Ecology, 79(1), 1998, pp. 213–225

LONG-TERM DYNAMICS OF SMALL-MAMMAL POPULATIONS IN ONTARIO

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Abstract. We analyzed 43 yr of live-trapping data for eight species of small mammals in Algonquin Provincial Park, Ontario. Our primary objective was to test whether complex nonlinear models are necessary to describe dynamics of the Algonquin rodent populations. Variation in abundance among species was related to mean abundance by a simple power function with an exponent of 1.77, implying that population variability did not increase with mean density as much as one might expect for strictly statistical reasons. Time-series analyses of annual population densities indicated no significant autocorrelation functions for five species. Southern red-backed voles, red squirrels, and flying squirrels had significant autocorrelations, but only flying squirrels had an autocorrelation function suggestive of cyclic population dynamics. Per capita rates of population growth were density-dependent in all eight species, although in most cases there was substantial deviation around the fitted regression lines. Response surface models with one- and two-year lags significantly improved the statistical fit to data for three species, but only one of these response surface models was sustainable in the face of realistic stochastic variation in per capita growth. These results suggest that simple logistic models are adequate for predicting the long-term dynamics of the Algonquin small-mammal assemblage. All eight species showed evidence of synchronized population fluctuations over time, suggesting trophic linkages due to shared food resources, shared predators, or both.

Key words: cycles; density dependence; mammal, small; Ontario; population dynamics; recruitment; response surface; time series.

Introduction

One of the most persistent and challenging questions in population biology concerns the degree to which natural populations are characterized by complex or even chaotic dynamics due to inherent nonlinear relationships among key demographic variables (Schaffer and Kot 1986, Berryman and Millstein 1989, Turchin and Taylor 1992, Hanski et al. 1993, Ellner and Turchin 1995, Constantino et al. 1995). This issue is of considerable theoretical and practical importance. If deterministic chaos is common in natural populations, then predictability over long time scales is essentially impossible, even though short-term predictability can be enhanced by strong density dependence (Ellner and Turchin 1995). An alternate hypothesis is that complex population dynamics arise from stochastic environmental variation. This does not offer much improvement for short-term predictability unless we understand the sources and dynamics of environmental variability, but at least stochastic effects will not propagate over time, as they do for chaotic systems (Ellner and Turchin 1995).

Recent studies of several rodent populations have shown both marked variability in abundance and sensitivity to initial conditions—hallmarks of deterministic chaos (Hanski et al. 1993, Turchin 1993, Ellner and Turchin 1995). Other rodent populations have shown evidence of simple cycles or non-periodic fluctuations over time (Garsd and Howard 1981, 1982, Henttonen et al. 1985, Marcström et al. 1990, Turchin 1993, Lindström and Hörnfeldt 1994). Complex dynamics seem to be more common in arctic than temperate species (Turchin 1993), but long-term data are more common from the arctic than from the temperate zone, particularly in North America. In this paper, we use time-series analysis to describe the temporal dynamics over the past 43 yr of eight species of small mammals in Algonquin Provincial Park, Ontario, Canada.

Response surface methodology (hereafter termed RSM) has been developed as a means to reconstruct intrinsic time dynamics from complex and presumably noisy data sets (Turchin and Taylor 1992, Hanski et al. 1993, Perry et al. 1993, Turchin 1993, Ellner and Turchin 1995). This method consists of fitting flexible power functions (where the response is measured by the per capita rate of population growth) to lagged population densities (Turchin and Taylor 1992, Ellner and Turchin 1995). It is attractive because it has a remarkable degree of flexibility, it is relatively efficient to implement on microcomputers, and it relates to demographic models commonly used by ecologists. Response surface methodology offers one of the most

Manuscript received 13 June 1996; revised 10 January 1997; accepted 17 February 1997.

promising approaches to understanding the kinds of nonlinear dynamics that probably predominate in population ecology (Turchin and Taylor 1992, Ellner and Turchin 1995). It is not yet clear, however, whether lagged models obtained using RSM significantly improve on the predictive power obtained from simpler density-dependent models (Dennis and Taper 1994). Using our time-series data from Algonquin Park, we compare the predictive power of traditional models of density dependence with more complex RSM models incorporating lagged density dependence (Turchin and Taylor 1992, Turchin 1993).

Methods

Data

Live-trapping of small mammals was conducted in a standardized manner over the past 43 yr at the Wildlife Research Station near Lake Sasajewun, Algonquin Provincial Park, Ontario, Canada (48°30′ N, 78°40′ W). At each of 10–15 forested sites, a 90-m trapline was established with either one or two Sherman traps at stations 10 m apart. The physical dimensions of the Sherman traps were 7.5 × 7.5 × 30.5 cm, of sufficient size to catch even large rodents, such as red or flying squirrels. Single lines had 10 traps in total, whereas double lines (two traps per trapsite) had 20 traps. Lines were sampled either once or twice a month for three nights from mid-May until the end of August or September, yielding a maximum of 10 of these 3-d trapping periods per year. Over the years a few lines were abandoned or moved, but otherwise the trapping protocol was quite consistent.

Lines were set out in a variety of forest stands, ranging from pure deciduous hardwoods through mixed forest to pure coniferous stands. Care was taken at the beginning of the study to locate traps in forest types typical of the region. Common tree species included sugar maple (*Acer saccharum*), speckled alder (*Alnus rugosa*), red maple (*Acer rubrum*), trembling aspen (*Populus tremuloides*) balsam fir (*Abies balsamea*), white spruce (*Picea glauca*) and black spruce (*Picea mariana*). It would be enormously difficult to quantitatively assess how representative our study sites were of forests throughout the southern Ontario region, but in our collective experience the sites were certainly not atypical in any obvious way.

During the early years of the study, three lines in the hardwood forest stands were double lines that were sampled once every two weeks, whereas the other habitats had single lines sampled monthly. In 1979, three single lines were abandoned and the remaining lines were converted to double lines and sampled once every two weeks. The original double lines in hardwood stands were unaltered. One additional line was dropped in 1980. There is a 1-yr gap in the time series (1988), so our time-series analysis and tests of density dependence are confined to the first 36 yr of study. Subsequent population monitoring has closely followed the pre-1988 procedures, allowing additional estimates of per capita rates of increase between 1989 and 1995.

Traplines were ≥0.3 km apart and few marked animals have been captured on more than one trapline. The total study area is ~8 × 2.5 km, comprising several stands in a continuously forested region of the Park that has not been logged or burned since the 1930s.

Gross trapping effort was calculated by multiplying the number of lines by trap stations per line, trapping periods, and nights per trapping period. Comparative studies (E. A. Falls, *unpublished data*) showed that double trap lines yielded ~1.5× the captures made by comparable single lines. We accordingly multiplied the trapping effort from double lines by 1.5 to account for differences in the effectiveness of double vs. single lines. For example, a double line would have 45 trap nights of effective effort per 3-d sampling period whereas a single line would have 30 trap nights of effective effort.

Traps were opened on the first day of each sampling period. Before 1991, traps were left open throughout the sampling period. After 1991, traps were closed during the middle of the day to reduce trap mortality of the few animals entering traps during that time. Our recent data show little indication that this affected captures of diurnal species, such as the sciurids, but it is a potential source of additional variation in the time series. For most of the study period, traps were baited with a mixture of peanut butter and rolled oats. The trap bait was changed in 1991 to sunflower seeds, which seemed to be as attractive to small mammals as the previous bait, but were less attractive to bears or slugs. Bait was renewed before each sampling period. Traps were provided with a fist-sized wad of polyester quilt batting to allow animals to build nests in the metal traps. Bait and nesting material were replenished as needed during each sampling period. When a trap was set, the treadle was checked to ensure that it was sensitive enough to capture animals as small as shrews. Captured animals were identified to species and individuals were ear-tagged, weighed, sexed, and examined for reproductive condition. These demographic details will be published separately.

To use the entire time series for all mammal species, we have chosen a simple annual index of population density for each species: captures per 1000 nights of trapping effort summed over the summer and early autumn. Hence, our population totals pertain to calendar years. More elegant assessment models were not applicable in this context for several reasons. First, the level of effective effort varied considerably over the years, ranging from 1000–1500 trap nights in the 1950s to 3500–4500 trap nights in more recent years. Second, several species were rather rare, with accordingly low frequencies of recapture. Third, some species were not tagged in the early years of the study, eliminating the possibility of using mark–recapture techniques for estimating the abundance of all species in the assemblage. In the interests of retaining the fullest information possible, we have therefore restricted our analysis to catch per unit effort.

Models

Animal population dynamics are often depicted as a dynamic interaction between per capita rates of change and population density, for the simple reason that the population rate of growth depends on both the ''interest rate'' and the ''capital'' upon which this rate exerts its effect (e.g., Royama 1992, Turchin and Taylor 1992, Ellner and Turchin 1995). Moreover, observed patterns of variation often show that logarithmic transformation of per capita rates of change produces more even distributions of error around fitted demographic functions (Turchin and Taylor 1992, Ellner and Turchin 1995). We therefore estimated the relationship $N_t = N_{t-1} \exp(r_t) = N_{t-1} f(N_{t-1}, N_{t-2}, \varepsilon_t)$, where $r_t = \ln(N_t/N_{t-1})$ is the per capita rate of population growth between years $t - 1$ and t, N_t is population density in year t, ε_t is stochastic variation in the rate of increase in year t, and f is a polynomial function of both population density and stochastic variability.

Response surface methodology involves fitting flexible functions for $f(N_{t-1}, N_{t-2}, \varepsilon_t)$, such that one can account for both lags in demographic response to changes in population density and various forms and intensity of nonlinearity in the demographic response (Box and Draper 1987, Turchin and Taylor 1992). We followed Turchin and Taylor's (1992) procedures in fitting the following formulation:

$$r_t = \alpha_0 + \alpha_1 X + \alpha_2 Y + \varepsilon_t,$$

in which X and Y are simply polynomial transformations of population densities in preceding years: $X = N^{\theta 1}{}_{t-1}$ and $Y = N^{\theta 2}{}_{t-2}$. The power terms θ_1 and θ_2 were evaluated at $\{-1, -0.5, 0, 0.5, 1.0, 1.5, 2.0\}$, using natural-log transformation when $\theta_i = 0$. To avoid any problems with zero values, we added one to each estimate of catch per unit effort.

We wished to evaluate the explanatory power of demographic models of increasing complexity. In one of our simple density-dependent models, we assumed that $Y = 0$ and $\theta_1 = 1$, and omitted the second-order term in X, a formula often called the Ricker logistic model (Ricker 1954). We also considered a second simple model, sometimes termed the Gompertz logistic model, in which $Y = 0$ and per capita rate of growth is a linear function of $\ln(N_{t-1})$. For the more complex lagged model, we fitted X and Y terms and the full range of values for θ_i, following Turchin and Taylor's (1992) procedure. We used a Gause-Jordan elimination algorithm to find linear solutions, with least squares as the maximum likelihood estimator (Press et al. 1992:672–675).

The logic of the Ricker and Gompertz models is most compatible with univoltine species that have strict separation of generations (adults dying before the next generation is recruited). This is at best a rough approximation for the biology of our small mammal species, in which adults often have several litters each summer and some adults survive the winter to breed again. Nonetheless, it is common for population ecologists to use logistic models without age structure for long-lived species as a first approximation for predicting long-term dynamics. Alternatively one can view any of the density-dependent models as a discrete time analogue of continuous population growth (Turchin 1993, Ellner and Turchin 1995).

The most reasonable null hypotheses for population time series such as ours are that the populations are simply undergoing a random walk or stochastic exponential increase. As a consequence of the resulting nonindependence between population densities in sequential years, simple regression tests of density-dependent relationships are inappropriate (Dennis and Taper 1994). For the same reason, one should not use simple regression tests to compare more complex lagged models derived from response surface methodology with simpler models.

To solve this statistical problem, we used the parametric bootstrap likelihood ratio (PBLR) test outlined by Dennis and Taper (1994) to evaluate the predictive power of a series of models of increasing complexity. The first stage in the PBLR test procedure is to estimate parameters for both the hypothesized and null models. These parameters are used to calculate the likelihood of the hypothesized model relative to the null model for the observed data. This is a measure of the improvement in predictive power obtained by using the hypothesized model. One then simulates replicate time series using the parameters of the null model. For each simulated data set of the same length as the original time series, the likelihood ratio of the hypothesized vs. null model is recalculated. We repeated this process 1000 times to estimate the probability of obtaining a likelihood ratio as extreme as that estimated from the observed data if the null hypothesis were indeed true.

We started with an exponential growth model as our null hypothesis and a simple density-dependent growth model as our alternate hypothesis. We did this for both the Ricker and Gompertz forms of the discrete-time logistic model, since both density-dependent models have been widely used by population ecologists. Both logistic models yielded significant improvement in predictive power over the exponential model, so we then tested models of greater complexity (Dennis and Taper 1994). At this stage, the Ricker logistic model became the null hypothesis used to generate Monte Carlo time series and the lagged response surface model was our alternate hypothesis. This procedure is in many ways analogous to the cross-validation procedures outlined by Turchin (1993) and Ellner and Turchin (1994), with the additional advantage that it is based on a standard parametric test of statistical inference.

RESULTS

The raw totals (listed in Appendix 1) for all eight species of small mammals suggest substantial variability in

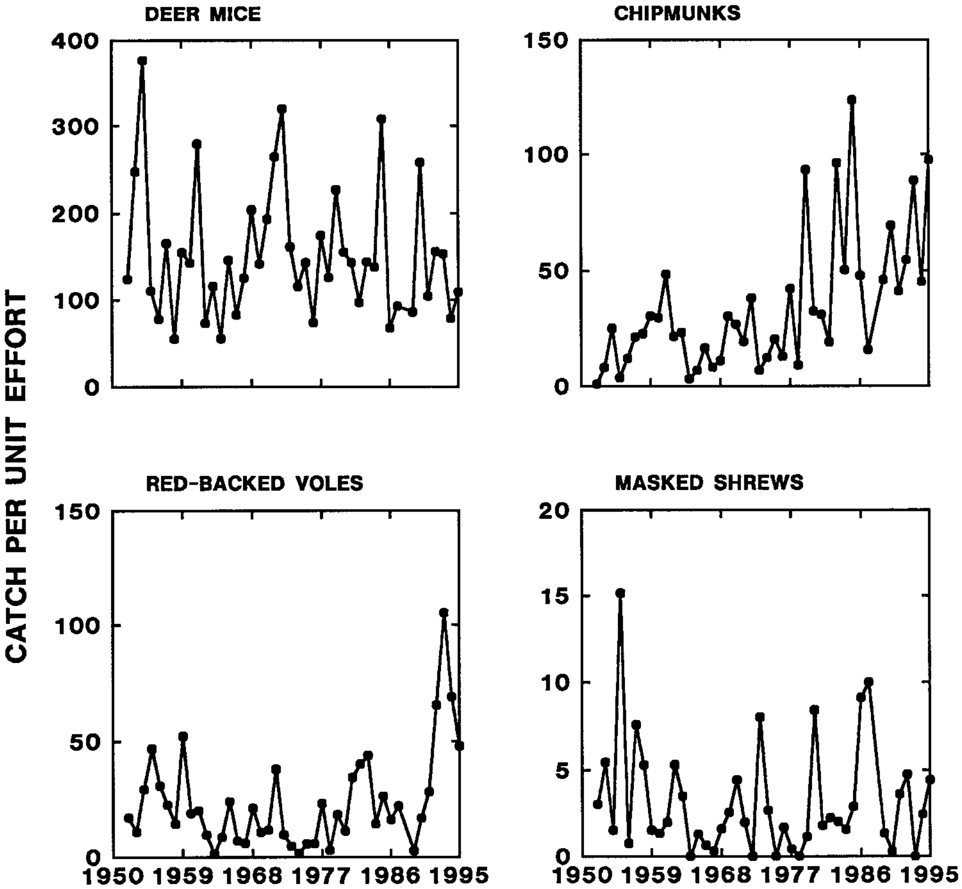

FIG. 1. Catch per 1000 trap nights of effective effort for eight species of small mammals in Algonquin Park, Ontario, between 1952 and 1995.

abundance over the 43-yr study period (Fig. 1). Deer mice (*Peromyscus maniculatus*) were consistently more abundant than any other species, followed in order of mean abundance by eastern chipmunks (*Tamias striatus*), southern red-backed voles (*Clethrionomys gapperi*), woodland jumping mice (*Napaeozapus insignis*), short-tailed shrews (*Blarina brevicauda*), red squirrels (*Tamiasciurus hudsonicus*), masked shrews (*Sorex cinereus*), and northern flying squirrels (*Glaucomys sabrinus*).

Taylor (1961) showed that population variability is often related to mean abundance by a power function ($y = ax^b$, where y = variance in density and x = mean density for a given species, and b is a calculated exponent). The best-fit power function for the Algonquin small mammal community was $y = 1.63x^{1.77}$ ($r^2 = 0.944$, $P < 0.001$ for the log-transformed function). The value for the exponent was <2, implying that variability changed less with increasing mean density than one might expect on purely statistical grounds (i.e., variability was density dependent sensu Hanski 1990). The magnitude of the exponent for the Algonquin populations was similar to that of other taxa whose populations are moderately to highly variable (Hanski 1990). In principle, the retrapping of surviving individuals might bias the records of long-lived species, such as chipmunks, red squirrels, or flying squirrels, toward greater numerical constancy from year to year than short-lived species, but our data suggested a similar degree of population variability across taxa, once mean density had been taken into account.

The population trajectories illustrate numerous examples of exceptional recruitment events (Fig. 1). Maxima for all species were $>2.5\times$ those recorded on average and in several cases the ratio of maximum to mean density was considerably greater (Table 1). Perhaps the most commonly accepted index of population variability is the standard deviation of log-transformed population densities. At the species level, the value of this variability index ranged between 0.204 and 0.576 with deer mice being the least variable and woodland jumping mice the most variable species (Table 1). The observed values for all the Algonquin populations are intermediate in the vertebrate spectrum and are typical of small mammals in general (Ostfeld 1988, Hanski 1990).

Time-series analysis assumes that populations are stationary, i.e., showing no consistent net change over time. Increasing population trends over time, such as that exhibited by chipmunks, southern red-backed voles, woodland jumping mice, or short-tailed shrews (based on linear

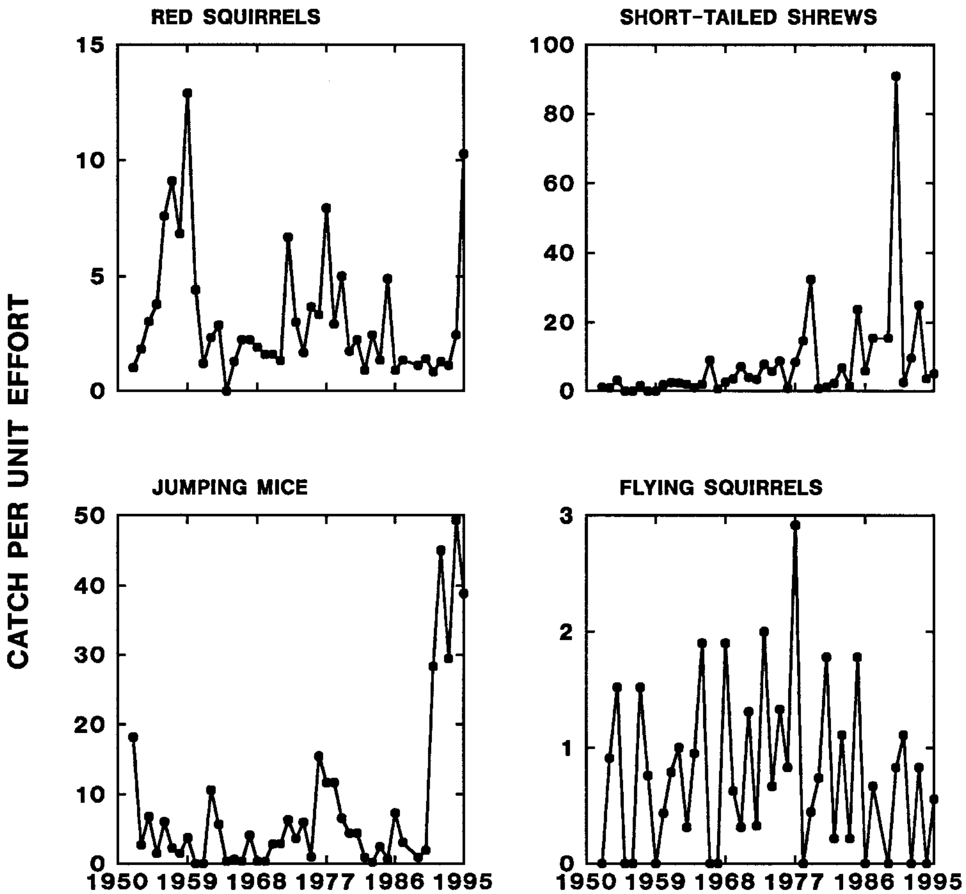

FIG. 1. Continued.

regression of N vs. t, where in all cases $P < 0.05$), might distort the autocorrelation functions (Diggle 1990). For these four species, we performed our time-series analysis on detrended population data obtained by using deviations around the regression of N_t vs. time.

Autocorrelation functions of five species showed no significant lagged terms: deer mice, chipmunks, masked shrews, woodland jumping mice, and short-tailed shrews (Fig. 2). Southern red-backed voles and red squirrels had significant autocorrelation between population densities in sequential years and each exhibited decaying autocorrelation functions with an 8-yr period (Fig. 2). Lack of significant higher order lags in these species suggests at most weak, phase-forgetting cycles with an 8-yr period. Flying squirrels had significant autocorrelation between population densities with a 4-yr lag and showed some evidence of a recurrent wavelike form to the autocorrelation function (Fig. 2). We conclude that at least five species, and most likely seven species, were noncyclic. Strong evidence of periodic population dynamics was limited to flying squirrels, the rarest species in the assemblage.

TABLE 1. Interannual variability over 43 yr in catch per thousand trap nights of effort for eight small mammal species in Algonquin Park, Ontario.

Species	Max N	Mean N	CV N	SD $(\log_{10}[N])$
Deer mice	376.5	152.8	0.49	0.204
Red-backed voles	105.3	23.7	0.89	0.409
Woodland jumping mice	49.3	8.2	1.49	0.576
Chipmunks	123.8	34.0	0.85	0.402
Red squirrels	12.9	3.2	0.89	0.321
Flying squirrels	2.9	0.8	0.93	0.306
Short-tailed shrews	90.8	7.8	1.91	0.491
Masked shrews	15.2	3.1	1.04	0.443

Time-series analysis of per capita rates of increase indicated that the population dynamics of most species were synchronized. Nineteen of the 28 possible pairwise interspecific combinations showed significant crosscorrelations for at least one lag (Table 2), and in most cases there were several significant lag terms. Typical patterns of association are depicted in Fig. 3, showing the per capita rate of increase of chipmunks, red squirrels, short-tailed shrews, and flying squirrels plotted against that of deer mice, the predominant member of the small mammal assemblage. These comparisons across species indicate that population changes among Algonquin small mammals were synchronized, presumably either through tro-

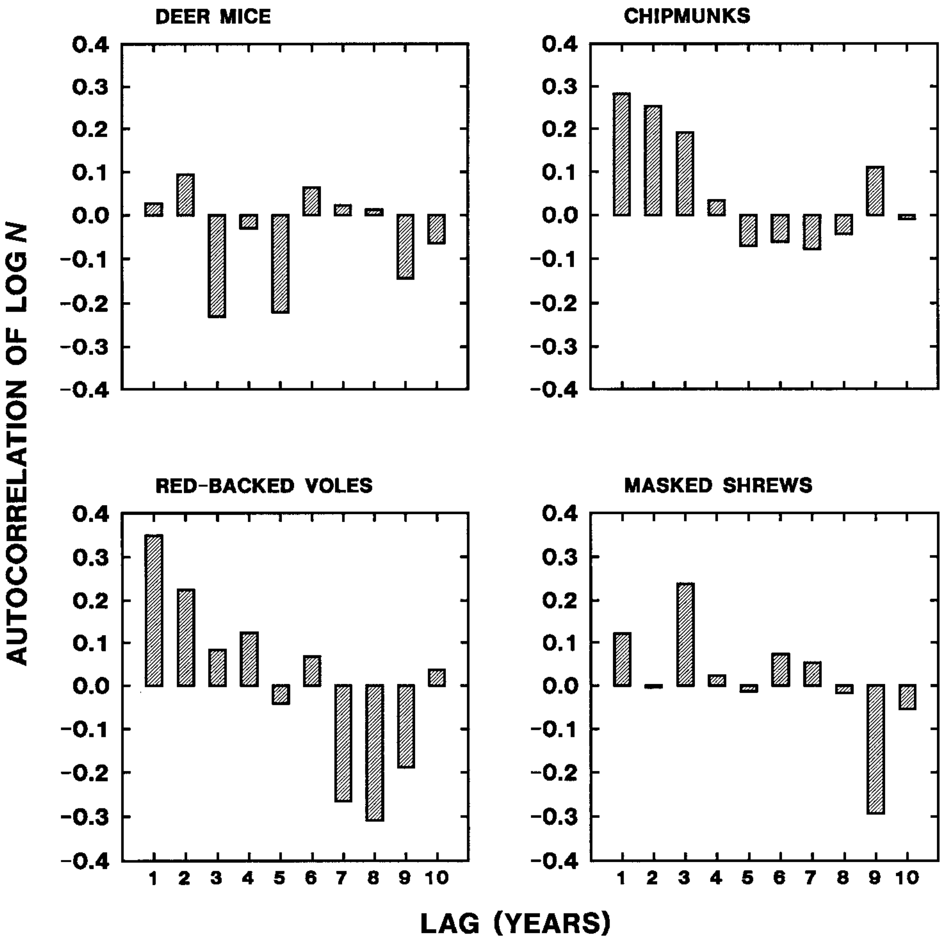

FIG. 2. Correlograms for log N_t of eight species of small mammal in Algonquin Provincial Park, Ontario, for data during 1952–1987. The height of each bar indicates the positive or negative autocorrelation between density estimates with different time lags. Southern red-backed voles and red squirrels showed a significant autocorrelation coefficient at a lag of 1 yr, and flying squirrels had a significant autocorrelation coefficent at lags of 1 yr and 4 yr. Autocorrelations for other species were all nonsignificant.

phic interactions or through common responses to environmental variability.

All of our rodent populations showed statistically significant logistic relationships between r and N (Table 3) or r and log N (Table 4). There was little difference in the predictive power of the Ricker formulation vs. the Gompertz formulation, based on the likelihood ratios shown in Tables 3 and 4. Hence, the Algonquin data fairly convincingly demonstrate simple density-dependent changes in recruitment from year to year, regardless of logistic formulation.

For the parameters observed in the Algonquin populations, the Ricker model always yields deterministically stable solutions (Ricker 1954, Royama 1992). It is more instructive, however, to consider the patterns that would emerge in the presence of typical levels of environmental noise. We used the Ricker model to reconstruct population dynamics over the next 100 yr under moderately stochastic conditions, by adding a random normal deviate of the same magnitude as that estimated for each Algonquin population.

Model dynamics were generally similar to the field observations. Population time series derived from the Ricker equation yielded rapidly damping autocorrelation functions without significant time lags. Scatterplots of r vs. N obtained from the model data were reminiscent of field data, exhibiting weak negative slopes and showing wide variability at low population densities but smaller variability at high population densities. These features suggest that simple logistic models captured most of the salient dynamical features of the Algonquin populations.

Response surface models significantly improved predictive power ($P < 0.05$) relative to the Ricker model in three species: chipmunks, masked shrews, and short-tailed shrews (Table 5). In both shrew species, however, stochastic computer simulations based on the response surface models inevitably led to cycles of violently increasing amplitude and rapid extinction. This sug-

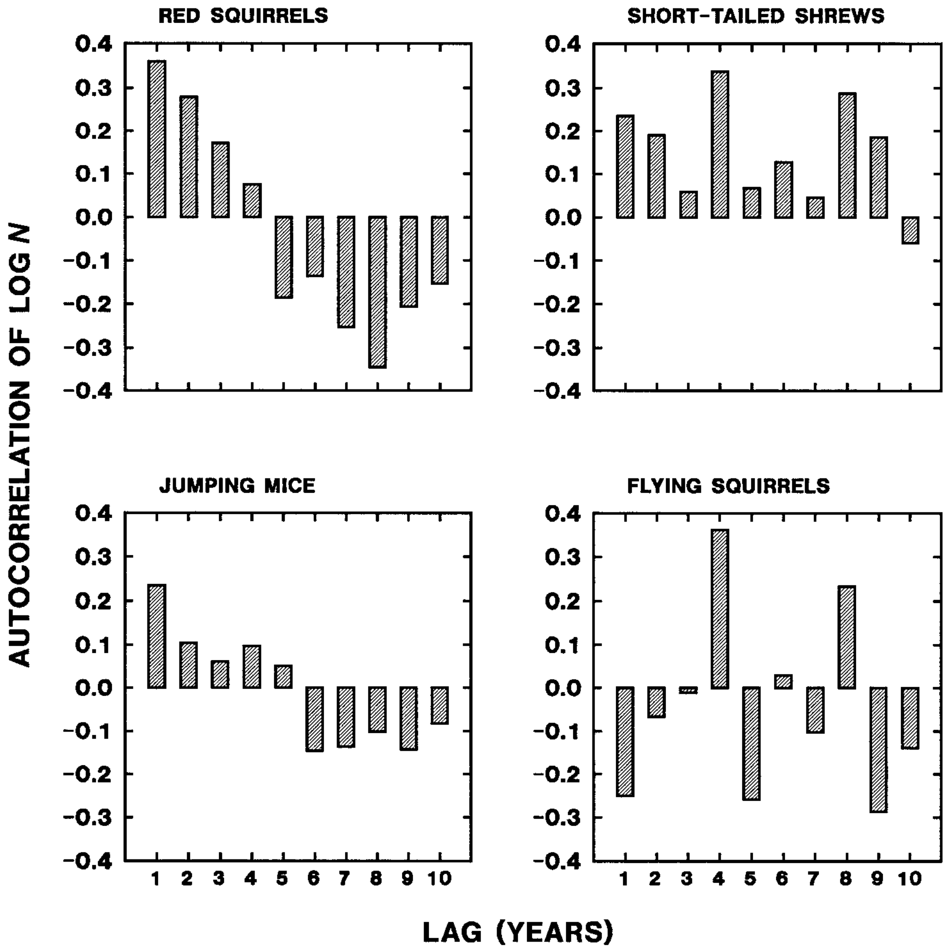

FIG. 2. Continued.

gests that lagged terms significantly improved forecasting of temporal population trends only in chipmunks. In this latter species, simulations using response surface parameters quickly converged on point stability under deterministic conditions and under stochastic conditions produced autocorrelation functions similar to those seen under simple logistic models. These test results are consistent with the hypothesis that our study populations had relatively simple dynamics, adequately predicted by population density or log-transformed population density the previous year. In all cases, however, there was appreciable variability around the fitted density-dependent relationships (Fig. 4), suggestive of stochastic environmental noise.

DISCUSSION

Our field observations suggest that populations of small mammals in Algonquin Park fluctuated considerably over time, with little evidence of long-term periodicity in seven out of eight species. Pronounced

TABLE 2. Cross correlation between annual rates of increase ($r_t = \ln[N_t/N_{t-1}]$) for pairs of small mammal species in Algonquin Park, Ontario, during 1952–1995 (+ indicates significant correlation among populations of different species, and 0 indicates no significant correlation).

Species		1	2	3	4	5	6	7	8
Deer mice	1								
Red-backed voles	2	+							
Woodland jumping mice	3	+	+						
Chipmunks	4	+	+	0					
Red squirrels	5	+	+	+	+				
Flying squirrels	6	+	+	+	0	+			
Short-tailed shrews	7	+	+	+	+	+	+		
Masked shrews	8	0	0	0	0	0	0	0	

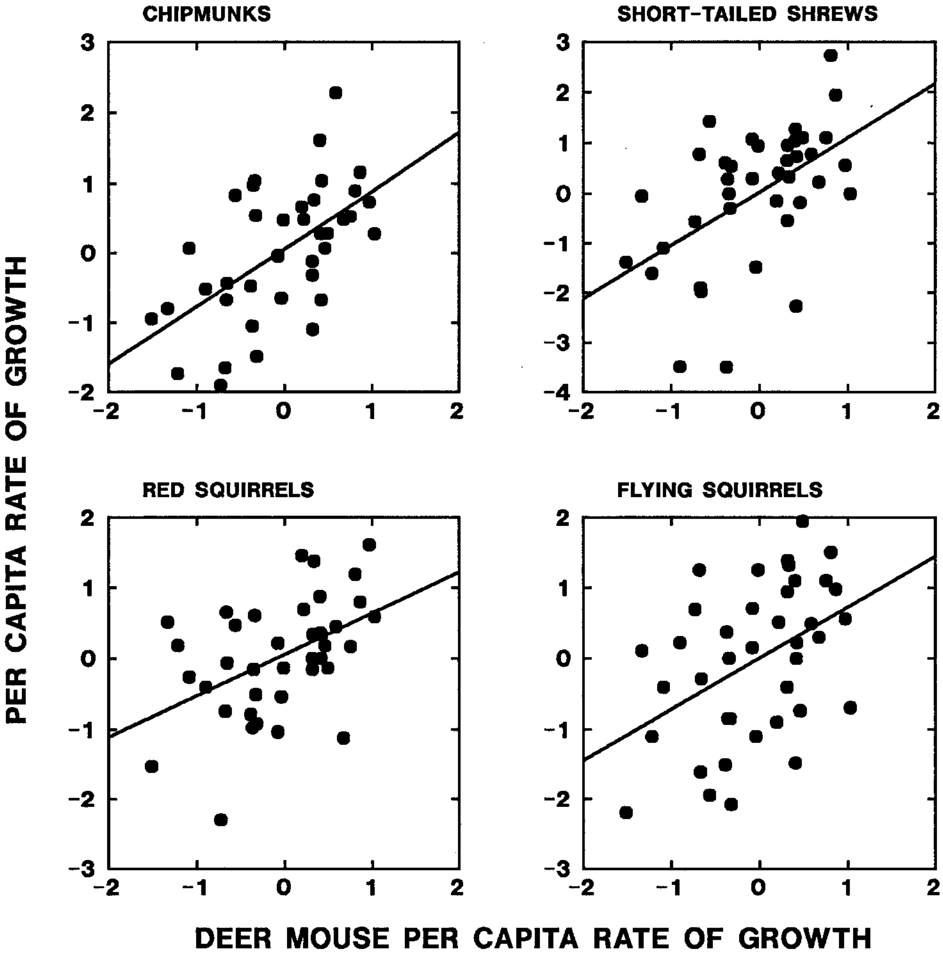

FIG. 3. Per capita rates of increase by chipmunks, short-tailed shrews, red squirrels, and flying squirrels in relation to the per capita rate of increase of deer mice in Algonquin Provincial Park over 43 yr (chipmunks vs. deer mice: $y = 0.062 + 0.829x$, $P < 0.001$; short-tailed shrews vs. deer mice: $y = 0.033 + 1.073x$, $P = 0.001$; red squirrels vs. deer mice: $y = 0.060 + 0.581x$, $P = 0.003$; flying squirrels vs. deer mice: $y = 0.008 + 0.722x$, $P = 0.005$).

variability has been documented many times in populations of small mammals (for examples in recent literature see Garsd and Howard 1981, 1982, Hansson and Henttonen 1985, Henttonen et al. 1985, Taitt and Krebs 1985, Saitoh 1987, Schaffer 1987, Marcström et al. 1990, Gilbert and Krebs 1991, Hanski et al. 1993, Pucek et al. 1993, Turchin 1993, Lindström and Hörnfeldt 1994, Elkinton et al. 1997). Pronounced variability per se is therefore not in question with

TABLE 3. Maximum likelihood estimates of parameters for the Ricker logistic model of r_t vs. catch per unit effort the previous year, and the probability that one would observe such a likelihood ratio if population changes were due to the null hypothesis, using Dennis and Taper's (1994) PBLR† test.

Species	a_0	a_1	Ratio	P
Deer mice	0.905	−0.0059	1.873	<0.001
Red-backed voles	0.726	−0.0364	1.358	0.009
Woodland jumping mice	0.682	−0.1556	1.257	0.026
Chipmunks	0.571	−0.0185	1.339	0.011
Red squirrels	0.464	−0.1254	1.228	0.030
Flying squirrels	1.425	−1.1562	3.032	<0.001
Short-tailed shrews	0.677	−0.1159	1.640	0.001
Masked shrews	0.777	−0.2200	1.439	0.003

† Parametric bootstrap likelihood ratio.

TABLE 4. Maximum likelihood estimates of parameters for the Gompertz logistic model of r_t vs. ln(catch per unit effort the previous year), and the probability that one would observe such a likelihood ratio if population changes were due to the null hypothesis, using Dennis and Taper's (1994) PBLR test.

Species	a_0	a_1	Ratio	P
Deer mice	4.749	−0.9640	1.949	<0.001
Red-backed voles	1.740	−0.6458	1.474	0.002
Woodland jumping mice	0.760	−0.7566	1.609	0.001
Chipmunks	2.291	−0.7401	1.607	0.001
Red squirrels	0.673	−0.6306	1.449	0.005
Flying squirrels	0.011	−1.2487	2.702	<0.001
Short-tailed shrews	0.921	−0.7530	1.565	0.001
Masked shrews	0.732	−0.8878	1.770	<0.001

TABLE 5. Maximum likelihood estimates of parameters for the response surface model of r_t vs. catch per unit effort the previous year and the year before that. The probability that one would observe such a likelihood ratio if population changes were due to the null hypothesis was evaluated using Dennis and Taper's (1994) PBLR test.

Species	θ_1	θ_2	a_0	a_1	a_2	P
Deer mice	0.5	−2.0	2.048	−0.1582	−1843.4	0.166
Red-backed voles	0.0	0.5	1.578	−0.6885	0.0670	0.286
Woodland jumping mice	−0.5	2.0	−1.730	2.2713	0.0031	0.009
Chipmunks	0.0	0.5	2.066	−0.8250	0.0994	0.022
Red squirrels	0.0	0.0	0.530	−0.6953	0.1929	0.072
Flying squirrels	0.5	2.0	3.128	−2.7852	−0.0819	0.299
Short-tailed shrews	0.5	0.0	1.344	−0.7462	0.1986	0.445
Masked shrews	−0.5	2.0	−1.696	2.1553	0.0037	0.043

respect to small mammals, but robust statistical evidence of cycles in small mammals is less common than popularly supposed.

Ecologists studying small mammal populations often rely on indirect indices, such as variation in log N, to discriminate between cyclic and noncyclic populations. The statistical inadequacy of such indices raises serious doubts about the reliability of cyclicity assessments in the historical literature (Sandell et al. 1991). A less ambiguous statistical approach is to use the standard methodology of time series or spectral analyses to assess periodicity in small mammals, as is commonly done for univoltine insects or other taxa (e.g., Turchin 1990, Turchin and Taylor 1992). Several appropriate time-series analyses from northern Europe have shown evidence of recurrent periodic fluctuations over time (Garsd and Howard 1981, 1982, Henttonen et al. 1985, Marcström et al. 1990, Hanski et al. 1993, Turchin 1993, Lindström and Hörnfeldt 1994). Indisputable evidence of small mammal cycles from North America is much scantier.

We found strong evidence of direct density dependence in all eight species. The Ricker logistic and Gompertz logistic models described the Algonquin time series equally well. The Gompertz logistic model is highly stable, so its correspondence to our observed population data in some sense implies deterministic stability. The Ricker logistic model is capable of producing cyclic population dynamics due to overcompensatory responses (Ricker 1954), provided that organisms have a sufficiently high rate of increase as population densities approach zero ($r_{max} = 2$ in the Ricker formulation). Our field estimates of the maximum per capita rate of increase for the eight species in Algonquin ranged between 0.46 and 1.31, placing them squarely in the stable category in the absence of stochastic environmental variation (Ricker 1954), although environmental stochasticity of sufficent magnitude can induce damped oscillations in simple density-dependent models (Royama 1992, Kaitala et al. 1996). In accordance with predictions from the deterministic model, we found little evidence of cycles in our field populations.

Our conclusions regarding density-dependent relationships could be biased by an unavoidable feature of most free-living populations: sampling error in both the dependent and independent variables. This characteristic, sometimes termed the ''error in variables'' problem, has troublesome implications for any attempt at modeling ecological data. Uncertainty in the independent variable (i.e., population density) due to sampling error tends to obscure the true underlying relationship with annual rates of change (Ludwig and Walters 1981, Walters and Ludwig 1981). This suggests that our estimates of maximum rates of increase and slope were probably biased downward by sampling error in the annual estimates of population abundance, implying in turn that we underestimated the strength of density dependence.

Our results suggested that there is little statistical justification for invoking complex lagged models to explain the observed temporal variation in small mammals in Algonquin Park. Adding lagged terms to any population model must, by definition, improve predictive power. Nonetheless, the PBLR test showed that predictions obtained from either of the response surface models were rarely distinguishable from the simpler logistic formulations. This result, in conjunction with our time-series analysis, suggested that the Algonquin species exhibited fairly simple deterministic dynamics: stability or weak cycles. In a constant world, we would therefore expect to see a stable equilibrium for most of these rodent species. In a more realistic stochastic world, we would expect a stationary probability distribution of population densities, with each population tracking a continually shifting target. Some of the variability in population growth rates that we saw arose no doubt from biotic interactions in the community and was therefore predictable using broader ecological models. The source of these biotic interactions is a major focus of our current research efforts.

Perry et al. (1993) found little difference in predictive power between the Gompertz logistic model and the RSM model. Perry et al. (1993) commented on the instability of parameter estimates, pointing out that RSM results can change dramatically with further information. This is a good reason for cautious interpretation of any short time series, regard-

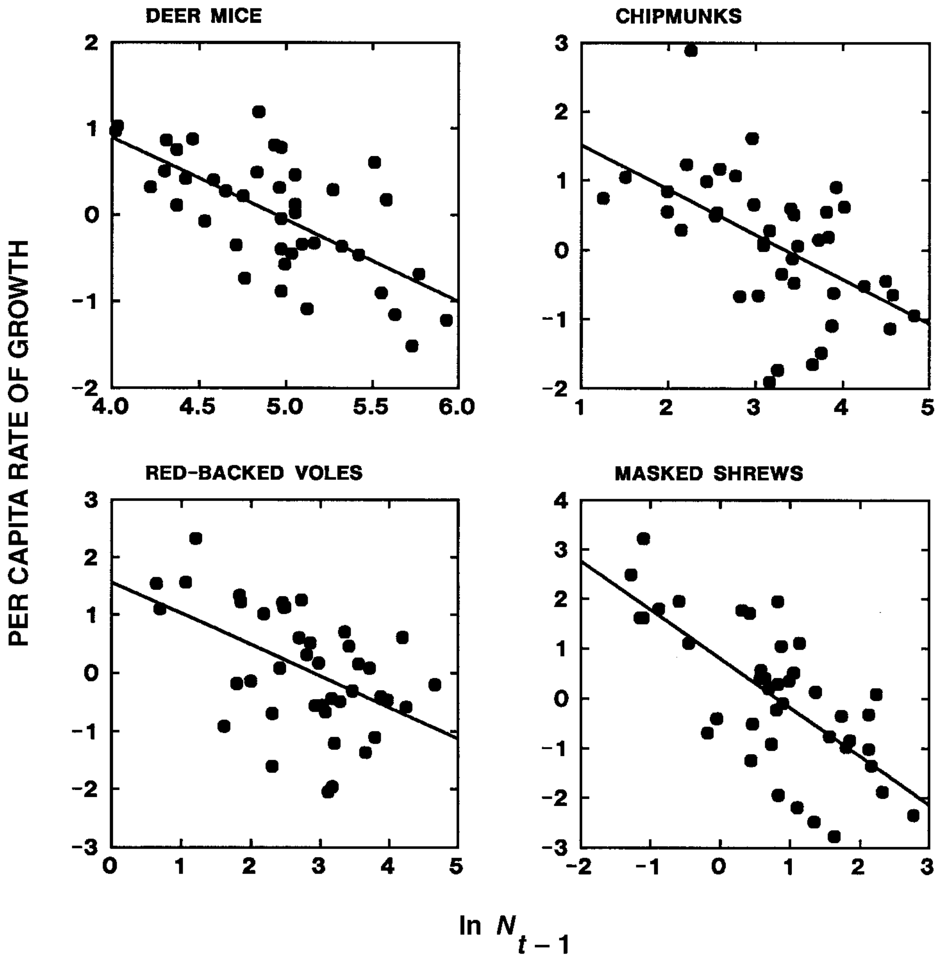

FIG. 4. Per capita rates of population growth (r_t = ln[N_t/N_{t-1}]) in relation to ln(N_{t-1}) for eight species of small mammals in Algonquin Provincial Park, Ontario, obtained during 1952–1995 (deer mice: $y = 4.672 - 0.946x$, $r^2 = 0.437$; southern red-backed voles: $y = 1.560 - 0.538x$, $r^2 = 0.250$; chipmunks: $y = 2.153 - 0.645x$, $r^2 = 0.297$; masked shrews: $y = 0.796 - 0.981x$, $r^2 = 0.494$; red squirrels: $y = 0.585 - 0.533x$, $r^2 = 0.229$; woodland jumping mice: $y = 0.665 - 0.466x$, $r^2 = 0.215$; short-tailed shrews: $y = 1.037 - 0.712x$, $r^2 = 0.351$; flying squirrels: $y = -0.074 - 1.210x$, $r^2 = 0.602$). Note that these regression lines pertain to the full data set from 1952–1995, whereas the PBLR test results in Table 4 pertain to the 36 yr of continuous data from 1952–1987. We justify use of the full data set on the basis of significant relationships found in the first 36 yr (Table 4).

less of the hypothesized model. There has been little consideration of the statistical significance of complex vs. simple ecological models (Morris 1990, Dennis et al. 1995), perhaps because methodologies for statistically discriminating among fundamentally different nonlinear models have only recently received attention (Dennis and Taper 1994, Dennis et al. 1995).

We found evidence of synchronized population dynamics among the small mammal species in Algonquin Park, which seems most likely to stem from two biological mechanisms. First, all of the species in our system are subject to predation. Recent work from northern Europe suggests that complex interactions between voles and their specialist predators could be responsible for population fluctuations (Hanski et al. 1993, Turchin 1993). Second, several of the populations in our study area share common food supplies. Studies from both North America (Wolff 1996, Elkinton et al. 1997) and Poland (Pucek et al. 1993) suggest that annual fluctuations in forest small mammals are influenced by seed crops. Seed crops alone are insufficient to explain all the correlations in rates of change we observed in the Algonquin populations, because some species (e.g., shrews) are not granivorous. The North American studies suggest higher trophic links between population fluctuations of rodents and outbreaks of arthropod-borne disease and forest pests (Ostfeld et al. 1996, Elkinton et al. 1997). Variability in food supplies, predators, and/or pathogens could explain both the high degree of synchronization and the substantial noise in the logistic relationships recorded for the Algonquin populations. We are currently con-

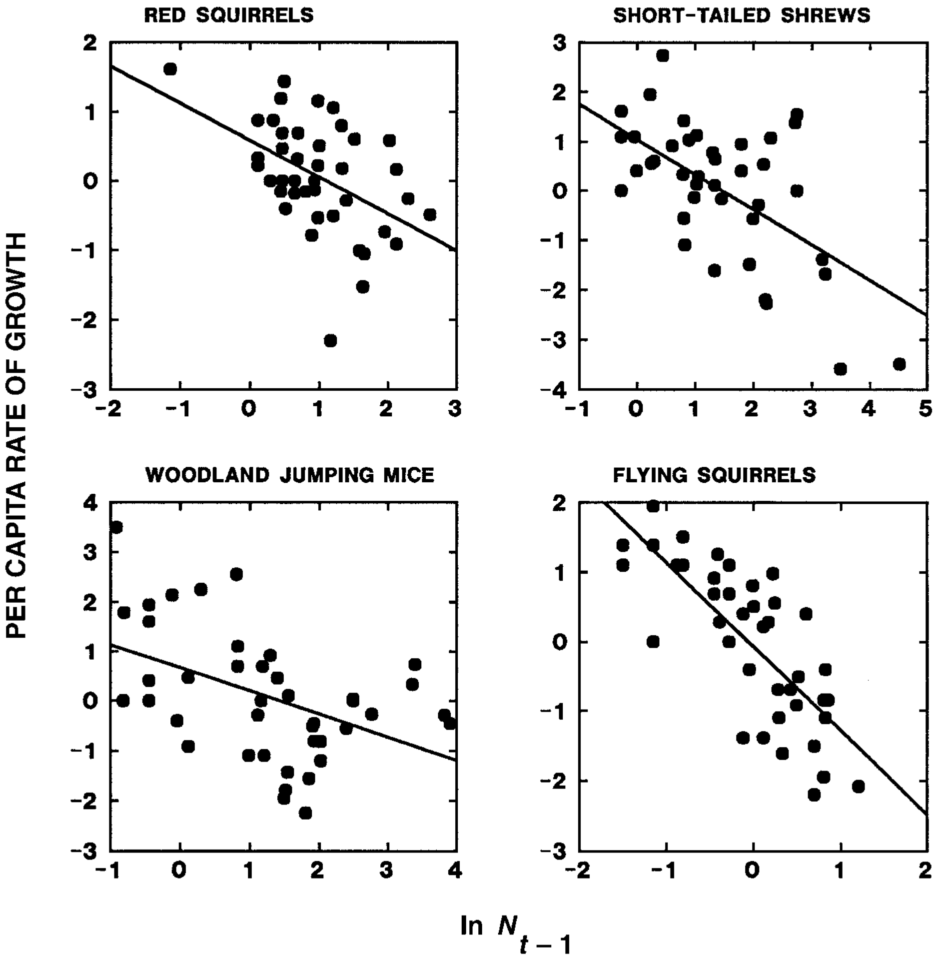

FIG. 4. Continued.

ducting further studies to test these causal mechanisms.

Acknowledgments

The field studies were supported through funding by the Ontario Ministry of Natural Resources, the Natural Sciences and Engineering Research Council of Canada, and the Ontario Environmental Youth Corps. Logistic support was provided by the Wildlife Research Station in Algonquin Provincial Park. We thank R. Ostfeld, J. Paloheimo, J. Wilmshurst, C. Bergman, and two anonymous reviewers for their valuable comments on the manuscript.

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APPENDIX

Annual trapping totals during 1952–1995 for eight species of small mammals in Algonquin Provincial Park, Ontario.

		Species†							
Year	Effort	*P.m.*	*C.g.*	*T.s.*	*S.c.*	*T.h.*	*N.i.*	*B.b.*	*G.s.*
1952	990	123	17	1	3	1	18	1	0
1953	1100	272	12	9	6	2	3	1	1
1954	1320	497	39	33	2	4	9	4	2
1955	1320	146	62	5	20	5	2	0	0
1956	1320	103	41	16	1	10	8	0	0
1957	1320	219	30	28	10	12	3	2	2
1958	1320	73	19	30	7	9	2	0	1
1959	1320	205	69	40	2	17	5	0	0
1960	2265	324	43	67	3	10	0	4	1
1961	2520	704	51	122	5	3	0	6	2
1962	3015	221	29	65	16	7	32	7	3
1963	3150	365	5	73	11	9	18	6	1
1964	3150	175	27	10	0	0	1	3	3
1965	3150	461	76	22	4	4	2	6	6
1966	3150	261	22	52	2	7	1	28	0
1967	3150	395	19	26	1	7	13	2	0
1968	3150	642	67	35	5	6	1	8	6
1969	3150	447	34	95	8	5	1	11	2
1970	3150	609	37	84	14	5	9	22	1
1971	3060	809	117	59	6	4	9	12	4
1972	3000	960	29	114	0	20	19	10	1
1973	3000	485	14	21	24	9	11	23	6
1974	3000	347	5	37	8	5	18	17	2
1975	3000	430	17	61	0	11	3	26	4
1976	2400	177	14	31	4	8	37	2	2
1977	2400	419	56	101	1	19	28	20	7
1978	2400	303	7	22	0	7	28	35	0
1979	4410	998	81	411	5	22	29	143	2
1980	4050	630	46	131	34	7	18	3	3
1981	4500	645	156	139	8	10	20	5	8
1982	4500	436	182	86	10	4	4	10	1
1983	4500	649	198	433	9	11	1	30	5
1984	4500	621	65	226	7	6	11	6	1
1985	4500	1387	119	557	13	22	3	107	8
1986	4500	304	73	215	41	4	33	26	0
1987	4500	417	100	71	45	6	14	69	3
1989	4500	387	12	207	6	5	4	69	0
1990	3600	927	61	250	1	5	7	327	3
1991	3600	375	102	148	13	3	102	9	4
1992	3150	492	206	172	15	4	142	30	0
1993	3600	552	379	319	0	4	106	90	3
1994	4500	353	310	203	11	11	222	16	0
1995	3600	393	173	351	16	37	140	18	2

† Symbols for each species are as follows: *P.m.* = *Peromyscus maniculatus* (deer mouse), *C.g.* = *Clethrionomys gapperi* (southern red-backed vole), *T.s.* = *Tamias striatus* (eastern chipmunk), *S.c.* = *Sorex cinereus* (masked shrew), *T.h.* = *Tamiasciurus hudsonicus* (red squirrel), *N.i.* = *Napaeozapus insignis* (woodland jumping mouse), *B.b.* = *Blarina brevicauda* (short-tailed shrew), and *G.s.* = *Glaucomys sabrinus* (northern flying squirrel).