

Population Cycles and the Chitty Syndrome

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Abstract—Data are presented on the long-term population dynamics of small mammals (1982–2019) and variation in the body weight and length of the bank vole, a dominant species, in southern taiga forests of the Middle Urals. Spontaneous change in the pattern of dynamics observed in our previous study—transition from regular 3-year cycles to noncyclic regime—provided the possibility to estimate the influence of different factors on the Chitty effect (increase in body size at high population numbers) under different regimes. This effect was clearly manifested in the bank vole population with cyclic dynamics: the average body weight and length of the animals were greater at the phases of population growth and peak than at the trough (low) phase, while the same parameters of voles from the noncyclic regime had intermediate values. The body size of animals depends not so much on population density as on factors determining their physiological status (including reproductive status).

Keywords: small mammals, rodents, cyclic dynamics, bank vole, body weight and size, southern taiga, Middle Urals

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The cyclic pattern of long-term population dynamics in many animal species has been attracting attention over centuries. Lemming population outbreaks in Scandinavia were recorded as early as the 16th century [1], and illustrations of fluctuations in purchases of hare and lynx pelts in Canada in the 19th and 20th centuries have been included in ecological textbooks [2]. However, identification of mechanisms behind long-term population cycles—recurrent peaks and drops of animal numbers—is still an unsolved problem in population ecology [3–5].

Observations on small mammal population dynamics in boreal ecosystems are one of the sources of data for heated debates on the potential drivers of these cycles. This follows from the fact that there are consistent numbers of relevant publications and dozens of hypotheses proposed to explain these dynamics [6–8]. Some researchers relate fluctuations of animal abundance to abiotic (e.g., weather-climatic) environmental factors; others, to biotic factors (food supply, competition, stress, predation pressure, diseases) [9–14]. On the whole, it is considered that population dynamics depend on the combined effect of abiotic and biotic factors, but the relevant mechanisms have not yet been studied in detail.

In the mid-20th century, Dennis Chitty proposed the hypothesis that the population cycle is determined genetically [15, 16]. In the same period, he described the phenomenon of increase in the body weight and size of rodents at high population density, known as the Chitty effect. This finding was based on his previ-

ous observations on *Microtus agrestis* population in Montgomeryshire, Wales, and similar features were subsequently observed in other species from other regions [17–23]. Chitty hypothesized that populations of rodents at different stages of population cycle are subject to very rapid alternative selection for genotypes for either early or late sexual maturation, even though this idea was objected by David Lack, who supported the concept of trophic limitation [24], and criticized by geneticist, who emphasized that natural selection proceeds at a very low rate and cannot produce any significant effect on the ecological time scale.

Variation in many morphophysiological (exterior and interior) traits has also been comparatively studied in noncyclic populations of different species, in different habitats, and at different population numbers [20, 25, 26]. However, no studies have yet been performed on changes in body size traits in populations of the same species under different regimes of their dynamics. We have previously found the pattern of small mammal population dynamics may change spontaneously [27], which allows such a study to be performed. However, it is necessary to take into account the age and reproductive characteristics of animals to avoid the risk to confuse the consequences of substantial shift in the reproductive and age structure at different phases of population cycle with the Chitty effect, i.e., selection for different genotypes

The purpose of this study was to quantitatively evaluate the effects of relevant factors such as animal age, sex, reproductive status, population cycle phase,

and the pattern of population dynamics on body size in the bank vole.

MATERIAL AND METHODS

The study was based on the results of long-term observations (1982–2019) on the population dynamics of small mammals inhabiting primary fir–spruce forests of the Visim State Biosphere Reserve (southern dark conifer taiga, the Middle Urals; 57°22' N, 59°46' E, 538 m a.s.l.). Animal censuses were taken in permanent plots by the trap line method (with snap traps and wooden live traps) three times a year: in spring summer, and autumn. Beginning from 2004, winter censuses were also performed.

To analyze long-term population dynamics, our own data (1995–2019, 200 trap–days per round) and the results obtained by Yu.F. Marin in other areas of the reserve, at a distance of ≤ 14 km, in 1982 to 2006 (by 1000 trap–days in spring and autumn only). To extend the observation series, it was important to estimate congruence between the results of censuses taken by standard methods and the possibility of pooling several observation series into one. We estimated mismatch between the results obtained by two groups of researchers in censuses performed in parallel over 12 years (1995–2006). The results showed that the corresponding time series may be pooled together without any special correction, since their bias (in logit scale) relative to each other does not statistically differ from zero (0.25 ± 0.34 , 95% confidence interval (CI) = -0.44 to -0.95).

The bank vole (*Clethrionomys glareolus* Schreber, 1780) [28] dominated among small mammals inhabiting the study area, with its proportion in catches varying from 30 to 100% (median 70%), which allowed us to consider that the data on the dynamics of the total small mammal community are adequate for the dominant species. All bank voles trapped during our study (1995–2019, $n \leq 1834$) were examined to determine their sex, reproductive status, and type of ontogeny (maturing or immature in the year of birth).

Identification of reproductive status is important for murine rodents of the boreal zone characterized by bivariate ontogeny (a special case of polyvariant ontogeny), which provides for allocation of reproductive efforts in the population [29], with part of animals reaching maturity in the year of birth and the other part, in the next year after overwintering. One of the two variants (ontogenetic pathways) is implemented depending on the time of birth, the state of the population, and other factors [30].

Animal body weight and length (from the tip of the nose to the anus) were measured to accuracies of 0.1 g and 1 mm, respectively. The calendar age of voles was determined according to [31], with the accuracy of estimation (5–35 days) depending on animal age.

The results of measurements (body length and logarithm of body weight) were processed using generalized linear models GRM/GLM [32], which makes it possible to evaluate an effect of certain factor taking into account the effects of other factors: $Y = b_0 + \sum b_i X_i + \varepsilon$. Among a set of competitive models, the statistically optimal model was selected based on the minimum value of Mallows' C_p statistic, which is interpreted as effective dimension (see Supplement, Tables 1s, 2s). Predictors (X_i) included one continuous trait (the \log_{10} of calendar age in days) and up to six binary traits: sex, reproductive status, visually detectable pregnancy, ontogenetic pathway, and markers of population cycle phase or noncyclic regime. Phases of the population cycle—trough (low), growth, and peak—and noncyclic regime (NC) were parameterized either as a categorical factor with four levels or using k-1 binary variables (0 or 1) marking the corresponding phases. Since the animals could be classified by cycle phases at the time of either their trapping or their birth, the values of this factor for young of the year were identical, but for the overwintered animals there was a one-year lag. The collinearity of predictors was controlled by the value of Variance Inflation Factor ($VIF = 1/[1 - R^2(X_i, X_j)]$, $VIF \leq 3$ in all cases). It should be noted that winter censuses made it possible to avoid collinearity between the calendar age and reproductive status and the last not use as a predictor.

To visualize contrasts between mean values for different phases of the population cycle (Fig. 2), we used one-way ANOVA with a new dependent variable—residuals (deviations from the expected value) from the model of nonlinear growth or from the reduced model with all relevant predictors except the factor of interest (the phase and regime). Thus, we used several ways to statistically evaluate and remove particular effects of accessory factors (of no interest in this study) such as calendar age, ontogenetic pathway, etc. The most conservative assessment of the contrast “trough (low) vs. other years” was made based on censored data (only on overwintered animals) using nonparametric median X^2 (chi-square) and Kruskal–Wallis H tests. Statistical analysis was performed using software packages Statistica (StatSoft, Inc., 2001) [33] and PAST [34].

RESULTS AND DISCUSSION

Until 2006/2007, the long-term population dynamics of small mammals were characterized by simple 3-year cycles with strikingly regular sequence of three phases: trough, increase, and peak (Fig. 1). These phases differed from each other not only in the characteristic level of animal abundance but also in specific seasonal dynamics and reproductive age structure [35, 36]. For example, animal abundance in the years of population increase reached a maximum in autumn, while in the peak years this occurred in

Table 1. Parameters of best-fit regression models ($C_p = \min = 8.0$) for variation in bank vole body weight and size

Predictors, x_i	β	b	$se(b)$	$t(df^*)$	$p \leq$	Exp(b)	95% CI	
$\ln(\text{body weight, g}) = b_0 + \sum b_i x_i + \varepsilon; R = 0.84, F(7; 1145) = 384.6, MSR = 0.02$								
$\log_{10}(\text{age})$	0.58	0.42	0.020	21.43	0.001	1.52	1.46	1.58
Maturity	0.32	0.16	0.014	11.64	0.001	1.18	1.14	1.21
Ontogeny	0.20	0.13	0.017	7.27	0.001	1.14	1.10	1.17
Pregnancy	0.16	0.13	0.016	8.46	0.001	1.14	1.11	1.18
Trough	-0.16	-0.17	0.018	-9.45	0.001	1.19^{-1}	1.23^{-1}	1.15^{-1}
NC	-0.13	-0.08	0.010	-7.77	0.001	1.08^{-1}	1.11^{-1}	1.06^{-1}
Sex	0.05	0.02	0.009	2.66	0.008	1.02	1.01	1.04
b_0		2.07	0.040	51.91	0.001	7.95	7.35	8.59
$\text{Body length, mm} = b_0 + \sum b_i x_i + \varepsilon; R = 0.84, F(7; 968) = 319.3, MSR = 26.3$								
$\log_{10}(\text{age})$	0.47	12.1	0.735	16.54	0.001		10.7	13.6
Maturity	0.45	8.4	0.544	15.44	0.001		7.3	9.5
NC	-0.19	-3.9	0.389	-10.05	0.001		-4.7	-3.1
Trough	-0.15	-6.7	0.773	-8.61	0.001		-8.2	-5.1
Ontogeny	0.07	1.5	0.678	2.27	0.02		0.2	2.9
Pregnancy	0.06	2.0	0.652	3.11	0.002		0.7	3.3
Sex	0.05	0.9	0.357	2.45	0.01		0.2	1.6
b_0		67.7	1.500	45.15	0.001		64.8	70.6

Reference level b_0 refers to immature females (remaining immature in the year of birth) trapped at increase and peak phases; predictors are ranked by the absolute value of β coefficient; (*) degrees of freedom of t -statistic correspond to those of the denominator of F -statistic.

midsummer (Supplement, Fig. 1s). Moreover, the so-called Kalela–Koshkina effect [37, 38] was observed in the peak years; i.e., maturation of young of the year was suppressed at high density of overwintered animals in spring [35]. It is noteworthy that change in the pattern of dynamics was preceded by increase in the amplitude of changes in animal abundance in the late

1980s and an ascending trend of abundance in the 1990s and 2000–2005 (Fig. 1).

After 2006/2007, the dynamics with regular 3-year cycles acquired a different pattern characterized by “quasi-2-year” periodicity and more distinct seasonal component, and maturation of young of the year was no longer blocked in the peak years [39]. This allowed

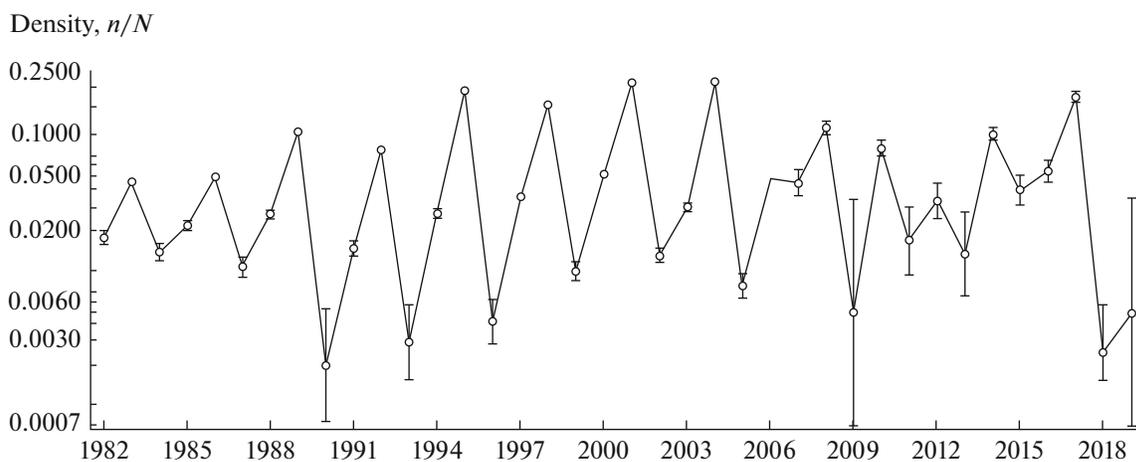


Fig. 1. Long-term dynamics of small mammal density index n/N (ind./trap day) on logit scale. Whiskers show 95% CI; years with noncyclic dynamics are underlined. Visim reserve, spring censuses (May 1982–2019).

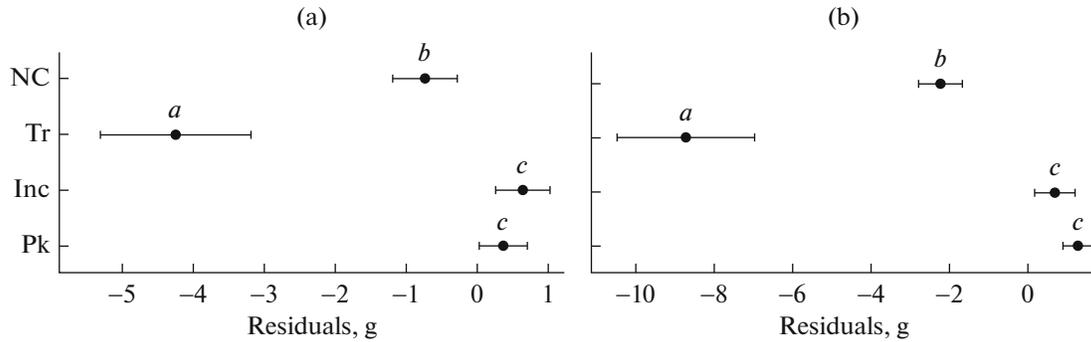


Fig. 2. Comparison of mean values of residuals from the nonlinear model of biphasic growth for (a) body weight and (b) body length of bank voles at phases of population trough (Tr), increase (Inc), and peak (Pk) and in noncyclic regime (NC). Bars show 95% CI; letters in italics (*a*, *b*, *c*) indicate statistically significant differences (Bonferroni test).

us to divide the entire observation series into two parts differing in the regime of dynamics [27] (Fig. 1; Supplement, Fig. 2s).

The Chitty effect in the bank vole was clearly manifested under conditions of cyclic dynamics: the average body weight of animals at the increase and peak phases was greater than at the trough phase by 1.9 g (95% CI, 0.1–3.7) and 4.2 g (2.4–6.0), and the respective differences in body length were 3.5 mm (0.1–7.1) and 8.3 mm (4.8–11.9). The same traits of voles from the noncyclic regime had intermediate values (Fig. 2), with a significant drop in the amplitude of fluctuations in the annual average values of body weight and length: $s_{1995-2006}^2/s_{2007-2019}^2$ (Bartlett's test $X^2(1)$: 27.5 and 6.2, respectively). Thus, variation in dimensional traits also reflects changes in the pattern of long-term population dynamics, but in the dimensions of exterior traits of animals.

Estimates of standardized (dimensionless) coefficients of regression (β_i) allow the magnitude of the effect of factor “cycle phase” (“Chitty effect”) to be collated with other factors, but it is more convenient for biological interpretation to use “natural” b_i coefficients. For example, *et ceteris paribus*, when predictor “logarithm of age” changes by unity, the body weight increases by a factor of 1.52 (95% CI, 1.46–1.58). The body weight of sexually mature voles is higher than in immature ones by a factor of 1.2 (1.14–1.21), and the weight of animals at the phase of depression is, on average, lower by a factor of 1.2 (1.15–1.23). Young of the year that reach maturity in the year of birth have a 14% (10–17%) “advantage” in body weight over those that remain immature, etc. (Table 1). Thus, we demonstrated conclusive statistical significance of the specific Chitty effect and compared its magnitude with factors of the physiological status of animals. A similar result was obtained when describing the body length of bank voles (Table 1).

The scatterplot of the body length and logarithm of body weight of overwintered voles (Fig. 3b) shows that

animals trapped at the trough phase (born at the peak phase) are characterized by below-median values of both body weight (\leq/\geq Me/Depression: 173/186/20/1, $X^2(1) = 17.6$ and $H(1, n = 380) = 22.75$, $p \leq 0.0001$) and body length (141/149/11/1, $X^2(1) = 8.54$ and $H(1, n = 302) = 18.9$, $p \leq 0.0001$). Voles with such parameters as well as larger ones were also observed at other phases of the cycle (in other years). It should be noted that senile animals and voles with a pathological deficit in body weight were not excluded from analysis (Fig. 3b, several points outside the confidence ellipsoid).

In our opinion, it would be more logical (at least in the case *Cl. glareolus*) to consider not so much the increase of animal body size at the peak phase (the Chitty effect per se) but rather its decrease at the trough phase, i.e., a kind of idiopathic dwarfism among overwintered voles (Fig. 3b). By analogy with medical symptomatic diagnostics that allows the patient's state to be determined, e.g., from the Kettle's body weight index, it appears that the term “syndrome” (a complex of symptoms) is preferable to “effect” as more adequate to the essence of the observed phenomenon.

Evaluating ontogenetic pathways for voles remaining immature in the year of birth, a dichotomy was revealed between the average pathways of animals born at the peak phase and animals trapped in other years (Fig. 3a). The observed picture may well reflect the results of “selection” (or an illusion of selection) for smaller mammals during wintering and in spring, upon transition from population peak to trough under conditions of maximum predation pressure, oligotrophic habitats (but with good protective conditions), higher energy expenditures for finding a mate at the extremely low population density during the trough phase, etc. As a result, we observe only subnormal individual pathways in the lower part of the “ontogenetic corridor” (Fig. 3a (insert), 3b).

Thus, our results appear to support the opinion of some authors that genetic mechanisms are superfluous for generating the Chitty effect [40, 41], since it

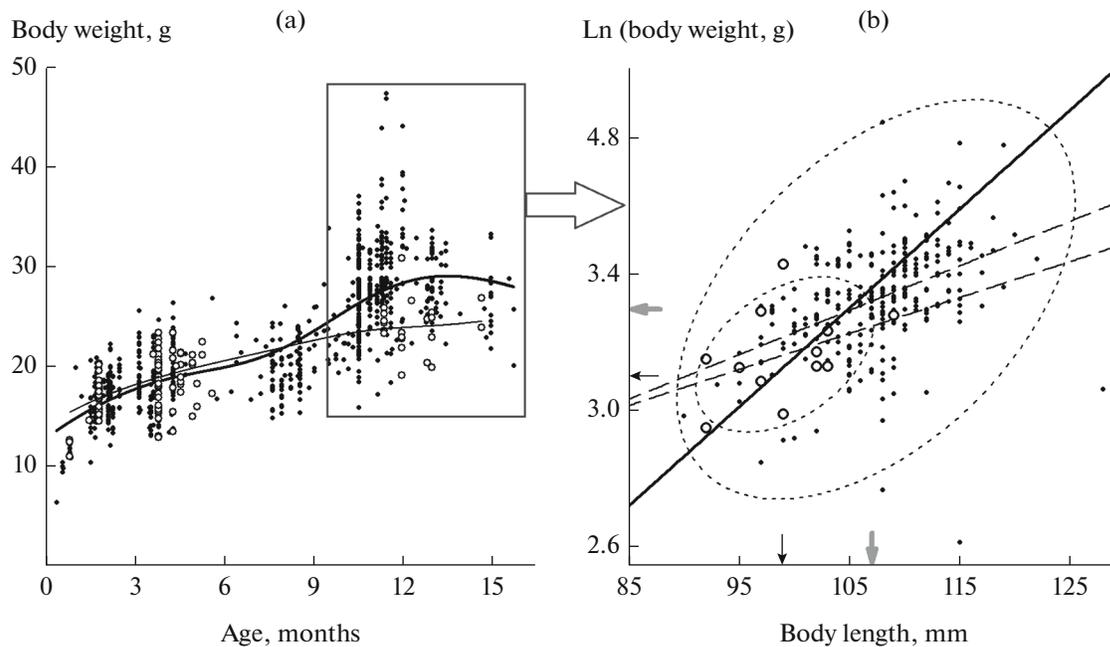


Fig. 3. Average and individual ontogenetic trajectories of bank voles remaining immature in the year of birth: (a) in “age–body weight” coordinates, (b) in projection onto the “body length–Ln(body weight)” plane (only for overwintered animals). Circles indicate animals trapped at the trough (low) phase (born at the peak phase); dots, animals trapped in other years. Key to panel (b): thick line, major axis regression (MAR): $y = 0.26 + 0.029x$; dashed lines, least squares regressions: circles, $y = 1.93 + 0.01x$; dots, $y = 2.12 + 0.01x$, $\Delta b_0 = 0.2 \pm 0.02$; ellipses, 95% PIs; gray arrows, total median; black arrows, trough phase.

can be easily and adequately explained in terms of normal ecological physiology. The Chitty syndrome may be interpreted as an ecophysiological phenomenon conditioned by variation in a number of factors during the population cycle, including population density, amount of stress, predation pressure, time of birth (photoperiod and maternal effect), habitat quality and trophic level, etc.

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COMPLIANCE WITH ETHICAL STANDARDS

Statement on the welfare of animals. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

Conflict of interest. The authors declare that they have no conflict of interest.

SUPPLEMENTARY INFORMATION

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