

# Relationships between the Individual Growth Rate and the Population Spatial Structure and Dynamics in Rodents

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The effects of the population density on individual animal growth, development, and reproduction has been extensively studied and reported in detail [1]. However, the existing explanations of these phenomena are incomplete and often inconsistent. The population dynamics of small rodents (especially at northern latitudes) exhibits large-amplitude oscillations called population cycles [2]. Their emergence is often attributed to the operation of intrapopulation mechanisms involved in the regulation of the rate of growth and maturation of young animals [3, 5]. In each population cycle, a short period of high abundance, or a peak, is followed by a long low-abundance period (depression), which, in view of the high fertility of small rodents, seems enigmatic [4]. Stress, lack of food and shelter, epizootics, and other factors are known to inhibit population growth [5]. However, the problem of population cycles remains a key problem of population ecology. The purpose of this study was twofold: (1) to clarify the relationship between the growth rate of young animals and the probability of meeting conspecifics; and (2) to develop a mathematical model to describe the obtained ecologic relationship in energy terms.

The most common method for studying natural rodent populations that allows researcher to derive a lot of diverse information is the mark–recapture technique in plots with regularly spaced traps. This technique was used to study a population of the bank vole *Clethrionomys glareolus* inhabiting Ural forests. We also analyzed the vole population data from the southern Urals kindly provided by G.V. Olenov. Capture sessions were carried out at intervals of four to seven weeks. Each capture session lasted for three to five days; traps were inspected twice a day. From weight gains of marked animals from session to session, the relative rate of their growth was estimated. The probability of meeting conspecifics was estimated from the area of home range overlap. The configurations of home ranges were estimated by the harmonic mean transformation method

from the coordinates of the points where marked animals were caught [6]. This method, along with the kernel one, is generally accepted as that most adequately assessing the patterns of home range use by individual animals [7].

Analysis of the data showed that the specific growth rate of young voles was maximum if the area of overlap of their home ranges with the home ranges of other animals was 5000 to 7000 m<sup>2</sup>. If the overlap area was smaller or larger, the specific rate was lower (Fig. 1).

According to the conservation laws, growth is the difference between matter and energy taken up with food and those expended on various activities [8].

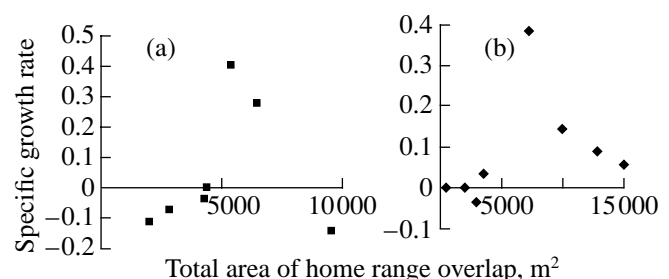
$$E_G = E_M - E_R, \quad (1)$$

where  $E_M$  is the metabolizable energy,  $E_R$  is the energy expenditure on daily living activities, and  $E_G$  is the energy of growth. Energy expenditures on daily living activities include the energy expended in interactions with conspecifics  $E_C$ :

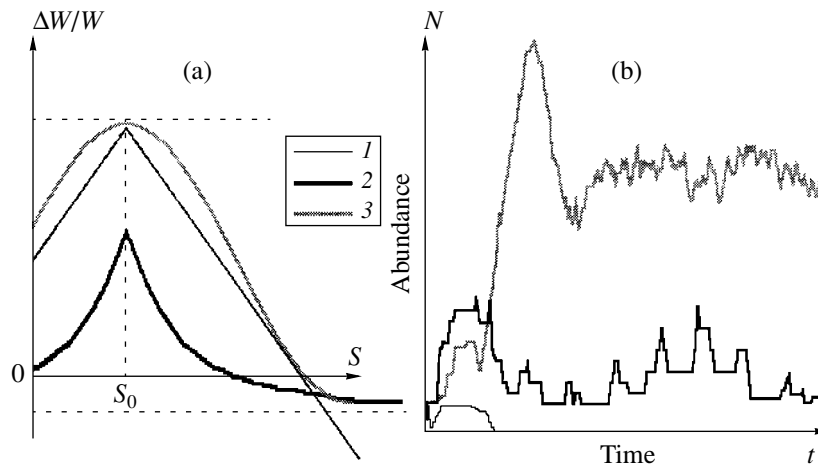
$$E_R = E_C + E_0, \quad (2)$$

where  $E_0$  is the energy expended in activities other than interactions with conspecifics. On the other hand, the metabolizable energy can be expressed as

$$E_M = E_P - E_C, \quad (3)$$



**Fig. 1.** Dependence of the specific growth rate of individual bank voles on the total area of overlap of their home ranges with home ranges of other animals: (a) May–July, 1989 (Central Urals); and (b) August–September, 1978 (Southern Urals).



**Fig. 2.** (a) Three types of the dependence of the specific growth rate of individual bank voles on the total area of overlap of their home ranges with home ranges of other animals and (b) the population dynamics calculated in the model for each of the three types: (1) linear dependence, (2) logistic dependence ( $\mu_0 \geq 1$ ), and (3) logistic dependence ( $\mu_0 \leq 1$ ).

where  $E_p$  is the energy that an animal would have expended on its growth (under the given conditions) had there been no interaction with conspecifics, and  $E_C$  is a fraction thereof that is either expended in interactions with conspecifics or wasted in search for them [9]. Hence, interactions between animals may affect the individual growth rate via a change either in the rate of energy intake or in the rate of energy expenditure.

Let  $S$  and  $S_0$  be the observed area and the optimal area of home range overlap, respectively; and let  $s = [(S - S_0)^2]^{0.5}$  be the absolute difference between them. Assuming that  $E_C$  linearly increases with  $s$ , we arrive at the linear relationship between  $E_G$  (or the specific growth rate) and  $s$ :

$$E_G = E_0 - cs, \quad (4)$$

where  $c$  is a proportionality coefficient, and  $E_0 = E_p - E_s$ .

The lower rates of energy intake by animals too frequently or too rarely interacting with conspecifics may result from their spending too much time of their daily budget on either interactions or search for contacts [9].

Energy expended on interactions is part of the metabolizable energy

$$E_C = \mu E_M. \quad (5)$$

Assume that the greater the coefficient  $\mu$  (and, hence, the  $E_C$ ), the higher the rate of its increase with an increase in  $s$ . If so,  $\mu$  is related to  $s$  exponentially:

$$\mu = \mu_0 e^{cs}, \quad (6)$$

where  $\mu_0$  is the  $\frac{E_C}{E_M}$  ratio for  $S$  within the optimum range ( $s = 0$ ). By definition,  $\mu_0$  can be interpreted as an optimum growth window; its width depends on the environmental conditions. Greater  $\mu_0$  values corre-

spond to worse environmental conditions and narrower ranges of overlaps favorable for growth of individuals. The coefficient  $c$  describes the strength of intrapopulation regulation of the individual growth rate. The relationship of the latter with  $s$  is described by an S-shaped (logistic) curve (Fig. 2a):

$$E_G = \frac{E_p}{(1 + \mu_0 e^{cs}) - E_R}. \quad (7)$$

To assess how this relationship affects the vole population dynamics, we constructed a simulation model and performed a series of computations using this model. In its construction, a number of simplifying assumptions were made, such as a fixed life span, onset of sexual maturity on attaining a certain body weight, fixed fertility, fixed intervals between consecutive parturitions, areas of overlaps within the optimum range, and the highest possible growth rate of individuals. Negative growth rates were assumed to be lethal. Based on the data on herbivores [10], the home range radius was taken to be proportional to the body weight of its host. Each home range was shifted toward or away from the mean center if the area of its overlap with other home ranges was smaller or larger than the lower or upper limit of optimum values, respectively. The initial conditions were body weights and distances between home range centers.

As can be seen from Fig. 2b, a group rapidly dies out if the growth rate linearly depends on the area of home range overlap. With an S-shaped dependence, we varied the optimal growth range. If it was narrow (large  $\mu_0$  values), large-amplitude population cycles fraught with demographic catastrophes were observed in the model. If it was broad (small  $\mu_0$  values), the population size stabilized at a relatively constant level (Fig. 2b). These results suggest that the same mechanisms of intrapopulation regulation of individual growth are responsible

for large- and small-amplitude population cycles. The narrower the optimal growth range, the larger the population cycle amplitude. Thus, the cyclic population dynamics and the cycle amplitude are determined by the shape of the dependence of the growth rate of young animals on the local population density, which, in turn, depends on the environmental conditions. Unfavorable environmental conditions enhance the population size cyclicality. The growth rate of young animals depends on the local population density nonmonotonically: at low densities, voles grow more slowly, prolonging the period of low abundance (the depression phase). In addition, the logistic model describing the relationship between the growth rate and the frequency of interaction among conspecifics does not contradict the data suggesting that there are two types of small rodent ontogeny [11].

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