

## Direct and indirect effects of masting on rodent populations and tree seed survival

Jaclyn L. Schnurr, Richard S. Ostfeld and Charles D. Canham

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Many plant species are thought to benefit from mast seeding as a result of increased seed survival through predator satiation. However, in communities with many different masting species, lack of synchrony in seed production among species may decrease seed survival by maintaining seed predator populations through the inter-mast cycle. Similarly, masting by different plant species may have different effects on the seed predator community. We conducted a three-year study in a northeastern USA temperate deciduous forest to determine if production of large seed crops by several tree species was synchronous, and if they had similar effects on all small mammal species. We found that red oak mast crops resulted in increased densities of *Peromyscus leucopus* and *P. maniculatus*, but had no effect on *Clethrionomys gapperi* abundance. Conversely, *C. gapperi* populations, but not *Peromyscus* populations, appeared to increase in response to a large red maple seed crop. Differences in small mammal abundance resulted in changes in species-specific seed survival: in the year of abundant *C. gapperi*, experimentally placed red oak acorns had significantly higher survival than in the year of high *Peromyscus* abundance. Red oak acorn removal was positively correlated with *Peromyscus* abundance, while red maple seed removal was significantly higher with increased *C. gapperi* abundance. Thus, species-specific seed production had differential effects on subsequent small mammal abundance, which in turn affected seed survival. We suggest that at the level of the community, even short-term lack of synchrony in production of large seed crops can cause variation in postdispersal seed survival, through differential effects on the community of small mammal seed predators.

J. L. Schnurr, Savannah River Ecology Laboratory, Drawer E, Aiken, SC 29802, USA (schnurr@srel.edu). – R. S. Ostfeld and C. D. Canham, Inst. of Ecosystem Studies, Millbrook, NY 12545, USA.

Mast seeding is the infrequent, synchronous production of large seed crops by most individuals within a plant population (Silvertown 1980, Kelly 1994). Swamping the environment with seeds benefits plant populations through predator satiation, allowing some seeds to survive and germinate (Janzen 1971, Jensen 1985, Nilsson 1985, Hughes and Fahey 1988, Crawley and Long 1995, McKone et al. 1998). However, mast seeding produces a large pulse of food resources for seed predators, increasing survival and reproduction, and in some cases, abundance (Jensen 1982, Pucek et al. 1993, Jedrzejewski et al. 1995, Elkinton et al. 1996, Ostfeld et al. 1996, Wolff 1996, Jones et al. 1998, McCracken et

al. 1999, Curran and Leighton 2000, Curran and Webb 2000, Ostfeld and Keesing 2000). In intermast years decreased food production is unable to sustain high seed predator populations (Jensen 1982, Pucek et al. 1993, Jedrzejewski et al. 1995, Elkinton et al. 1996, Ostfeld et al. 1996, Wolff 1996, Jones et al. 1998, McCracken et al. 1999, Ostfeld and Keesing 2000). Thus, abundances of seed predators are low during the next mast, increasing the probability of predator satiation and successful seedling recruitment.

Plant communities often consist of a number of different masting species. Within communities, plant species that share generalist seed predators should

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evolve synchronous masting to maintain the “boom and bust” cycle of seed predator abundance (Lalonde and Roitberg 1992). Community-wide synchronized masting is seen among the common deciduous tree species in the Bialowieza Primeval Forest in Europe (Pucek et al. 1993, Jedrzejewska and Jedrzejewski 1998), as well as in southeastern Asia, where many dipterocarp species may facilitate “regional escape” from nomadic seed predators (Curran and Leighton 2000, Curran and Webb 2000). The consequences for asynchrony between masting populations could be large: species producing seed out of synchrony may experience 100% seed predation (Curran and Leighton 2000).

In the temperate deciduous forests of northeastern North America, masting by oak species (*Quercus*) causes the predicted increases in seed predator populations, mainly generalist small mammals such as *Peromyscus leucopus* (white-footed mice), *P. maniculatus* (deer mice), and *Tamias striatus* (eastern chipmunks) (Elkinton et al. 1996, Ostfeld et al. 1996, Wolff 1996, Jones et al. 1998, McCracken et al. 1999). The increased small mammal populations have cascading effects on the rest of the animal community: abundant *P. leucopus* impact populations of birds, insects and, through their capacity as a reservoir for the spirochete that causes Lyme disease, humans (Elkinton et al. 1996, Ostfeld et al. 1996, Jones et al. 1998, McShea 2000, Ostfeld and Keesing 2000). Thus, oak mast is important in structuring the dynamics of these forests.

Even in oak-dominated forests of the northeastern United States, there are other masting species, such as hickory (*Carya glabra*) and American beech (*Fagus grandifolia*) (Silvertown 1980, Sork 1983, Sork et al. 1993), as well as species that more regularly produce large seed crops, such as sugar maple (*Acer saccharum*), red maple (*Acer rubrum*), white pine (*Pinus strobus*) and white ash (*Fraxinus americana*) (Silvertown 1980, Hughes and Fahey 1988, Koenig and Knops 2000). McCracken et al. (1999) found that large seed crops of red maple were correlated with increased abundance of *P. leucopus*, although abundance of another generalist seed predator, *Clethrionomys gapperi* (southern red-backed voles), was unaffected by red maple seed crops. Thus, mast by species other than oak may also be important for structuring temperate forest communities. Seed production by several tree species may differentially affect populations of seed predators, which may alter competitive interactions between species (Halvorson 1982). If high abundances of seed predators are maintained through masting by several tree species, then other tree species producing seed crops asynchronously may experience low seed survival.

We designed a study to examine the relationships among production of large seed crops by different, co-occurring tree species, the assemblage of small mammal seed predators, and seed removal in forests of the

northeastern United States. Over a three-year time period, we asked to what degree these forest communities displayed synchronous seed production. Since the major seed predators are generalists, we expected masting to be synchronous across tree species. We also asked if production of large seed crops by different tree species caused similar responses in all small mammal seed predators: does a large red maple seed crop cause similar proportional increases in seed predator populations as a red oak mast? Similarly, we asked if all small mammal species respond in like fashion, or if there are different responses of each small mammal species to large seed crops of different tree species. Finally, we tested whether mast seeding by one tree species affected survival of heterospecific seeds. We expected that predator satiation would cause any masting species to have decreased seed removal. In general, because both canopy trees and small mammals occur as multi-species assemblages, we asked to what extent it is appropriate to simplify this system into seed-producer and seed-consumer guilds.

## Methods

### Study area

This study was conducted in northwestern Connecticut, USA, at Great Mountain Forest (GMF) (41° 57' N, 73° 15' W), a 2500-ha tract of predominately second growth (~80–120 yr old) stands. Major tree species (in order of decreasing seed size) include *Quercus rubra* L. (red oak), *Fagus grandifolia* Ehrh. (American beech), *Prunus serotina* Ehrh. (black cherry), *Acer saccharum* Marsh. (sugar maple), *Acer rubrum* L. (red maple), *Fraxinus americana* L. (white ash), *Pinus strobus* L. (white pine), *Tsuga canadensis* (L.) Carr. (Eastern hemlock) and *Betula alleghaniensis* Michx.f. (yellow birch).

The major small mammal species in this area are *Peromyscus maniculatus* (deer mice), *P. leucopus* (white-footed mice), *Clethrionomys gapperi* (red-backed voles) and *Tamias striatus* (eastern chipmunks). The *Peromyscus* species were combined for these analyses, since they are morphologically and ecologically similar at similar sites (Wolff et al. 1985). All of these species consume seeds during at least part of the year (Martell 1981, Martell and Macaulay 1981, Ostfeld et al. 1996). Another study conducted at GMF indicated that post-dispersal seed removal by birds and insects is rare (Ostfeld et al. 1994).

In the summer of 1995 nine 1-ha sites were chosen throughout GMF. These sites were chosen on the basis of the adult tree composition: three were in locations dominated by red oak (“oak” sites), two were in locations dominated by sugar maple (“SugMap”), two were in locations dominated by Eastern hemlock (“hem-

lock”), and two were mixed red maple, red oak and black cherry stands (“mixed”). Minimum distance between sites was 200 m, and most sites were at least 1 km apart. These tree compositions were chosen on the basis of resource production: red oak produces large seeds (average 3600 mg), sugar maple and black cherry produce moderate sized seeds (average 65 and 113 mg, respectively), red maple produces small seeds (20 mg), and Eastern hemlock produces seeds too small for rodent consumption. We mapped and measured the diameter at breast height (DBH) of all canopy trees (DBH > 10 cm) and used these measurements to calculate the basal area (basal area =  $(DBH/2)^2\pi$ ) of all potentially seed producing trees (Table 1) to allow us to estimate seed production of specific tree species within each site type.

### Seed rain

To determine the overall interannual patterns of seed production, seed rain was measured from 1994 through 1996 at two of the nine 1-ha sites. One was a mixed site and the other a sugar maple site. Seventy-two mesh seed baskets 1 m in diameter were placed directly beneath the canopy of target tree species representing the most common tree species at GMF (sugar maple, red maple, American beech, white ash, red oak, Eastern hemlock). The baskets were supported 1 m above the ground by fiberglass T-posts and nylon-fishing line to keep small mammals from entering baskets. The contents of the seed baskets were removed monthly from June through September, and every 2 weeks from September to November when seed rain was maximal. Seeds were separated from the debris in the basket, identified to species, counted, and tested for viability by checking for a green embryo.

### Small mammal live trapping

Within each 1-ha site we established a nine-by-nine small mammal live-trapping grid with 12.5-m spacing between stations. Folding Sherman live traps (8 cm × 9 cm × 23 cm) were opened at 1700 and checked and closed at 0700 daily. We live-trapped each site for three consecutive days, four times from June to November in 1995 and three times from June to November in 1996. Because trapping effort was different in 1995 and 1996, we estimated the overall summer/fall animal densities by averaging the number of individuals captured per hectare divided by the number of trapping sessions. Captured small mammals were identified to species, given a numbered ear-tag (Monel fingerling tags, #1 size), weighed, checked for reproductive condition, and released at the point of capture.

### Seed removal experiment

In the falls of 1995 and 1996 seed removal experiments were conducted within each site. In 1995, nine locations were randomly chosen within each site for a total of 81 seed removal quadrats. In 1996, we randomly chose 15 locations within each site, for a total of 135 quadrats.

We established a 1 × 1 m seed removal quadrat at each location. In each quadrat we chose 25 random points with a minimum of 10 cm between points. These 25 points were then randomly assigned to have one of five different tree seeds: red oak, black cherry, sugar maple, red maple, or white pine. The five locations for each tree seed were marked with a colored wooden coffee stirrer, and the seed was placed directly on the ground at the base of the stirrer. The top 1 cm of the coffee stirrers was painted to aid in identifying the species of seed. Latex examination gloves were worn whenever touching the seeds and the coffee stirrers to

Table 1. Characterization of the major tree species found at all site types.

Tree species		Oak sites <i>n</i> = 3	Sugar maple sites <i>n</i> = 2	Eastern hemlock sites <i>n</i> = 2	Mixed sites <i>n</i> = 2
American beech	% density	18.3	2.0	10.7	5.6
	% basal area	7.5	0.9	7.2	2.1
Black cherry	% density	0.8	5.2	2.7	18.0
	% basal area	1.4	11.3	4.7	21.2
Eastern hemlock	% density	7.9	6.3	52.2	9.9
	% basal area	7.0	6.7	48.2	10.7
Red maple	% density	15.9	7.8	16.6	28.1
	% basal area	9.7	11.0	18.7	26.9
Red oak	% density	39.8	1.3	4.4	11.0
	% basal area	67.0	3.1	13.2	18.5
Sugar maple	% density	2.5	50.8	3.9	1.1
	% basal area	0.9	38.6	1.9	0.4
Across species	average <i>n</i> (stems/ha)	651	558	647	522
	average basal area (m <sup>2</sup> /ha)	33.6	46.8	54.3	52.3

avoid scent contamination since the animals are thought to rely on olfaction to locate seeds. Seeds were checked daily for three days, and the number removed per quadrat at the end of the trial was used in analyses. Other longer-term studies conducted at GMF have determined that the majority of seed removal occurs within the first three days of exposure to predators (Canham et al. unpubl.).

### Data analyses

Differences in small mammal capture rates and seed removal rates were analyzed using ANOVA to determine differences between stand type and year. For the year comparisons and between stand comparisons, stand types were considered the experimental unit. When applicable, Bonferroni pairwise comparisons were performed to determine differences between stand types. Linear regression was used to test for relationships between mammal populations and seed removal across sites. All data were analyzed using SYSTAT v. 6.1 for Windows.

## Results

### Seed rain

Numbers of seeds produced varied among the three years, as did the species with the largest individual contribution (Fig. 1A). Red maple was the only tree species to produce a seed crop in all three years, although the number of seeds produced in 1995 was much reduced compared to the large seed crops of 1994 and 1996. Four of the six tree species had crop failures in 1995. The large red oak mast crop in 1994 (about 5 acorns per m<sup>2</sup>) was synchronous with large crops of red maple, sugar maple and black cherry seeds. However, in this short-term study there was no apparent community-wide synchrony in seed production among species and years (Fig. 1A).

Seed biomass reflected somewhat different patterns than total seed numbers (Fig. 1B). Red oak had the largest biomass production in 1994, followed by red maple and beech. In 1995, red oak still produced a large biomass of seeds, even though total numbers was much decreased from 1994. Beech seed biomass was highest in 1996, followed both by red maple and red oak (Fig. 1B).

### Small mammal live-trapping

Pooling all species, small mammal abundance was not significantly different between 1995 and 1996 (ANOVA,  $df = 1,16$ ;  $F = 0.15$ ,  $P = 0.70$ ; Fig. 2A). *Peromyscus* species were significantly more abundant in 1995, after the

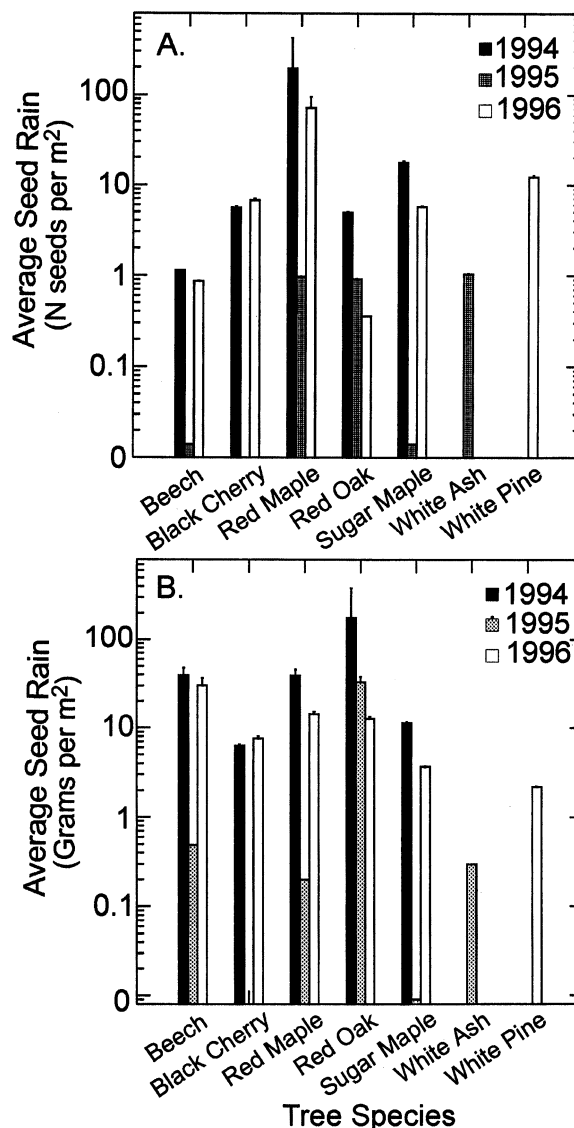


Fig. 1. A. The average seed rain per m<sup>2</sup> at Great Mountain Forest 1994 through 1996. B. The average biomass of seeds per m<sup>2</sup> at Great Mountain Forest 1994 through 1996. Note the log scale on the y-axis. Error bars are 1 standard error.

community wide mast crop in 1994, than in 1996, after the seed crop failure in 1995 (ANOVA,  $df = 1,16$ ;  $F = 12.3$ ,  $P = 0.003$ ; Fig. 2B). On a stand-by-stand basis, *Peromyscus* displayed a significant population decrease from 1995 to 1996 only at the hemlock stands (ANOVA,  $df = 1,2$ ;  $F = 250$ ,  $P = 0.004$ ; Fig. 2B). Numbers of *Peromyscus* did not differ among stand types in 1995 (ANOVA,  $df = 3,5$ ;  $F = 1.15$ ,  $P = 0.41$ ), 1996 (ANOVA,  $df = 3,5$ ;  $F = 2.50$ ,  $P = 0.17$ ) or in both years combined (ANOVA,  $df = 3,14$ ;  $F = 0.545$ ,  $P = 0.66$ ; Fig. 3A), indicating that *Peromyscus* did not differentiate among habitats based on canopy tree composition of these forests.

Total *Clethrionomys gapperi* abundance did not change between 1995 and 1996 (ANOVA,  $df = 1,16$ ;  $F = 0.99$ ,  $P = 0.34$ ; Fig. 2C). In 1995, average numbers of *C. gapperi* captured across all stand types were similar (ANOVA,  $df = 3,5$ ;  $F = 2.56$ ,  $P = 0.17$ ; Fig. 2C). However, in 1996, differences existed among stand types (ANOVA,  $df = 3,5$ ;  $F = 14.1$ ,  $P = 0.007$ ; Fig. 2C); more *C. gapperi* were captured in hemlock stands than in oak stands ( $P = 0.023$ ) or sugar maple stands ( $P = 0.025$ ). Summing both years, significantly more *C. gapperi* were captured in hemlock and mixed stand types than in the oak and sugar maple stands (ANOVA,  $df = 3,14$ ;  $F = 9.70$ ,  $P = 0.001$ ; Fig. 3B).

*Tamias striatus* populations remained relatively constant between 1995 and 1996 (ANOVA,  $df = 1,16$ ;  $F = 0.66$ ,  $P = 0.43$ ; Fig. 2D). Across both years, *T. striatus* displayed differences among stands (ANOVA,  $df = 3,14$ ;  $F = 4.94$ ,  $P = 0.015$ ; Fig. 3C); they were more abundant at the mixed sites than in oak ( $P = 0.031$ ) or sugar maple stands ( $P = 0.025$ ).

## Seed removal experiments

Since total small mammal abundance did not change between 1995 and 1996 (Fig. 2A), we predicted that seed removal would be similar between years. Total seed removal across all stand types was similar in 1995 and 1996 ( $t = 0.97$ ,  $P = 0.35$ ), as was removal of each seed species separately, except red oak ( $t = 3.76$ ,  $P = 0.002$ ), which had a lower level of seed removal in 1996 (Fig. 4F).

Seed removal was high across all stand types in 1995; no acorns remained after three days at the hemlock and mixed stands. In 1996, there was a significant effect of stand type on total seed removal (ANOVA,  $df = 3,5$ ;  $F = 5.51$ ,  $P = 0.048$ ; Fig. 4A) and on red maple seed removal (ANOVA,  $df = 3,5$ ;  $F = 5.43$ ,  $P = 0.050$ ; Fig. 4C), with the lowest seed removal occurring at the sugar maple sites, but none of the pairwise comparisons were significant. Significantly fewer sugar maple seeds were removed in 1996 at the sugar maple stands than in the other stand types (ANOVA,  $df = 3,5$ ;  $F = 14.0$ ,

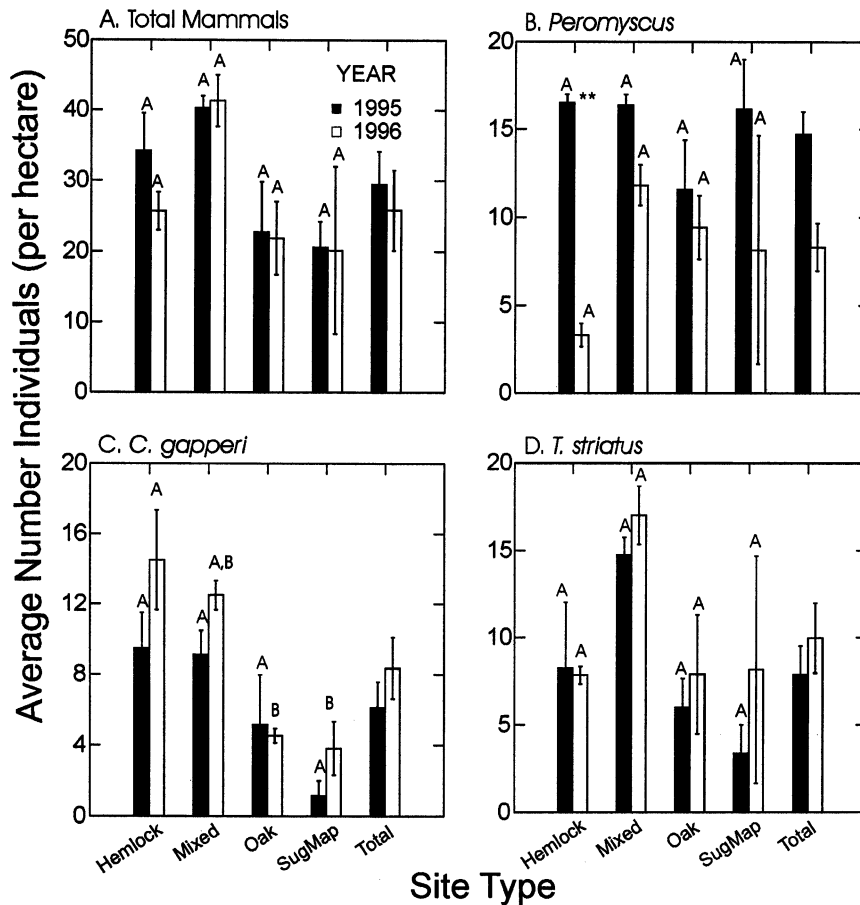


Fig. 2. Average numbers of small mammals captured at each site type. The filled bars are 1995 captures and the empty bars are 1996 captures. Error bars are standard errors. A. Total numbers of mammals, B. *Peromyscus* sp., C. *Clethrionomys gapperi*, and D. *Tamias striatus*. Within each graph, bars with different letters indicate significant differences ( $P < 0.05$ ) between sites within a year, and asterisks indicate significant differences between years at a site type.

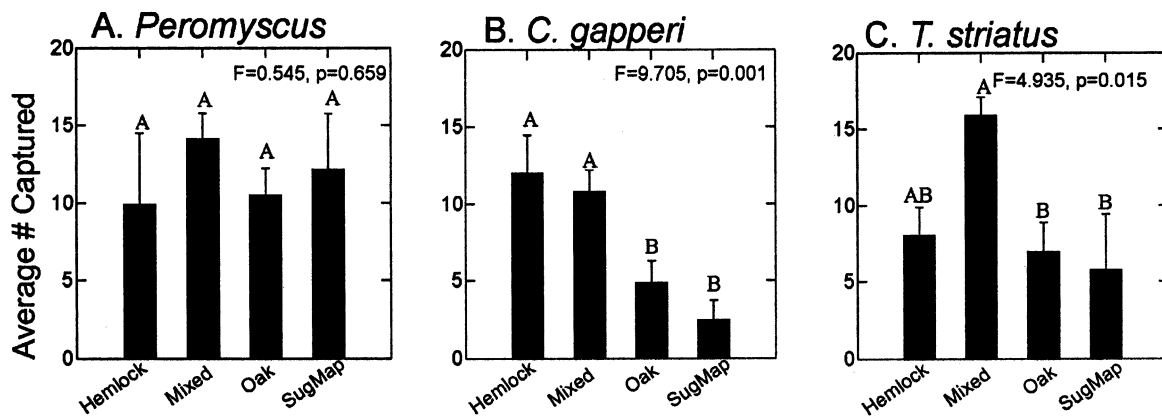


Fig. 3. The total average number of individuals captured at each site (1995 + 1996), for A. *Peromyscus* sp., B. *C. gapperi*, and C. *T. striatus*. Error bars are standard errors. Within each graph, bars with different letters are significantly different at the 0.05 level.

$P = 0.007$ , and all pairwise comparisons  $P < 0.05$ ; Fig. 4D). Red oak acorn removal was equal across all stand types in 1996 (ANOVA,  $df = 3,5$ ;  $F = 2.04$ ,  $P = 0.23$ ; Fig. 4F); acorns changed from the most frequently removed seed species in 1995 to the least frequently removed seed species in 1996. White pine consistently displayed high removal across both years and stand types (Fig. 4E).

Within each stand type, species-specific seed removal differed between 1995 and 1996. No acorns survived at the hemlock and mixed stands in 1995, whereas some survived at the oak and sugar maple stands. Acorn removal was significantly lower at the sugar maple stands in 1996 than in 1995 (ANOVA,  $df = 1,2$ ;  $F = 20.1$ ,  $P = 0.046$ ; Fig. 4F). Acorn removal was not significantly different between 1995 and 1996 at the red oak stands. Significantly fewer sugar maple seeds were removed in 1996 than in 1995 at the sugar maple stands (ANOVA,  $df = 1,2$ ;  $F = 24.3$ ,  $P = 0.039$ ; Fig. 4D). The only other change in seed removal within stand types was an increase in the removal of black cherry seeds at the hemlock stands between 1995 and 1996 (ANOVA,  $df = 1,2$ ;  $F = 57.4$ ,  $P = 0.017$ ; Fig. 4B).

We combined stands and years ( $n = 18$ ) to determine if the numbers of small mammals of each species influenced removal of specific seed species. We found a positive correlation between the number of *C. gapperi* and removal of red maple seeds ( $F = 5.03$ ,  $P = 0.039$ ,  $df = 1,16$ ; Fig. 5A); for each additional *C. gapperi* captured per hectare, red maple seed removal increased 2.0%. Similarly, acorn removal was positively correlated with *Peromyscus* density ( $F = 6.95$ ,  $P = 0.018$ ,  $df = 1,16$ ; Fig. 5B); for each additional *Peromyscus* captured per hectare, acorn removal increased 2.4%. Although a non-linear regression of these data was also significant, it was not a better fit than a linear regression for either data set. There were no other significant correlations among small mammal species and seed species.

## Discussion

The major tree species at our site in northeastern Connecticut asynchronously produced large seed crops, at least over our short-term study. Differential seed production caused changes in the populations of the major postdispersal seed predators. Although densities of *Peromyscus* were higher in 1995, after heavy production of red oak acorns, than in 1996, after an acorn failure, the total numbers of all rodents remained consistent between 1995 and 1996. The similarity between years in total rodent abundance was due to an increase in *C. gapperi* between 1995 and 1996. Red maple produced a large seed crop in 1996, and this tree species disperses seeds throughout the late spring and summer (USDA 1975). Similar to the response of *Peromyscus* to mast seeding by oak, *C. gapperi* increased population size apparently in response to the red maple seed crop in 1996. *T. striatus* displayed characteristics of being a true generalist seed predator: they had high populations in both 1995 and 1996 and did not change population size in response to seed production by any tree species.

*Peromyscus* and *C. gapperi* inhabit the same habitat types, but *Peromyscus* is thought to prefer more xeric areas and *C. gapperi* more mesic areas (Morris 1996). Although there are several accounts of these species coexisting non-competitively (Grant 1976, Miller and Getz 1977, Vickery 1979, Morris 1983, Wolff and Dueser 1986, Morris 1996), there are also reports that *C. gapperi* is competitively dominant to *Peromyscus* (Crowell and Pimm 1976, Halvorson 1982). For study sites on the border of Idaho and Montana, Halvorson (1982) concluded that *C. gapperi* was competitively dominant to *Peromyscus*, except in years following mast seeding by coniferous trees. A similar dynamic appears to occur at our sites in northwestern Connecticut in response to red oak mast. At all sites in 1995, *Peromyscus* was the most abundant rodent. In 1996,

*Peromyscus* populations decreased most at the hemlock-dominated sites, which is where *C. gapperi* increased most (Fig. 2B, C). Both populations had the smallest change at the oak sites: perhaps even the small acorn crop in 1995 was enough to maintain the competitive hierarchy.

Changes in the abundance of small mammals led to differences in seed removal between 1995 and 1996. The low removal rate at the sugar maple stands in 1996 probably resulted from the low mammal abundance at one of the replicates (total animals captured: 24). In 1995, high populations of *Peromyscus* resulted in very high removal of acorns at all stand types except for the red oak stands, possibly indicating predator satiation under conditions of high acorn abundance (Fig. 4F). In

1996 acorns had the lowest removal rates of all seed types. This demonstrates the important differences between specific small mammal seed predators: in the year of high *Peromyscus* abundance, red oak acorns had the highest removal rates among all seed species. In the year of high *C. gapperi* abundance, red oak acorns had the lowest removal rates of all seed species. The importance of *Peromyscus* as a seed predator on red oak is well known (Elkinton et al. 1996, Ostfeld et al. 1996, Wolff 1996); our study shows that as the number of *Peromyscus* increased, acorn removal also increased (Fig. 5B).

The importance of red maple seed as a food source for rodents in temperate deciduous forests has only recently been recognized. In Maine, McCracken et al.

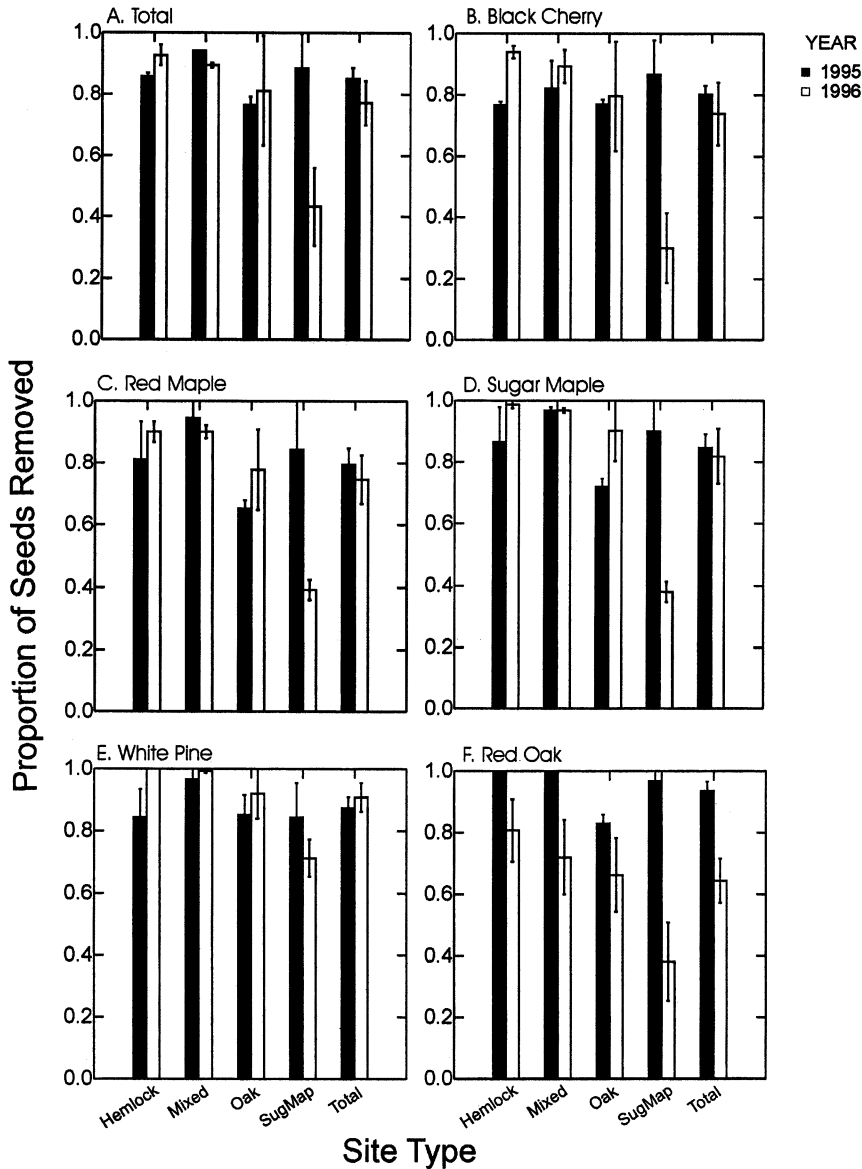


Fig. 4. The proportion of seeds removed at each site type after three days of exposure for A. all seed types combined, B. black cherry, C. red maple, D. sugar maple, E. white pine, and F. red oak. Error bars are standard errors.

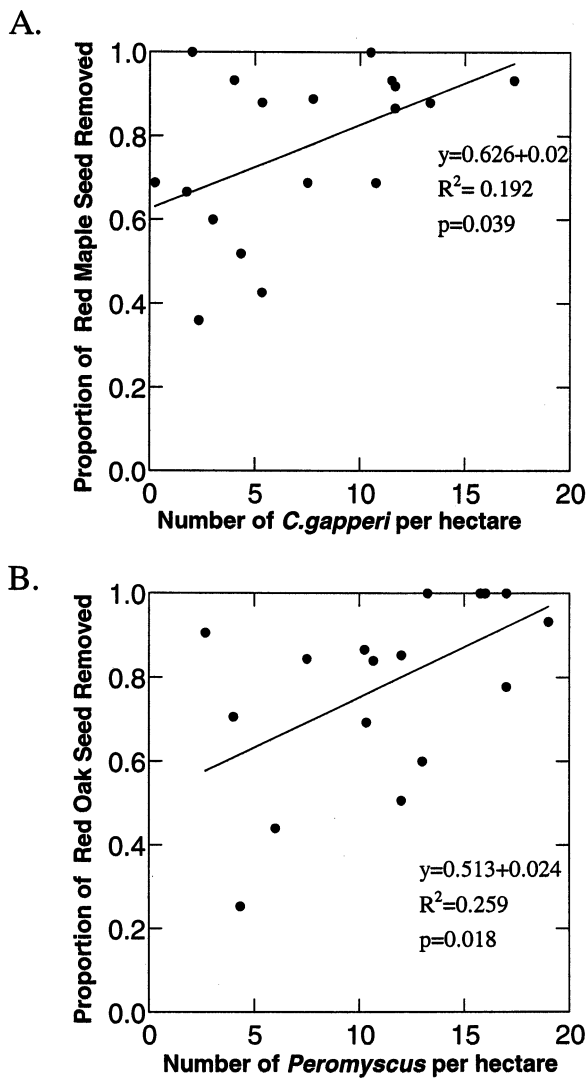


Fig. 5. The effects of specific small mammal species on seed removal across both sites and years. A. Relationship between density of *C. gapperi* and removal of red maple seeds. B. Relationship between density of *Peromyscus* and acorn removal.

(1999) found that summer density of *P. leucopus* increased in response to red maple seed production; however, they found no effect of seed rain of either red maple or red oak on *C. gapperi* populations. In our study, both *T. striatus* and *C. gapperi* had consistently higher population densities in stands with more red maple basal area (Table 1, Fig. 3B, C); thus, red maple may be important for structuring habitat choice. Large seed crops of red maple may sustain *C. gapperi* and *T. striatus* populations at high levels even after a year with low overall seed production. Production of large seed crops by red maple and red oak had differential effects on small mammal populations

at each particular site, which in turn influenced seed survival.

It is surprising that *C. gapperi* did not respond numerically to the red oak masting event of 1994. This suggests that either *C. gapperi* does not cache seeds, which would be necessary to increase over-wintering survival, or simply that *C. gapperi* does not eat acorns. Several studies have suggested that *C. gapperi* cache seeds for a winter food source (Abbott and Quink 1970, Merritt and Merritt 1978); however, these studies did not observe caching by *C. gapperi*. Instead they documented seed caches in areas where red-backed voles had been captured or found seed fragments in the winter diet. We found no study that provides direct evidence that *C. gapperi* cache food for the winters. Also, although many studies have indicated that *C. gapperi* consumes seed when it is readily available in the environment (Merritt and Merritt 1978, Martell 1981, Hansson 1985; Fig. 5A), no studies have examined seed preferences of wild *C. gapperi* (but see Vickery 1979 for a field study documenting frugivory by red-backed voles). The question of why *C. gapperi* did not respond to red oak mast is still unanswered.

Predator satiation is one of the proposed mechanisms for the evolution of mast seeding in plant populations (Silvertown 1980, Lalonde and Roitberg 1992, Koenig et al. 1994, Shibata et al. 1998). This study indicates that mast seeding by one plant species may have detrimental effects on the survival of another plant species through a mechanism akin to apparent competition (Holt 1977). Such an indirect, negative interaction should discourage asynchronous masting of tree species in multi-species assemblages. Indeed, most long-term studies that have presented results of community-wide seed production have found synchronous mast seeding (Pucek et al. 1993, Jedrzejewska and Jedrzejewski 1998, Shibata et al. 1998, Curran and Leighton 2000, Curran and Webb 2000). During our short-term study we did not observe synchronous mast production at our site in the northeastern United States. One reason plant populations may asynchronously produce large seed crops may be the differential affects of species-specific seed rain on seed predator populations, and the resulting competitive interactions among seed predators.

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## References

- Abbott, H. G. and Quink, T. F. 1970. Ecology of eastern white pine seed caches made by small forest rodents. – *Ecology* 51: 271–278.
- Crawley, M. J. and Long, C. R. 1995. Alternate bearing, predator satiation and seedling recruitment in *Quercus robur* L. – *J. Ecol.* 83: 683–696.
- Crowell, K. L. and Pimm, S. L. 1976. Competition and niche shifts of mice introduced onto small islands. – *Oikos* 27: 251–258.
- Curran, L. M. and Leighton, M. 2000. Vertebrate responses to spatiotemporal variation in seed production of mast-fruiting Dipteroecarpaceae. – *Ecol. Monogr.* 70: 101–128.
- Curran, L. M. and Webb, C. O. 2000. Experimental tests of the spatiotemporal scale of seed predation in mast-fruiting Dipteroecarpaceae. – *Ecol. Monogr.* 70: 129–148.
- Elkinton, J. S., Healy, W. M., Buonaccorsi, J. P. et al. 1996. Interactions among gypsy moths, white-footed mice, and acorns. – *Ecology* 77: 2332–2342.
- Grant, P. R. 1976. An 11-year study of small mammal populations at Mont St. Hilaire, Quebec. – *Can. J. Zool.* 54: 2156–2173.
- Halvorson, C. H. 1982. Rodent occurrence, habitat disturbance, and seed fall in a larch-fir forest. – *Ecology* 63: 423–433.
- Hansson, L. 1985. *Clethrionomys* food: generic, specific and regional characteristics. – *Ann. Zool. Fenn.* 22: 315–318.
- Holt, R. D. 1977. Predation, apparent competition and structure of prey communities. – *Theor. Popul. Biol.* 12: 197–229.
- Hughes, J. W. and Fahey, T. J. 1988. Seed dispersal and colonization in a disturbed northern hardwood forest. – *Bull. Torrey Bot. Club* 115: 89–99.
- Janzen, D. H. 1971. Seed predation by animals. – *Annu. Rev. Ecol. Syst.* 2: 465–492.
- Jedrzejewska, B. and Jedrzejewski, W. 1998. Predation in vertebrate communities: the Bialowieza primeval forest as a case study. – Springer-Verlag.
- Jedrzejewski, W., Jedrzejewska, B. and Szymura, L. 1995. Weasel population response, home range, and predation on rodents in a deciduous forest in Poland. – *Ecology* 76: 179–195.
- Jensen, T. S. 1982. Seed production and outbreaks of non-cyclic rodent populations in deciduous forests. – *Oecologia* 54: 184–192.
- Jensen, T. S. 1985. Seed-seed predator interactions of European beech, *Fagus sylvatica* and forest rodents, *Clethrionomys glareolus* and *Apodemus flavicollis*. – *Oikos* 44: 149–156.
- Jones, C. J., Ostfeld, R. S., Richard, M. P. et al. 1998. Chain reactions linking acorns to gypsy moth outbreaks and Lyme disease risk. – *Science* 279: 1023–1026.
- Kelly, D. 1994. The evolutionary ecology of mast seeding. – *Trends Ecol. Evol.* 9: 465–470.
- Koenig, W. D. and Knops, J. M. H. 2000. Patterns of annual seed production by northern hemisphere trees: a global perspective. – *Am. Nat.* 155: 59–69.
- Koenig, W. D., Mumme, R. L., Carmen, W. J. and Stanback, M. T. 1994. Acorn production by oaks in central coastal California: variation within and among years. – *Ecology* 75: 99–109.
- Lalonde, R. G. and Roitberg, B. D. 1992. On the evolution of masting behavior in trees: predation or weather? – *Am. Nat.* 139: 1293–1304.
- Martell, A. M. 1981. Food habits of Southern red-backed voles (*Clethrionomys gapperi*) in Northern Ontario. – *Can. Field-Nat.* 95: 325–328.
- Martell, A. M. and Macaulay, A. L. 1981. Food habits of deer mice (*Peromyscus maniculatus*) in Northern Ontario. – *Can. Field-Nat.* 95: 319–324.
- McCracken, K. E., Witham, J. W. and Hunter, M. L., Jr. 1999. Relationships between seed fall of three tree species and *Peromyscus leucopus* and *Clethrionomys gapperi* during 10 years in an oak-pine forest. – *J. Mammal.* 80: 1288–1296.
- McKone, M. J., Kelly, D. and Lee, W. G. 1998. Effect of climate change on mast-seeding species: frequency of mass flowering and escape from specialist insect seed predators. – *Global Change Biol.* 4: 591–596.
- McShea, W. J. 2000. The influence of acorn crops on annual variation in rodent and bird populations. – *Ecology* 81: 228–238.
- Merritt, J. F. and Merritt, J. M. 1978. Population ecology and energy relationships of *Clethrionomys gapperi* in a Colorado subalpine forest. – *J. Mammal.* 59: 576–598.
- Miller, D. H. and Getz, L. L. 1977. Comparisons of population dynamics of *Peromyscus* and *Clethrionomys* in New England. – *J. Mammal.* 58: 1–16.
- Morris, D. W. 1983. Patterns and scale of habitat use in two temperate-zone, small mammal faunas. – *Can. J. Zool.* 62: 1540–1547.
- Morris, D. W. 1996. Coexistence of specialist and generalist rodents via habitat selection. – *Ecology* 77: 2352–2364.
- Nilsson, S. G. 1985. Ecological and evolutionary interactions between reproduction of beech *Fagus sylvatica* and seed eating animals. – *Oikos* 44: 157–164.
- Ostfeld, R. S. and Keesing, F. 2000. Pulsed resources and community dynamics of consumers in terrestrial ecosystems. – *Trends Ecol. Evol.* 15: 232–237.
- Ostfeld, R. S., Lewin, N., Schnurr, J. et al. 1994. The roles of small rodents in creating patchy environments. – *Pol. Ecol. Stud.* 20: 265–276.
- Ostfeld, R. S., Jones, C. G. and Wolff, J. O. 1996. Of mice and mast: ecological connections in eastern deciduous forests. – *BioScience* 46: 323–330.
- Pucek, Z., Jedrzejewski, W., Jedrzejewska, B. and Pucek, M. 1993. Rodent population dynamics in a primeval deciduous forest (Bialowieza National Park) in relation to weather, seed crop, and predation. – *Acta Theriol.* 38: 199–232.
- Shibata, M., Tanaka, H. and Nakashizuka, T. 1998. Causes and consequences of mast seed production of four co-occurring *Carpinus* species in Japan. – *Ecology* 79: 54–64.
- Silvertown, J. W. 1980. The evolutionary ecology of mast seeding in trees. – *Biol. J. Linn. Soc.* 14: 235–250.
- Sork, V. L. 1983. Mammalian seed dispersal of pignut hickory during three fruiting seasons. – *Ecology* 64: 1049–1056.
- Sork, V. L., Bramble, J. and Sexton, O. 1993. Ecology of mast-fruiting in three species of North American oaks. – *Ecology* 74: 528–541.
- USDA 1975. Silvics of forest trees of the United States. – United States Dept of Agriculture, Agriculture handbook No. 271. pp. 57–62.
- Vickery, W. L. 1979. Food consumption and preferences in wild populations of *Clethrionomys gapperi* and *Napaeozapus insignis*. – *Can. J. Zool.* 57: 1536–1542.
- Wolff, J. O. 1996. Population fluctuations of mast-eating rodents are correlated with the production of acorns. – *J. Mammal.* 77: 850–856.
- Wolff, J. O. and Dueser, R. D. 1986. Noncompetitive coexistence between *Peromyscus* species and *Clethrionomys gapperi*. – *Can. Field-Nat.* 100: 186–191.
- Wolff, J. O., Dueser, R. D. and Berry, K. S. 1985. Food habits of sympatric *Peromyscus leucopus* and *Peromyscus maniculatus*. – *J. Mammal.* 66: 795–798.