

SONGBIRD POPULATIONS IN FLUCTUATING ENVIRONMENTS: PREDATOR RESPONSES TO PULSED RESOURCES

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Abstract. In response to mast production of acorns, populations of small mammals, such as the white-footed mouse and eastern chipmunk, greatly increase and, in turn, initiate cascades of direct and indirect effects that permeate throughout forest communities. To examine the strength of the effects stemming from acorn crops, we conducted studies in oak-dominated deciduous forest of the Hudson Valley, New York, documenting the connections between predator abundance (small mammals and raptors) and the abundance and reproductive success of five woodland songbirds. Nest predation rates increased at high rodent densities for Veeries, Red-eyed Vireos, and Wood Thrushes. Analysis of Breeding Bird Survey (BBS) data from surrounding counties demonstrated a unimodal relationship between rodent density (year t) and songbird abundance (year $t + 1$), rather than a monotonic decline. Regional Christmas Bird Count data for Sharp-shinned and Cooper's Hawks showed a positive correlation between rodent density and accipiter abundance the following winter, suggesting that hawks exhibit a numerical response to rodents. Taken together, we suggest that predation by accipiters when rodents are scarce, in combination with high nest predation when rodents are abundant, may explain the unimodal relationship between rodents and songbirds. Nonlinear relationships between predator and prey abundance and indirect interactions appear to characterize this system.

Key words: *Breeding Bird Survey; direct and indirect effects; eastern chipmunk; nest predation; oak mast; pulsed resources; songbird populations; temporal variability; Veery; white-footed mouse.*

INTRODUCTION

A key feature of temperate deciduous forests is the production of variable seed crops (i.e., pulsed resources) and their consequential effects on mast-consuming species (Curran and Leighton 2000, Ostfeld and Keesing 2000, Schaubert et al. 2002). In particular, populations of mast-consuming mammals, such as the white-footed mouse (*Peromyscus leucopus*) and eastern chipmunk (*Tamias striatus*), initiate cascades of direct and indirect effects that permeate throughout these forest-based food webs (Elkinton et al. 1996, Ostfeld et al. 1996, Ostfeld 1997, Jones et al. 1998, McShea 2000, Schmidt et al. 2001). Masting seed crops have the potential to exert strong indirect effects on songbird populations mediated through small-mammal populations and their effects on nest predation rates (Ketterson et al. 1996, McShea 2000, Schmidt et al. 2001), nest productivity, and the recruitment of breeding adults (Sherry and Holmes 1992, Jędrzejewska and Jędrzejewski 1998, McShea 2000). For instance, McShea (2000) found significant negative correlations between acorn crops (fall of year t) at Front Royal, Virginia, and the Breeding Bird Survey's (BBS) index of population abundance (summer of year $t + 2$) for ground- or low-shrub-nesting Worm-eating Warblers (*Helmitheros ver-*

mivorus) and Hooded Warblers (*Wilsonia citrina*). Three remaining ground- or low-shrub-nesting species, Veery (*Catharus fuscescens*), Ovenbird (*Seiurus aurocapillus*), and Kentucky Warblers (*Oporornis formosus*) had negative, but nonsignificant correlations, as did Red-eyed Vireos (*Vireo olivaceus*). Thus, McShea argued that autumn seed crops increase rodent populations during the succeeding spring and summer, which in turn have cascading effects on songbird nest productivity through increased rates of nest predation. That these effects are seen two years following acorn mast indicates reduced recruitment into the adult breeding songbird population.

Summarizing long-term studies of the reproductive ecology of nesting forest songbirds, Jędrzejewska and Jędrzejewski (1998) also found high nest predation by rodents during outbreak years in the Białowieża Primeval Forest (BPF) at the border of Poland and Belarus. However, during rodent population crashes at BPF, aerial-foraging raptors and carnivorous mammals, such as the marten (*Martes martes*), switched from a diet consisting primarily of rodents to a diet of primarily songbirds. Thus, in contrast to the monotonic relationship between rodent densities and reproductive success suggested by McShea's study (see also Ketterson et al. 1996), breeding songbird abundance at BPF peaked following years of moderate rodent densities (or alternatively stated as 2 yr post-mast).

The connections between variable seed crops, temporal variability in rodent populations, and nest pre-

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datation rates on songbirds are well established at Front Royal and BPF. However, the influence of rodents on the future recruitment of breeding songbirds is apparently contingent upon the presence of alternative, generalist predators that may further mediate indirect effects through behavioral (i.e., prey-switching) or numerical responses to high rodent densities. We have examined the interactions between acorn production in oak forest, rodent populations, and songbird nesting success for two primary species, the Veery and Wood Thrush (*Hylocichla mustelina*), although we include preliminary data on Ovenbirds, Red-eyed Vireos, and American Redstarts (*Setophaga ruticila*), nesting in temperate deciduous forest of the Hudson Valley, New York. During the 4 yr of our study, rodent populations have fluctuated by two orders of magnitude. In this paper, we (1) document variation in nest mortality as a function of rodent density; (2) correlate the regional abundance of several forest songbird populations in surrounding counties (based on the Breeding Bird Survey, Sauer et al. 2001) to rodent and acorn abundance from long-term monitoring plots; and (3) correlate the regional abundance of Cooper's (*Accipiter cooperii*) and Sharp-shinned Hawks (*A. striatus*) to acorn and rodent abundance.

METHODS

General approach and study location.—We used original field data and analyses of available data from the Breeding Bird Survey to examine the degree to which interannual variation in nest mortality and the abundance of forest songbirds is explained by fluctuating abundance of rodents that are known to depredate nests. Because of the tight correlation between summer rodent densities and the production of acorns the prior fall (Ostfeld et al. 1996, 2001, Wolff 1996), we further examined whether variation in songbird nest predation can be explained by fluctuating acorn production in prior years.

Field studies were conducted on the property of the Institute of Ecosystem Studies (IES) in Dutchess County, southeastern New York (41°50' N, 73°45' W). IES property includes ~325 ha of continuous eastern deciduous forest. Forest canopy is dominated by oaks (*Quercus rubra* and *Q. prinus*), and with oaks, sugar maple (*Acer saccharum*), eastern hemlock (*Tsuga canadensis*), maple-leaved viburnum (*Viburnum acerifolium*), and witch hazel (*Hamamelis virginiana*) common in the understory.

Small-mammal population studies.—We used six 2.25-ha forest plots (separated by 0.5–4 km) as sites for live-trapping rodents in order to estimate population sizes. Each plot consisted of an 11 × 11 array of grid points with 15 m between points. We placed two Sherman live traps (7.6 × 8.9 × 22.9 cm) at each point for a total of 242 traps per plot. Small mammals (white-footed mice, eastern chipmunks, and shrews) were trapped each May through November on the study plots

since 1995 or earlier. From the trapping data, we enumerated densities of white-footed mice as minimum number known alive (MNA) per plot. Lower capture probabilities for chipmunks necessitated more sophisticated techniques for estimating densities. We used the program POPAN5 (e.g., Arnason and Schwarz 1999) to estimate population densities within a Jolly-Seber framework, allowing trappability and survival rates to vary with time and avoid bias (at the cost of precision). Detailed protocols for trapping small mammals can be found in Schmidt et al. (2001).

Songbird population studies.—We monitored populations of five songbird species at IES from 1998 through 2001. These include Veery, Wood Thrush, Ovenbird, Red-eyed Vireo, and American Redstart. To date, our population studies have concentrated on measuring breeding productivity and nest predation rates of primarily Veeries and Wood Thrushes. Due to low sample sizes, we combined nesting data for vireos and redstarts (henceforth called pensile nesters), which build very similar nests that differ slightly in their placement. Red-eyed Vireos build their nests toward the outer tips of branches, whereas American Redstart nests are placed against the main trunk. In addition, three ground-nesting warbler nests were included with the Ovenbird data: two Worm-eating Warblers (1999 and 2001) and a Black-and-white Warbler (1998). During mid-May through July, we searched IES' grounds extensively for Veery and Wood Thrush nests by concentrating in areas with singing males. We monitored all active nests approximately every three days until depredated or until all fledglings had left the nest. We quantified rates of nest predation as the nest daily mortality rate (DMR), calculated by dividing the number of depredated nests by the total number of nest exposure days (Mayfield 1975). A handful of Wood Thrush nests ($n = 4$ nests) failed as a result of apparent abandonment during the incubation phase of a full clutch. We considered these as depredated, since they likely failed as a result of the female bird being killed by predators. From the DMR, we calculated the probability of a successful nest attempt (i.e., producing at least one fledgling) as: $(1 - \text{DMR})^d$, where d gives the number of days in the nesting cycle. During nest visits, we also determined nest productivity, which will be detailed in a forthcoming manuscript (K. A. Schmidt, unpublished manuscript).

Regional population trends using the Breeding Bird Survey.—To assess regional population trends of forest songbirds, we used data from the Breeding Bird Survey (BBS; Robbins et al. 1986, Sauer et al. 2001). The BBS is a roadside survey that uses permanent sampling routes randomly located throughout the United States and Canada to census adult songbird populations by visual and auditory identification of singing males. We examined all routes used in an ~150 km radius extending out from Dutchess County, New York. This range was chosen somewhat ar-

bitrarily, but oak species are known to show synchronous mast production over distances of 300–600 km (Koenig et al. 1999, Koenig and Knops 2000, Schaubert et al. 2002). We considered our selection of routes close enough for mast production to be synchronized. To ensure as high a quality of route selection as possible, we restricted our analyses to routes surveyed continuously from 1994 to 2000 (covering a period of two cycles of acorn production [see next paragraph]), or that had no more than a single year of data missing over this period. This resulted in discarding a number of routes due to irregular censusing. We retained 20 routes that have been regularly surveyed in the following counties: Litchfield and Fairfield counties in Connecticut; Hampshire, Franklin, and Berkshire counties in Massachusetts; Passaic and Sussex counties in New Jersey; Wayne and Pike counties in Pennsylvania; and Dutchess, Columbia, Greene, Ulster, and Rensselaer counties in New York State.

For our analyses, we regressed standardized songbird abundances in year t against acorn abundance in year $t - 2$ or rodent density in year $t - 1$. To standardize songbird abundance for comparisons between species, we divided annual mean abundances (i.e., BBS counts) by the highest abundance recorded over the time period considered. Determination of acorn abundance at IES began in 1992 (Ostfeld et al. 2001; C. Canham, unpublished data), and consisted of 20 0.5-m² seed traps per plot. A single trap was deployed under each of five randomly chosen mature individuals of four dominant canopy species: *Quercus rubra*, *Q. prinus*, *Q. alba*, and *Carya glabra* (for more details, see Ostfeld et al. [2001]). Placing seed traps below seed-producing trees is not ideal for assessing total seed production per unit area, but it is sufficient for monitoring the temporal trends in seed production as we use it here. We regressed songbird densities between 1994 and 2000 against red oak acorn abundance between 1992 and 1998. This period covered two cycles of acorn production; 1992–1994 (low, intermediate, and high acorn production, respectively) and 1995–1998 (low, intermediate, intermediate, and high acorn production, respectively). Red oak acorns were chosen because previous results indicate the annual peak of mice in the summer is highly correlated with the number of red oak acorns produced the previous fall ($r^2 = 0.87$, $P < 0.01$; Ostfeld et al. 1998).

Rodent densities were calculated from averaging across six 2.25-ha trapping grids (see Schmidt et al. 2001) monitored since 1995. We regressed songbird abundance against rodent densities between 1996 and 2000. Mean rodent densities were calculated for the target date of approximately 10 June in each year. Because the three pairs of plots were generally trapped on alternate weeks, densities were taken from the trapping period nearest the target date, often the week before or after, or when trapping dates spanned the target

week, densities were averaged between them. When regressing against acorn or rodent densities, we included both a linear and quadratic term but dropped the quadratic term if nonsignificant ($P > 0.10$) and used the simpler model.

Because bird species showed different relationships between nest predation and rodent density (see *Results: Nest survivorship*), we ran three separate regressions: thrushes (Veery, Wood Thrush, and American Robin), ground-nesting warblers (Ovenbird and Black-and-white Warbler), and the small, pensile-nesting Red-eyed Vireo and American Redstart as the third group. All these species are common breeders at IES, although we lack extensive nesting data for several of them. We tested for differences between species in each group both as a main effect and by the interaction between species and the covariate (acorns or rodents), and as before, we dropped the interaction term(s) if nonsignificant. For pensile nesters and ground-nesting warblers we also included a year effect in the model, as these species exhibited an increasing trend over the time period we considered. Finally, we ran separate regressions of songbird abundance against mouse and chipmunk densities to compare against our results when using the composite rodent variable.

Regional accipiter abundance.—Regional variability in rodent densities might also lead to numerical responses in the number of hawks. Because hawks are poorly censused by the BBS, we used data from the National Audubon Society Christmas Bird Count to assess regional population trends of Cooper's and Sharp-shinned Hawks. The Christmas Bird Count, while subject to its own biases (Bock and Root 1981), provides the most comprehensive database available for regional hawk abundance. Counts are standardized to specific 24 km diameter plots that are censused for one day located within a 2-wk window around 25 December. Data were taken from the Audubon web site⁴ and standardized for sampling effort by dividing counts by the number of party hours. We used 37 routes occurring within the approximate geographic area used for the regional songbird analysis. We regressed hawk abundance (year t) against rodent (year $t - 1$) or acorn abundance (year $t - 2$) using ANCOVA, and tested for effects of the covariate (rodents or acorns), hawk species, and their interaction. Both interaction terms were nonsignificant ($P > 0.15$) and were subsequently dropped from the analysis.

RESULTS

Nest survivorship.—Over a 4-yr period (1998–2001) in which we measured nesting success and nest productivity, rodent densities at IES spanned approximately two orders of magnitude (Fig. 1). We analyzed these data using ANCOVA with rodent density as a covariate, bird species as the group variable, and the

⁴ URL: <http://www.audubon.org/bird/cbc>

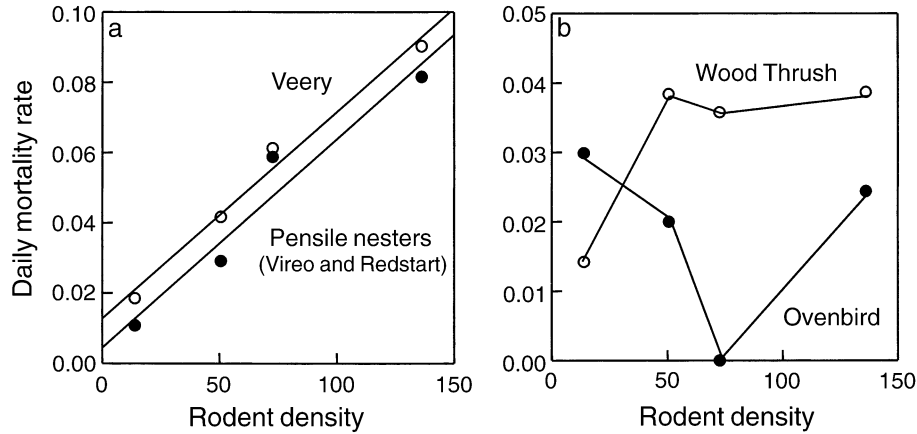


FIG. 1. Daily nest mortality rates on songbird nests as a function of the summer rodent density (number of animals/2.25 ha).

interaction between the two terms. Rodent density had a highly significant influence on daily mortality rates ($r^2 = 0.903$, $F_{1,8} = 29.8$, $P = 0.001$), but species did not ($F_{3,8} = 0.64$, $P > 0.50$). The species \times rodent interaction was likewise significant ($F_{3,8} = 6.97$, $P = 0.013$). For the Veery and the pensile-nesting group, DMR was a strongly increasing function of the density of rodents (Fig. 1a). Wood Thrush nest mortality rates increased from low-rodent (33% of nests depredated when extrapolating the DMR to a 28-d nesting cycle) to moderate- or high-rodent years ($\sim 65\%$ of nests depredated; Fig. 1b, Table 1), whereas predation rates on Ovenbird nests were low and insensitive to variability in rodent density.

During routine nest checks, we made a number of observations, exclusive to Wood Thrushes in all but one occasion, suggesting that predators had killed nestlings and/or adult birds while on or guarding a nest. Evidence included direct observation (by K. A. Schmidt) of a Sharp-shinned Hawk attacking Wood Thrush nestlings and dead birds (both juveniles and adults) with feathers plucked out underneath the nests, as well as indirect evidence, such as clutch abandonment in the middle of incubation and continuous sing-

ing thereafter by the male. The percentage of attempted Wood Thrush nests that failed due to suspected marauding from raptors approximately doubled in low-rodent years (13.3%) relative to intermediate- (7.9%) or high- (7.4%) rodent years.

Regional songbird population trends.—The regional abundance of thrushes (Veery, Wood Thrush, and American Robin) peaked the summer following intermediate rodent densities (Table 2, Fig. 2a) and two summers following intermediate acorn densities (Table 2, Fig. 2b). Rodent density or acorn abundance was not significantly related to the abundance of pensile nesters or ground-nesting warblers (Table 2). For comparison, when either mice or chipmunks were substituted for the composite rodent density the ANCOVA results remained significant (thrushes only). However, variation in chipmunk abundance explained considerably more of the variation in thrush abundance than did variation in mouse abundance ($r^2 = 0.586$ vs. $r^2 = 0.929$ for mice and chipmunks, respectively).

When the two acorn cycles were analyzed separately, similar patterns were observed. Each thrush species peaked in density two summers following intermediate

TABLE 1. Daily mortality rates (DMR) for forest songbird populations nesting at the Institute of Ecosystem Studies in each year of study (pensile nesters include the Red-eyed Vireo and American Redstart).

Species	1998			1999			2000			2001		
	N	DMR	Nests depredated (%)	N	DMR	Nests depredated (%)	N	DMR	Nests depredated (%)	N	DMR	Nests depredated (%)
Wood Thrush	43	0.0358	64.0	27	0.0387	66.9	15	0.0142	33.0	46	0.0384	66.6
Veery	21	0.0613	78.1	19	0.0903	89.7	12	0.0185	36.2	23	0.0417	64.0
Ovenbird	5	0	0	4	0.0244	44.7	7	0.0299	54.5	12	0.0200	40.9
Pensile nesters	6	0.0588	76.6	9	0.0816	87.0	5	0.0108	22.9	17	0.0291	49.2

Notes: The percentage of nests depredated is calculated as $[1 - (1 - \text{DMR})^d] \times 100\%$, where d gives the number of days in the nesting cycle. For calculations, Wood Thrush $d = 28$; Veery $d = 24$; Ovenbird $d = 24$; pensile nesters $d = 24$. N = number of nests.

TABLE 2. Results of ANCOVA regressing standardized songbird abundance (from BBS routes) against either rodent density the previous summer or acorn abundance two autumns previous.

Effect	df	MSE	F ratio	P
A) Thrushes; $r^2 = 0.952$				
Species	2	0.001	46.45	0.139
Rodents	1	0.073	167.9	<0.001
(Rodents) ²	1	0.082	188.2	<0.001
Error	10	<0.001		
Regression using acorn abundance; $r^2 = 0.688$				
Species	2	0.009	2.885	0.087
Cycle	1	0.011	3.451	0.083
Acorns	1	0.059	19.08	0.001
(Acorns) ²	1	0.072	23.12	<0.001
Error	15	0.003		
B) Pensile-nesters; $r^2 = 0.958$				
Species	1	0.043	109.2	<0.001
Year	1	0.005	12.48	0.012
Rodents	1	0.001	1.442	0.275
Error	6	<0.001		
Regression using acorn abundance; $r^2 = 0.927$				
Species	1	0.012	8.39	0.018
Year	1	0.007	4.70	0.058
Cycle	1	0.001	0.45	0.518
Acorns	1	<0.001	0.35	0.571
Error	9	0.001		
C) Ground-nesting warblers; $r^2 = 0.191$				
Species	1	0.002	0.320	0.590
Year	1	0.014	1.942	0.213
Rodents	1	0.003	0.407	0.550
Error	6	0.007		
Regression using acorn abundance; $r^2 = 0.305$				
Species	1	0.008	1.233	0.296
Year	1	<0.001	0.016	0.902
Cycle	1	<0.001	0.001	0.981
Acorns	1	0.002	0.236	0.639
Error	9	0.007		

acorn abundance during each bust to boom acorn cycle (Fig. 3). However, despite the apparent synchrony among thrush populations as shown in Fig. 2, the relationships appear more idiosyncratic when broken down into the two separate masting cycles. Wood Thrush abundance fell dramatically ($\sim 30\%$) 2 yr following high acorn production during the 1992–1994 cycle (Fig. 3). However, in the 1995–1998 cycle, abundance following high acorn production was only $\sim 7\%$ below the peak abundance during intermediate acorn production. Veeries, in contrast, showed strong consistency between cycles, whereas American Robins were intermediate.

Regional accipiter population trends.—The regional abundance of Sharp-shinned and Cooper's Hawks was positively related to the previous summer's rodent density ($r^2 = 0.750$, $P = 0.012$; Fig. 4a) and acorn abundance two autumns previous ($r^2 = 0.701$, $P = 0.018$; Fig. 4b). These relationships suggest a numerical response by accipiters to rodents (1-yr lag) and, indirectly, to acorns (2-yr lag).

DISCUSSION

Our study integrates the concepts of pulsed resources and variability in songbird population dynamics over time. Pulsed resources in deciduous forest communities are generated in the form of interannual variability in the production of seed crops, principally acorns. In turn, highly productive years temporarily release generalist consumers (e.g., mice and chipmunks) from food limitation and their populations explode. For instance, the annual peak of mouse abundance in the summer is highly correlated with the density of red oak acorns produced the previous fall (Ostfeld et al. 1998, 2001, Wolff 1996). Likewise, chipmunks covary positively

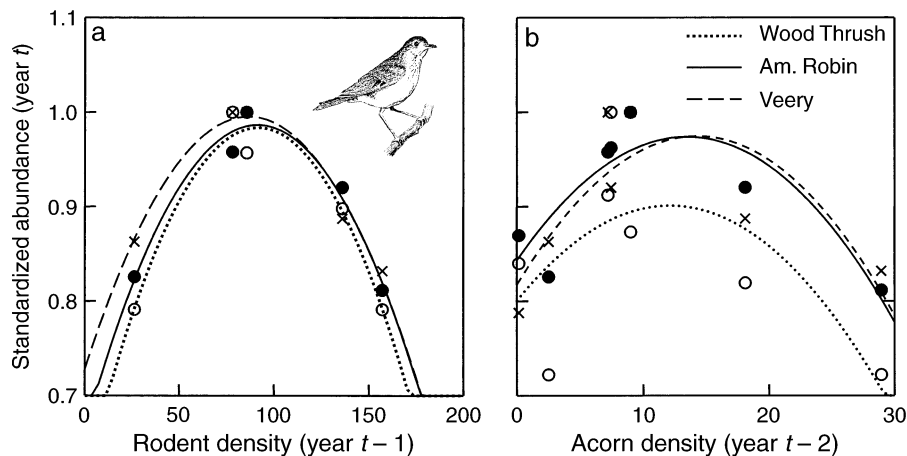


FIG. 2. Standardized thrush abundance on Breeding Bird Survey (BBS) routes from Dutchess County (New York) and surrounding counties as a function of (a) rodent or (b) red oak acorn abundance measured at the Institute of Ecosystem Studies (IES). Thrush abundances are plotted against rodent densities (number of animals/2.25 ha) from the previous summer or against acorn densities (acorns/0.5 m²) from two autumns previous.

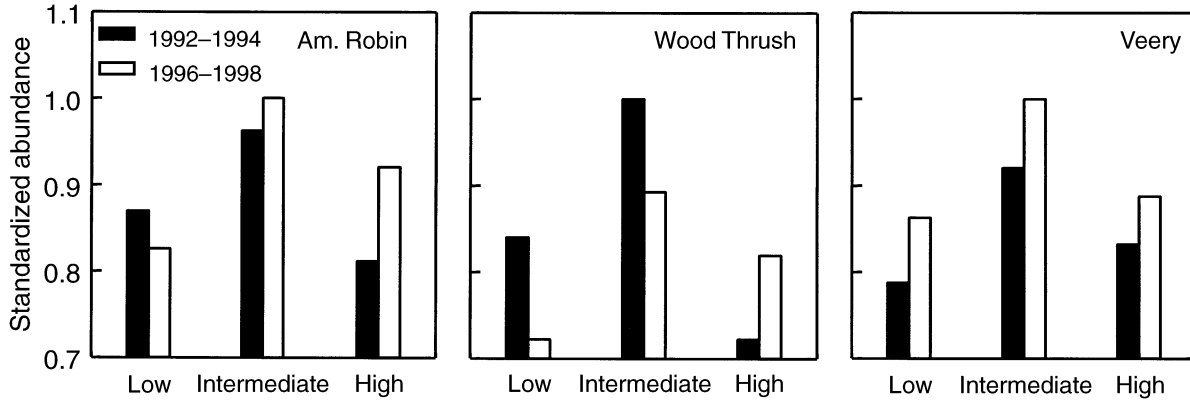


FIG. 3. Standardized thrush abundance on BBS routes from Dutchess County (New York) and surrounding counties vs. acorn production two autumns previous, broken into low, intermediate, and high designations. The period of this study covers two cycles of acorn production; 1992–1994 (low, intermediate, and high acorn production, respectively) and 1995–1998 (low, intermediate, intermediate, and high acorn production, respectively).

with mouse populations, but at approximately half their abundance (Schmidt and Ostfeld 2001; also see Wolff 1996). Past results, therefore, indicate that population densities of mast-consuming rodents increase dramatically in the year following mast production (Elkinton et al. 1996, Wolff 1996, Jones et al. 1998, McShea 2000). This study has concentrated on illuminating further cascading interactions between seed crops and songbirds. While our study concentrates on songbird populations, cascading impacts of pulsed resources are ubiquitous in a number of community types (Jones et al. 1998, Curran and Leighton 2000, Ostfeld and Keesing 2000).

Nest predation and rodent populations.—We have demonstrated that nest mortality increases with the density of rodents for the Veery and the Red-eyed Vireo/American Redstart group, species with very different

nest placement (Fig. 1). Veeries nest on or close to the ground, whereas Red-eyed Vireo and American Redstart nests we found were between 2–4 m in trees and sapling either against the trunk (redstart) or in the outer tips of branches (vireo). The Ovenbird also nests on the ground, but showed no relationship between nest predation and rodent density and, in fact, had the lowest nest predation rate of any species we examined. Wood Thrushes nest at similar heights as Red-eyed Vireos, but nest predation increased from low to intermediate rodent densities and remain high thereafter. Thus the shape of the relationship between rodent density and nest predation is not predictable from nesting height (i.e., ground- vs. shrub-nesting birds), although we urge caution in interpreting these results for Red-eyed Vireos and Ovenbirds, as the data are based on few nest attempts in most years.

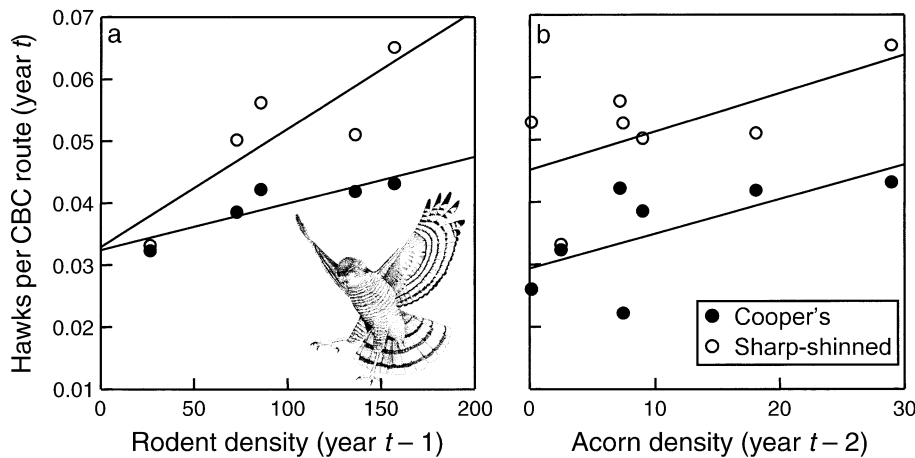


FIG. 4. Sharp-shinned and Cooper's Hawk abundance (standardized to party hour) from 37 Christmas Bird Count regions surrounding Dutchess County (New York), as a function of (a) rodent or (b) red oak acorn abundance measured at the Institute of Ecosystem Studies. Hawk abundances are plotted against rodent densities (number of animals/2.25 ha) from the previous summer or against acorn densities (acorns/0.5 m²) from two autumns previous.

Observations of dead adults/nestlings at Wood Thrush nests also suggest that raptors (Sharp-shinned, Cooper's, and Broad-winged Hawks are all present at the site) may be an additional source of nestling mortality and/or nest failure when the female is killed before the young fledge. That these observations were made only at Wood Thrush nests (with one exception) likely reflects the higher vulnerability of this species. Wood Thrushes build fairly large nests that are often conspicuously placed in shrubs, and it is not uncommon for raptors to raid active nests for chicks (Nelson 1968, Rosenfield and Bielefeldt 1993, McCallum and Hannon 2001; K. A. Schmidt, *personal observation*).

Pulsed resources and population interactions.—Despite the linkages we observed between nest mortality and rodent density, songbird population dynamics in the surrounding region do not show a simple monotonic relationship with rodent density. Instead, our data indicate that the abundance of adult thrushes (we discuss the patterns for other songbirds below) peaks following years with moderate densities of rodents (Fig. 2). The strong unimodal peak in thrush abundance following moderate rodent years (or two years after moderate acorn production; Fig. 3), suggests that songbirds (thrushes in particular) are (1) limited by rodent predation on nests during summers of high rodent density; and (2) limited by predation by alternative predators on adult and juvenile birds during summers with few rodents (or, alternatively, 2 yr post-mast). The latter may be caused by a behavioral response, such as prey-switching (in raptors see Jędrzejewska and Jędrzejewski 1998, Selås 2001) and/or a numerical response of alternative predators. The monotonic relationship between Cooper's and Sharp-shinned Hawk abundance and rodent densities the prior year (Fig. 4) suggests the numerical response of raptors likely plays an important role; however, we cannot rule out prey-switching. Interestingly, despite the large literature on the diet of American raptors, apparently little is known about fluctuations in their diet caused by annual variability in the abundances of their prey (see e.g., Johnsgard 1990, Bildstein and Meyer 1993, Rosenfield and Bielefeldt 1993), and this stands in stark contrast to European raptors (e.g., Jędrzejewski et al. 1994, Jędrzejewska and Jędrzejewski 1998, Selås 2001).

Regression of adult songbird abundance vs. mouse or chipmunk density (rather than pooled rodent density) also yielded significant results, with chipmunk density explaining far more of the variation in thrush abundance than did mouse density. We cautiously interpret these results as indicating that adult songbird abundance may track chipmunk densities more closely than white-footed mouse densities. This does not suggest that chipmunks are more important nest predators, an interpretation that would contradict the results of previous artificial nest studies (Schmidt et al. 2001). Rather, if predation by raptors varies inversely with the abundance of diurnal chipmunks (e.g., Tomiałojć 1994,

Wesołowski 1995 for a similar observation at Białowieża Primeval Forest), chipmunk densities may capture more of the underlying sources of songbird mortality in all stages of their life history.

In summary, our data support the indirect pathways of interactions between seed crops and songbirds as noted by Jędrzejewska and Jędrzejewski (1998) rather than the pathway postulated by McShea (2000). Thrush populations remain low following rodent population crashes, consistent with Jędrzejewska and Jędrzejewski; however, whereas Jędrzejewska and Jędrzejewski concluded that prey switching by predators was responsible, our data indicate that numerical responses by raptors to peak rodent density cause heavy songbird losses in subsequent years.

We depict these relationships in Fig. 5 as a sequence of years in which acorn production proceeds from low to intermediate to high. This matches the temporal sequence of acorn production at IES; however, it may not be typical of other systems. For instance, records of acorn production indicate that Front Royal and Mountain Lake (both in Virginia) experience more frequent mast failures than our study site (Wolff 1996, McShea 2000). The decrease in songbird abundance following low rodent densities may be due to the failure of acorn production in the year immediately following a heavy masting event setting up the worst possible scenario for songbirds: abundant raptors owing to last year's rodent peak, and a concurrent crash in the supply of rodent prey, eliminating this alternative food supply for raptors.

An alternative explanation for the unimodal relationship between acorns and thrush abundance is simply that masting events might correlate with climatic variables (e.g., Schaubert et al. 2002) that likewise influence breeding bird densities through changes in food abundance. This alternative seems unlikely, since the acorns of red oaks mature in the second year after flowering and thus red oaks are, at least partially, using cues from two years prior to maturation. Furthermore, the relationship between songbirds and acorn crops appears to be driven by acorn-rodent and rodent-accipiter interactions, of which there is good observational and experimental evidence (Jones et al. 1998). It is also interesting that the three species of thrushes have different migratory strategies and/or nonbreeding habitats. American Robins are short-distance migrants, whereas Veeries and Wood Thrushes are neotropical migrants, overwintering in southern Brazil (Remsen 2001) and Central America (Roth et al. 1993), respectively. All three species coexist in the eastern temperate forest of the United States for only a fraction of their annual cycle. That they show very similar patterns of regional abundance in relation to acorns and rodents strongly suggests that these populations are regulated by the events that are occurring in their breeding habitat.

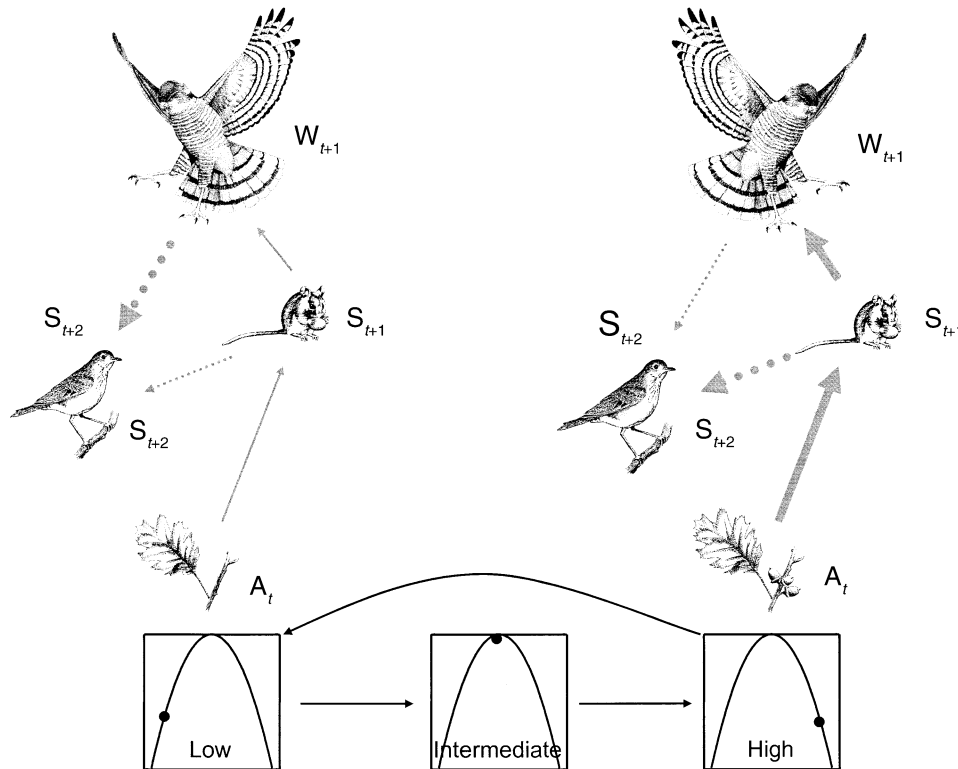


FIG. 5. Schematic diagram of the connections between oaks, mast-consuming rodents, songbirds (thrushes in particular), and hawks. The figure goes through a masting cycle (left to right) from low to intermediate to high acorn production. Positive and negative effects highlighted in the study are designated by solid and dashed arrows, respectively. The notations beside the arrows designate the period over which abundances were examined: A_t = Autumn of year t , S_{t+1} = Summer year $t + 1$, W_{t+1} = Winter year $t + 1$. Songbirds have two negative inputs: rodents, primarily via nest predation, and hawks, primarily via predation on fledglings, juveniles, and adults.

The remaining two groups of birds we examined, pensile nesters and ground-nesting warblers, did not show any clear relationship to either acorn or rodent abundance. Ground-nesting warblers were solely represented by the Ovenbird in our nest predation studies, which showed no relationship between nest mortality and either rodents or acorns. Pensile nesters, despite a strong relationship between rodents and nest mortality, showed no population relationship at the regional scale. There are a number of potential reasons for this inconsistency. First, given their current regional population increases, Red-eyed Vireos and American Redstarts may be regulated at either a different spatial scale or through different factors. For example, American Redstarts appear to peak in mid-successional forests and decline in older stands (Holmes and Sherry 2001). Second, both species may build a significant number of nests above 4 m (e.g., Marshall et al. 2002), and thus our sample (generally below 4 m) may be a poor representation of the population. Third, the small body mass of warblers and vireos renders them less vulnerable to raptors, which target larger species (Johnsgard 1990 and references therein, Rosenfield and Bielefeldt 1993, although see McCallum and Hannon 2001).

In conclusion, the results of our study suggest (1) songbird species differ tremendously in their direct and indirect interactions with rodent populations, and the form of the relationship is not predictable from nest placement (i.e., ground- vs. shrub-nesting birds); (2) moderate to high rodent densities can strongly reduce songbird nesting success; (3) accipiters, and possibly other species of raptors, show numerical responses to increased rodent densities following acorn masting; and (4) variable acorn crops, through their direct and indirect effects on rodent and hawk populations, result in strong top-down regulation of several songbird populations in eastern forests. Finally it is worth pointing out that if raptors are exerting strong, but temporally variable, top-down effects on songbird populations, increasing raptor populations in the eastern United States (e.g., Sharp-shinned and Broad-winged Hawks have increased in New York State by 11.3% and 4.9% per annum, respectively, since 1966; Sauer et al. 2001) may be having substantial effects on songbird populations. A thorough understanding of the mechanism(s) that contribute to the decline in breeding songbird abundance following rodent population explosions and crashes is necessary to formulate a general theory of

forest songbird population dynamics. This, in turn, is critical if we hope to understand how continued changes to our forested landscapes will impact songbirds into the future.

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