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Chapter 2

**EXTRINSIC AND INTRINSIC FACTORS
OF REGULATION OF REPRODUCTIVE POTENTIAL
IN THE WATER VOLE (*ARVICOLA AMPHIBIUS*)
POPULATION FROM WESTERN SIBERIA**

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ABSTRACT

The European water vole (*Arvicola amphibius*) dominates in rodent assemblies in Northern Baraba Lowland (Western Siberia) where its populations exhibit pronounced 4–9 year-long cyclic fluctuations in numbers. One of the principle peculiarities of water voles ecology in West Siberia is usage of different habitat sites during reproductive season and wintering. In summer they are aquatic and live and reproduce in wetlands, while in winter they are fossorial and live underground in meadows. The water vole has proved an excellent model species to investigate the role of both extrinsic and intrinsic mechanisms in driving population cycles. Using data from multi-annual study, we investigated the dependence of female's breeding success on extrinsic conditions influencing the availability of wet biotopes, food resources and intrinsic factors (density dependent). We also investigated the relation of winter survival to mass of food storage.

Abiotic factors have a direct influence on the availability of habitat-related resources. In summer, the main extrinsic factor influencing reproductive potential of the water vole is hydrological regime, i.e. variable water supply determining the area of suitable biotopes. Our analysis has revealed correlation between flow intensity of the Om River in the study area and population dynamics, average number of live embryos in overwintered females, and percentage of mature young-of-the-year females in different years of study. Female reproductive characteristics appeared to be sensitive to effects of both extrinsic (availability of suitable biotopes) and intrinsic (density) factors. It was found that

interaction of these factors determines the level of competition among reproductively active females as detected by number of injuries on skins and consequently embryonic losses and decline of population numbers.

In severe continental Siberian climate winter survival of voles depends on amount of food stores which, in turn, depends on population density influencing competition level. Participating of the young-of-the-year females in reproduction has effect on their winter survival. They stay in wet biotopes for late summer and have not enough time to gather necessary for safe wintering amount of food stores. Because of higher female winter mortality, sexual structure of the population in spring is unbalanced. This leads to high level of inter-male competition for receptive females and strong selection among overwintered males.

Thus, the obtained data indicate that in the water vole from Western Siberia the extrinsic and intrinsic factors closely interact both in summer and in winter regulating reproductive potential and density of the population.

INTRODUCTION

Regular cycles of animal numbers are well known in northern populations of lemmings and voles [Krebs & Myers 1974]. A central issue in population studies lies in determining the mechanisms of density regulation. Discussing causes, factors, and mechanisms of cyclic population dynamics, ecologists have not yet agreed upon the role of external factors in fulfillment of biological potential of populations [Duhamel *et al.* 2000, Krebs 2002, Zhigal'skii 2002, Rogovin & Moshkin 2007]. Because none of the more than 20 proposed hypotheses is sufficient to explain the cycles' phenomenon [Saucy & Gabriel 1998], it is obvious that in general a combination of factors acts to regulate population numbers [Lidicker 1999]. In practice, populations respond to both extrinsic factors such as climatic oscillations and habitat heterogeneity, and intrinsic factors such as density, sexual structure and behavioral tendencies. The effect of external factors is mediated through individual physiological and behavioral responses of individuals and manifests at the level of local reproductive groups in different ecological conditions. Individual and "family" heterogeneity facilitates maintaining homeostasis in a population. Nevertheless, in particular situations one or a few regulating factors may be considered determinative [Lidicker 1999].

Multi-annual oscillations of population number may be related to climatic cycles which are known in the Northern Hemisphere [Saucy & Gabriel 1998]. In Western Siberia, they develop first of all into cycles of humidity [Maksimov 1982]. The humid phase is characterised by low summer temperature, high precipitation, extended surface of water-filled wetlands and maximal river flow. The expansion of the water-bearing wetlands suitable for reproduction of water voles provides condition for the outbreaks of their "mass breeding" and increase in the numbers [Maksimov 1982].

Widespread in Eurasia, the European water vole (*Arvicola amphibius* (Linnaeus, 1758)) dominates in rodent assemblies in Northern Baraba Lowland (the forest-steppe zone of Western Siberia) where populations of this species exhibit pronounced regular cyclic fluctuations in numbers [Evsikov *et al.* 1997]. In the course of four- to nine-year cycles, their numbers changes drastically up to four orders of magnitude, comparing the maximal and minimal values [Rogov 1999]. In Western Siberia, water voles change their habitat sites twice during life cycle. In summer they are aquatic and live and reproduce in wetlands and along

banks of natural streams and artificial ditches, while in winter they are fossorial and live underground in meadows. Vast range, pronounced population dynamics, specific life style, and a huge body of accumulated data make the water a convenient model for solving theoretical problems of population ecology [Panteleyev 1971, 2001a, Maksimov 2001].

The first part of our work is aimed to determine how existing habitat hydrology affects intra-specific competition, reproduction, and population dynamics in the water vole, and differentiation of reproductive groups in density and demographic structure, i.e. structural and functional stability of the population of interest.

The aim of the second part of the present study was to test the hypothesis of winter food deficit as a possible cause for population decline and so as one of the main factors for cyclicity in Siberian water voles.

Since any biological system consists of interacting parts but functions as a unit in higher level context [Lidicker 1988], better understanding of population processes requires “looking in and looking out” of the system [Lidicker 1999]. We adopt this concept and try to “look in” – on different intrinsic demographic factors (density, the role of age/sex cohorts) and “look out” – on the interrelation of the population and its environment. We investigated the dependence of breeding success and survival on environmental conditions (water supply in summer and food availability in winter) and intrinsic effects in the water vole, using data from long-term study commenced in 1980 in Northern Baraba Lowland (vicinity of Lisii Norki village, Ubinskoye rayon, Novosibirsk oblast, 55°50' N, 80°00' E.).

POPULATION REGULATION IN REPRODUCTIVE SEASON

Material and Methods

Long-term hydro-meteorological data were obtained from State Institution “Novosibirsk Center for Hydrometeorology and Environmental Monitoring”. Since flow intensity of minor Baraba rivers can be an indicator of the humidity, or amount of water in the study area [Maksimov *et al.* 1979], we used data on summer total runoff and monthly, May through July, flow intensity of the Om River measured at the gauging station in Kreshchenskoye village, the nearest point to the study area. An index of area of watered biotopes was calculated from summer runoff raised to the power of 2/3.

Population numbers (voles/km²) were estimated in May and August every year [Rogov 1999, Rogov *et al.* 1999]. From these data we calculated the rate of population growth over the breeding season. Percentage of males in May indicated intensity of inter-male competition for reproductive resource. Percentage of females, taking into account the total population numbers allowed us to estimate female density per 1 km² of the studied area. Female density divided by the area index of watered biotopes indicated strength of inter-female competition for essential resources.

When studying the effect of local hydrology on the structure of reproductive settlements, we used data obtained in 1994, 1997, 1999, 2008, and 2009. Wetlands, characteristic habitats of the water vole, have seasonal and year-to-year hydrological fluctuations. In years of low water they may remain uninhabited by water voles. The banks of perennial water bodies, e.g.

lakes, streams, rivers, anabranches, and man-made channels, were inhabited by reproductive groups during breeding seasons in all study years [Panteleyev 1971]. To obtain comparable data for the entire study period, we trapped voles with “Kulunda” live traps [Barbash *et al.* 1971] set at 10 m intervals in local settlements along the banks of irrigation channels that had been built decades ago. The trapping was conducted at the peak of breeding season, mid May through early June.

Evsikov and co-workers [1999b] showed that with pronounced population waves in total numbers, the average density of breeding individuals in reproductive groups remains relatively stable, while the average density of populations varies annually. Nevertheless, the intra-annual variability of local densities allows their classification. Local density of the animals in the settlements was calculated as the number of reproductively active voles per 100 m of bank line [Plyusnin 1985, Plyusnin & Evsikov 1985, Evsikov *et al.* 1999b]. Each settlement was identified as “dense” if its numbers were higher than local mean annual density or “sparse” if its numbers were lower. Data on 318 individuals of 26 local populations were analyzed. Water depths measured at 0.5 m from the water edge perpendicular to the live traps were supplied with data on the amount of water at every settlement.

At autopsy, the captured animals and their internal organs were weighed, and animals’ reproductive status was determined. The voles were identified as either overwintered or young-of-the-year according to the external traits and reproductive organs. Female reproductive characteristics were estimated from the state of the uterus and ovaries. Embryo loss was calculated as the difference between the number of corpora lutea in the ovaries and live embryos in the uterus, divided by the number of corpora lutea. The number of injuries (wounds and scars) on the inner side of the skins in females and males served as measure of intensity of intra-specific aggressive interactions [Rose 1979, Plyusnin 1985].

Results and Discussion

Some authors supposed that the role of a “pace maker” of the population dynamics is played by changing amount of water in the habitat [Maksimov 1959, Evsikov & Moshkin 1994]. However the effect of varying hydrology on population structure has not been studied well.

Our analysis of the effect of total amount of water in the habitats on the population numbers revealed that May–August population growth correlates positively with the Om flow intensity in the study area in May ($r_{16} = +0.60$, $p < 0.01$), June ($r_{16} = +0.67$, $p < 0.01$), and July ($r_{16} = +0.47$, $p = 0.05$). This is evidence that reproduction rate is dependent on climate (habitat hydrological regime). Nevertheless, the multi-year data show that the numbers may continuously grow at different levels of humidity and may decline even at high humidity [Evsikov *et al.* 1999a]. Thus, Maksimov’s [1982] hypothesis alone cannot explain the cause of regular population crashes in this species. Explaining the causes of decline is important for understanding the phenomenon of cyclicity in species with high reproductive capacity

Water vole populations are known to be structured and consist of numerous local vole settlements in breeding season, which inhabit areas with heterogeneous biotic and abiotic conditions [Nikolaev *et al.* 1976, Evsikov *et al.* 1999b, 2001, Zav’yalov *et al.* 2007].

Reproduction in a population and maximum adaptation of water voles to considerable changes in land capacity are maintained through feedback in ethological and genetic-physiological mechanisms of animals' adaptive potential.

Density of reproducing individuals in local habitats correlates in all study years with the amount of water at the settlements estimated from average depths of the water bodies ($r_{24} = +0.83$, $p < 0.05$). The results are consistent with those obtained by Zav'yalov and co-workers [2007]. This work, however, gives data on one settlement studied in different years, whereas our data show variation among settlements with different amount of water. Similarly to larger rodents, the muskrat or the beaver, that occur in watered habitats too, and use water as a temporal refuge to hide from possible enemies and predators, the water vole also needs that water body be sufficiently deep near its nest during breeding season. Hence bottom shape and water level adjacent to a specific area determine how suitable and attractive this area is to the water vole.

According to the hypothesis proposed by Ostfeld [1985], the structure of spatial distribution of reproductive groups in voles is formed by breeding females. Female small rodents often are territorial; this is widely accepted to result from competition by females for resources [Ostfeld 1985, 1990, Ims 1987, 1988, Wolff 1993, Keesing & Ostfeld 1999]. Particularly, territoriality of females comprises defense of habitat-related resources: forage [Ostfeld 1985, 1990, Ims 1987], and/or nest sites to deter intra-specific infanticide [Wolff 1993, Wolff & Peterson 1998].

Breeding-season ranges of female water voles are small and non-overlapping, whereas ranges of males are larger, may overlap with each other and with the ranges of several females [Pelikán & Holisova 1969, Stoddart 1970]. To have enough resources, female water voles have to establish sufficient-sized territories within an available area [Stoddart 1970, Evsikov *et al.* 1997, Moorhouse & Macdonald 2005], which results in inter-female competition for more preferable, deeper parts of a water body along the bank line. The effect of habitat hydrological regime on a population's reproductive potential is produced therefore through inter-female competition for territory.

Our results have shown that the water supply determines the intensity of competition among females for the most preferable watered biotopes. The more females there are per a unit of watered area suitable for reproduction of the species, the more injuries are received in the aggressive competition ($r_{17} = +0.59$, $p = 0.007$; Fig. 1). Along with that, tougher competition for territories results in decreased reproductive output: the number of injuries in females correlates with embryo loss ($r_{17} = +0.73$, $p < 0.001$).

Population growth depends on fertility of overwintered females and rate of sexual maturity of young-of-the-year ones [Evsikov *et al.* 1999a]. Puberty is reached in the birth year by females that had been born before June, similar to other seasonally breeding rodents [Schwarz *et al.* 1964, Boonstra 1989; Nazarova & Evsikov 2007]. Data obtained showed that intensity of reproduction depends on the amount of water in a biotope: the more the territory is watered in May, the more young-of-the-year females are reproductively active (Fig. 2). Our data are in accordance with those of Moorhouse and co-workers [2008] showing that reduced maturation rates in female water voles are accounted by reduction of mean range size and limited availability of forage.

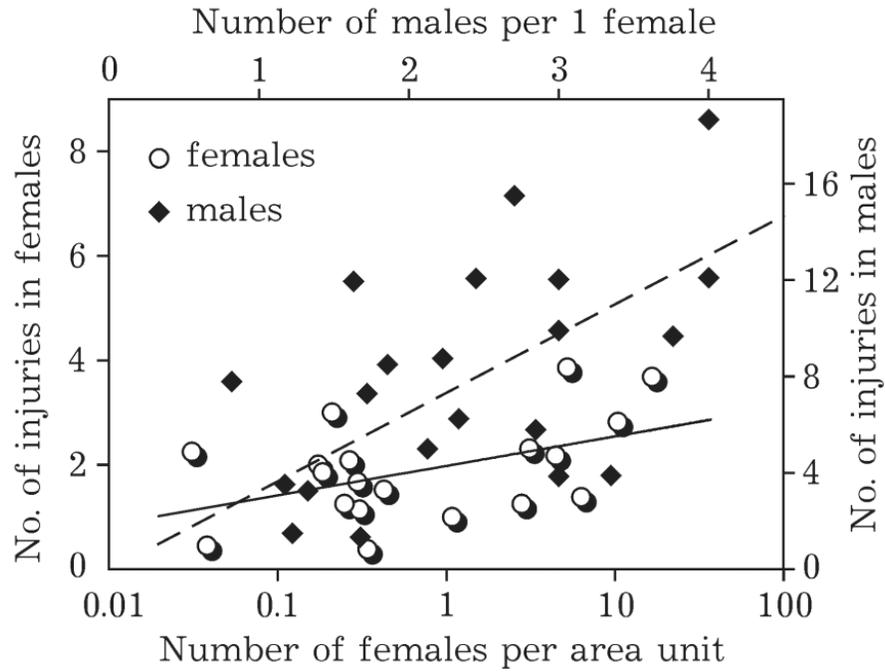


Figure 1. The dependence of the number of injuries on males' skins on the number of males per 1 female among overwintered animals. The dependence of the number of injuries on females' skins on the number of females per area unit of watered biotopes [Muzyka *et al.* 2010].

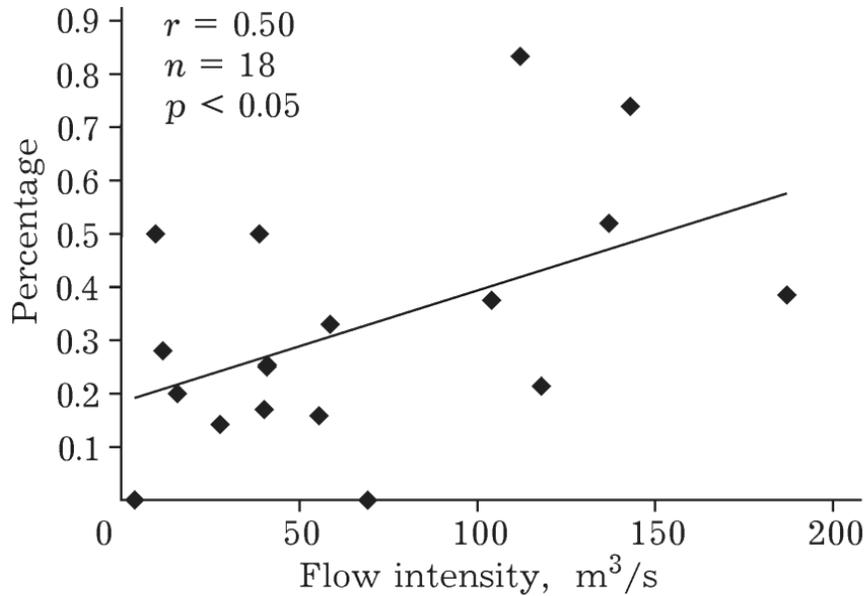


Figure 2. The effect of Om flow intensity in May on the percentage of mature young-of-the-year females [Muzyka *et al.* 2010].

When the local density of breeding voles increases, inter-male competition for females toughens, resulting in a greater number of aggressive contacts. According to Ostfeld [1985], males compete for “reproductive resource”: the number of injuries depends on intensity of the competition, i.e. on the number males per 1 female of reproductively active animals ($r_{19} = +0.53$, $p = 0.013$; Fig. 1). Competition results in a rigid hierarchy that maintains stable density in local reproductive settlements [Potapov & Muzyka 1994, Evsikov *et al.* 1999b]. Larger dominant males occupy areas closer to females and have breeding advantages [Evsikov *et al.* 1997].

When we studied local settlements, we obtained similar data. We found that the frequency of aggressive contacts, i.e. the number of injuries on overwintered males' skins, is affected by local density of breeding voles ($r_{27} = +0.63$, $p < 0.05$). The density determines the intensity of inter-male competition for reproductive females. Here, it was shown that the denser is the breeding segment within a settlement, the better is reproductive state of overwintered males. Mass of seminal vesicles correlates positively with settlement density ($r_{27} = +0.41$, $p < 0.05$). Taking into account that dominant males live closer to reproductive females and high-ranking males have better reproductive qualities [Evsikov *et al.* 1994, 1999b], one may reasonably assume that vesicle mass predicts male competitiveness and adaptive value.

The comparison of age-class structure of settlements with various densities of breeding individuals showed that the ratio of the young-of-the-year males per 1 overwintered female is higher in settlements with relatively low density than in those with high density (4.05 and 0.87, respectively).

This may be evidence of either of the following processes: (1) pregnant females move out of dense habitats to sparser ones before parturition to provide their expected young with essential resources [Stoddart 1970, Jeppsson 1986]; (2) the young-of-the-year are driven out of dense settlements by breeding individuals, as was assumed by Solomonov [1980], and settle in vacant areas or move to meadows and prepare for winter; (3) the young-of-the-year more frequently die in dense settlements.

Existing local settlements with low-density of breeding voles can support excessive numbers of non-breeding animals. If conditions are good for breeding, young-of-the-year females may breed in new areas, replacing overwintered ones who left these areas.

WINTER FACTORS OF POPULATION REGULATION

Material and Methods

To estimate the significance of food supply during winter for the population demography, we studied: (1) the burrow systems and the dynamics of foraging activity at different phases of the population cycles; (2) the inter-sexual differences of tunnel length and mass of food stores; (3) age differences in daily consumption of natural food in captivity; (4) the change of body mass during winter; (5) winter survival.

In different years, a total of 46 burrows were studied in September and 93 burrows in October (Table 1). We dug up the burrows and recorded the natural wet mass of food stores.

Table 1. Number of excavated burrows (Burr), the burrows with determined tunnel length (Tunn) and mass of food stores (Store) and number of captured water voles (Anim) in different years and months of the study [Potapov *et al.* 2004]

Year	Cycle phase	September				October			
		Burr	Tunn	Store	Anim	Burr	Tunn	Store	Anim
1986	Peak	10	10	10	10				
1987						10	7	10	5
1988	Decline	7	–	7	6	4	–	4	2
1990	Increase	2	2	2	2				
1991		1	1	1	–				
1992		9	9	–	–	8	7	8	6
1993		9	7	8	4	10	10	10	9
1994		8	4	4	8				
1995	Peak					26	26	26	20
1998	Increase					4	4	4	3
1999						21	21	21	20
2001						10	10	10	9
Sum		46	33	32	30	93	85	93	74

The majority of burrows were mapped and the tunnel length was measured. Usually, animals were caught by hand and their sex and age were recorded. Water voles are attached to their burrows and when they were not caught immediately, they often returned and were captured with traps. The voles can only get rhizomes from the upper soil layer before it freezes. To determine the length of time voles were feeding on their stored food, we used average multi-year dates of soil freezing down to a depth of 10 cm (15 November) and that of the appearance of thawed patches (17 April) when the voles are able to feed on the soil surface [Anonymous 1978].

Food consumption was studied in October 1999 and 2001. On the day of capture, 16 young-of-the-year and three overwintered voles in 1999 and nine young-of-the-year voles in 2001 were weighed and placed in a field vivarium in separate stainless steel meshed cages supplied with water and measuring 22 × 45 × 22 cm. In the vivarium room air temperature was maintained at +10 ± 3 °C. Each cage was provided with two blind plastic tubes 24 cm long with a square cross-section 8 × 8 cm. One of these tubes served as a shelter and it was supplied with nest material, while the other served as a pantry and it was supplied with weighed quantity of food storage (100–150 g). Both the nest and food were taken from the burrow of a given animal. To control for natural drying of food, one similarly prepared cage was left unoccupied. Every day all animals, nests and food remains in the tubes plus minor quantities on the cage bottoms were weighed. Then the tubes were reloaded with fresh nest material and food. The animals were kept under such conditions for two to seven days. The daily consumption of each animal was determined by calculating the mean difference in the mass of the food provided and the remaining food, considering its water loss. Obviously, the voles almost did not consume their nest material because its mass did not change appreciably in consecutive days. The nest mass was ignored later on.

To determine the mean body mass change during winter, the October and the next May samples of captured animals were used. Embryo mass was subtracted from the body mass of pregnant females.

To determine winter survival, ratios (%) between population densities defined by standard capture procedures with the use of “Kulunda” live-traps and pitfall grooves [Rogov 1999] in May and in the previous October were calculated. The density data were borrowed from Evsikov and co-workers [1999a] and augmented with additional data.

We carried out statistical analyses using ANOVA, Student’s test for independent samples, Mann-Whiney U-test, Pearson linear and Spearman rank correlations. Because distributions of the tunnel length (L, m) and food stores’ mass (S, kg) are asymmetrical [Airoldi 1976, Rogov *et al.* 2000], nearly normally distributed logarithms were used when computing parametric statistics: $\ln(100 \times L)$ for tunnel length and $\ln(S+1)$ for food stores (“one” was added to take stock of “zero” stores). To estimate the amount of stored food on 15 November (average date of soil freezing), we extrapolated it from a linear regression based on the September and October data. Means are given ± 1 SD. Statistical significance was considered at $p < 0.05$ level.

Results and Discussion

During autumn, young-of-the-year water voles move from wetlands to meadows and prepare for wintering by constructing a system of underground galleries and storing food (mainly rich roots and grass rhizomes) [Sasov 1965, Panteleyev 1971]. The size of food storage depends on the productivity of the habitats they occupy since both the structure of burrow systems and the quantity of food available depend on habitat richness, particularly, on abundance of plant biomass in the soil [Airoldi 1991, Rogov *et al.* 2000].

Usually water voles build individual burrows. During the study we found only two burrows shared by two voles, an overwintered female and a young male in both cases [Rogov *et al.* 2000]. The adult and subadult voles were caught in different parts of the burrows, which were connected by single paths. Because the individuals differed markedly by size in both cases, the burrows were divided to parts belonging likely to each of them according to the diameter of connecting tunnels.

The majority of tunnels are at a depth of 5–15 cm (from the ceiling to the ground surface). One-third of the October burrows had one or two deep (30–115 cm) tunnels, 1–5 m long, and terminated by an enlarged chamber with a dry and well-developed nest inside (in 75 % of the deep tunnels). The absence of deep tunnels or the lack of nests in the other burrows corresponds probably to incomplete constructions by mid October. Cavities with food stores were dispersed throughout the burrow and consisted of unenlarged blind passages densely packed with roots and rhizomes of meadow plants.

The average length of burrow systems was 18.2 ± 11.9 m ($n = 33$) in mid September and 41.0 ± 28.5 m ($n = 85$) in mid October. The tunnel length was significantly different between the peak and increase phases of population density both in September (11.9 ± 11.0 m, $n = 10$ and 21.0 ± 11.4 m, $n = 23$, respectively; Student’s test for log data: $t_{31} = 2.82$, $p = 0.008$) and October (23.6 ± 13.3 m, $n = 33$ and 52.0 ± 30.2 m, $n = 52$; Student’s test for log data: $t_{83} = 5.56$, $p < 0.001$).

Seasonal changes in food stores show that water voles begin gathering food in early September (Fig. 3). By mid September the food stores weighed on average 0.27 ± 0.56 kg ($n = 32$), and there were no marked differences between the phases (peak, decline and increase) of population density (respectively: 0.01 ± 0.03 kg, $n = 10$, 0.25 ± 0.15 kg, $n = 7$

and 0.45 ± 0.77 kg, $n = 15$; ANOVA for log data: $F_{2,29} = 3.29$, $p = 0.052$). In about 40 % of burrows no stores were found in September. By mid October the mean mass of the food stores per burrow reached 3.0 ± 2.6 kg ($n = 93$). Overall, there was a significant difference among the density phases (peak: 1.9 ± 2.4 kg, $n = 36$; decline: 2.0 ± 1.5 kg, $n = 4$; increase: 3.8 ± 2.4 kg, $n = 53$; ANOVA for log data: $F_{2,90} = 11.67$, $p < 0.001$). However, only the difference between the increase phase and the peak phase was statistically significant (LSD test: $p < 0.001$). The peak and the decline phases did not differ (LSD test: $p = 0.49$) and they were combined for further consideration. Thus food stores in October were 1.9 ± 2.3 kg ($n = 40$) during years of population peak and decline combined, and they were twice as high during years of increase (Student's test for log data: $t_{91} = 4.80$, $p < 0.001$). The linear extrapolation shows that by the date of soil freezing food stores may reach on average 3.4 kg at the peak and decline phases and 7.0 kg at the increase phase (Fig. 3). In October, we only caught seven voles that had overwintered previously. They had rather small stores (1.9 ± 1.8 kg, $n = 7$) compared to those of young voles (3.3 ± 2.7 kg, $n = 67$; two-way ANOVA for log data: "AGE" – $F_{1,70} = 4.85$, $p = 0.031$; "PHASE" – $F_{1,70} = 12.96$, $p < 0.001$; "AGE×PHASE" – $F_{1,70} = 1.13$, $p = 0.29$).

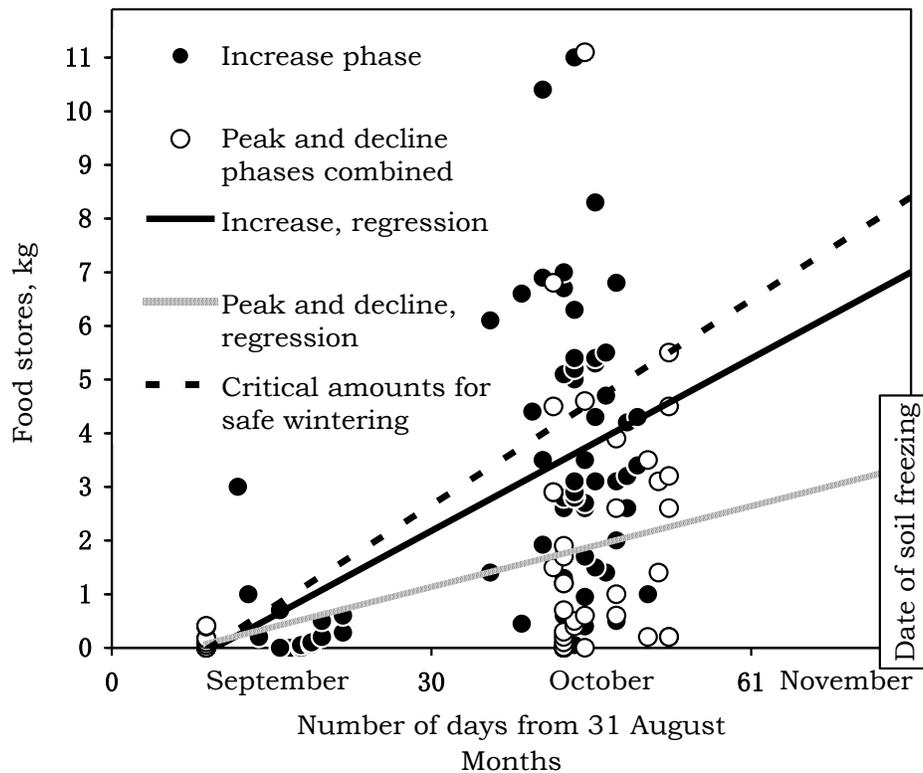


Figure 3. The mass of food stores per individual burrow at different phases of the population cycle and the linear regression of food stores (FS) on the number of days from 31 August ($D = 0$). The equations of linear regressions look as follows. Increase phase: $FS = -1.0 + 0.11 \times D$; $n = 68$, $r = 0.48$, $p = 0.0005$. Peak and decline phases combined: $FS = -0.4 + 0.05 \times D$; $n = 57$, $r = 0.41$, $p = 0.001$. Critical amounts for safe wintering (see text): $FS = -1.2 + 0.13 \times D$ [Potapov *et al.* 2004].

When feeding animals with natural food in captivity, the daily consumption was 57.3 % of the body mass or 54.7 ± 8.0 g ($n = 25$) in the young-of-the-year voles and 42.0 % or 68.3 ± 9.3 g ($n = 3$) in the overwintered ones. Although the overwintered voles consumed less per g of body mass (ANOVA: $F_{1,26} = 4.70$, $p = 0.04$), their absolute consumption exceeded that of the young (ANOVA: $F_{1,26} = 7.45$, $p = 0.01$). It was found that the absolute daily consumption positively depended on body mass (Pearson linear correlation: $r_{27} = +0.48$, $p < 0.01$), while the relative one depended on body mass negatively (Pearson linear correlation: $r_{27} = -0.72$, $p < 0.001$). The estimations of the experimentally defined levels of consumption (54.7 g per day in young voles) show that the critical value of food stores necessary during the under-snow period (153 days) is at least 8.4 kg in mid November. Assuming a linear rate of storage accumulation (starting on 10 September), voles should have about 4.5 kg of food in their burrows by mid October (Fig. 3). Only a small fraction of individuals had sufficient food supply.

Both tunnel length and mass of food stores in mid October were greater in young males than in females: 49.8 ± 29.1 m, $n = 39$ vs. 33.2 ± 26.8 m, $n = 26$ (two-way ANOVA for log data: “SEX” – $F_{1,61} = 10.90$, $p = 0.002$; “PHASE” – $F_{1,61} = 21.77$, $p < 0.001$; “SEX×PHASE” – $F_{1,61} = 2.43$, $p = 0.12$) and 3.9 ± 2.9 kg, $n = 41$ vs. 2.3 ± 1.9 kg, $n = 26$ (two-way ANOVA for log data: “SEX” – $F_{1,63} = 6.99$, $p = 0.01$; “PHASE” – $F_{1,63} = 19.78$, $p < 0.001$; “SEX×PHASE” – $F_{1,63} = 1.66$, $p = 0.20$).

The body mass in May of overwintered voles did not correlate with the previous October body mass (Spearman rank correlations: $r_s = +0.02$, $n = 8$, $p = 0.96$ in males and $r_s = -0.05$, $n = 8$, $p = 0.91$ in females). At the same time, the winter body mass change correlated with the average October food store both in males and females (Spearman rank correlations: $r_s = +0.74$, $n = 8$, $p = 0.035$ and $r_s = +0.82$, $n = 7$, $p = 0.023$, respectively; Fig. 4).

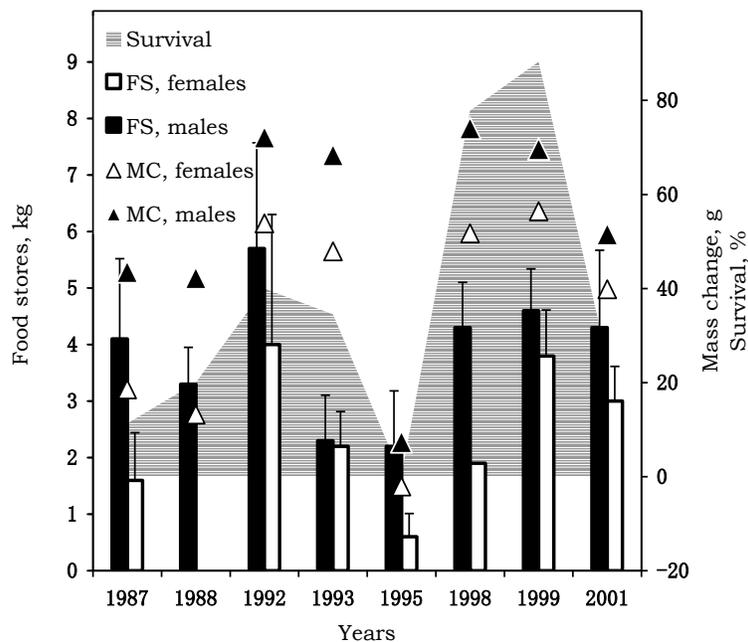


Figure 4. Food stores in October (FS), changes in body mass (MC) and survival during the subsequent winters. Bars represent SE [Potapov *et al.* 2004].

Winter survival of water voles varied widely among the years of our study (Fig. 4). The density phases differed by the survival: peak and decline combined - $10.5 \pm 9.9\%$, $n = 3$; increase - $53.1 \pm 28.1\%$, $n = 5$ (ANOVA: $F_{1,6} = 6.10$, $p < 0.05$). The winter survival correlated with the mean size of food stores (Spearman rank correlation: $r_s = +0.86$, $n = 8$, $p = 0.007$). Also, the survival correlated with the winter body mass change both in males and females (Spearman rank correlations: $r_s = +0.95$, $n = 8$, $p = 0.0003$ and $r_s = +0.90$, $n = 8$, $p = 0.002$, respectively). Thus, one of the possible causes for the decline in numbers of water vole populations may be increased winter mortality which results from winter food deficit [Evsikov *et al.* 1995, 2001, Evsikov & Ovchinnikova 1999, Rogov *et al.* 2000, 2003, Potapov *et al.* 2004]. During the phase of high vole density, the biomass of the underground parts of vegetation in meadow habitats decreases three times or more, and its recovery then takes at least three years [Evsikov & Ovchinnikova 1999, Evsikov *et al.* 2001]. The intensive exploitation of food resources, leading to their depletion at high population density is also considered a cause for population crashes in the fossorial water voles, *A. scherman*, from Switzerland [Airoidi 1991]. Furthermore, long-term data indicate that in Western Siberia the mortality among females from birth to the beginning of the next-year reproductive season is three times greater than in males. The maximal losses occur during winter [Rogov *et al.* 1999], which is a critical period in the life history of female water voles.

The data on burrow systems of water voles are still fragmentary [Panteleyev 1971, 2001a, Mesch 1984], except for those of the fossorial form, *A. scherman*, studied by Airoidi [1976, 1991, 1992]. The average length of burrow systems we obtained is lower than that for the fossorial voles from Switzerland [Airoidi 1976]. Nevertheless, the values per individual vole are comparable taking into account that the majority of the burrows in the fossorial voles are inhabited not by solitary voles but by adult pairs or by females with young [Airoidi 1976, 1991, Saucy 2001]. Moreover, a burrow system in a terrarium has been shown to be longer when inhabited by a couple [Airoidi 1992]. In the fossorial voles, winter breeding was recorded and could be responsible for population outbreaks [Meylan & Airoidi 1975]; this never has been documented in the aquatic voles from Siberia [Sasov 1965, Panteleyev 1971].

The foraging activity of water voles at the beginning of winter in Siberia is still poorly known. It was reported that in Western Siberia food stores in burrows amounted to 0.5 kg, the biggest one reaching 3.8 kg [Sasov 1965]. These data are close to those (0.2 to 4.0 kg) of Mesch [1984]. In the centre of European Russia the stores amount to only 0.2 kg on average [Panteleyev 1971]. On the other hand, they are of great importance for winter survival of water voles in Yakutia and average 2.8 kg. In some fertile sites such as lakeshores or potato fields they can even reach 18–30 kg per burrow [Solomonov 1980]. Our results indicate that water voles in Western Siberia accumulate rather large food reserves in their burrows by mid October, comparable to those in Yakutia. Nevertheless, the estimation of food consumption in the vivarium shows that animals could face a food deficit during winter.

Our data on food consumption are the first obtained from feeding water voles on their natural winter stores. According to Alekseyeva and co-workers [1959], the daily consumption of edible roots and juicy grasses by water voles in different seasons is 76–91 g or 50–75 % of the vole's body mass. When feeding separately on grasses or vegetables, voles consumed about 59 g or 80 % of body mass [Drozd *et al.* 1971]. Voles weighing 100 g consumed about 85 g of succulent feed per day [Mesch 1984]. The revealed dependence of daily consumption on animals' age and/or body mass is very close to that reported by Panteleyev [2001b]. According to the calculated critical amounts of winter feed, almost all overwintered animals

had insufficient food stores for a safe second overwintering. Moreover, their relatively high daily consumption would not allow surviving a second winter. Among the young, only 15% have sufficient stores during peak and decline phases and less than 50% during the years of increasing numbers [Rogov *et al.* 2000]. Indeed, these figures are very close to those on winter survival during different phases of population dynamics.

In Siberia, contrary to the European part of the range [Mesch 1984], water voles cannot get rhizomes from frozen soil. During the five months from the date of soil freezing to the first thaw, they have to feed on their stores. Of course, these dates may vary from year to year and a decrease in metabolic rate and food consumption may occur in winter. However, Panteleyev [2001b], who kept captive voles on juicy roots throughout winter, showed that their food consumption was rather stable and only depended negatively on air temperature, which, in its turn, was stable in shelters. In any case, the correlations between the food stores, the change in body mass and survival during winter demonstrates the dependency of animals' welfare on their forage activity in autumn. The voles may additionally feed on withered plants and green sprouts under the snow cover [Sasov 1965]. However, the poor nutritional quality of last year's vegetation and the small quantity of sprouts limit such possibility.

The quantity of stored food may be dependent both on its availability in the soil [Rogov *et al.* 2000] and on the density of wintering voles. Indeed, the situation is aggravated during peaks in population numbers, when habitats lack sufficient amounts of root biomass to feed all the voles adequately [Evsikov & Ovchinnikova 1999, Evsikov *et al.* 2001]. Furthermore, the high density of voles and consequently that of their burrows in the occupied habitats increases the risk that hungry neighbours will compete with each other for forage [Panteleyev 2001a]. The depletion of the food supply at the peak probably determines the prolonged effect of winter under-nourishment for subsequent years, thus being one of the reasons for the deepening of the population decline [Airoldi 1991, Evsikov & Ovchinnikova 1999, Evsikov *et al.* 2001].

The females are those which strongly suffer from the winter food deficiency because they do not manage to prepare adequately for wintering. It is the most important demographic factor, determining high female mortality in winter, greatly exceeding that in males. In May the number of overwintered males is almost always twice or more as high as those of females [Rogov *et al.* 1999]. The loss of 2/3 of the females during winter leads to a decrease in the reproductive potential of water vole populations. As a result, the increase phase, despite the pronounced r-strategy of the species, stretches for three to six years. Analysis of the multi-year data shows that the duration of the whole population cycle of water voles in Siberia varies from four to nine years [Rogov 1999], and it is longer on average than that in most other vole species [Krebs & Myers 1974].

Thus, the conditions of winter food availability are rather severe, especially during the peak and decline of numbers in populations of the water vole from Siberia. Over-exploitation of under-ground phytomass reserves at the peak keeps the situation critical during one or two subsequent years. It is slightly better in meadows with restored fertility, but during years of density increase, about half of animals still suffer from food deficit. The data presented suggest that the winter food deficit is a real factor affecting dynamics of numbers, sexual and age structures, and reproductive potential in the water vole population in Western Siberia.

CONCLUSION

The water vole has proved a convenient species to investigate the role of both extrinsic and intrinsic mechanisms in driving population cycles. Both in reproductive season and in winter well-being of water voles strongly depends on climatic conditions having a direct influence on the availability of resources and the carrying capacity of the environment. In summer, the main extrinsic factor influencing realization of reproductive potential of the water vole is hydrological regime, i.e. variable water supply determining the area of suitable biotopes.

The level of the water vole population reproductive output, estimated by ratio of autumn to spring population numbers, correlates with hydrological fluctuations in summer reflecting the availability of suitable habitats. Taking in account the extremely high amplitude of inter-annual numbers fluctuations in the water vole, the extrinsic conditions interact with intrinsic factors such as density predetermining a level of competition for the limiting resources. At different population numbers and flooding levels, habitats vary in attractiveness and suitability for the animals. As a result, the intensity of intra-specific competition naturally varies with habitat heterogeneity. It is possible to state that the amount of water at breeding sites in Northern Baraba Lowland affects local density of the breeding animals and rate of population growth.

It was found that the most variable characteristics determining reproductive output of the population are a portion of participating in breeding young-of-the-year females and a rate of embryonic losses during pregnancy. These characteristics appeared to be essentially sensitive to effects of both extrinsic (availability of suitable biotopes) and intrinsic (density) factors. The interaction of these factors determines the level of competition among reproductively active females as detected by number of injuries on skins and consequently embryonic losses and reproductive output of the population.

The data obtained indicate that climate (habitat hydrological regime) affects individual qualities (reproductive characteristics, aggression) of animals and results in differentiation of reproductive groups in density and demographic structure. Land capacity directly depends upon the amount of water in the biotope. In turn, local settlements with different densities provide a "reserve" of reproductive individuals to maintain population homeostasis.

Participating of the young-of the-year females in reproduction has its effect on their winter survival. They stay in summer biotopes and have not enough time to gather necessary for safe wintering amount of food stores. Indeed, Siberian climate is severe continental, with long and cold winter. This fact is responsible for the dependence of winter survival of voles on amount of gathered beforehand food stores which, in its turn, depends on density influencing competition level. Because of higher female winter mortality, sexual structure of the population in spring is unbalanced. This leads to high level of inter-male competition for receptive females and strong selection among overwintered males.

During the multi-year study of wintering burrows of water voles in Western Siberia it was found out that the size of food stores are smaller at the peak and the decline phases of the population cycle compared to that at the increase. Females have smaller stores compared to males. Comparison of the mass of stores in burrows and the daily consumption of natural foods indicates that only a small fraction of individuals have sufficient food supply for safe

wintering. In support, it is shown that the size of food stores in October affects both winter change in body mass and winter survival. Our results support the hypothesis of winter food deficit as a cause of population decline.

Thus, the obtained data indicate that in the water vole from Western Siberia the extrinsic and intrinsic factors closely interact regulating reproductive potential and density of the population and affecting competition level, efficiency of natural selection and formation of demographic structure.

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