===== **SHORT COMMUNICATIONS** =====

Density-Dependent Regulatory Mechanisms in the Sexual Maturation of Male Red-Backed Voles

O. A. Zhigalskii and V. P. Mamina

Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences,
ul. Vos'mogo Marta 202, Yekaterinburg, 620144 Russia
e-mail: zig@ipae.uran.ru
Received December 11, 2014

The modern concept for regulation of the abundance of mammals is based on the combined influence of two radically different processes: accidental and regular changes in the environmental conditions; regulatory mechanisms employing the feedback principle and striving to level these fluctuations. Accordingly, there are modifying (beyond the control of the population density) and regulatory (determined by the population density) ecological factors. The first group of factors can influence living organisms either directly or through changes in the biocenotic components. They only cause changes in the abundance level, while the regulatory factors maintain it at a particular level corresponding to abiotic environmental conditions. The regulatory density-dependent mechanisms are likely to transform the effect caused by external factors through changes in the spatiotemporal structure, thereby "balancing" the population and the environment (Zhigalskii, 2014). Population density can be controlled by direct changes in reproductive activity and mortality of animals or migration flows (Naumov, 1965; Zhigalskii and Bernstein, 1986; Zhigalskii, 2002; Rogovin and Moshkin, 2007; Elton, 1924; Wynne-Edwards, 1962; Ims and Andreassen, 2005).

The reproductive function of most mammalian species depends on their population density. The suppression of sexual maturation in young individuals and the decreased reproductive activity of adults takes place when the population density reaches its maximum level under the given conditions and can terminate the reproduction process. The reproductive abilities of males in regulating the population density are beyond the scope of researchers. At the same time, males contribute significantly to the fertilization process and embryonic losses (Mamina and Zhigalskii, 2009).

Previously, we demonstrated (Zhigalskii, 2011) that, depending on the stage in the seasonal reproduction cycle and population density, the proportion and number of young immature males in populations of *C. glareolus* living in the central and peripheral parts of the habitat differed in a statistically significant manner. In the population, which settled in the central part of the habitat (Udmurtia), the abundance of young immature males in June–July at different phases was as follows: low, 9.1; growth, 42.3; and peak, 68.7 individuals per 100 traps/day. A similar situation is observed in the population on the periphery of the habitat (Karelia). In July, the abundance of immature males during various phases of the population dynamics was 8.6, 20.2, and 36.7 inviduals per 100 traps/day, respectively. In August, these differences were even more significant: 18.9, 49.15, and 91.7 individuals per 100 traps/day. The decrease in the proportion of young individuals in the reproduction process accompanied by a high population density is mainly caused by the suppression of sexual maturation (Wynne-Edwards, 1962; Zhigalskii and Berstein, 1986). The sexual maturation of young males is determined by the duration of spermatogenesis (31.0 ± 0.7 days in *C. glareolus*) (Grocock and Clarke, 1976). Spermatogenesis includes four periods: (1) the multiplication period (mitotic division of spermatogonia); (2) the growth period (DNA replication); (3) the ripening period (meiosis); (4) the shaping period (early and late stages of spermatogenesis). Each spermatogenesis period corresponds to a particular level of sexual maturation. In recent studies, there are almost no data on density-dependent changes in the system of "spermatogenesis—sexual maturation" of animals in nature. This work presents the results of an analysis of separate spermatogenesis periods in immature underyearlings, which determine the degree of their sexual maturation at different levels of population abundance.

We studied immature males of *C. glareolus* trapped in the Middle Urals (Sverdlovsk oblast, Revda district) during April–September 1990–1995 (Karaseva et al., 2008). Based on the comprehensive demographic

Changes in weight of body, testicles, and diameter of testicular tubules in *C. glareolus* at different phases of abundance in the population

Phase of abundance	Body weight, g	Weight of testicles, g	Diameter of tubules, mm
Low	14.8 ± 1.50*	12.8 ± 0.80*	41.7 ± 6.5*
Growth	17.2 ± 2.30	35.0 ± 4.80	49.3 ± 6.01
Peak	16.4 ± 1.80	13.7 ± 0.90*	42.7 ± 5.8*

* Significant differences with phase of population growth ($p < 0.05$).

characteristics, 1990 and 1993 is the low abundance phase (2.45 ind. per 100 traps/day); 1991, 1994, and 1995 is the growth phase (4.34 ind. per 100 traps/day); and 1992 is the peak phase (9.31 ind. per 100 traps/day).

Analysis of the morphophysiological and morphometric characteristics of the testicles demonstrated a statistically significant ($p < 0.05$) decrease in weight and diameter of testicular tubules in the peak abundance phase compared to the growth phase. The low abundance phase is marked by a decrease in body weight, testicular weight, and diameter of testicular tubules (see table). In males with the diameter of testicular tubules up to 37 μm, spermatogenesis should be included in the multiplication period; up to 42 μm, growth; up to 50 μm, ripening; up to 60 μm, shaping of spermatozoids (early stage); up to 70 μm, maturation (late stage).

Each stage of abundance is characterized by a particular distribution of separate periods of spermatogenesis, all characterizing the degree of sexual maturation in animals (see figure). In the of low and peak abundance phases, up to 95% of immature voles are at the beginning of spermatogenesis. In the phase of

Occurrence of spermatogenesis periods

Occurrence of animals with different levels of sexual maturation (periods of spermatogenesis) in various phases of abundance of population. (*1–4*) Periods of spermatogenesis: (*1*) multiplication; (*2*) growth; (*3*) ripening; (*4*) shaping (early and late stages of spermatogenesis).

peak, spermatogenesis of only 5% of immature males reaches the stage of formation of spermatozoids, which are hardly able to take part in the process of reproduction. In the low abundance phase, spermatogenesis of 5% of immature males are at the ripening stage (see figure), i.e., in the earlier period of spermatogenesis compared to the peak phase; thus, males in the population exhibit suppressed sexual maturation. It is only in the growth phase that the majority of males reach a higher level of sexual maturation (the development of germ cells is at later stages of development), which allows them to become actively involved in the population growth process in the year of birth (see figure).

Changes in the distribution of spermatogenesis periods or degree of sexual maturation in different phases of abundance may be associated with physiological stress (intrapopulation pressing), leading to the suppression of sexual maturation in individuals. It is assumed that reduction in the rates of sexual maturation and suppression of reproduction result from the inhibition of gonadotropin secretion by the anterior lobe of the hypophysis during the period of active ACTH formation. In addition, the endocrine status of an animal and its reproductive potential are influenced by the demographic structure of the population, including the abundance in previous periods. Neuroendocrine mechanisms that decelerate population growth begin to develop at the growth stage, which is manifested in early differentiation of the hypothalamus–hypophysis–adrenal system. This, in turn, leads to hyperfunctioning of this system in the peak phase, as well as to a decrease in reproductive activity (Tkachev, 1980; Chernyavskii and Lazutkin, 2004). It is known that males develop some neuroendocrine complex, which further determines their reproductive potential, in the embryonic and early postnatal periods (Tkachev, 1980).

Therefore, the results indicate that the group of immature males is heterogeneous according to the degree of sexual maturation. The degree of polymorphism is associated with the phase of the population size. A similar pattern is observed in females (Zhigalskii and Berstein, 1986; Zhigalskii, 2011). For this reason, it can be said with a high probability that fluctuations in abundance taking place in different years are more associated with changes in the rates of sexual maturation in young voles than with an increase in the mortality rate of individuals in different sex and age groups. The results of the study also demonstrated that testicular weight cannot itself indicate the degree of sexual maturation in males and the phase of the abundance cycle of the population.
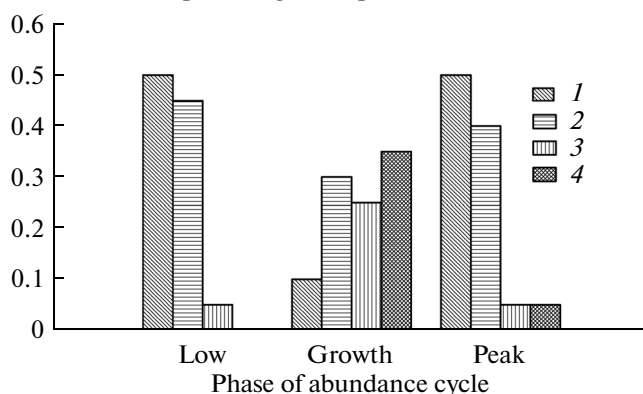
REFERENCES

Chernyavskii, F.B. and Lazutkin, A.N., *Tsikly lemmingov i polevok na Severe* (Population Cycles of Lemmings and Voles in the North), Magadan: Nauka, 2004.

Elton, C.S., Periodic fluctuations in the numbers of animals: Their causes and effects, *Br. J. Exp. Biol.*, 1924, vol. 2, pp. 119−163.

Grocock, C.A. and Clarke, J.R., Duration of spermatogenesis in the vole (*Microtus agrestis*) and bank vole (*Clethrionomys glareolus*), *J. Reprod. Fertil.*, 1976, vol. 47, pp. 133−135.

Ims, R.A. and Andreassen, H.P., Density-dependent dispersal and spatial population dynamics, *Proc. R. Soc. London B*, 2005, no. 272, pp. 913−918.

Karaseva, E.V., Telitsyna, A.Yu., and Zhigal'skii, O.A., *Metody izucheniya gryzunov v polevykh usloviyakh* (Methods for Field Studies on Rodents), Moscow: LKI, 2008.

Mamina, V.P. and Zhigal'skii, O.A., Reproductive losses in small mammals: The roles of females and males, *Dokl. Biol. Sci.*, 2009, vol. 425, pp. 164−166.

Naumov, N.P., Spatial features and mechanisms of population dynamics in terrestrial vertebrates, *Zh. Obshch. Biol.*, 1965, vol. 26, no. 6, pp. 625−633.

Rogovin, K.A. and Moshkin, M.P., Self-Regulation of Population Size in Mammals and Stress: Strokes to the Picture Painted Long Ago, *Zh. Obshch. Biol.*, 2007, vol. 68, no. 4, pp. 244−267.

Tkachev, A.V., Endocrine characteristics of lemming population cycle on Wrangel Island, in *Mekhanizmy regulyatsii chislennosti lemmingov i polevok na Krainem Severe: Mat-ly soveshch* (Mechanisms of Population Regulation in Lemmings and Voles in the Far North: Proc. Conf.), Vladivostok: Dal'nevost. Nauch. Tsentr Akad. Nauk, SSSR, 1980, pp. 119−126.

Wynne-Edwards, V.C., *Animal Dispersion in Relation to Social Behaviour*, Edinburgh: Oliver and Boyd, 1962.

Zhigal'skii, O.A., Analysis of small mammal population dynamics, *Zool. Zh.*, 2002, vol. 81, no. 9, pp. 1078−1106.

Zhigal'skii, O.A., Structure of the bank vole (*Myodes glareolus*) population cycles in the center and periphery of its distribution area, *Biol. Bull.* (Moscow), 2011, vol. 38, no. 6, pp. 629−641.

Zhigalski, O.A., Ecological mechanisms maintaining the demographic and spatial structure of small mammal populations, *Russ. J. Ecol.*, 2014, vol. 45, no. 5, pp. 441−444.

Zhigal'skii, O.A. and Bernshtein, A.D., Populyation factors regulating reproduction in the bank vole (*Clethrionomys glareolus* Schreb.), *Dokl. Akad. Nauk SSSR,* 1986, vol. 291, no. 1, pp. 250−252.

Translated by A. Karmazina