

PEROMYSCUS LEUCOPUS ABUNDANCE AND ACORN MAST: POPULATION FLUCTUATION PATTERNS OVER 20 YEARS

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Summer abundance of white-footed mice (*Peromyscus leucopus*) fluctuated periodically during 20 years (1983–2002) at the Holt Research Forest, Maine, USA, a pine-oak forest within 125 km of the northern edge of this species' range. The oscillation period of the series was 4.0 years, with fluctuations greater than in *P. leucopus* populations in Indiana, Virginia, Ohio, and Pennsylvania. Abundance always increased after a low population phase coupled with a large acorn (*Quercus*) crop, but in 3 summers population declines followed population peaks despite large acorn crops. We used linear autoregression to identify periodicity after accounting for the relationship between mice and acorn mast. Among 3 candidate models, a 2nd-order lagged abundance (AR[2]) model fit the data better and had greater predictive value (total $r^2 = 0.69$) than either a 1st-order (AR[1]) or an acorns-only model. The AR(2) term could represent unknown limiting factors, such as response of predators.

Key words: acorns, cycles, density dependence, periodicity, *Peromyscus leucopus*, population, time-series analysis, white-footed mice

Acorns (*Quercus*) are an important mast crop for white-footed mice (*Peromyscus leucopus*); investigators have demonstrated that high acorn mast crops typically precede an increase in *P. leucopus* breeding season abundance (McCracken et al. 1999; McShea 2000; Ostfeld et al. 1996; Wolff 1996). Via time-series analysis or empirical observation, others (Kesner and Linzey 1997; Wolff 1993) have demonstrated regular interannual (yearly) fluctuations in *P. leucopus* populations. The relationship between interannual periodic fluctuations in *P. leucopus* and acorn mast is the focus of this study.

Based on 10 years of data (1983–1992) from the Holt Research Forest, a pine-oak forest in mid-coast Maine, McCracken et al. (1999) showed that summer abundance of *P. leucopus* was positively correlated with previous autumn acorn crop size. Since that study, we have accumulated an additional 10 years of data on *P. leucopus* and acorn mast at the Holt Research Forest, which has permitted a more complex analysis.

Although *P. leucopus* abundance on the Holt Forest increased and declined following large or small acorn crops, respectively, there were exceptions when *P. leucopus* declined in 1992, 1996, and 1998 despite large acorn crops. This suggested an underlying periodic fluctuation driven by unknown factors (other than acorn mast) but that could be

modeled as 1st- or 2nd-order lags in abundance, respectively. Therefore, we modeled the relationship between mice and acorns under an autoregressive scheme. Our purpose was to determine the periodicity and strength of the *P. leucopus* time series; to select, based on Akaike information criterion (AIC) scores, the best among 3 models: a 2nd-order (AR[2]), 1st-order (AR[1]), or acorns-only model; to test the probability that the selected model arose from a random versus periodic process; and to compare the Holt Forest *P. leucopus* population time series to other rodent series.

MATERIALS AND METHODS

The Holt Research Forest is a 120-ha, mature (trees about 70–90 years old) pine-oak forest in Arrowsic, Maine (43°45'N, 69°46'W), within about 125 km of the northern edge of the range of *P. leucopus*. The 6 most common tree species were eastern white pine (*Pinus strobus*), northern red oak (*Quercus rubra*), red maple (*Acer rubrum*), red spruce (*Picea rubens*), eastern hemlock (*Tsuga canadensis*), and white oak (*Q. alba*). Total basal area was 30 m²/ha. In 1983 we mapped the study area and divided it into 40 1-ha blocks (Fig. 1). See Kimball et al. (1995) for a more detailed description of the study area.

Small-mammal trapping.—We trapped small mammals in the first 2 weeks of August 1983–2002. We placed 144 stations on 6 parallel, north–south, 400-m transect lines and trapped for 5 nights during the 1st week of each trapping session. At the beginning of the 2nd week, we placed 140 stations on 4 parallel, 567-m assessment lines running diagonally at 45° to the transect lines (Fig. 1) and trapped for 3 nights. We used this census-assessment line method for efficiency (O'Farrell and Austin 1978; O'Farrell et al. 1977). Specifically, our configuration

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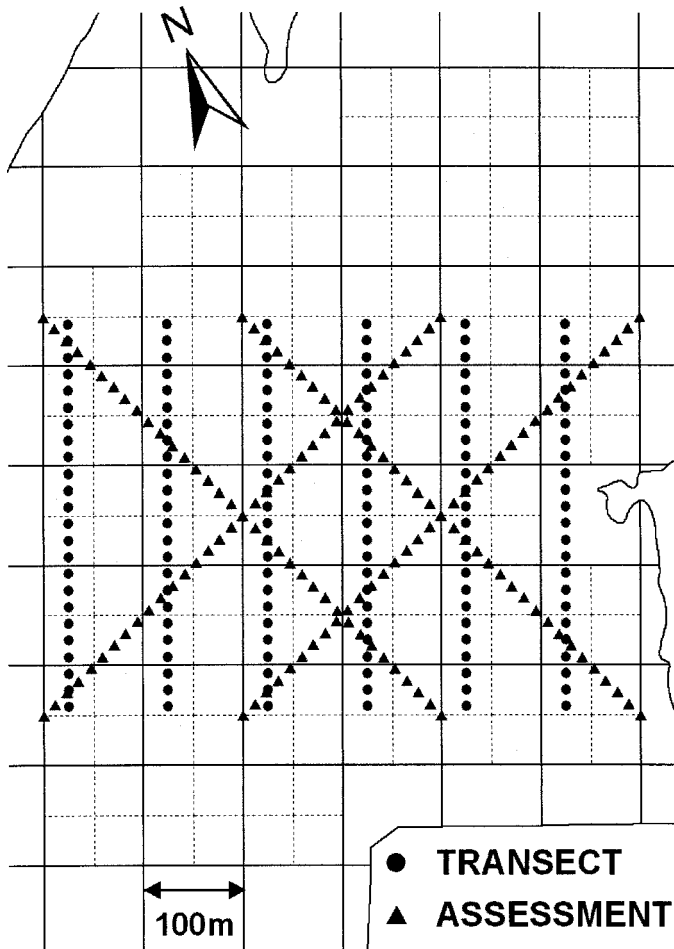


FIG. 1.—Study area (shaded gray) and small-mammal trapping and assessment line stations on the Holt Research Forest, 1983–2002.

allowed us to trap more than half (about 24 ha) of the 40-ha study area; given the same amount of labor and materials, a grid system would have limited sampling to <25% of the study area.

Stations on trap lines were 16.7 m apart (6 traps/100 m). At each station, we baited two $9 \times 8 \times 23$ -cm Sherman live traps with a mixture of rolled oats and peanut butter. We put a 5.1×5.1 -cm square pad of cotton (Nestlets, Ancare Corporation, Bellmore, New York) in each trap for nesting material. We checked traps daily between 0600 and 1000 h, recorded traps snapped but empty, and rebaited traps. We aged, sexed, and weighed *P. leucopus*, then marked them with metal ear tags (National Brand and Tag Company, Newport, Kentucky). We computed the number of *P. leucopus* per 100 trap nights for each year (to account for snapped traps and adjust for trapping effort). We did not use mark-recapture estimators of abundance because there were too few animals in the low phases of the series. However, Slade and Blair (2000) found that counts represented density and population fluctuations just as well as jackknife, Lincoln-Peterson, and Jolly-Seber estimators as long as comparisons of abundance were intraspecific, with site and trapping protocol invariant.

Acorn collection.—We constructed seed traps from 1.5-m tall tomato cage wire serving as frames and UV-resistant nylon netting bags suspended within the frames to collect seeds. From 1983 to 1990, we used seed traps with 0.5-m^2 openings randomly located in each 1-ha block ($n = 40$). From 1988 to 2001, we used traps with 0.042-m^2 openings, placing 1 at each of the 144 small-mammal trapping stations

and at stations at 10-m intervals along two 600-m, east–west transects across the study area ($n = 264$ traps). No evidence of depredation of seed traps was found. Though white oak was present on the Holt Research Forest, red oak was more abundant by almost an order of magnitude, whether measured by basal area (86.2%), stem count (84.4%), or acorn counts (87.3%). In peak acorn years (1983, 1984, 1988, 1992, 1998, and 1999), red oak acorns were roughly 90% of the total acorn count. We tested the relationships between *Peromyscus* and each oak species separately, but it was significant only for red oak acorns. Thus, while white oak mast did contribute meaningful mast volume across the years, red acorn mast accounted for most of the annual variation. Therefore, we pooled the 2 oak species. We calculated annual acorn mast as thousands of acorns per ha.

Statistical analyses.—We obtained simple summary statistics for both *P. leucopus* abundance and acorn crops. From a principal components analysis on local weather data, we derived 4 variables representing cold, snowy winters; cold, snowy springs; rainy springs; and spring extremes of hot and cold. Because these weather terms were highly insignificant ($P > 0.8$) in a model relating them to *P. leucopus* numbers, we did not pursue further analysis of weather data.

Using the minimum number alive, we calculated s , the index of fluctuation, according to Henttonen et al. (1985). Hansson and Henttonen (1985) considered an s value >0.50 characteristic of a strongly fluctuating population. For the time-series analysis, we added 1 and log-transformed all observations of *P. leucopus* and acorn abundance. Both time series exhibited trends (nonstationarity). Since trends may generate spurious significant 2nd-order lag effects (Saitoh et al. 1997), we used locally weighted regression scatter-plot smoothing to fit a curve to long-term trends (Trexler and Travis 1993), then output the residuals as the new, detrended series. We used autoregression with maximum likelihood to model the detrended input series (acorns) and found no evidence of autocorrelation in this series. Using a periodogram, we estimated the apparent oscillation period (Priestley 1981) of the detrended *P. leucopus* series. Via autoregression, we modeled abundance versus acorns plus animal abundance from the 2 previous years. We compared 3 competing models:

$$\text{Acorns, AR(2): } N_t = \beta_0 + \beta_1 \text{Acorns} + -\phi_1 v_{t-1} - \phi_2 v_{t-2} + \varepsilon$$

$$\text{Acorns, AR(1): } N_t = \beta_0 + \beta_1 \text{Acorns} + -\phi_1 v_{t-1} + \varepsilon$$

$$\text{Acorns only: } N_t = \beta_0 + \beta_1 \text{Acorns} + \varepsilon,$$

where N_t is animal abundance; β_0 is the intercept coefficient; β_1 is the acorn coefficient; v_{t-1} and v_{t-2} represent lags of N_t and are the autoregressive terms AR(1) and AR(2), respectively, and $-\phi_1$ and $-\phi_2$ are their coefficients; and ε is unexplained error. We used the Akaike information criterion (AIC) to assess model fit and rank models (Hurvich and Tsai 1989). The best model is that with the lowest AIC score.

Our purpose was to select the most parsimonious model. We did not attempt to detect statistical density dependence with a battery of tests because of their lack of agreement and power (Shenk et al. 1998). However, to integrate model selection with hypothesis testing (Zeng et al. 1998), we applied nonparametric bootstrap statistical inference to assign a probability value to the selected model based on a generated distribution of AIC scores. This is in concept similar to the parametric bootstrap likelihood ratio test of Dennis and Taper (1994). We bootstrapped (random selection with replacement) the *P. leucopus* abundance data, producing 1,000 new series (Efron and Tibshirani 1993). We held the acorn data constant as a fixed input and used the actual 1st value of the *Peromyscus* series as the starting value, then modeled each of the 1,000 series as specified by the most

parsimonious model of the original series. We output the 1,000 AIC scores, thus building a distribution of scores. Where the original AIC score fell within the 5th percentile of the generated distribution of AIC scores, we considered $P_{\text{crit}} \leq 0.05$ and concluded that the time series came from an n -order autoregressive rather than random process. All analyses were carried out using SAS (SAS Institute 1999).

RESULTS

Summer *P. leucopus* abundance (N_t) on the Holt Research Forest averaged 8.2 mice/100 trap nights ($n = 20$ years, $SE = 1.63$). Abundance ranged from 0.5 to 23.1 mice/100 trap nights, a 46-fold difference. The index of fluctuation, s , was 1.19, indicating a strong fluctuation in this population. The estimated oscillation period was 4.0 years.

Acorns ($n = 19$ years) averaged 45,114/ha ($SE = 7,498$) and ranged from 0 (in autumn 1983) to 91,441/ha.

There were 5 low and 5 high phases in the *P. leucopus* series and 4 periods of high acorn crops the previous autumn: 1 brief (1986), 2 sustained (1990–1992, 1994–1998), and 1 beginning in 2001 (Fig. 2). The start of each high phase in the *P. leucopus* series followed a large acorn crop the previous autumn and a low phase in the *P. leucopus* series. High phases lasted across 2 summers except for the 1-year high phase of 1986. The precipitous drop to 1987 N_t appeared to follow the drop in previous acorn abundance, but thereafter declines in the 1992, 1996, and 1998 N_t followed high *Peromyscus* population phases despite large previous autumn acorn crops (Fig. 2).

In the model selection process, the AR(2) model fit the data better than the acorns-only model ($\Delta\text{AIC} = 1.8$) and better than the AR(1) model ($\Delta\text{AIC} = 2.8$; Table 1). In the AR(2) model, previous autumn acorn crop explained 53%, and the 2nd-order autoregressive term 15%, of the variation in N_t , for a total r^2 of 0.68 (Table 1). This was an improvement over the acorns-only model ($r^2 = 0.55$) and the AR(1) model (total $r^2 = 0.58$; Table 1). The nonparametric bootstrap procedure indicated that the probability that the pattern in the original *P. leucopus* series could have arisen from a random process versus an AR(2) process was very small ($P = 0.001$).

DISCUSSION

Food.—Acorns are clearly a staple food for *P. leucopus*. During a 14-year study at the Mountain Lake Biological Station in southwestern Virginia, Wolff (1996) found a strong relationship between *P. leucopus* numbers and acorn crops ($r^2 = 0.79$) and observed that peak crops allowed stores of acorns to last and mice to breed throughout the winter. McCracken et al. (1999) found a similar but weaker relationship at the Holt Research Forest ($r^2 = 0.46$, $P = 0.05$) with a 10-year series, and with 10 more years of data in this study, the N_t –acorn relationship improved slightly (regression $r^2 = 0.55$; Table 1). Correlations were lower than Wolff's (1996) because, in our study, the case of low mouse densities at above-average mast levels was apparently more common.

McShea (2000) found that acorn crop was 1 of 4 significant predictors of summer *P. leucopus*. He noted that large mast crops coincided with high small-mammal densities but also that low densities occurred at all mast levels. Related phenomena

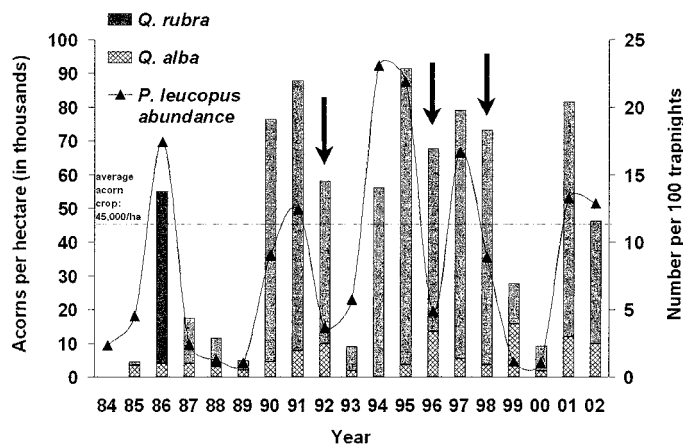


FIG. 2.—Time series for white-footed mouse (*Peromyscus leucopus*) and acorn (*Quercus rubra* and *Q. alba*) abundance time series, Holt Research Forest, 1983–2002. Bold arrows point to years in which *P. leucopus* numbers were low (1992, 1996, 1998) despite high acorn crops the previous autumn.

have been observed in other studies: in a Virginia population of *P. leucopus*, surplus supplemental food did not prevent suppression of reproduction in early summer (Terman 1999), and in Ohio, *P. leucopus* populations declined sharply in late summer amidst plentiful food (Vessey 1987). Food supplementation in the Yukon (Gilbert and Krebs 1991) increased *Peromyscus maniculatus* density but had only a 2- to 3-fold effect. Four *P. leucopus* food supplementation studies listed by Vessey (1987) included 1 study where density increased and another where density stayed the same, and in the remaining 2, female but not male densities increased.

It is difficult to interpret these findings without knowing more about the state of the population (high or low phase) at the time of the experiments. Our results are consistent with the concept that extra food can boost population densities, but only at low or moderate densities. In other words, large acorn crops appeared to boost *P. leucopus* numbers at the Holt Forest after low phases in the population time series, yet unobserved factors systematically drove numbers back down during 3 periods of consecutive years of large acorn crops.

At the Holt Forest we observed 2 periods of high previous autumn acorn crops (1990–1992, 1994–1998) but no sustained (e.g., 4- or 5-year) period of small acorn crops. Should this scenario arise, and in the absence of other bumper crops (such as white pine seeds [Abbott and Quink 1970] or insect outbreaks), we predict that the *P. leucopus* high phase would be truncated, the amplitude diminished, and the low phase prolonged.

Periodicity of the series.—The 4-year periodicity of the Holt Forest *P. leucopus* population was consistent with cycles of 3.6–3.9 years found in microtine rodents in southern Fennoscandian latitudes (60.5°N–64.0°N) and shorter than the cycles of 4.4–4.8 years farther north (67°N–69°N—Bjørnstad et al. 1995). Interannual cycling is not considered typical of *P. leucopus*; still, several studies illustrate cases of periodicity. Kesner and Linzey (1997) presented statistical evidence for regular interannual fluctuations in Pennsylvania *P. leucopus*, although

Table 1.—Linear autoregressive models of the relationships between *Peromyscus leucopus* number per 100 trap nights (N_t) and previous autumn acorn^a crop and N_t at past lags on the Holt Research Forest, Arrowsic, Maine, 1984–2002^b. The *Peromyscus* and acorn series were log-transformed and detrended before modeling. Models are ranked by AIC^c (lower is better).

Model rank	Model specification	Parameter	d.f.	Estimate	SE	t	P	AIC ^c	r^2	
									Regression	Total
1	N_t f (acorn crop size, N_{t-1} , N_{t-2}) ^d	Intercept	1	0.00	0.05	−0.08	0.94	21.7	0.53	0.68
		Acorns	1	0.47	0.123	3.83	<0.01			
		AR (1)	1	0.33	0.240	1.39	0.18			
		AR (2)	1	0.49	0.227	2.16	0.05			
2	N_t f (acorn crop size) ^d	Intercept	1	0.01	0.098	0.06	0.95	23.5	0.55	0.55
		Acorns	1	0.56	0.121	4.59	<0.001			
3	N_t f (acorn crop size, N_{t-1}) ^d	Intercept	1	0.00	0.080	0.03	0.98	24.5	0.58	0.58
		Acorns	1	0.56	0.134	4.17	<0.001			
		AR (1)	1	0.23	0.273	0.86	0.40			

^a *Quercus rubra* and *Q. alba*.

^b The acorn crop of 1982, prior to the 1st trapping summer of 1983, is unknown since the analysis is based on the 19-year series, 1984–2002.

^c Akaike information criterion (AIC) = $-2 \ln(L) + 2k$, where L is the value of the likelihood function evaluated at the parameter estimates and k is the number of parameters.

^d $N_t = \beta_0 + \beta_1(\text{acorns}) + -\phi_1 v_{t-1} - \phi_2 v_{t-2} + \varepsilon$, where v_{t-1} and v_{t-2} are lags of N_t and are represented by autoregressive terms, AR(1) and AR(2).

the series was very short (9 years). Wolff (1993) reported a 4- to 6-year periodicity in *Peromyscus* in the mountains of southwestern Virginia. The 46-fold difference between peak- and low-density years at the Holt Forest was greater than for *Peromyscus* at sites (6- to 30-fold differences) south and west of Maine (Wolff 1993). The Holt population fluctuation index ($s = 1.19$) was similar to those of cyclic microtines (Hansson and Henttonen 1985) and stronger than for *Peromyscus* in Indiana, Virginia, Ohio, and Pennsylvania (Krohne et al. 1988). s -Values from the latter studies ranged from 0.20 to 0.38, similar to those of noncyclic microtine populations (Krohne et al. 1988).

Other investigators have reported lack of regular interannual periodicity in *Peromyscus* populations. For example, in a 17-year study in southwestern Yukon, *P. maniculatus* showed little interannual variation (Gilbert and Krebs 1991). Based on a 43-year series from Ontario, Fryxell et al. (1998) concluded that *P. maniculatus* populations did not cycle across years. Lewellen and Vessey (1998a, 1998b) identified intra-annual (i.e., seasonal within years) density dependence related to weather in Ohio *P. leucopus* but found little evidence of delayed density dependence in interannual cycles.

The contradictory evidence raises the question: does *P. leucopus* exhibit periodicity only at the northern extremes of its range and/or at higher altitudes? An investigation into latitudinal and altitudinal gradients in North American *P. leucopus* population fluctuations is warranted.

Declines and low phases.—Declines and low phases within our *P. leucopus* time series could indicate a numerical response of predators (e.g., mustelids) to *P. leucopus* density with a time delay (Hanski et al. 1991). The 2nd-order lagged abundance term in our model supports this in theory. Mustelids (*Mustela erminea* and *M. frenata*), owls (*Bubo virginianus* and *Strix varia*), and other predators have been regularly censused at the Holt Forest, but the low frequencies did not allow for statistical testing.

Current consensus is that predation and/or self-regulation may drive declines in small-mammal populations (Krebs 1996; Stenseth et al. 1996). Self-regulation in microtines is likely

mediated through spacing behavior that in turn affects processes such as delayed maturation, senescence, death, birth, and emigration (Boonstra et al. 1998; Krebs 1985, 1996; Oli and Dobson 2001). Evidence indicates that intrinsic regulation is probably not a population regulation factor in rodents such as *Peromyscus* (Wolff 1997). While extrinsic factors probably play the most important roles in the population fluctuations observed at the Holt, we would not unequivocally rule out all forms of intrinsic regulation without a more intensive demographic study of both *P. leucopus* and its predators.

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