

The effect of winter food stores on body mass and winter survival of water voles, *Arvicola terrestris*, in Western Siberia: the implications for population dynamics

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A b s t r a c t. The study was performed to test the hypothesis that winter food deficit can act to reduce a water vole, *Arvicola terrestris*, population in Western Siberia. During 12 years, a total of 139 wintering burrows were examined at different phases of population cycles. The size of food stores was found to be greater during increases of the population compared to that at the peak and the decline. Comparison of the mass of stores in burrows and the daily consumption of natural foods under controlled conditions shows that only a small fraction of individuals have sufficient food supply for safe wintering. Females have smaller stores compared to males, and this is possibly responsible for their higher winter mortality. The size of food stores in October affects both winter change in body mass as defined by difference between average mass in samples of animals captured in October and in May of the next year and winter survival determined as a ratio between population densities in May and October. The deficiency of food during winter is likely to be a strong factor affecting body mass change, density, sexual and age structures, and reproductive potential in the water vole population in Western Siberia.

Key words: burrow system, food consumption, population cycles

Introduction

The aquatic form of the water vole, *Arvicola terrestris* L., is known to exhibit marked cycles in the forest-steppe zone of Western Siberia (E v s i k o v 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 (R o g o v 1999). Regular cycles of animal numbers are well known in northern populations of lemmings and voles (K r e b s & M y e r s 1974). Because none of the more than 20 proposed hypotheses is sufficient to explain the cycles' phenomenon (S a u c y & G a b r i e l 1998), it is obvious that in general a combination of factors acts to regulate population numbers (L i d i c k e r 1999). Nevertheless, in particular situations one or a few regulating factors may be considered determinative (ibid.).

Climatic cycles are known in the Northern Hemisphere (S a u c y & G a b r i e l 1998). In Western Siberia, they develop first of all into cycles of humidity, which are considered a possible cause for the outbreaks of "mass reproduction" in the water vole (M a k s i m o v 1982). The humid phase is characterised by low summer temperature, high precipitation, extended surface of water-filled bogs and maximal river flow. The expansion of the water-bearing wetlands suitable for reproduction provides condition for an increase in the numbers of voles (ibid.). Nevertheless, the multiyear data show that the numbers may continuously

grow at different levels of humidity and may decline even at high humidity (E v s i k o v et al. 1999). Thus, M a k s i m o v ' 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.

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 (E v s i k o v et al. 1995, 2001, E v s i k o v & O v c h i n n i k o v a 1999, R o g o v et al. 2003). 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) (S a s o v 1965, P a n t e l e y e v 1968). 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 (E v s i k o v & O v c h i n n i k o v a 1999, E v s i k o v 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. t. scherman*, from Switzerland (A i r o l d i 1991). The voles are dependent 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 (A i r o l d i 1991, R o g o v et al. 2000). 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 (R o g o v et al. 1999), which is a critical period in the life history of female water voles.

The aim of the present study was to test the hypothesis of winter food deficit as a possible cause for population decline and so as the main factor for cyclicity in Siberian water voles. Since any biological system consists of interacting parts but functions as a unit in higher level context (L i d i c k e r 1988), better understanding of population processes requires “looking in and looking out” of the system (L i d i c k e r 1999). We adopt this concept and try to “look in” – on the role of different age/sex cohorts and “look out” – on the interrelation of the population and its environment. 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 intersexual 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.

Material and Methods

The material was collected in the vicinity of Lisii Norki village in the north of Novosibirsk region (55°50'N, 80°00'E) at different phases of the population cycles (E v s i k o v et al. 1999 augmented with three years of additional data): peak (1986–87, 1995), decline (1988), and increase (1990–94, 1998–99, 2001). A total of 46 burrows were studied in September and 93 burrows in October (Table 1). During the study we found only two burrows shared by two voles, an overwintered female and a young male in both cases (R o g o v 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 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 multiyear 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 (A n o n y m o u s 1978).

We dug up the burrows and recorded the natural wet mass of food stores. The majority of burrows were mapped and the tunnel length was measured (Table 1). 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.

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.

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

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 weight 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 live-traps and pitfall grooves (R o g o v 1999) in May and in the previous October were calculated. The density data were borrowed from E v s i k o v et al. (1999) and augmented with three years of additional data.

We carried out statistical analyses using ANOVA, Student's test for independent samples, Mann-Whitney U-test, Pearson linear and Spearman rank correlations. Because distributions of the tunnel length (L, m) and food stores' mass (S, kg) are asymmetrical (A i r o l d i 1976, R o g o v et al. 2000), nearly normally distributed logarithms were used when computing parametric statistics: $\ln(100L)$ 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 \pm 1 SD. Statistical significance was considered at $p < 0.05$ level.

Results

Usually water voles build individual burrows. We found only two shared by two voles. 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. 1). 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. 1). 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 \times PHASE" – $F_{1,70}=1.13$, $p=0.29$).

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. 1). Only a small fraction of individuals had sufficient food supply.

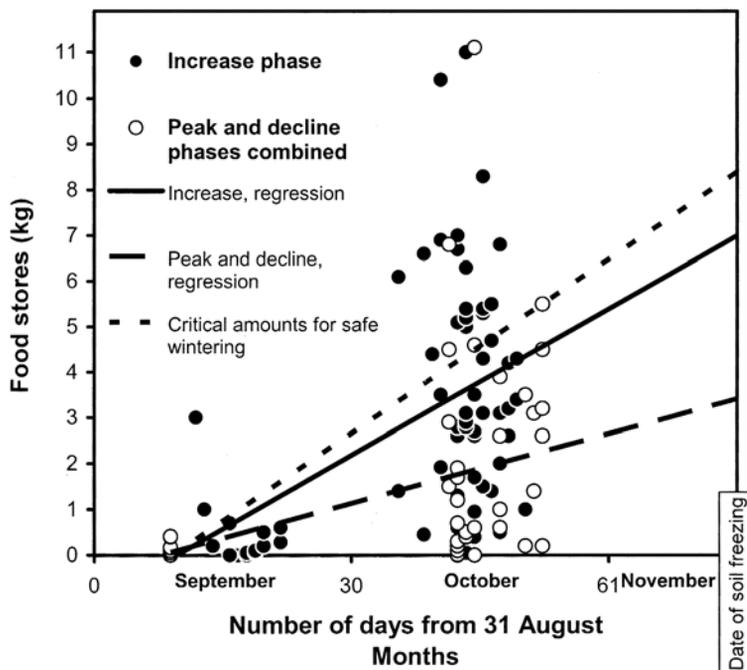


Fig. 1. The mass of food stores per individual burrow at different phases of the population cycle and the linear regression of food stores (S) on the number of days from 31 August (D=0). The equations of linear regressions look as follows. Increase phase: $S=-1.0+0.11D$; $n=68$, $r=0.48$, $p=0.0005$. Peak and decline phases combined: $S=-0.4+0.05D$; $n=57$, $r=0.41$, $p=0.001$. Critical amounts for safe wintering (see text): $S=-1.2+0.13D$.

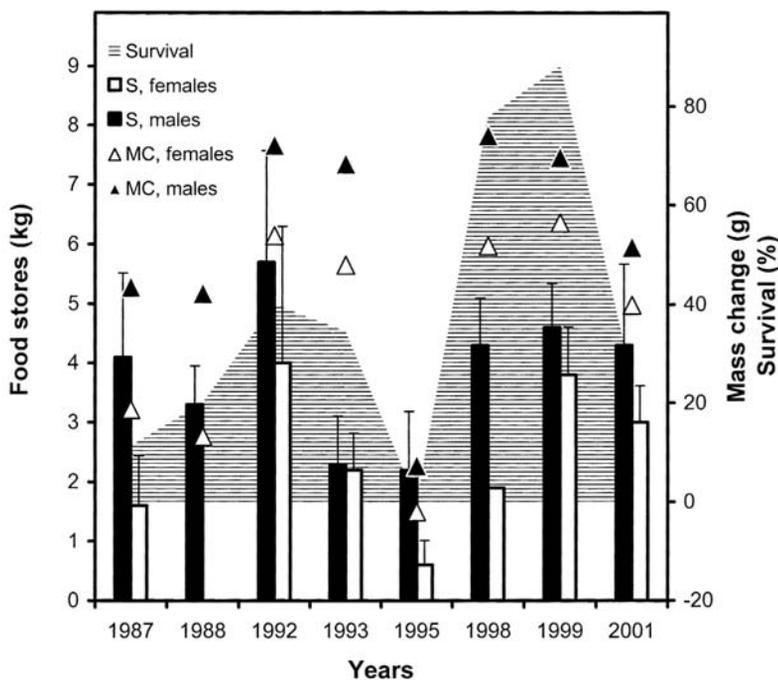


Fig. 2. Food stores in October (S), changes in body mass (MC) and survival during the subsequent winters. Bars represent SE.

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 \pm 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 \pm 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. 2).

Winter survival of water voles varied widely among the years of our study (Fig. 2). The density phases differed by the survival: peak and decline combined – 10.5 ± 9.9 %, $n=3$; increase – 53.1 ± 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).

Discussion

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. Thus, obtained data support the hypothesis of winter food deficit as a cause of population decline.

The data on burrow systems of water voles are still fragmentary (Panteleyev 1968, 2001a, Mesch 1984), except for those of the fossorial form, *A. t. scherman*, studied by Airoldi (1976, 1991, 1992). The average length of burrow systems we obtained is lower than that for the fossorial voles from Switzerland (Airoldi 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 (Airoldi 1976, 1991, Saucy 2001). Moreover, a burrow system in a terrarium has been shown to be longer when inhabited by a couple (Airoldi 1992). In the fossorial voles, winter breeding was recorded and could be responsible for population outbreaks (Meylan & Airoldi 1975); this never has been documented in the aquatic voles from Siberia (Sasov 1965, Panteleyev 1968).

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 1968). 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 Alekseeva et al. (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 (ibid.). 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 (S a s o v 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 (R o g o v 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 (E v s i k o v & O v c h i n n i k o v a 1999, E v s i k o v 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 (P a n t e l e y e v 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 (A i r o l d i 1991, E v s i k o v & O v c h i n n i k o v a 1999, E v s i k o v 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 (R o g o v 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 multiyear data shows that the duration of the whole population cycle of water voles in Siberia varies from four to nine years (R o g o v 1999), and it is longer on average than that in most other vole species (K r e b s & M y e r s 1974, L i d i c k e r 2002).

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.

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