POPULATION ECOLOGY

Acorn mast drives long-term dynamics of rodent and songbird populations

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Abstract Resource pulses can have cascading effects on the dynamics of multiple trophic levels. Acorn mast is a pulsed resource in oak-dominated forests that has significant direct effects on acorn predators and indirect effects on their predators, prey, and pathogens. We evaluated changes in acorn mast, rodent abundance, raptor abundance, and reproductive success of a ground-nesting songbird over a 24-year period (1980–2004) in the southern Appalachian Mountains in an effort to determine the relationships among the four trophic levels. In particular, we examined the following: acorn mast from red oaks (*Quercus rubra*) and white oaks (*Q. alba*), abundance of white-footed mice (*Peromyscus leucopus*) and deer mice (*P. maniculatus*), population estimates of seven raptor species from three feeding guilds, and nest failure and number of juveniles of dark-eyed juncos (*Junco hyemalis*). Finally, we recorded seasonal temperature and precipitation to determine the effects of weather on each trophic level. We found that weather patterns had delayed effects of up to 3 years on these trophic interactions. Variation in acorn mast, the keystone resource in this community, was explained by weather conditions as far back as 2 years before the mast event. Acorn mast, in turn, was a strongly positive predictor of rodent abundance the following year, whereas spring and summer temperature and raptor abundance negatively affected rodent abundance. Dark-eyed junco nests were more likely to fail in years in which there were more rodents and raptors. Nest failure rate was a strong predictor of the number of juvenile juncos caught at the end of the summer. Our results improve our understanding of the complex ecological interactions in oak-dominated forests by illustrating the importance of abiotic and biotic factors at different trophic levels.

Keywords Resource pulse · *Quercus* · *Peromyscus* ·
Dark-eyed junco · Raptor · Weather

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Introduction

Resource pulses, or temporary periods of high resource availability, occur throughout terrestrial ecosystems and may serve a stabilizing or keystone role in structuring community dynamics (Ostfeld and Keesing 2000). Pulsed resources, such as the irruption of insects or the deposition of nutrients, can have dramatic long-term direct and indirect

effects on many members of a community (Helfield and Naiman 2001; Stapp and Polis 2003; Yang 2004). The ecology of oak-dominated forests is significantly influenced by the periodic production of large quantities of acorns. This crop of fruits, known as "mast" after the acorns dry in autumn, is a key food supply for numerous mammals and birds. Highly productive mast events typically occur every 2–6 years. Mast cycles vary among and within species (Sork et al. 1993; Herrera et al. 1998) as a function of weather conditions (Lalonde and Roitberg 1992). For some species, such as red (*Quercus rubra*) and white (*Q. alba*) oaks, spring temperatures are significant predictors of annual variation in mast patterns (Sork et al. 1993; Koenig and Knops 2002). Mast production can be relatively synchronized within species (Koenig et al. 1999a, 1999b; Liebhold et al. 2004), and it has been proposed that masting evolved as a means of satiating seed predators or facilitating dispersal (Silvertown 1980; Kelly 1994).

The temporal and spatial heterogeneity of mast events has profound implications for many species, influencing population dynamics, social structure, and disease prevalence. Most notable among these are rodents, including mice (*Peromyscus* spp.), squirrels (*Sciurus carolinensis*), and chipmunks (*Tamias striatus*) (Elkinton et al. 1996; Wolff 1996; McShea 2000; Schnurr et al. 2002). Experimental manipulations have demonstrated that mast events can cause three- to sevenfold increases in population densities owing to enhanced survival and increased reproduction in mast-supplemented areas (Jones et al. 1998). In addition, some large mammals use acorn mast to build up winter fat deposits (Eiler et al. 1989; McShea and Schwede 1993). Population dynamics and social structures of several species of birds are also profoundly affected by acorn availability (Hannon et al. 1987; DeGange et al. 1989).

Not surprisingly, changes in the population sizes of acorn consumers have significant effects on other components of oak forest communities (Ostfeld 2002). For example, mice are predators of gypsy moth (*Lymantria dispar*) pupae (Elkinton et al. 1996); increases in mouse populations following mast events have an inhibitory effect on gypsy moth outbreaks. Removal of mice by Jones et al. (1998) resulted in defoliation by gypsy moths, and acorn supplementation consequently increased mouse density and suppressed moth populations. An even more complicated interaction involves deer and blacklegged ticks (*Ixodes scapularis*), the vector for the Lyme disease bacterium *Borrelia burgdorferi*. During mast years, oak stands attract deer that are host to adult ticks (McShea and Schwede 1993). Larval ticks feed on mice, which are also attracted to acorns, which can lead to increased transmission of *B. burgdorferi* to humans (Ostfeld et al. 1996).

Changes in rodent populations due to mast events are also likely to have consequences for songbird populations.

Numerous studies have demonstrated that rodents are significant predators of eggs and nestlings (Reitsma et al. 1990; Leimgruber et al. 1994; Schmidt et al. 2001a). Nest predation is a strong determinant of adult population density, dispersal distance, and life history evolution in birds (Newton 1993; Martin 1995; Powell and Frasch 2000). Several studies examining the dynamics among acorn mast, rodent density, and songbird populations have found that increases in rodent density following mast events were followed by declines in ground- or shrub-nesting birds (McShea 2000; Schmidt 2003; Schmidt and Ostfeld 2003).

Our study examines the interactions among acorn mast, abundance of three rodent species, and reproductive success of a ground-nesting bird, the dark-eyed junco (*Junco hyemalis*). Ketterson et al. (1996) demonstrated that chipmunk abundance was positively correlated with junco nest failure over an 8-year period in an oak-dominated forest in southwestern Virginia, USA. In the current study, we have added 12–17 years of data from the same site and expanded our analyses to include data on mast events, raptor abundance, and weather conditions. We predict that acorn mast causes increases in rodent populations and thus a time-lagged decrease in junco reproductive success due to nest failure via predation. We also investigate interactions among trophic levels in this forest community, and assess the effects of weather conditions on each trophic level and the duration of such effects.

Materials and methods

Study site and species

Our research was conducted at the Mountain Lake Biological Station (MLBS) and surrounding areas. Located at 37°22′32′′ N, 80°31′20′′ W at an elevation of 1,100–1,200 m, the montane deciduous forest of MLBS is dominated by red and white oaks, which represent 54 and 10% of the canopy tree species, respectively (Wolff 1996). Other oak species in the immediate area include *Q. velutina* and *Q. prinus* (=*montana*), but these occur at much lower densities. With regards to mammals, our efforts were focused on the three most abundant mast-consuming rodents in the study area: white-footed mice (*P. leucopus*), deer mice (*P. maniculatus*), and eastern chipmunks. Dark-eyed juncos are the most common ground-nesting bird at MLBS.

Mast index

Acorn production data from a combination of red and white oaks were obtained from the Virginia Department of Game and Inland Fisheries for the period 1980–2003 (D. Martin, personal communication). Red and white oaks produce

acorns that mature and fall every 2 years or every year, respectively. MLBS is within 5 km of the Stony Creek census site, and previous research has shown that the Stony Creek mast index is highly positively correlated with an independent measure of mast production at MLBS ($r = 0.997$; Wolff 1996). The census was taken every August–September before the acorns dropped and consisted of monitoring ten red oaks and ten white oaks that were permanently marked at each site. For each marked oak, ten branches in the upper half of the crown were randomly selected and all acorns on those branches were counted. The mast index was then calculated as the average number of acorns per branch (200 branches) and denoted "$t - 1$" to indicate the mast crop the year before rodent and junco populations were measured.

Rodent censuses

Data on the abundances of *P. leucopus*, *P. maniculatus*, and *T. striatus* were collected as a part of three separate studies on a series of permanent trapping grids at MLBS. The first set of data from 1980–1989 was collected by Wolff (1996); the other data sets were collected from 1990–2000 (J.A.C.) to 2001–2004 (A.B.P. and J.A.C.). Mice were live-trapped in Sherman traps on 1–6 permanent trapping grids from April to October or November each year, with two exceptions when the yearly censuses were not taken (1992, 1998).

The trapping grids contained 100 traps spaced 10 or 15 m apart, in a 10×10 trapping array (except 1980–1983, where each grid had 64 traps with 12.5 m spacing), giving grid sizes of 1–2.25 ha. Trapping was conducted over 2–4 days every 2–6 weeks (varied by year). Traps were baited with crimped oats or solid shortening and set from 1600 to 1800 h. Permanent ear tags were applied to all captured animals and the following demographic data were collected for each: species, age, body and tail length, weight, and reproductive condition.

Abundances of *P. leucopus* and *P. maniculatus* were standardized as the minimum number known alive (MNKA) per hectare and represent both spatial (multiple grids) and temporal (multiple trapping periods from late spring through summer) averages. Chipmunk MNKA was also estimated for the years when data were available on the same trapping grids. In addition to mouse MNKA (all years except 1992, 1999), mouse abundance was estimated using Lincoln–Peterson mark–recapture methods (1990–1998; 2000–2002). Mouse MNKA was highly positively correlated with the Lincoln–Peterson estimates (Pearson's $r = 0.96$, $P < 0.001$, $n = 11$ years) and with chipmunk MNKA ($r = 0.66$, $P = 0.01$, $n = 14$ years). Because the mouse MNKA data set was most complete, it was used as our measure of rodent abundance in all subsequent analyses.

Dark-eyed junco reproductive success

We searched for nests daily between 1 May and 15 July, 1984–2003. Once found, nests were marked and the attending adults were identified. We checked nests regularly (alternate days in early years, daily in more recent years) until clutches were completed. Clutches were deemed complete when no new eggs were added for 24 h. Thereafter, nests were checked at least every 2–3 days until nestlings were 12 days old (hatching = day zero). A successful nest was one in which at least one young fledged or reached 12 days old with no evidence of predation or starvation. If an empty nest was found where there should have been nestlings nine days old or older, the area was searched to determine if they fledged early and if their parents were feeding them. If no feeding activity was observed, we assumed that nest predation had occurred.

From 1990 to 2002, some adults in the population were treated with subcutaneous testosterone implants (Ketterson et al. 1991, 1996). It has been demonstrated previously that hormone treatment does not significantly affect nest failure in this population of juncos (Ketterson et al. 1996; Reed et al. 2006). Thus, data from both treated and untreated birds were combined in the analyses presented here.

Between 15 July and 15 August of each year, juvenile (hatched that summer) juncos were caught using 12-m mist nets. Forty-five to 50 nets per year were placed at standardized locations. Depending on the number of nets operated and the number of field assistants, 483–1,559 net-hours of catching effort were accumulated per year (mean ± 1 SE = 1153.7 ± 78.6 net-hours, $n = 14$ years; no net-hour data for 1984–1989), resulting in 38–700 juvenile juncos being caught and individually marked (mean ± 1 SE = 276.5 ± 45.3 juveniles, $n = 19$ years; no data available for 1984). A linear regression showed that the number of juvenile juncos caught per year was unrelated to the number of net-hours ($r^2 = 0.15$, $t = -1.46$, $P = 0.17$); furthermore, the negative coefficient suggests no causal relationship between catching effort and number of juveniles caught. For these reasons, and because the numbers of net-hours are unavailable for the first few years of the study, only the raw numbers of juvenile juncos caught per year are included in the following analyses.

Raptors

As there are no long-term concurrent studies of rodent or junco predators at the Mountain Lake Biological Station, we obtained counts of raptor abundance from the Audubon Society's Christmas Bird Count (CBC; http://www.audubon.org/bird/cbc) (Schmidt and Ostfeld 2003). Annual counts of three guilds of raptors were determined from CBC data. The three guilds were accipitrine hawks (sharp-shinned

hawk, *Accipiter striatus*; Cooper's hawk, *A. cooperii*), buteo hawks (red-shouldered hawk, *Buteo lineatus*; red-tailed hawk, *B. jamaicensis*), and owls (Eastern screech-owl, *Megascops* (=*Otus*) *asio*; great-horned owl, *Bubo virginianus*; barred owl, *Strix varia*). These raptors were selected on the basis of two criteria: their abundance at MLBS (Mountain Lake Biological Station library, unpublished data) and the importance of small mammals in their diet. Accipitrine hawks are known as bird specialists, but their diets may include up to 40% small mammals (Rosenfield and Bielefeldt 1993; Bildstein and Meyer 2000). Small rodents comprise 10–60% of the diet of buteo hawks (Preston and Beane 1993; Crocoll 1994) and are also significant prey items for the three owl species (Gehlbach 1995; Houston et al. 1998; Mazur and James 2000).

Raptor abundance data were obtained in two ways. First, a local estimate of raptor abundance (hawks and owls/hour) was taken from the nearest CBC site in Blacksburg, VA (21 km from MLBS). Second, a regional estimate was calculated from six CBC sites, each with a 24-km-diameter circle, located within 100 km of MLBS (see also Schmidt and Ostfeld 2003). We calculated raptor abundance separately for each of the three guilds as the total number of all individuals observed divided by the total observation party-hours on a single day during a two-week period in late December to early January of each year 1980–2003. In addition, we created a composite measure of raptor abundance, which included all three guilds. For both local and regional abundance estimates, accipitrine and buteo hawks were correlated ($n = 24$, $r = 0.59$, $P = 0.002$, and $r = 0.64$, $P = 0.0006$, respectively), while neither was correlated with the local owl estimates. In addition, the local composite measure of raptors (accipiters, buteos and owls combined) was significantly correlated with the regional composite measure ($n = 24$, $r = 0.76$, $P = 0.0001$). In all analyses presented here we used the local composite estimate of raptor abundance. Raptor abundance estimates are denoted with the subscript "*t*" and reflect counts from December$_{(t-1)}$ through January$_{(t)}$.

Weather variables

Mean temperature (°C) and total precipitation (mm; rain or melted snow) were recorded by meteorological season (winter: December–February, spring: March–May, summer: June–August, fall: September–November) from the MLBS weather station. Last spring frosts were determined by the latest Julian calendar date on which minimum air temperature fell below −5 °C (Sork et al. 1993). For periods in which weather data were unavailable (sporadically in 1991–1993), we used data from a weather station 5.81 km away and 200 m lower in elevation (Horton Research Station, Virginia Polytechnic and State University). Temperatures

from Horton Station were corrected by −1.94 °C (coefficient from regression of MLBS–Horton data from 1994 to 2003; $n = 98$ months). Weather variables are denoted "$t - 1$," "$t - 2$" or "$t - 3$" to indicate conditions 1, 2 or 3 years, respectively, before the rodent and junco populations were measured.

Statistics

Data were analyzed using SPSS 11.0.1 (SPSS, Inc., Chicago, IL, USA). All data were checked for normality, means are presented ± SE, and differences were considered significant at $P < 0.05$. A principal components analysis was conducted on the weather variables and four principal components that explained 73% of the variance were obtained. The factor loadings of these components, however, were not related significantly to any of our dependent variables (acorn mast, rodent abundance, or junco reproductive success). Thus, only the original variables were included in our analyses.

We then built a series of nested models to test the importance of abiotic and biotic factors in influencing the annual dynamics of acorn mast, *Peromyscus* abundance (MNKA), dark-eyed junco nest failure, and dark-eyed junco juvenile abundance. For the acorn mast analysis, we ran all possible model combinations of the following 34 variables and present the best-fitting models. For year $t - 1$ we included winter, spring and summer precipitation and temperature, and date of last frost; for years $t - 2$, $t - 3$ and $t - 4$ we included winter, spring, summer and fall precipitation and temperature and date of last frost. Fall weather data in year $t - 1$ was not included because it occurred after the mast data were collected in August–September. Univariate regressions were conducted to determine what weather variables affected ($P \leq 0.15$) *Peromyscus* abundance, junco nest failure, and number of juvenile juncos, using all weather variables from the current year. To test for possible temporal autocorrelations in the times series data, we ran autocorrelations for each of the dependent variables for 1-, 2- and 3-year time lags. In cases when there was evidence of a significant temporal autocorrelation within a dependent variable, we then included the lagged time series as an independent variable in the model sets, forcing them to remain in all the nested models. Multiple regressions were then used to analyze how these independent variables (e.g., temperature, precipitation, acorn mast, and raptor abundance) were related to the dependent variables at the three trophic levels. *Peromyscus* (MNKA) abundance, acorn mast index, and dark-eyed junco juvenile abundance were log-transformed to conform to the Gaussian assumptions of the models. Relative model fit was examined using AIC (Akaike's information criterion) statistics (Hurvich and Tsai 1989), where the lowest AIC value indicates the best

fit model. Model selection analyses were conducted within a structural equation-modeling framework (MPlus: Muthén and Muthén 2005) using full information maximum likelihood, and incomplete data was treated as missing at random.

Results

Acorn mast

During 1980–2004, red and white oak trees at MLBS produced 3 years of very abundant mast crops (1980, 1985, 1989) and 3 years of near or complete mast failure (1987, 1992, 1997). A visual inspection of Fig. 1a reveals that mast dynamics around MLBS were less defined after 1990, and many years showed intermediate mast productivity, with a mean mast index of 23.9 ± 4.9 ($n = 24$ years).
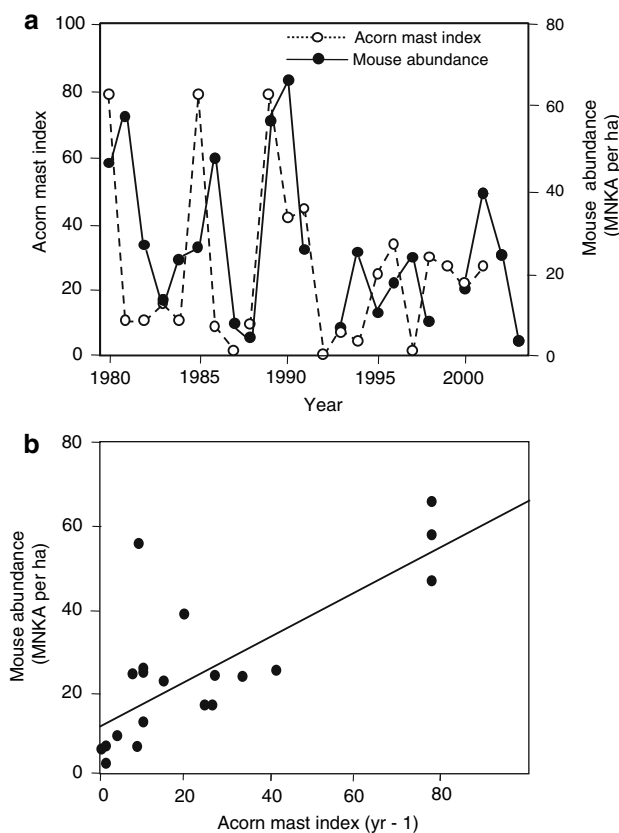

Fig. 1 a The long-term patterns between acorn mast index (*open circle*) and mouse (*Peromyscus* spp.) abundance (*filled circle*) during 1980–2004 at the Mountain Lake Biological Station (MLBS) in Virginia, USA. **b** The linear relationship between acorn mast index in 1 year ($t - 1$) and mouse abundance the following summer ($r^2 = 0.55$, $\beta = 0.74$, $P < 0.001$). Acorn mast index was obtained from counting acorns on marked trees each autumn, and mouse abundance was estimated as the minimum number known alive (MNKA) per ha on standardized trapping grids at MLBS (see "Materials and methods" for more details)

There was evidence of a significant temporal autocorrelation within the acorn mast time series only for a 2-year time lag (1-year: $r = 0.003$, $P = 0.99$; 2-year: $r = -0.41$, $P < 0.05$; 3-year: $r = -0.13$, $P = 0.59$). Thus we included both a 1-year ($t - 2$) and 2-year ($t - 3$) time lag in all possible model sets to account for this relationship. Autoregression alone explained 18% of the variation in acorn mast patterns (Model 1: $r^2 = 0.18$, AIC = 2823, Table 1). However, weather conditions up to 2 years prior to the mast event also had significant independent effects on the quantitative acorn mast index. We present the two best-fit models of acorn mast patterns (Table 1). Of the 25 weather variables that were measured, seven of them had strong effects on mast patterns (Model 2: $r^2 = 0.80$, AIC = 2807, ΔAIC = 16). The best-fit model, however, included just five weather variables (summer temperature$_{(t - 1,\ t - 2)}$, spring precipitation$_{(t - 2)}$, and date of last spring frost$_{(t - 2,\ t - 3)}$), and explained 80% of the variation in acorn mast patterns over the 24-year time series (Model 3: $r^2 = 0.80$, AIC = 2803, ΔAIC = 20).

Peromyscus dynamics

The mean of the summer estimates of *Peromyscus* abundance (MNKA) per hectare was 25.5 ± 3.8 ($n = 23$ years) and fluctuated between 3 and 66 mice per hectare (Fig. 1a). Temporal patterns of acorn mast and mouse abundance showed a positive relationship with a 1-year time lag, with mast from the previous autumn ($t - 1$) having a significant effect on mouse abundance (t) ($r^2 = 0.55$, $\beta = 0.74$, $P < 0.001$, Fig. 1a, b). Local raptor abundance (hawks and owls/hour) in winter was also significantly negatively related to the abundance of *Peromyscus* the following summer ($F_{(1,21)} = 4.59$, $r^2 = 0.19$, $\beta = -0.43$, $P = 0.045$).

We found a strong trend for a 2-year temporal autocorrelation within the *Peromyscus* time series (1-year: $r = -0.11$, $P = 0.65$; 2-year: $r = -0.44$, $P = 0.06$; 3-year: $r = -0.25$, $P = 0.32$). As in the acorn mast models, we included both a 1-year ($t - 1$) and 2-year ($t - 2$) time lag in all possible model sets to account for this relationship, and these variables alone explained 25% of the variation in mouse abundance (Model 1: $r^2 = 0.25$, AIC = 835.6, Table 2). With the addition of acorn mast to the model, an additional 35% of the variance was explained (Model 2: $r^2 = 0.60$, AIC = 823.3, ΔAIC = 12.3). However, the model that best fit the 24-year time series of *Peromyscus* abundance included acorn mast$_{(t - 1)}$, raptor abundance, and three weather variables (spring temperature, summer temperature, and date of last spring frost), and explained more than 90% of the annual variation in *Peromyscus* abundance (Table 2, Model 4: $r^2 = 0.92$, AIC = 811.2, ΔAIC = 24.4).

Table 1 Comparison of the best-fit models for the quantitative index of oak acorn mast$_{(t-1)}$ from 1980 to 2004

Model rank	Model	Parameters	Estimate	SE	AIC	ΔAIC	r^2
1	Model 3: Temporal autocorrelations and weather	Summer temperature$_{(t-1)}$	−0.31*	0.08	2,803	20.0	0.80
		Summer temperature$_{(t-2)}$	0.11	0.09			
		Spring precipitation$_{(t-2)}$	0.01*	0.001			
		Date of last spring frost$_{(t-2)}$	0.01*	0.004			
		Date of last spring frost$_{(t-3)}$	−0.03*	0.01			
		Acorn mast$_{(t-2)}$	−0.23	0.122			
		Acorn mast$_{(t-3)}$	−0.57*	0.12			
2	Model 2: Temporal autocorrelations and weather	Summer temperature$_{(t-1)}$	−0.36*	0.12	2,807	16.0	0.80
		Summer temperature$_{(t-2)}$	0.10	0.10			
		Spring precipitation$_{(t-2)}$	0.01*	0.001			
		Date of last spring frost$_{(t-2)}$	0.01*	0.004			
		Date of last spring frost$_{(t-3)}$	−0.03*	0.01			
		Spring temperature$_{(t-2)}$	−0.02	0.07			
		Fall temperature$_{(t-2)}$	0.04	0.08			
		Acorn mast$_{(t-2)}$	−0.24	0.13			
		Acorn mast$_{(t-3)}$	−0.59*	0.13			
3	Model 1: Temporal autocorrelations	Acorn mast$_{(t-2)}$	0.06	0.18	2,823		0.18
		Acorn mast$_{(t-3)}$	−0.43*	0.18*			

The sign of each parameter estimate indicates the directionality of the relationship with the dependent variable; * denotes the significance for each parameter ($P < 0.05$); AIC represents the Akaike's information criterion; ΔAIC is the difference in AIC values between a model and the base model in the candidate set, which has a ΔAIC = 0; r^2 values represent the amount of variation explained by the model

Table 2 Comparison of the best-fit models for *Peromyscus leucopus* and *P. maniculatus* abundance (N$_t$) 1980–2004

Model rank	Model	Parameters	Estimate	SE	AIC	ΔAIC	r^2
1	Model 4: Temporal autocorrelations, acorn mast, raptor abundance and weather	Spring temperature$_{(t)}$	−0.08*	0.03	811.2	24.4	0.92
		Summer temperature$_{(t)}$	−0.20*	0.40			
		Date of last spring frost$_{(t)}$	−0.01*	0.004			
		Raptor abundance$_{(t)}$	−1.4*	0.27			
		Acorn mast$_{(t-1)}$	0.27*	0.06			
		Mouse abundance$_{(t-1)}$	0.39*	0.13			
		Mouse abundance$_{(t-2)}$	−0.35*	0.07			
2	Model 3: Temporal autocorrelations, acorn mast and raptor abundance	Raptor abundance$_{(t)}$	−0.71	0.41	822.5	13.1	0.65
		Acorn mast$_{(t-1)}$	0.40*	0.10			
		Mouse abundance$_{(t-1)}$	−0.18	0.15			
		Mouse abundance$_{(t-2)}$	−0.29*	0.14			
3	Model 2: Temporal autocorrelations and acorn mast	Acorn mast$_{(t-1)}$	0.44*	0.10	823.3	12.3	0.60
		Mouse abundance$_{(t-1)}$	−0.13	0.16			
		Mouse abundance$_{(t-2)}$	−0.24	0.15			
4	Model 1: Temporal autocorrelations	Mouse abundance$_{(t-1)}$	0.20	0.19	835.6		0.25
		Mouse abundance$_{(t-2)}$	−0.45*	0.20			

The sign of each parameter estimate indicates the directionality of the relationship with the dependent variable; * denotes the significance for each parameter ($P < 0.05$); AIC represents the Akaike's information criterion; ΔAIC is the difference in AIC values between a model and the base model in the candidate set, which has a ΔAIC = 0; r^2 values represent the amount of variation explained by the model

Dark-eyed junco dynamics

An average of 116.8 ± 6.1 junco nests ($n = 20$ years, range = 64–177, Fig. 2a) were found per summer, of which $60.3 \pm 4.2\%$ failed each year, the vast majority (95%) due to nest predation. An average of 276.5 ± 45.3 juvenile juncos ($n = 19$ years, range = 38–700, Fig. 2c) were caught in 1153.7 ± 78.6 net-hours of effort per year. Fluctuations in

Peromyscus abundance affected dark-eyed junco reproductive success, having a significant effect on the proportion of junco nests that failed ($r^2 = 0.23$, $\beta = 0.48$, $P = 0.044$, Fig. 2a, b) and the number of juvenile juncos captured ($r^2 = 0.24$, $\beta = -0.49$, $P = 0.046$, Fig. 2c, d) each summer. Univariate regression showed a nearly significant indirect effect of acorn mast$_{(t-1)}$ on junco juveniles ($r^2 = 0.20$, $\beta = -0.45$, $P = 0.055$), but not on nest failure rate ($r^2 = 0.07$, $\beta = 0.27$, $P = 0.25$) (Fig. 3).

Fig. 2 Relationship between mouse (*Peromyscus*) abundance (*filled circles*) and reproductive success of dark-eyed juncos (*Junco hyemalis*) (*open circles*) during 1984–2003. **a** The time series and **b** the linear relationship between mouse abundance and the percentage of junco nests that failed to produce any young ($r^2 = 0.23$, $\beta = 0.48$, $P = 0.044$). **c** The time series and **d** the relationship between mouse abundance and the number of juvenile juncos trapped in late summer of the same year ($r^2 = 0.24$, $\beta = -0.49$, $P = 0.046$)
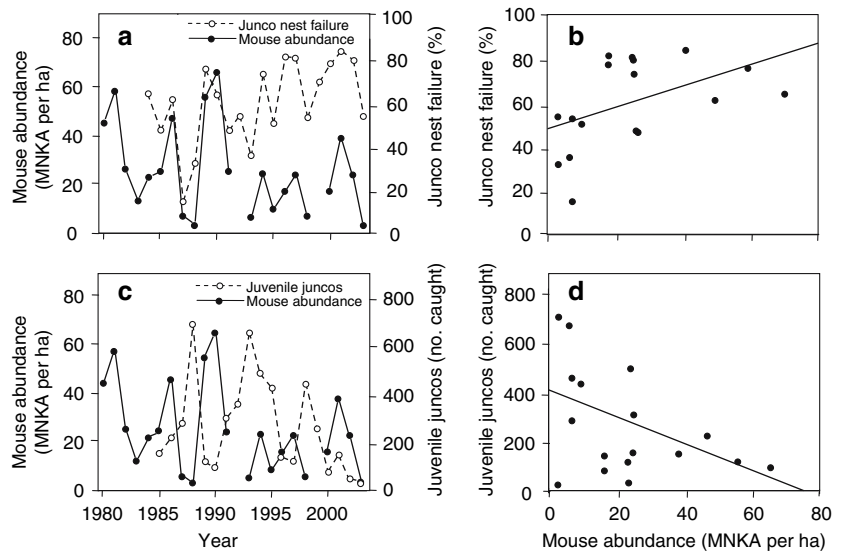
Fig. 3 Schematic representation of the complex interactions in an oak-dominated forest. *Arrows* designate the abiotic (*ovals*) and biotic (*shaded oval*) factors that were included in the best-fit models for acorn mast, mouse abundance, dark-eyed junco nest failure, and abundance of dark-eyed junco juveniles, where t = current year. *Curved arrows* indicate the temporal autocorrelations
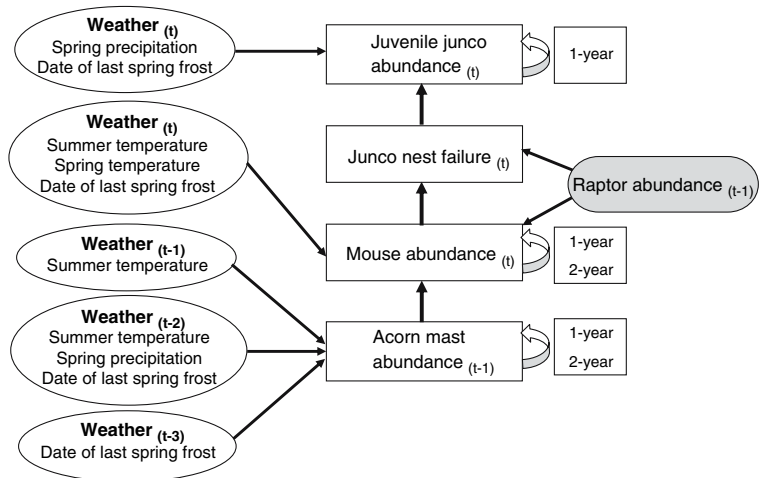
We found no evidence of temporal autocorrelations in the nest failure time series (1-year: $r = 0.21$, $P = 0.40$; 2-year: $r = 0.02$, $P = 0.94$; 3-year: $r = 0.03$, $P = 0.92$) and thus did not include any time-lagged variables in the model set. The best fit model of dark-eyed junco nest failure, which explained over 50% of the year-to-year variance, included *Peromyscus* abundance (MNKA) and raptor abundance (Table 3a, Model 2: $r^2 = 0.51$, AIC = 765.2, ΔAIC = 4.2).

In contrast to nest failure, we did find a significant 1-year temporal autocorrelation in the juvenile junco times series (1-year: $r = 0.47$, $P = 0.05$; 2-year: $r = 0.02$, $P = 0.94$; 3-year: $r = 0.06$, $P = 0.84$), and this variable explained 25% of the variation in juvenile abundance (Table 3b, Model 1: $r^2 = 0.25$, AIC = 761.7). However, the addition of nest failure and two key weather variables (summer precipitation and date of last spring frost) increased the fit to 56% (Model 3: $r^2 = 0.56$, AIC = 757.3, ΔAIC = 4.4).

Discussion

Our results demonstrate strong links across multiple trophic levels in an oak-dominated forest. Acorn mast production was significantly affected by temperature, precipitation, and frost 2 years prior to the mast events. This keystone resource pulse, in turn, was a significant positive determinant of rodent abundance patterns, while avian predators, warm spring and summer temperatures, and late spring frosts negatively affected their abundance. Subsequently, abundant rodents and raptors contributed to elevated nest failure rates in dark-eyed juncos, and ultimately, in combination with high summer precipitation and late spring frosts, led to lower abundance of juvenile juncos. This study demonstrates the complex interactions between weather patterns and resource pulses and their dynamic and cascading effects on key species within oak-dominated forests.

Table 3 Comparison of the best fit models

Model rank	Model	Parameters	Estimate	SE	AIC	ΔAIC	r^2
(a) Proportion of dark-eyed junco (*Junco hyemalis*) nests that failed							
2	Model 3: Weather, mouse and raptor abundance	Summer temperature$_{(t)}$	−0.06	0.05	765.4	4.0	0.54
		Raptor abundance$_{(t)}$	0.49	0.32			
		Mouse abundance$_{(t)}$	0.28*	0.11			
1	Model 2: Mouse and raptor abundance	Raptor abundance$_{(t)}$	0.74*	0.27	765.2	4.2	0.51
		Mouse abundance$_{(t)}$	0.38*	0.09			
3	Model 1: Mouse abundance only	Mouse abundance$_{(t)}$	0.29*	0.09	769.4		0.32
(b) The number of juvenile juncos caught from 1984 to 2003							
1	Model 3: Temporal autocorrelations, nest failure and weather	Summer precipitation$_{(t)}$	−0.001*	0.001	757.3	4.4	0.56
		Date of last spring frost$_{(t)}$	−0.01	0.007			
		Nest failure$_{(t)}$	−0.95*	.316			
		Juvenile junco abundance$_{(t-1)}$	0.16	0.29			
2	Model 2: Temporal autocorrelations and nest failure	Nest failure$_{(t)}$	−0.89*	0.33	757.5	4.2	0.46
		Juvenile junco abundance$_{(t)}$	0.55*	0.19			
3	Model 1: Temporal autocorrelations	Juvenile junco abundance$_{(t)}$	0.53*	0.23	761.7		0.25

The sign of each parameter estimate indicates the directionality of the relationship with the dependent variable; * denotes the significance for each parameter ($P < 0.05$); AIC represents the Akaike's information criterion; ΔAIC is the difference in AIC values between a model and the base model in the candidate set, which has a ΔAIC = 0; r^2 values represent the amount of variation explained by the model

Weather effects on acorn mast

We found that temperature, precipitation, and late spring frost conditions up to 2 years prior to the mast year, and particularly the year before ($t − 2$), explained a highly significant proportion (80%) of the variance in total acorn crops. Similar relationships have been found in other *Quercus* spp. (Sork et al. 1993; Koenig et al. 1996; Cecich and Sullivan 1999). We were able to detect significant weather effects on masting in spite of the fact that our data set combined data from a 1-year (*Q. alba*) and a 2-year (*Q. rubra*) masting oak species. Although we cannot speculate on the relative importance of acorn predation or weather in the evolution of masting (Lalonde and Roitberg 1992), our data suggest that weather conditions play a significant role in interannual variation in acorn crops. Furthermore, the significantly negative temporal autocorrelations we observed between acorn masts$_{(t − 2, t − 3)}$ are consistent with the idea that masting events require the sequestration of resources in intervening years (Sork et al. 1993).

The observation that oak species do not necessarily share peak or failure years has led some to argue that masting is unrelated to weather conditions (Silvertown 1980). There is substantial evidence, however, that within-stand synchrony is high among conspecifics (Liebhold et al. 2004) or among species whose acorns require the same amount of time (1 or 2 years) to develop (Mohler 1990; Koenig et al. 1994), suggesting that common environmental factors play a significant role. Koenig and Knops (2002) reviewed the evidence for weather effects on mast production, and found myriad factors associated with masting in both 1- and 2-year oak species.

In the early years (pre-1990) of our study, near-complete mast failures were common, but in recent years the oscillations have been damped, resulting in lower peak mast years and fewer years of mast failure. This apparent change in the mast pattern could be due to differences in masting periodicity of the two oak species (Sork et al. 1993). Masting asynchrony within an oak community may function to reduce competition among sympatric species (Mohler 1990), and may secondarily buffer animal populations from years of complete mast failure.

Biotic and abiotic effects on mice

Like many previous studies, we found a strong positive relationship between summer *Peromyscus* abundance estimates and acorn mast crops from the preceding autumn (Elkinton et al. 1996; Wolff 1996; Jones et al. 1998; McShea 2000; Schnurr et al. 2002). This increase in mouse abundance after a high mast year is caused by increased over-winter survival and increased reproduction in the spring (Wolff 1996). However, this study also demonstrates that multiple factors affect *Peromyscus* abundance and long-term population dynamics. By including raptors, abiotic variables and temporal autocorrelations in mouse abundance$_{(t − 1, t − 2)}$, the model fit was significantly improved and explained more than 90% of the variation in *Peromyscus* abundance over the 24-year duration of our study.

While we did not have data on all predators of *Peromyscus*, we found that raptor abundance was a significant negative determinant of mouse abundance. In the best-fit model, the winter "non-breeding" abundance of a composite local group of raptor predators (accipitrine hawks, buteo hawks, and owls) was negatively related to *Peromyscus* abundance, even though for some of the raptors, particularly accipitrines, rodents comprise less than half of their diet (Rosenfield and Bielefeldt 1993; Bildstein and Meyer 2000). Abiotic factors, particular spring and summer temperature, and the date of the last spring frost were negative predictors of mouse abundance. Breeding patterns of *Peromyscus* vary greatly throughout their North American range (Millar 1989). Warm temperatures have been found to have significant effects on structuring the initiation and cessation of reproductive activity in natural populations (Millar and Gyug 1981), and may decrease density due to lower in utero and pup survival through reduced plant productivity (Lewellen and Vessey 1998). While there is strong evidence that acorn masting events are the dominant factor driving changes in *Peromyscus* abundance, this study demonstrates that additional biotic and abiotic factors are likely to be important in determining abundance, and that single-factor explanations are incomplete descriptions of the complex interactions that affect rodent population dynamics.

Biotic and abiotic effects on juncos

We found that *Peromyscus* abundance explained a significant proportion of the variation in dark-eyed junco nest failure, which is consistent with other correlational studies of ground- and shrub-nesting songbirds (Ketterson et al. 1996; Jędrzejewska and Jędrzejewska 1998). Experimental attempts to relate rodent abundance to success of real bird nests, however, have been relatively few. Several studies by Schmidt and colleagues (Schmidt 2003; Schmidt and Ostfeld 2003; Schmidt et al. 2006) found that rodent abundance was a significant predictor of nest predation rates in some, but not all, of a group of woodland passerines. Martin and Joron (2003) report that nest predation on ground- and shrub-nesting songbirds was greater on islands with red squirrels (*Tamiasciurus hudsonicus*) than on islands without squirrels. They also found a significant interaction with island habitat type: islands with mature Sitka spruce (*Picea sitchensis*) stands, which produce more cones than immature stands, had much lower nest survival rates, suggesting a similar mast–rodent–songbird interaction to that we observed.

Raptor abundance was also positively related to junco nest failure, which could indicate that raptors are significant predators of junco nests or of incubating females. Alternatively, it could be due to covariation between mouse and raptor abundances. Studies relating predator removal to avian reproductive success have been primarily focused on medium-sized mammals and gamebirds (reviewed in Côté and Sutherland 1997). Mammal trapping does increase productivity of gamebirds, but provides few benefits for passerine birds nesting in the same area. Dion et al. (1999) actually found evidence of compensatory increases in predation by ground squirrels on passerine nests following the experimental removal of larger mammalian predators. A recent study in Arizona, however, provides evidence that small predator removal increases passerine nesting success. Fontaine and Martin (2006) found a significant decline in daily predation risk for 12 passerine species over 4 years in areas from which rodent predators had been removed.

Not surprisingly, increased failure of dark-eyed junco nests led to significantly fewer juvenile juncos at the end of the breeding season. Juvenile abundance was also decreased in cooler, wetter years. Cold weather has also been shown to decrease juvenile survival in numerous passerine species (Tyler and Green 2004; Stokke et al. 2005; Robinson et al. 2007), though in our study precipitation was a more significant determinant of juvenile survival than was temperature (see also Chase et al. 2005).

Several studies have documented the effects of rodent populations on adult songbirds using breeding bird survey (BBS) estimates of songbird abundance (McShea 2000; Schmidt and Ostfeld 2003). Schmidt and Ostfeld (2003), for example, found a negative relationship between mouse and chipmunk abundance in 1 year and roadside counts of five woodland songbirds in the following year. However, the evidence for such a relationship in ground-nesting birds was mixed. Neither McShea (2000) nor Schmidt and Ostfeld (2003) found an effect of rodent abundance on ovenbirds (*Seiurus aurocapillus*), but McShea (2000) found a significant negative effect of rodents on populations of worm-eating warblers (*Helmitheros vermivorus*), another ground-nesting species. Data on abundance of adult dark-eyed juncos in our study area in either summer (BBS) or winter (CBC) were largely unavailable. The total abundance of 51 species of songbirds recorded along a BBS route at MLBS (1992–1999) was slightly negatively related to *Peromyscus* abundance ($\beta = -0.87$, $P = 0.075$), suggesting that rodents do have a suppressive effect on songbird productivity in our study system.

Role of additional predators and competitors

Some years of high junco nest failure and low juvenile recruitment appear related to rodent abundance, while others do not. What accounts for poor junco production in years with relatively few mice? Perhaps predators that ordinarily feed on rodents switch to nestling or fledgling juncos when rodents are rare. Several authors have reported that

when rodent abundances decrease, rodent predators such as hawks and mustelids increase their consumption of songbirds (Dunn 1977; King 1983; Jędrzejewska and Jędrzejewska 1998; Schmidt and Ostfeld 2003). In addition to the raptors discussed above, several common predators of both rodents and birds are found at MLBS, including longtail weasels (*Mustela frenata*), black rat snakes (*Elaphe obsoleta*), and timber rattlesnakes (*Crotalus horridus*). The importance of summer temperature suggests that snakes, whose metabolic rate increases with temperature (Huey 1982), may play a particularly important role. In warm summers, snakes may take more rodents (Bozinovic and Rosenmann 1988) in their primary diet, thereby decreasing junco nest failure rates. Snakes are widely known predators of nestling birds, but the numerical significance of snake predation on birds is poorly understood (Weatherhead and Blouin-Demers 2004).

Competition between mice and other nest predators may also be important. *Peromyscus* at many sites, including MLBS, numerically dominate other rodents (Wolff 1996; Schmidt et al. 2001a), and thus may minimize the ecological role of other species as nest predators except in years of low mouse abundance. Schmidt et al. (2001a, 2001b) report data to support this assumption; predation of artificial bird nests was negatively related to mouse density in study plots with natural variation in rodents, despite the fact that experimental removal of mice in different plots significantly reduced nest predation. Increased nest predation by chipmunks in years of low mouse abundance may also explain the weak relationship between mice and junco nest failure.

In this study, we have focused on describing the complex interactions between weather phenomena and resource pulses and their dynamic and cascading effects on key species within an oak-dominated forest. This is one of the first studies to document time-lagged effects of weather, in some cases by several years, across multiple trophic levels of predators and prey, and it highlights the need for community ecologists to include weather variables in their analyses of predator–prey interactions. In addition, it clearly demonstrates the complex and strong interactions between predators and prey that are driven by periodic resource pulses, and the role of these pulses in structuring ecological communities.

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