Population Cycles of the Bank Vole in the Range Optimum

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Abstract—Patterns of seasonal and long-term dynamics of the size and structure of the bank vole population were studied in the European subtaiga subzone, the optimum of the species range. The dynamics of this population proved to undergo complex fluctuations with cyclic components, which have periods of one year and about three years. The one-year fluctuations of the population size and structure are accounted for by animal adaptation to seasonal changes in environmental factors. The fluctuations with the three-year quasi-period are determined by intrapopulation density-dependent mechanisms.

Key words: bank voles, population cycles, regulation mechanisms.

Population dynamics of small mammals is determined by a combination of endo- and exogenous factors and is characterized by complex seasonal and long-term fluctuations. Ecologists discovered periodic fluctuations of population size in small mammals as early as in the first half of the 20th century. However, it was not until Elton's (1924) classical paper was published that periodic fluctuations were found to be typical of northern ecosystems where animal reproduction cycles occur in spring and summer. This timing determines the discreteness of population dynamics and, hence, may be regarded as one of the main factors responsible for a delay in population response to variations in external and internal conditions. According to the theory of population dynamics (Maynard Smith, 1974; May, 1975), this delay, together with a high reproductive potential, density-dependent intraspecific competition, effects of predators, and many other factors, may cause population autooscillations. As a result, population dynamics can even become chaotic.

Although population dynamics and mechanisms of its cyclicity have been extensively studied, modern ecologists differ on the causes and main mechanisms of this phenomenon. This may be explained by both the intrinsic complexity of population phenomena and numerous methodological problems. The main methodological factor is an insufficient number of long-term stationary observations on both population size and demographic structure. Even fewer studies dealt with the simultaneous monitoring of population demographic characteristics and environmental conditions (weather, food supply, predator pressure, etc.). Another factor preventing the development of a general theory of population regulation is that most researchers try to explain all the diverse population phenomena by influences of a single group of factors. Hansson (1984) rightly notes that single-factor hypotheses of population-size oscillations are so popular because they are easier to test and interpret in biological terms. Long-term cycles of population dynamics and their mechanisms are among the topical problems of population ecology (Krebs, 1996).

The purpose of this study was to analyze the dynamics of bank vole population and the mechanisms responsible for its cyclicity in the optimum of species range on the basis of data obtained during long-term stationary surveys.

MATERIALS AND METHODS

Data on the size and structure of the bank vole (*Clethrionomys glareolus* Scherb. 1780) population were obtained on a stationary plot in the Udmurt Republic (56°20′ N, 52°40′ E) between 1973 and 1991. The plot was located in the subzone of linden–fir–spruce subtaiga forests, which is regarded as the optimum of the bank vole range (Zhigalski, 1992). Population dynamics was monitored using the standard trapline method each April, June, August, and October. We used the data on 76 time points (four studies per year during 19 years) and 2×10^4 trap-days; a total of 2.5×10^3 animals were caught. The state of populations in each year was described by 19 demographic parameters (Table 4). In some variants of analysis, we used logarithms of relative numbers. The data were treated using univariate and multivariate statistical methods, including spectral analysis (Kendall and Steward, 1976), ANOVA, regression analysis (Afifi and Azen, 1982; Sokal and Rolhf, 1995), principal component
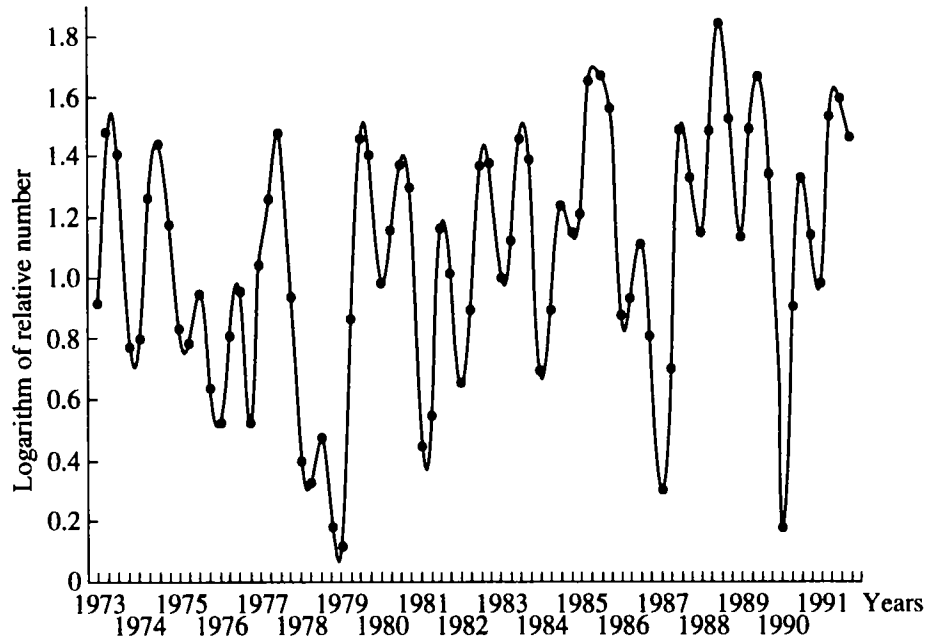
Fig. 1. Relative numbers of bank voles in April, June, August, and October (Udmurt population, 1973–1991).

analysis (Iberla, 1980), and discriminant analysis (Aivazyan *et al.*, 1989).

RESULTS AND DISCUSSION

Dynamics of Population Size and Structure and Mechanisms of Its Cyclicity

The data on bank vole population dynamics (Fig. 1) arose a question as to whether the observed fluctuations are stochastic or are underlain by certain regularities. To answer this question, we used spectral analysis of a long-term series of the bank vole population size. We found two peaks of spectral density corresponding to the periods of one year and about three years (Fig. 2). The presence of two distinct harmonic components indicated that the changes of population size were two-component cyclic oscillations. To estimate these two components, we used ANOVA (a model with random factors, with gradations of the first and second factors being 19 years of monitoring and 4 months of recording, respectively). The interannual (long-term) component of the total variance was the highest (42.6%; $F(18; 54) = 7.64$; $p < 0.0001$), seasonal variation accounted for 31.7% of the variance ($F(3; 54) = 7.64$; $p < 0.0001$), and the residual variance (25.7%) was determined by the factors unaccounted by the model used. Both components were statistically significant; therefore, the observed changes in population size reflected a complex process consisting of the sum of two oscillations (long-term and seasonal) and a random component. Changes in animal numbers during the year resulted from the seasonal reproduction pattern, which is typical of animals living in the temperate zone. To clarify the mechanisms of long-term oscillations, it

is necessary to formulate the corresponding hypotheses and to test them statistically. This was one of the main tasks of our study.

If there are statistically significant interannual and seasonal components of variation in population size and two peaks of spectral density in population dynamics, there must be years with similar seasonal dynamics, as their alternation accounts for the long-term population cycle.

To reveal the years with similar seasonal dynamics, we used two methods of pattern recognition: (1) without a teacher, i.e., component analysis, and (2) with a teacher, i.e., discriminant analysis. Table 1 shows the results of the component analysis. The figures in the "load" columns are coefficients of correlation between the demographic parameters studied and three principal components (PCs); the last column shows the proportions (in percent) of the parameter variance explained by the three-component model.

The first three PCs explained 72.2% of the total variance of the parameters (Table 1). The first PC explained 48.2% of the total variance. It positively correlated with population size (in any period studied) and the proportion of nonreproductive males in June and August but negatively correlated with the proportion of reproductive females in June to October and with animal survival in winter. This was probably accounted for by the existence of an inverse relation between population density, on the one hand, and reproduction rate and winter survival, on the other. The second PC (14.2% of the variance) was related to the interannual variation in the age structure of population in June to August and the survival in winter. The third PC (10.8% of the total variance) was associated with the proportion of repro-

Table 1. First three eigenvectors of the correlation matrix and explained proportions of the total variance of population demographic parameters

No.	Demographic parameter	Load on the principal component ($df = 17$)			Explained proportion of variance (%), df (3; 15)
		1	2	3	
1	Population size in April	0.816*	−0.209	0.203	75.0*
2	Population size in June	0.821*	−0.346	0.256	85.9*
3	Percentage of reproductive females in June	−0.528*	0.300	0.677*	82.8*
4	Percentage of nonreproductive males in June	0.878*	−0.244	−0.171	86.0*
5	Percentage of one- to two-month-old animals in June	0.332	−0.847*	0.084	83.5*
6	Percentage of three- to six-month-old animals in June	0.621*	−0.470*	0.130	62.3*
7	Population size in August	0.789*	−0.008	0.538*	91.2*
8	Percentage of reproductive females in August	−0.744*	0.099	0.384	71.1*
9	Percentage of nonreproductive males in August	0.518*	0.046	−0.404	43.3*
10	Percentage of one- to two-month-old animals in August	0.753*	0.343	−0.240	74.2*
11	Percentage of three- to six-month-old animals in August	−0.700*	−0.556*	−0.061	80.3*
12	Population size in October	0.627*	0.067	0.591*	74.7*
13	Percentage of reproductive females in October	−0.534*	−0.419	0.207	50.4*
14	Percentage of one- to two-month-old animals in October	−0.857*	−0.153	0.077	76.4*
15	Percentage of three- to six-month-old animals in October	0.856*	0.191	−0.058	77.2*
16	Survival in winter	−0.421	−0.587*	−0.207	56.5*
Variance (V_i)		7.709	2.275	1.725	
V_i, %		48.2	14.2	10.8	73.2

* $p < 0.05$.

ductive females in June and the numbers of animals in August and October. Its dynamics exhibited a linear trend.

According to the model proposed by Krebs and Myers (1974), a population cycle consists of four alter- nating phases: growth, peak, decrease, and depression. Based on this assumption, each year included in the long-term series of the first PC values was assigned to one of the four phases. This preliminary classification of the years of surveys was then refined using stepwise
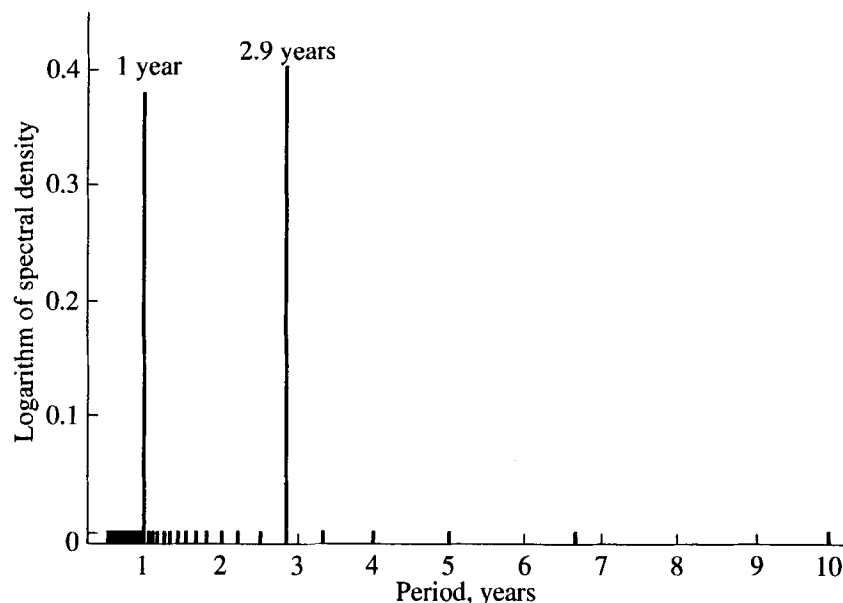

Fig. 2. Spectrum of the time series of bank vole relative numbers (Udmurt population, 1973–1991).

Table 2. Results of stepwise discriminant analysis. Comparison of three phases of the bank vole population cycle.

CDF	Eigenvalue	Canonical correlation coefficient (R)	Wilks's Λ	χ^2	df	p
1	17.96	0.973	0.006	61.43	18	0.000001
2	7.82	0.942	0.113	26.12	8	0.001

Phase	Years	Phase of population cycle*		
		Depression	Growth	Peak
Depression	1975, 1978, 1981, 1984, 1986, 1990		$F = 8.99$ $p = 0.0025$	$F = 15.78$ $p = 0.0003$
Growth	1973, 1976, 1979, 1982, 1987,1988, 1991	59.33		$F = 9.83$ $p = 0.0019$
Peak	1974, 1977,1980, 1983,1985, 1989	113.59	64.88	

* Elements under the diagonal show squared Mahalanobis distances between group centroids; elements above the diagonal show F-test values (df 9; 8) and significance levels (p).

discriminant analysis (Table 2). The first two canonical discriminant functions (CDFs) were statistically significant. The first CDF and the first PC correlated with each other ($r = 0.82, p < 0.001$); therefore, the interpretations of these canonical axes were similar. Each of these canonical variables integrally characterized the population state, estimated the effects of intrapopulation density-dependent mechanisms and, hence, identified the phases of the long-term population cycle. The resultant classification (Table 2) comprised only three phases of the cycle, each characterized by a specific set of the values of demographic parameters. Six years of observation were assigned to the depression phase; seven, to the growth phase; and six, to the peak phase of the cycle. All the phases significantly differed from one another with respect to the state of the population.

In contrast to the Krebs and Myers model, the decrease phase was not observed in our study (Fig. 3). After a peak was reached, the population always entered the depression phase in the next year, and the
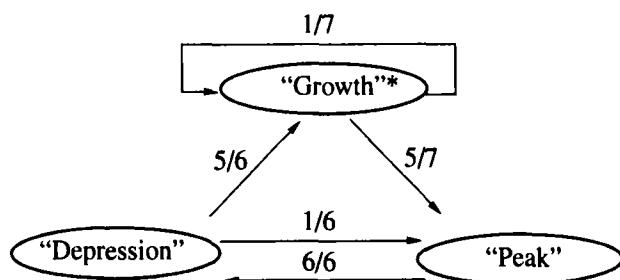

Fig. 3. Scheme of the alternation of seasonal phases in the population cycle. Arrows show the direction of transition. Figures before and after the slash are the number of transitions observed and the total duration (years) of the given phase, respectively. The asterisk refers to the last year in the survey series.

depression phase was usually replaced by the growth phase. We observed only one direct transfer from the depression (1984) to the peak phase (1985); however, this was a probable consequence of reproduction in winter, which is untypical of bank voles living in the region studied. The growth phase was usually replaced by the peak phase. The cycles that we observed in the bank vole population of the Udmurt station had the following periods: two years (one cycle), three years (three cycles), and four years (one cycle).

Regular oscillations are typical of the populations of small mammals that reproduce almost exclusively in spring and summer. This may be one of the main factors causing a delay in the population response to changes in environmental conditions (Maynard Smith, 1974; May, 1975; Krebs, 1996).

The response of the Udmurt bank vole population to changes in its state was delayed by one year (the first coefficient of the serial correlation $r_1 = -0.54, p = 0.011$). This may be explained by the seasonal reproduction pattern of small mammals in the temperate zone. As in the case of population dynamics, the first CDF exhibited oscillations with a period of three years. Fifteen out of 19 series of population demographic parameters had the only one spectral-density maximum, which corresponded to this period.

To determine the pattern of the relationship between the population states (characterized by the first CDF) in two consecutive years, we used regression analysis. The dependence of the population state in a given year on its state in the preceding year approximated by a polynomial function explained 82.4% of the variance. The regression was nonmonotonic (U-shaped; Fig. 4), which indicates the delay and effects of the density-dependent regulation (Williamson, 1975). In terms of the self-organizing criticality theory (Bak and Chen,

1991), this relationship may be interpreted as follows. If a population is in the subcritical state (the depression phase), it will increase its density and reach the critical state (the growth phase) in the next year. If the population is in the critical state, it will reach the supercritical state (the peak phase) in the next year. If the state of the population is supercritical, the current cycle will end in a "demographic collapse," which is characterized by a catastrophic decrease in population size during winter, and the population will return to the subcritical state, (i.e., the depression phase). The stationary state of the population, which corresponds to the intersection between the curve and the bisector of the angle between the axes (Fig. 4), is unstable: the tangent of the regression slope in this point is less than unity, which indicates that the population has self-oscillating dynamics (Svirizhev and Logofet, 1978). If the population dynamics has cycles with the three-year period, there must be cycles with other periods (Li and Yorke, 1974; cited from May, 1975). In addition to the three-year period, the time series of bank vole population dynamics contained two- and four-year periods; therefore, the population studied may be described as a system with chaotic dynamics.

The plateau in the peak–depression region (Fig. 4) may be explained by chaos-limiting mechanisms, which were earlier demonstrated in simulation models (Stone, 1993) and natural bank vole populations in the central and peripheral parts of the species range (Kshnyasev, 1998a, 1998b). The curve bend in the depression–peak region resulted from reproduction under snow in the winter of 1984–1985. This phenomenon has often been observed in other populations in the species-range optimum after the years of a low population size (Bernstein et al., 1989; Zhigalski, 1992; Kshnyasev, 1998a).

To determine the type of density-dependent regulation and to estimate the growth (increment) coefficient and the levels of animal abundance corresponding to the threshold of intraspecific competition and the stationary state of the Udmurt bank vole population, we used the model that took into account the rate of intraspecific competition (Maynard Smith and Slatkin, 1973; cited from Begon et al., 1989):

$$N(t+1) = N(t)\lambda\{1 + [aN(t)]^b\}^{-1},$$

where λ is the growth coefficient; parameter $a (a = [(\lambda - 1)^{1/b}]/K)$ determines the background level relative to which the oscillations occur; and b is the parameter determining the pattern of the relationship between population state and density: $b = 0$, $b < 1$, $b = 1$, and $b > 1$ correspond to the absence of density dependence, an incomplete compensation, an accurate compensation, and a supercompensation, respectively.

The value of b estimated from empirical data on the dynamics of the Udmurt bank vole population was significantly higher than unity. Therefore, the dependence of intraspecific competition on population density cor-
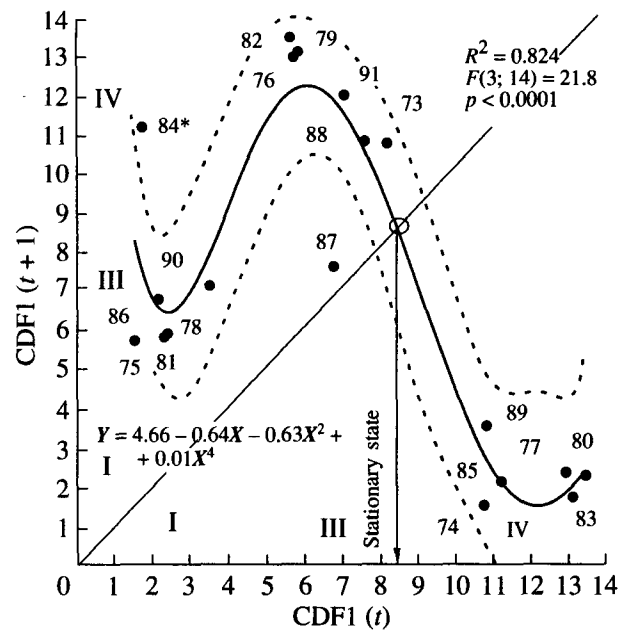

Fig. 4. Dependence of the state of population [CDF1($t + 1$)] on its state in the previous year [CDF1(t)].

responded to the supercompensation type, i.e., a strictly density-dependent regulation of population processes (Table 3).

Table 4 shows point estimates of relative population size that correspond to the threshold of intraspecific competition and the stationary state of the population. They were calculated from the regression of population size on CDF 1.

Population Demography at Different Phases of the Population Cycle

When the population was at the depression or growth phase in spring, its size at the onset of reproductive season was low; when it was at the peak phase, its size in this period was high and considerably exceeded the threshold value for "triggering" the intraspecific competition (Table 4). The proportion of reproductive females was slightly lower during the depression phase than during other phases, but this difference was statistically nonsignificant. In April, for example, the population comprised only overwintered animals if it was at the depression phase and animals of all age groups if it was at any other phase. This was apparently because reproduction at the depression phase began later than at other phases. This difference in the timing of reproduction could not be accounted for by exogenous factors alone, because years of the depression phase differed in environmental conditions.

Most of the animals that entered wintering after the peak phase and formed the core of the population at the next (depression) phase were from early summer generations. Therefore, they had grown and developed at

Table 3. Estimation of parameters of the population dynamics model taking into account intraspecific competition: $N(t + 1) = N(t)\lambda\{1 + [aN(t)]^b\}\}^{-1}$ ($R = 0.859$; $R^2 = 0.737$; $F(3; 15) = 14.0$; $p = 0.00013$)

Parameter	Estimate	Standard error	t ($df = 15$)	p
λ, growth coefficient	2.9377	0.4844	6.06	0.00002
a, parameter characterizing the stationary state $(a = [(\lambda - 1)^{1/b}]/K)$	0.1397	0.0143	9.78	0.00000
b, type of competition and density dependence	5.0044	1.1481	4.36	0.00056

high population densities, which probably determined the high mortality rate in winter and the low population reproductive potential in the next year. As a result, population size at the depression phase increased only 1.17 ± 0.15 times by June. This significantly differed from the increments observed at the growth and peak phases, when the population increased during the same period by factors of 2.93 ± 0.63 and 2.19 ± 0.08, respectively. Relatively slow population growth in April to June at the depression and peak phases, compared to the growth phase, was caused by different factors. During the depression phase, structural features of the population prevented a drastic increase in its size (the late onset of reproduction, low population size in spring, and low proportion of reproductive females). At the peak phase, density-dependent regulation limited population growth, as population size exceeded the threshold level. This is confirmed by the fact that, in June, the proportions of reproductive females and immature males during the peak phase were lower and higher, respectively, than during other phases. As is seen from Table 4, the population in June mainly consisted of overwintered animals and one- to two-month-old animals of the new generation at all phases of the population cycle.

From June to August, the population size at the depression, growth, and peak phases increased by factors of 2.52 ± 0.37, 2.97 ± 0.87, and 1.61 ± 0.11, respectively. Variation in population growth rate during the peak phase was significantly smaller than during other phases ($F(5; 5) = 15.74$, $p < 0.005$; $F(6; 5) = 34.56$, $p < 0.0007$), which is probably the effect of strict intrapopulation regulation.

Population size in August was also considerably lower at the depression phase than at other phases (Table 4). Male and female reproductive activities regularly decreased by August. In addition, the rate of sexual maturation and the proportion of reproductive animals decreased when population density exceeded the threshold level, which was especially characteristic of the peak phase. In this period, the population mostly consisted of one- to two-month-old and three- to six-month-old animals of the new generation at all phases of the population cycle.

By October, population size decreased approximately 1.6-fold, irrespective of the phase (the numbers of animals at the growth and peak phases were almost equal to each other and were almost three times higher than at the depression phase). Although October is the time when reproduction ceases at the given latitude, the population at the depression and peak phases still contained more than 16 and about 6% of reproductive females, respectively (Table 4). At the depression phase, one- to two-month-old animals accounted for the major part of the population in October (87.2%), whereas their proportion at the peak phase was only 23%. The growth phase was intermediate with respect to age structure. Such pronounced differences in age structure could not emerge unless reproduction at the peak phase drastically decreased as early as in July to August. Apparently, the survival rates in winter also differed because of differences in the age structure of population observed at early winter (Table 4). After the peak phase, less than one-fifth of the population survived winter (the population collapse), whereas the proportions of survivors after the depression and growth phases were about 50%.

The high mortality in winter after the "peak" years is the main factor responsible for the following depression. The small biotic potential of the population at the depression phase does not allow it to grow significantly during one reproduction season. Therefore, the subsequent growth phase has intermediate characteristics: during this phase, the population can recover its density and demographic structure to the extent that usually allows it to reach the peak phase in the next year. Thus, a three-year cycle is formed. We also observed a two-year cycle (Fig. 3), when the peak phase began immediately after depression; however, this transition was accompanied by reproduction in winter, which improved the biotic potential of the population. In addition, a four-year cycle of population dynamics was revealed in which the growth phase lasted for two years.

Apparently, these trends in population dynamics are only characteristic of bank voles in the optimum of their species range, where population size and structure are mainly determined by endogenous density-dependent regulatory mechanisms (Zhigalski, 1992, 1994).

Table 4. Demographic characteristics of the bank vole population cycle

Month	Demographic parameter	Mean value for the cycle phase ±1 standard error			Significant differences or contrasts ($p < 0.05$)
		I Depression	III Growth;	IV Peak	
April	1. Population size (4.7/6.9)*	3.3 ± 1.00	5.1 ± 1.75	10.1 ± 1.40	IV from all others
	2. Percentage of reproductive females	65.4 ± 15.89	81.5 ± 13.77	72.7 ± 11.11	No
	3. Percentage of one- to two-month-old animals	0.0 –	10.1 ± 5.50	7.4 ± 6.01	I from (III + IV)**
	4. Percentage of three- to six-month-old animals	0.0 –	10.7 ± 7.28	4.6 ± 2.29	I from (III + IV)**
June	5. Population size (11.1/16.5)*	5.0 ± 1.08	16.2 ± 5.02	22.1 ± 4.95	I from all others***
	6. Percentage of reproductive females	75.4 ± 7.26	54.8 ± 10.93	30.8 ± 5.51	I–IV
	7. Percentage of nonreproductive males	9.1 ± 3.90	42.3 ± 8.59	68.7 ± 3.81	All
	8. Percentage of one- to two-month-old animals	63.2 ± 3.42	73.1 ± 4.91	69.1 ± 3.95	No
	9. Percentage of three- to six-month-old animals	0.0 –	5.3 ± 1.56	4.0 ± 2.17	I from (III + IV)**
August	10. Population size (21.4/27.8)*	11.9 ± 2.59	31.0 ± 7.03	32.5 ± 4.08	I from all others***
	11. Percentage of reproductive females	27.7 ± 7.19	20.8 ± 8.79	4.8 ± 2.75	I–IV, IV from (I + III)
	12. Percentage of nonreproductive males	79.9 ± 7.76	77.5 ± 7.00	95.3 ± 2.47	IV from (I + III)**
	13. Percentage of one- to two-month-old animals	78.0 ± 2.16	79.6 ± 4.28	87.9 ± 2.39	IV from (I + III)
	14. Percentage of three- to six-month-old animals	19.4 ± 2.25	12.4 ± 3.84	6.2 ± 1.27	I–IV
October	15. Population size (13.4/16.9)*	7.4 ± 2.10	19.1 ± 4.25	19.9 ± 3.77	I from all others***
	16. Percentage of reproductive females	16.2 ± 5.57	9.9 ± 3.33	6.3 ± 2.30	I–IV, $p < 0.1$
	17. Percentage of one- to two-month-old animals	87.2 ± 2.65	60.1 ± 13.19	23.0 ± 6.55	I–IV, IV from (I + III)**
	18. Percentage of three- to six-month-old animals	12.2 ± 2.55	37.7 ± 13.07	74.1 ± 6.53	I–IV, IV from (I + III)**
	19. Survival in winter, %	45.2 ± 8.75	54.1 ± 982	14.7 ± 2.37	I–IV, IV from (I + III)**
	Principal component 1	−0.99 ± 0.104	0.02 ± 0.365	0.96 ± 0.145	I–IV
	Canonical discriminant function 1	−4.73 ± 0.281	−0.27 ± 0.402	5.04 ± 0.510	All
	Number of years	6	7	6	

* Estimates of the intraspecific competition threshold and the population stationary state (animals/100 trap-days).
** The nonparametric Kruskal–Wallis test was used.
*** Logarithms of the parameters were compared.

ACKNOWLEDGMENTS

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