

## THE INFLUENCE OF ACORN CROPS ON ANNUAL VARIATION IN RODENT AND BIRD POPULATIONS

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**Abstract.** I recorded mast production by oaks (*Quercus* sp.) at 12 forested sites in western Virginia for 6–12 yr and measured its impact on the abundance of small mammals, understory vegetation, and artificial-nest predation. White-tailed deer (*Odocoileus virginianus*) were excluded from half the 4-ha sites after at least one season of data collection. My hypothesis was that annual variation in acorn crops affected multiple species and that the strength of those interactions is mediated by white-tailed deer.

The acorn crop was variable across sites and year, with some of the between-site variability explained by differences in elevation. All sites experienced at least one mast failure, and mast failure years were generally consistent across sites. White-footed mouse (*Peromyscus leucopus*), eastern chipmunk (*Tamias striatus*), and gray squirrel (*Sciurus carolinensis*) populations were significantly correlated with annual fluctuations in the acorn crop. The exclusion of deer had a significant impact on *P. leucopus* and *T. striatus* populations by increasing the number of animals captured following low acorn mast years.

Annual fluctuations in the acorn crop, but not in rodent densities, were significantly correlated with the rates of predation on artificial nests the next summer. There was no significant interaction between predation rates and the exclusion of deer. An index from the Breeding Bird Survey (BBS) for Virginia was used to measure regional numbers for 11 common species captured at the sites. The index for two understory species was significantly negatively correlated with the mean acorn crop measured 2 yr previously. The effect of white-tailed deer on the forest community was not consistent across all conditions, as sites with large acorn crops were not strongly influenced by deer. These data are consistent with the hypothesis that mast crops from oaks serve as important determinants of community function within Appalachian forests.

**Key words:** acorn production; avian nest predation; eastern deciduous forests; *Odocoileus virginianus*; *Peromyscus*; *Quercus*; *Sciurus*; *Tamias*; white-tailed deer.

### INTRODUCTION

Much of eastern North America is dominated by deciduous forest (Braun 1950). These forests have undergone profound changes in the last 200 yr due to removal of both herbivore and predator species, extensive logging, and fragmentation. The conservation status of current forests is reflected by concern over the increase in ungulates (Stromayer and Warren 1997, Waller and Alverson 1997), the shift in canopy species (Healy et al. 1997), and the high predation rates on many forest birds (Robinson et al. 1995). Management of forest ecosystems has focused on how remaining species respond to the fluctuations of dominant or keystone species (Power et al. 1996), and in forested ecosystems these key species are often large predators (McLaren and Peterson 1994, Palomares et al. 1995, Boertje et al. 1996). Fluctuations in the productivity of dominant plant species should also have a significant impact on complex food webs in forest ecosystems (Power 1992). If the interactions of multiple species

are mediated through the productivity or abundance of a single species, then the effective management of this species can help maintain ecosystem stability (Polis and Strong 1996).

One consistent feature of deciduous forests has been the importance of the forest seed crops on mammal populations. In Appalachian forests, oaks have replaced the American chestnut (*Castanea dentata*) as the dominant tree species (Braun 1950), and acorns have become a major food resource for many mammals in North America (Martin et al. 1951). Acorns can form the bulk of the winter larder collected by small mammals (Goodrum et al. 1971, Gashwiler 1979). In Illinois, natural populations of gray (*Sciurus carolinensis*) and fox (*S. niger*) squirrels persist only in areas of abundant winter seed crops (Nixon and Hansen 1987). Deer movement (McShea and Schwede 1993) and feeding (Harlow et al. 1975), and reproduction in black bear (*Ursus americanus*; Eiler et al. 1989), are determined by seasonal mast patterns. For white-tailed deer, acorns are the primary food source supporting autumn fat deposition (Mautz 1978, Pekins and Mautz 1987).

The reliance of many mammals on the acorn crop, and the temporal heterogeneity of the crop, set the stage

for dynamic fluctuations in population density. Seed production of the American chestnut may have been regular (Diamond 1989), but the annual mast production of oaks is extremely variable (Downs and McQuilken 1944, Beck 1977). Mast failures in red (*Quercus rubra*) and white (*Q. alba*) oaks coincide with poor spring conditions that decrease flower abundance and seed set, but insect damage and endogenous rhythms also play a role in determining levels of seed production (Sork et al. 1993). At the site level, acorn production in the autumn has a significant effect on small mammal (*Peromyscus* and *Tamias*) populations the following summer (Wolff 1996). Between-site variation in spring populations of *Peromyscus leucopus* can be explained by differences in mast production the previous autumn (McShea and Rappole 1992). Mast failure in eastern forests is usually followed by low winter survival rates for mice (Hansen and Batzli 1978) and low population densities the subsequent summer (Ostfeld et al. 1996, Wolff 1996).

Complex interactions have been documented between gypsy moths (*Lymantria dispar*), mice, and oaks (Elkinton et al. 1996, Ostfeld et al. 1996). Low densities of gypsy moths, which feed on oak leaves, are regulated by mice which in turn are regulated by variable acorn crops. Similar interactions also exist for acorns, mice, and the transmission of Lyme disease through black-legged ticks (*Ixodes scapularis*) (Ostfeld et al. 1996, Ostfeld 1997). Large acorn crops increased the number of potential primary hosts through increased mouse numbers and changes in the distribution of deer. These shifts in host distribution and abundance affected the next year's distribution of juvenile ticks, and the potential for transmission of Lyme disease to humans (Jones et al. 1998).

The importance of small mammals as predators on bird nests (Leimgruber et al. 1994) leads to another potential pathway by which acorn production could impact multiple species within forest ecosystems. Nest predation is a primary constraint on bird life-history traits (Martin 1993), and predation risk may structure bird assemblages (Martin 1988). Mammalian predators on nests are diverse (Reitsma et al. 1990, Leimgruber et al. 1994, Keyser et al. 1998) and small mammals have been shown to be significant predators on artificial nests (Leimgruber et al. 1994). Early work on nest predation focused on microhabitat (Martin and Roper 1988) or landscape features (Wilcove 1985), with the abundance of predators a more recent focus (Reitsma et al. 1990, Heske 1995). Seed crops have been shown to impact predators in temperate forests of New Zealand (King 1983), where stoats (*Mustela erminea*) are significant predators on nestlings, and their annual abundance is correlated with fluctuations in mice (*Mus musculus*) and beech (*Nothofagus* sp.) seed production.

To examine how seed crops impact forest systems, it would be preferable to manipulate the amount of seed available to consumers. However, adding supplemental

food to natural populations of small mammals has not yielded consistent results, primarily because of rapid immigration or emigration at the site (Wolff 1986, Vessey 1987, Koford 1992). Jones et al. (1998) did succeed with increasing spring populations of *Peromyscus leucopus* through overwinter supplementation of acorns. An alternative test would be to exclude a mast consumer from sites and record the response of the remaining species. White-tailed deer have been shown to consume significant quantities of acorns and shift both their home range and habitat use in response to acorn crops (McShea and Schwede 1993). The response of seed-eating rodent species to the removal of white-tailed deer would provide insights into the complexity of oak dominated forests.

Ecosystem stability should be increased by food web complexity (Polis and Strong 1996). In order to understand complex communities and the importance of individual species, the first step is to map the interactions that exist across and within trophic levels (Power et al. 1996). By recording the response of species from more than one trophic level to fluctuations in the productivity of oak seeds, we can begin to map the complexity of food webs within oak forests. Interactions between species are often dependent on context (Power et al. 1996), and the removal of one seed consumer from the suite of species examined should alter the degree to which the remaining species interact. I report on a long-term study involving the exclusion of deer from multiple, large (4-ha) sites, dominated by mature oak forest. I examined the masting pattern of oaks, small mammal population size, vegetation density, and predation rate on artificial nests at these sites relative to control sites where deer were not excluded. The response of rodent populations to the exclusion of a major acorn consumer, and the implications of variable mast crops on small mammal, predator, and bird populations are discussed.

#### METHODS

*Study sites.*—Twelve study sites were located within 25 km of Front Royal, Virginia (38°54' N, 78°09' W), USA, within large forest tracts. The eight sites located on the Shenandoah National Park (SNP) or the Smithsonian Institution's Conservation and Research Center (CRC) were composed primarily of mature oak, hickory (*Carya* sp.), white ash (*Fraxinus americana*), and yellow poplar (*Liriodendron tulipifera*), with understory shrubs of *Cornus florida*, *Lindera benzoin*, and *Cercis canadensis* (SAF Types 52, Eyre 1980). The four sites located on the George Washington and Jefferson National Forests (GWF) were composed of mature oak and Virginia pine (*Pinus virginiana*) with an understory of *Vaccinium* sp., *Nyssa sylvatica*, and *Sassafras albinum* (SAF Type 59, Eyre 1980). All sites were 4 ha, either 200 × 200 m, or 160 × 250 m in shape, and were separated by at least 1 km. Data were collected at two sites since 1986, six sites since 1990, and four

sites since 1992. To examine site quality, 10 soil cores obtained at each site, and organic carbon and nitrogen levels were determined by flash combustion using a Carlo Erba NA-1500 Elemental Analyzer (CE Elantech, Milan, Italy) (Verardo et al. 1990).

*Deer density.*—Deer exclusion fences were erected around four sites at SNP and CRC in early 1991, with two grids in GWF fenced in early 1993. The 3-m fence, composed of farm fencing (with  $25 \times 25$  cm mesh at bottom) and high tensile wire, did not exclude medium and small vertebrates (Leimgruber et al. 1994). Each fenced grid was paired with a control site possessing similar understory vegetation (see *Methods: Vegetation index*). Deer density was estimated for SNP and CRC by walking at least 100 km of line transects and recording the number of deer sighted and their distance to the transect (Burnham et al. 1980). These annual estimates were based on at least 40 deer sightings each and have stayed consistently above 25 deer/km<sup>2</sup> (McShea and Rappole 1992; W. J. McShea, unpublished data). For the GWF sites, deer sightings were too low to generate a reliable estimate based on line transects, but were estimated by Forest Service personnel at 10 deer/km<sup>2</sup> based on check station returns (S. Klinger, personal communication). Deer hunting was prohibited in the forests surrounding the SNP and CRC sites, while hunting pressure was heavy in the remaining four sites at GWF.

*Small mammal trapping.*—At each 4 ha site, 100 trap stations were evenly placed at 20-m intervals, and permanently marked with stakes. Each year the sites were trapped during late March/early April and again during August. The spring trapping coincided with the emergence of green vegetation, while the August trapping concluded before the maturation of the annual mast crop (McShea and Schwede 1993). No trapping was conducted during spring 1991.

During each trapping period, two Sherman traps (Sherman Trap Company, Tallahassee, Florida) were placed on the ground at each station. Also, at nine evenly-spaced stations, Tomahawk traps (Tomahawk Trap Company, Tomahawk, Wisconsin;  $40 \times 15 \times 15$  cm) were placed on wooden platforms nailed to a tree. All traps were prebaited with rolled oats and sunflower seeds for 3 d prior to 72 h of trapping, and during the spring cotton was added to all traps for insulation. The traps were checked every 12 h and all rodents captured were marked with a unique eartag, weighed, sexed, examined for reproductive condition, and released at the station. Abundance estimates are given as the total number of rodents captured during the trapping session. Although nine species were captured at least 10 times during the study, the only granivorous mammals with sufficient sample size for analysis were *Peromyscus leucopus*, *Tamias striatus*, and *Sciurus carolinensis*. Additional species captured included *Glaucomys volans*, *Neotoma alleghensis*, *Clethrionomys gapperi*, *Microtus pinetorum*, *Blarina brevicauda*, and *Sorex fu-*

*meus*. There were strong seasonal differences in trapping success of *T. striatus* and *S. carolinensis*, so abundance was estimated using the highest annual estimate, which was always the August trapping for *T. striatus* and the spring trapping for *S. carolinensis*.

*Acorn production.*—At every other station at each site ( $N = 50$ ), I attached a wire basket to a 1-m pole to estimate the acorn crop. Each mast collector had a collecting surface of 2910 cm<sup>2</sup>. All captured acorns were removed every 2 wk from 1 September until 14 November. Mast collectors remained at the same stations throughout the study period. There was no evidence of the mast collectors being disturbed by animals. All removed acorns were air dried, caps removed, and weighed to the nearest gram. At each site, the mass of acorns produced per hectare was estimated based on the sampling surface of the collectors and the total mass of acorns collected. The mast production of red and white oaks are not congruent (Sork et al. 1993) and the sites differed in their relative abundance of red, white, and chestnut (*Q. prinus*) oaks. The species of oak sampled was determined for each collector, and was used to estimate the ratio of red/white oaks for the site. Chestnut oaks were aggregated within the white oak subgenus (*Leucobalanus*), and black oaks (*Q. velutina*) within the red oak subgenus (*Erythrobalanus*). At the initial two sites at CRC, mast estimates were based on 100 collectors for the years between 1986–1989.

*Vegetation index.*—A coverboard was used to estimate vegetation density at each site (Nudds 1977). The  $2 \times 0.5$  m board was divided into four equal sections, with each section divided into 25 squares of equal size. Only the two center sections (0.5–1.5 m above ground) were used for this study. The board was placed 16 m from the observer and the number of squares not containing green vegetation were counted for each section. Annually at each site, the readings were taken at the same 12 staked locations and averaged. I tested the relationship between the coverboard values and the density of understory shrubs at three periods during the study (1990, 1995, 1997), when I counted the number of woody stems within  $24 \times 24$  m plots at the 12 stations used for coverboard readings. The number of woody stems was significantly correlated with the average coverboard value for each site ( $F = 84.3$ ;  $df = 1, 30$ ;  $r^2 = 0.74$ ;  $P < 0.001$ ). For site characteristics, the slope and aspect were averaged from three points at each site, and the elevation for each site was derived from United States Geological Survey (USGS) topographic maps.

*Nest predation and bird populations.*—Between 1991 and 1997, artificial nests were placed at each site during June to estimate nest predation rates (Leimgruber et al. 1994). Nests contained two Bobwhite Quail (*Colinus virginianus*) eggs each, and were placed at 10 randomly selected trap stations on each site. Eggs were handled with rubber gloves to minimize transfer of odors, and nests were constructed by using a gloved

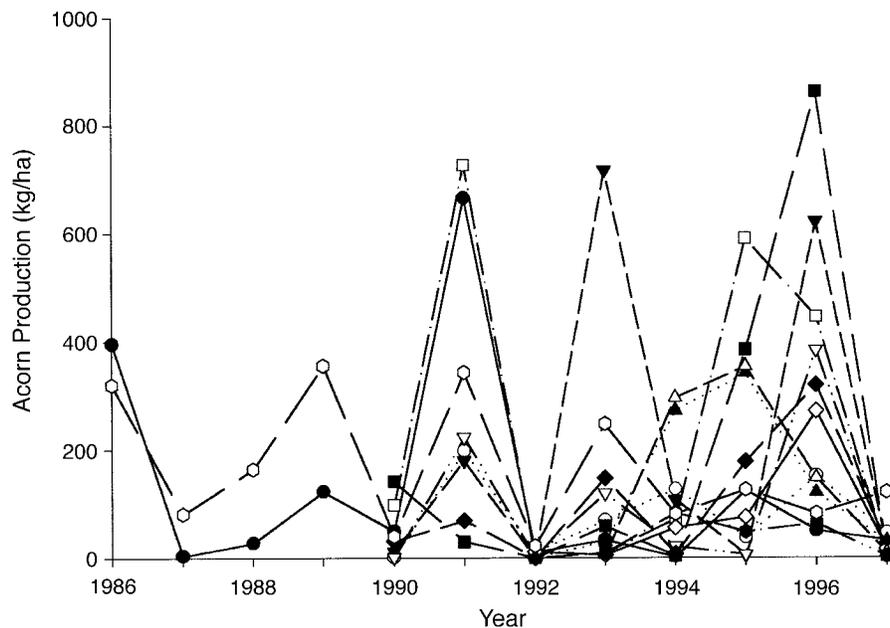


FIG. 1. The estimated acorn production (kg/ha) for 12 sites over a range of 10 yr, based on 50 baskets (each collecting surface = 2910 cm<sup>2</sup>) arrayed at each site. Each site is represented by a unique symbol and line.

first to make a depression in the leaf litter. After one week the nest was revisited, and if at least one egg was removed or destroyed, the nest was considered depredated. Percentage vegetation cover, estimated for a 1-m<sup>2</sup> area centered on the nest, and a coverboard placed at 5 m in each cardinal direction of the nest, were used as an index of vegetation density.

To examine bird populations at a regional scale, I used an annual index of abundance derived from Breeding Bird Survey (BBS) data (Sauer and Geissler 1990). This index has been used previously to estimate regional trends in bird populations (Holmes and Sherry 1988). The indices are estimated as residuals from route regressions for BBS routes run in the state ( $N = 72$ ; Sauer and Geissler 1990). If variability in acorn crops affects nest predation rates the following summer, then variability in nestling survivorship should be reflected in population counts of adults the subsequent summer. For example, a large mast crop in 1990 might produce high predation rates during the summer of 1991, which might decrease the number of adults detected in regional bird counts in 1992. To examine this relationship, I selected 11 species (see Table 6), all of which are captured at our sites (McShea and Rappole 1992). Six of the bird species nest on or near the ground, where nests are accessible to most mammal predators, and five species nest in trees where the nests are inaccessible. The nesting height of the species was based on Ehrlich et al. (1988).

*Analysis.*—To compare acorn production between sites, I created a matrix of the differences in acorn production and site characteristics between all possible pairs of sites and tested the relationship between the

matrix elements with linear regression. Discriminant function analysis and analysis of covariance was used to test for differences in vegetation cover, and mast crop between artificial nests that had, and those that had not, experienced predation. Analysis of covariance was used to compare the number of individuals for each rodent species captured at the 12 sites and the annual measures of the acorn crop, and vegetation density. The sites were divided into deer enclosure and control sites, and the interaction terms between deer status and the two independent variables (acorn crop and vegetation density) were used to examine the impact of excluding deer on the rodent populations. Comparisons of acorn crops and vegetation density between deer enclosure and control sites, and between high and poor quality sites, were tested in a repeated measures ANOVA. All data analyses were conducted using SAS Version 6.12 (SAS 1987). All ratio and percentage values were arcsine transformed and the amount of mast was log transformed prior to analysis.

## RESULTS

### *Acorn production and vegetation density*

Estimates of the acorn crop varied from 0 to 862 kg/ha (Fig. 1). All sites experienced at least one mast failure (<50 kg/ha), and nine sites experienced a bumper mast crop (>300 kg/ha) during the course of the study (Table 1). A comparison of mast production at the 12 sites revealed a significant positive correlation between 14 of 66 potential pairs (Table 2). With the average annual difference in mast production between each pair of sites as the dependent variable, a stepwise

TABLE 1. Summary of site characteristics. The sites are listed from north to south.

Site	Status	Location	Number of years sampled	Mean basal area of oaks (1 SD)†	Shrub density (1 SD)‡	Acorn production (kg/ha)	
						Mean (1 SD)	Range
Posey	Fenced	CRC	12	16.97 (10.38)	72 (10.5)	165.3 (120.4)	22–356
Bear	Control	CRC	12	78.32 (139.66)	108 (15.4)	126.5 (201.6)	2–666
North	Control	CRC	8	21.02 (2.34)	128 (65.1)	80.0 (71.1)	1–198
Forest1	Fenced	GWF	6	124.47 (13.58)	366 (15.5)	72.5 (101.1)	6–271
Forest2	Fenced	GWF	6	203.48 (0.20)	476 (69.8)	132.2 (142.5)	1–341
Forest3	Control	GWF	6	133.90 (26.2)	327 (44.4)	135.5 (157.9)	0–354
Forest4	Control	GWF	6	50.87 (16.4)	471 (89.8)	34.3 (35.5)	0–83
Keyser	Fenced	SNP	8	161.24 (9.82)	128 (47.8)	243.3 (296.9)	0–727
Dump	Fenced	SNP	8	244.28 (2.37)	47 (42.3)	185.6 (302.4)	0–862
Hilltop	Fenced	SNP	8	120.8 (24.69)	17 (25.0)	97.2 (111.1)	6–320
Range	Control	SNP	8	92.08 (10.97)	96 (54.1)	95.9 (140.6)	1–384
Elk	Control	SNP	8	89.3 (15.17)	34 (16.9)	207.5 (292.7)	0–717

† Basal area is calculated as the mean value (in square centimeters) for three 576-m<sup>2</sup> plots/1000.

‡ Mean number of shrub stems >1 m height for three 576-m<sup>2</sup> plots, counted the first year at each site.

(backwards) multiple regression for the difference in site characteristics; slope (degrees), aspect (degrees), elevation (m), distance (km), basal area of oaks, and the ratio of red to white oak trees, indicated that only the difference in elevation was a significant predictor of the difference in acorn production ( $F = 8.99$ ;  $df = 1, 64$ ;  $r^2 = 0.11$ ;  $P = 0.003$ ).

Despite the lack of a significant correlation between annual mast production at most sites, there appeared to be synchrony between sites with regards to mast failure (Fig. 1). To examine this pattern, I used the years when mast production was recorded on at least eight sites, and qualified production at each site with respect to mast failure (mast < 50 kg/ha; Table 3). The number of sites experiencing mast failure each year was not randomly distributed ( $\chi^2 = 39.5$ ,  $df = 7$ ,  $P < 0.001$ ), with only 1993 showing an equal distribution between the two levels of productivity.

Poorer quality soil is evidenced by a higher C:N ratio (Van Miegroet and Johnson 1993), and, based on analysis of 10 soil samples taken at each site, the GWF sites had poorer soil quality (ANOVA  $F = 136.8$ ;  $df = 1, 119$ ;  $P < 0.001$ ). However, these sites did not

produce significantly different numbers of acorns than did other sites (repeated measures ANOVA, interaction term; Year  $\times$  Site Quality,  $F = 2.13$   $df = 4$ ,  $P = 0.11$ ).

Sites without deer did not produce significantly different acorn crops from control sites (repeated measures ANOVA, interaction term; Year  $\times$  Deer Exclusion,  $F = 1.74$   $df = 6$ ,  $P = 0.52$ ). The exclusion of deer did increase vegetation density measures at the eight sites located at CRC and SNP (repeated measures ANOVA, interaction term Year  $\times$  Deer Exclusion,  $F = 3.30$ ,  $df = 6$ ,  $P = 0.005$ ), but had no significant impact at the low soil quality sites at GWF (repeated measures ANOVA, interaction term; Year  $\times$  Deer Exclusion,  $F = 1.35$ ,  $df = 4$ ,  $P > 0.10$ ).

Rodent populations

Annual variability in spring populations of *P. leucopus* can be explained by the independent variables measured ( $F = 3.23$ ;  $df = 15, 58$ ;  $r^2 = 0.45$ ;  $P = 0.0007$  [Fig. 2]), but the annual acorn crop accounts for most of the explained variability (Table 4). These same variables are also significant predictors of the summer density of *P. leucopus* ( $F = 9.81$ ;  $df = 16$ ,

TABLE 2. Pearson correlation coefficients ( $r$ ) for acorn production at 12 sites. The number of years sampled is shown next to the site name. The sites are listed from north to south.

Site	Site											
	1	2	3	4	5	6	7	8	9	10	11	12
1) Posey (12)												
2) Bear (12)	0.70**											
3) North (8)	0.62	0.64*										
4) Forest1 (6)	-0.25	0.25	0.73*									
5) Forest2 (6)	-0.08	0.56	0.27	0.23								
6) Forest3 (6)	-0.15	0.53	0.34	0.31	0.99**							
7) Forest4 (6)	-0.21	0.14	0.78*	0.60	0.78*	0.83*						
8) Keyser (8)	0.50	0.75**	0.59	0.66	0.67	0.69	0.52					
9) Dump (8)	-0.20	-0.13	0.24	0.95**	0.26	0.32	0.47	0.41				
10) Hilltop (8)	0.12	-0.03	0.34	0.82*	0.18	0.22	0.34	0.49	0.91**			
11) Range (8)	0.37	0.36	0.75	0.85**	0.26	-0.06	0.34	0.45	0.68*	0.75*		
12) Elk (8)	0.37	-0.05	0.42	0.43	-0.28	-0.26	0.08	0.03	0.69	0.69	0.72*	

\*  $P < 0.05$ , \*\*  $P < 0.01$ .

TABLE 3. The number of mast failures (estimated acorn production <50 kg/ha) among the 8–12 sites monitored since 1990.

Mast crop production	Year							
	1990	1991	1992	1993	1994	1995	1996	1997
<50 kg/ha	6	1	12	6	3	4	1	11
50–862 kg/ha	2	7	0	6	9	8	11	1

56;  $r^2 = 0.74$ ;  $P = 0.0001$ ). For the summer populations, the acorn crop remained a significant factor even after the variability due to spring population numbers was removed (Table 4). Shrub density was not a significant variable for either spring or summer populations of *P. leucopus* (Table 4).

The independent variables measured predicted population densities of both *T. striatus* ( $F = 3.74$ ;  $df = 15, 66$ ;  $r^2 = 0.46$ ;  $P = 0.0001$ ) and *S. carolinensis* ( $F = 1.85$ ;  $df = 15, 66$ ;  $r^2 = 0.30$ ;  $P = 0.045$ ) (Fig. 3), but again acorn crop production accounts for most of the explained variability (Table 4). Shrub density was not a significant predictor of *T. striatus* captures, but was a significant predictor for *S. carolinensis* captures (Table 4).

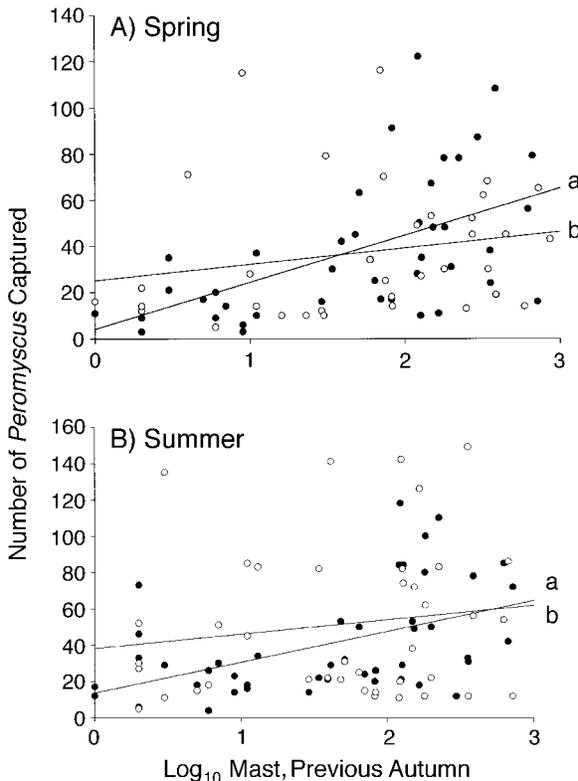


FIG. 2. The relationship between acorn production (kg/ha) and *Peromyscus leucopus* populations the next spring (A) and summer (B) for sites where deer are present (closed circles, control sites) and absent (open circles, experimental sites). Linear regression lines for both control (a) and experimental (b) sites are indicated.

TABLE 4. Results of analysis of covariance between small rodent populations, acorn crop productivity, and shrub density at the 12 study sites. The exclusion of deer from six sites is used as an interaction term with acorn crop and shrub density.

Source of variation	df	MS	F (partial)	P (partial)
<i>P. leucopus</i> (spring)				
Site	11	1149	1.96	0.046
Acorn crop	1	11 185	19.31	0.0001
Shrub density	1	1233	2.31	0.15
Deer × Acorn crop	1	2598	4.8	0.032
Deer × Shrub density	1	11	0.02	0.89
Error	58			
<i>P. leucopus</i> (summer)				
Site	11	3980	8.35	0.0001
No. of mice in spring	1	24 977	52.37	0.0001
Acorn crop	1	5806	12.17	0.001
Shrub density	1	14	0.03	0.86
Deer × Acorn crop	1	119	0.25	0.62
Deer × Shrub density	1	152	0.32	0.57
Error	56			
<i>T. striatus</i> (summer)				
Site	11	14.3	3.33	0.0011
Acorn crop	1	59.2	13.74	0.0004
Shrub density	1	1.3	0.30	0.58
Deer × Acorn crop	1	23.7	5.50	0.022
Deer × Shrub density	1	0.1	0.02	0.88
Error	66			
<i>S. carolinensis</i> (spring)				
Site	11	7.26	1.19	0.31
Acorn crop	1	34.91	5.72	0.019
Shrub density	1	22.94	3.76	0.056
Deer × Acorn crop	1	2.84	0.47	0.49
Deer × Shrub density	1	29.01	4.76	0.033
Error	66			

I observed a significant interaction between the exclusion of deer and annual variability in the acorn crop on densities of *T. striatus* populations and spring *P. leucopus* populations (Table 4; Fig. 2). Deer impact was most obvious during years following low acorn crops, where high numbers of mice were often found at deer exclusion sites, but not at control sites. During good mast years, high numbers of rodents could potentially be captured at any site, regardless of deer densities.

*Predation on artificial nests*

The proportion of artificial nests depredated was extremely variable between sites and years (Fig. 4). A stepwise (backwards) multiple regression revealed that only the acorn crop, and not the densities of the three rodent species, explained a significant portion of the variability observed between sites ( $F = 15.8$ ;  $df = 1, 74$ ;  $r^2 = 0.18$ ;  $P = 0.0002$ ; Fig. 5). A stepwise discriminant function analysis for predation at individual nests revealed that neither of the microsite vegetation indices, percentage ground cover or coverboard, explained the occurrence of predation, but the acorn crop recorded at the site the previous autumn was a significant predictor ( $F = 21.9$ ;  $df = 1, 378$ ;  $P < 0.001$ ). In

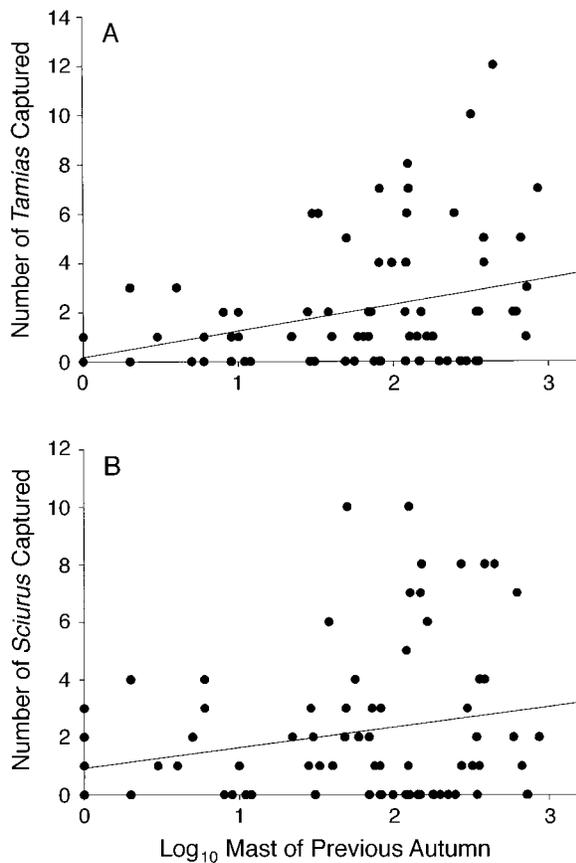


FIG. 3. The relationship between acorn production (kg/ha) and *Tamias* (A) and *Sciurus* (B) populations captured the next year. A linear regression line for each species is indicated.

an analysis of covariance for predation at individual nests, the year and the size of the mast crop the previous year were the best predictors, and not the vegetation density around the nest or the differences between sites (Table 5).

#### Regional bird populations

For two of the six ground- and understory-nesting species captured at our sites, the BBS index of bird abundances in Virginia was significantly predicted by the mast crop measured 2 yr previously (Table 6). For an additional three of the six species the correlations are negative, but not significant. Of the five canopy species examined, the abundance of none are significantly correlated with acorn production.

#### DISCUSSION

Acorn crops were variable and, although there was a correlation between sites, the degree of synchrony was not high. For this study, synchrony was only obvious during mast failures, with obvious differences in productivity between the sites during the alternate years. Regional synchrony for mast crops has been pos-

tulated by previous authors (Ostfeld et al. 1996, Wolff 1996). Sork et al. (1993) found that significant differences in annual mast production was due primarily to differences in seed set during the spring. The significance of elevation in this study may reflect similar spring temperatures for sites that share the same elevation. However, since acorns within the red oak subfamily mature over 2 yr, while acorns within the white oak subfamily mature during 1 yr, it is difficult for forests containing multiple oak species to have synchronized acorn production. The apparent synchrony during mast failures may result from landscape events, such as widespread gypsy moth defoliation, which cause both failure of seed-set and abortion of maturing nuts (Gottschalk 1989).

The variability in acorn crops affected mouse populations in the spring and summer following the mast crop, a finding in agreement with previous studies (Wolff 1996, Jones et al. 1998). Removal of a seed consumer (deer) from half the sites impacted both *P. leucopus* and *T. striatus* populations, but the impact was obvious only during years following low mast crops. Acorn crops >200–300 kg/ha did not result in significant increases in rodent populations at enclosure sites relative to the control sites. Exclusion of deer significantly increased the understory vegetation, and this affected the number of *S. carolinensis* captured, but not the number of *P. leucopus* or *T. sciurus*. *S. carolinensis* populations were affected by the acorn crop the previous year, but did not respond significantly to the removal of deer. The ability of squirrels to harvest seed crops before they fall to the ground may make them less sensitive to species interactions on the forest floor. Overall, the removal of deer had an impact on other seed consumers, but the interaction was weak compared to fluctuations in seed production.

Most analyses showed significant differences among the sites. These site differences may be partially due to abiotic factors. The four sites on the GWF showed significantly lower soil productivity, which did not result in lower acorn production, but did coincide with few *T. striatus* captures. The severity of winter storms and seasonal droughts was also probably variable for these sites, which were spread over a large distance and elevation. For both small mammal densities and nest predation rates, large mast crops coincided with large values, but low mammal densities and predation rates occurred at all mast levels. This phenomenon accounts for the low  $r^2$  values reported for several analyses. Mast crops appear to set the upper bounds for small mammal densities and predation rates, but do not determine the ability of populations to reach that potential.

The role of white-tailed deer populations in shaping the structure of the forest understory vegetation (McShea and Rappole 1997) has ramifications beyond seed-eating rodents. The density and diversity of forest understory vegetation may affect the ability of pred-

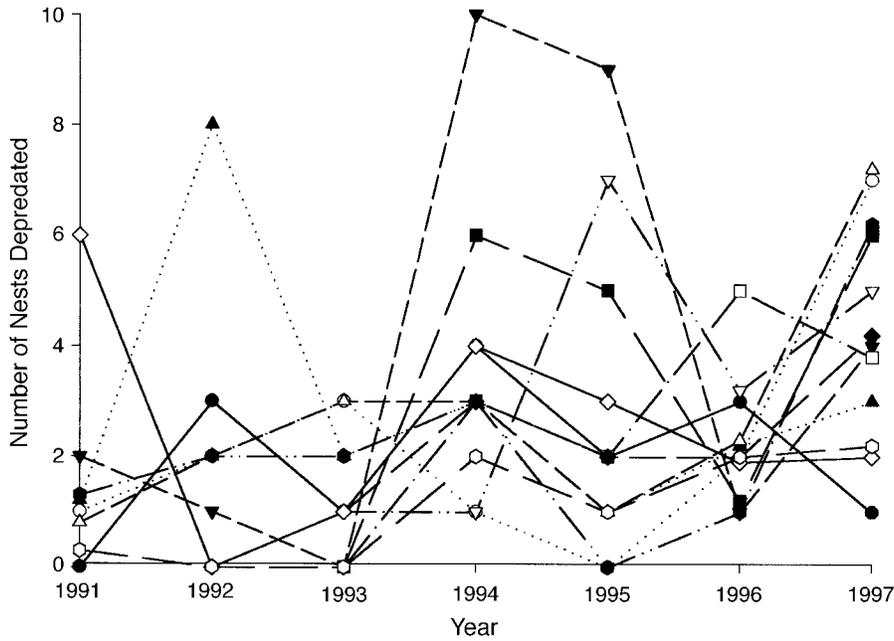


FIG. 4. The number of nests depredated at each site during the study. Ten nests of two quail eggs each were placed at each site for one week during June of each year. Each site is represented by a unique symbol and line.

ators to locate nests for forest birds (Martin and Roper 1988, Yahner and Morrell 1991). A previous study at these sites noted that artificial nests at sites with high vegetation density experienced low rates of predation (Leimgruber et al. 1994). However, annual predation rates at the sites were extremely variable, without dramatic changes in vegetation density. The best predictor of annual variation in the amount of nest predation was acorn production the previous autumn.

Interpretation of results from artificial nest studies is delicate (Storaas 1988, Reitsma et al. 1990, Keyser et al. 1998). Mast crops, and not densities of graniv-

orous mammals, were significant predictors of predation rates at the sites. My use of quail eggs probably underestimated predation by small rodents (Haskell 1995, Keyser et al. 1998), but it is also possible that acorn crops impact other species beyond seed consumers. Studies in large forest tracts have shown that artificial nest predation is caused by a combination of both small rodents and medium-sized carnivores (Leimgruber et al. 1994, Keyser et al. 1998). In a previous study conducted at these sites, 11 species of mammals were photographed at artificial nests (Leimgruber et al. 1994). Granivorous mammals (*Peromyscus*, *Tamias*, and *Sciurus*) were responsible for 25% of the predation events, while 65% were attributed to mammalian carnivores (Leimgruber et al. 1994). The abundances of the two types of nest predators are not necessarily independent, as rodents form the bulk of the prey for many medium carnivores outside the bird nesting season (King 1983, Hansson 1987). The temporal and spatial dynamics of abundant rodent species, such as *Peromyscus*, may result in variable predation

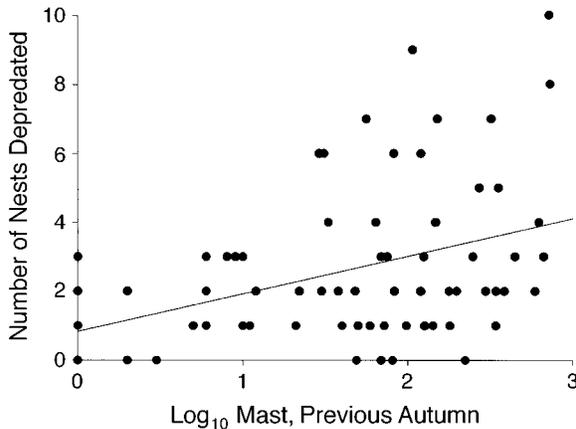


FIG. 5. The relationship between the amount of artificial nest predation at a site and the amount of acorns (kg/ha) produced at the site the previous autumn. A linear regression line is plotted.

TABLE 5. Analysis of covariance between predation at artificial nests and acorn crop and vegetation changes.

Covariables	df	MS	F (partial)	P (partial)
Year	5	1.07	6.47	0.0001
Site	11	0.26	1.58	0.1035
Acorn crop	1	1.58	9.53	0.0022
Vegetation density	1	0.03	0.18	0.660
Error	330	0.166		

TABLE 6. The index of bird populations based on Breeding Bird Surveys in Virginia for select species, and correlation of this index with average mast production measured two years before the index.

Species	Nest height	Year										Correlation ( <i>r</i> ) with acorn crop†
		1988	1989	1990	1991	1992	1993	1994	1995	1996		
Ovenbird ( <i>Seiurus aurocapillus</i> )	ground	9.6	9.7	8.9	10.2	10.1	10.6	11.9	12.5	11.9	-0.31	
Worm-eating Warbler ( <i>Helmitheros vermivorus</i> )	ground	1.1	1.2	1.1	1.0	1.2	1.1	1.3	1.2	1.2	-0.83**	
Hooded Warbler ( <i>Wilsonia citrina</i> )	low shrub	2.5	3.0	3.0	2.8	3.0	2.5	3.2	2.5	3.1	-0.77*	
Kentucky Warbler ( <i>Oporornis formosus</i> )	low shrub	0.9	0.9	0.9	0.9	0.9	0.9	1.0	0.8	0.7	-0.38	
Veery ( <i>Catharus fuscescens</i> )	low shrub	8.4	8.2	8.2	8.2	10.4	8.7	8.6	8.0	11.2	-0.12	
Wood Thrush ( <i>Hylocichla mustelina</i> )	high shrub	12.7	11.7	9.6	12.4	11.5	13.3	11.8	11.0	10.5	+0.28	
American Redstart ( <i>Setophaga ruticilla</i> )	high shrub	1.5	1.7	1.5	1.6	1.5	1.4	1.3	1.6	1.4	+0.27	
Red-eyed Vireo ( <i>Vireo olivaceus</i> )	high shrub	29.4	26.6	28.1	33.6	30.8	29.6	35.5	35.2	37.7	-0.23	
Scarlet Tanager ( <i>Piranga olivacea</i> )	canopy	6.3	5.8	6.7	7.7	6.4	6.7	6.5	7.8	6.8	+0.33	
Eastern Wood-pewee ( <i>Contopus virens</i> )	canopy	9.9	7.4	8.9	8.1	7.8	7.7	8.4	8.0	6.6	+0.18	
Blue-gray Gnatcatcher ( <i>Poliophtila caerulea</i> )	canopy	7.6	7.4	10.4	12.6	9.0	12.9	13.3	13.4	10.8	-0.11	
Mean acorn production (kg/ha) 2 yr previously		350	42	96	239	47	304	5	121	94		

\*  $P < 0.05$ , \*\*  $P < 0.01$ .

† The acorn estimates (kg/ha) were log-transformed prior to analysis.

pressures on migratory birds, both due to their role as a predator and as a food for other generalist predators.

The negative correlation between mast production and statewide indices for Worm-eating Warblers and Hooded Warblers, both understory forest birds, suggests that some interactions within forest communities may operate at the landscape scale. The hypothesis is that widespread mast failures produce pulses in bird productivity the next year due to low densities of nest predators. For this hypothesis to be true, there are at least two additional assumptions that must be tested. The first assumption is that mast crops and small mammal populations are synchronized across a wide range. In this study synchrony in the mast crop was only obvious during mast failure years, which occurred ~1 out of 4 yr. Synchrony in small mammal populations was observed across the landscape of Algonquin National Park in Ontario, Canada (Fryxell et al. 1998), although oak populations across this region were probably low. The second assumption is that juvenile recruitment into bird populations must operate at the same scale as mast production. In New Hampshire, pulses in productivity of migratory birds have been linked to pulses in food availability (i.e., defoliating caterpillars) at both the local (Holmes et al. 1986), and regional (Holmes and Sherry 1988) level.

Recent papers point to the wide-ranging impact of acorn production (Elkinton et al. 1996, Jones et al. 1998) and forest ungulates (Pastor et al. 1997, Waller and Alverson 1997, Ritchie et al. 1998) on forest sys-

tems. For both oaks (Braun 1950) and white-tailed deer (Warren 1997), present densities do not reflect historical levels, and determining the impact of present densities on forest systems is difficult. In this study, the impact of white-tailed deer on other forest vertebrates was dependent on context; at sites with high densities of acorns their influence on other forest vertebrates was minimal. Concerns that their present densities will result in suppressed productivity (Stromayer and Warren 1997, Waller and Alverson 1997) do not appear warranted with regards to food webs involving acorns. For oaks within Appalachian forests, numerical dominance is recent, but significant, and oaks may serve as an ecological replacement for American chestnuts. The connection between acorn crops, small mammals, and forest birds has been postulated (Ostfeld et al. 1996), but this study is the first empirical evidence for such connections. The productivity of oaks, and the reliance of many species on the seed crop, creates complex food webs that may serve to increase the stability of forest ecosystems (Polis and Strong 1996). Identifying the links between species, and the sensitivity of these links to fluctuations in productivity, are the first steps in effective management of complex ecosystems (Power et al. 1996).

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