

Is food quality responsible for the cold-season decline in bank vole density? Laboratory experiment with herb and acorn diets

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A b s t r a c t. We investigated, in a laboratory experiment, how natural food available in autumn influences the body mass, locomotor activity, and level of detoxification enzymes in the bank vole *Clethrionomys glareolus* (Schreber, 1780). In September and October 2001, two groups of bank voles were fed with herbs and acorns. A well-balanced mixed diet was a control. The animals fed with herbs showed high locomotor activity, compared to those fed control diet, a distinct increase of food consumption but loss of body mass. These voles also showed remarkably increased levels of detoxification enzymes (cytochrome P-450 and glutathione transferases) in their livers. Bank voles fed with acorns also lost weight and were more active, compared to the control (but less than the herb-fed group), and had higher levels of detoxification enzymes. Bank voles fed with the control diet showed the lowest level of locomotor activity and did not lose weight. We explain the increased activity of bank voles with stress response to low-quality food, especially as this effect ceased after changing the diet to the control one. Our results suggest that poor nutritional quality of herbs, the bank voles' main food under natural conditions, may be the main cause of seasonal decline in vole density in autumn-winter.

Key words: *Clethrionomys glareolus*, body mass, feeding experiments, locomotor activity, detoxification enzymes

Introduction

Populations of small rodents in Europe show seasonal and multi-year changes in numbers (Jędrzejewski & Jędrzejewska 1996, Löfgren et al. 1996). During a year, the critical period for rodents is autumn, winter, and early spring. Survival in these seasons determines the size and the reproductive potential of a population at the beginning of the next breeding season (Gliwicz 1983, Bujalska 2000). In forests of Central Europe mast years of deciduous trees, mainly oaks (*Quercus robur*), occur every 6–9 years and rapid growth of rodent populations is correlated with this phenomenon (Pucek et al. 1993, Hansson et al. 2000, Stenseth et al. 2002). Supplemental feeding also results in higher survival and increased number of individuals in the following season (Andrzejewski 1975, Bujalska 1975, Hansen & Batzli 1979, Banach 1986, Löfgren et al. 1996). These facts led to formulation of two hypotheses that attempt to explain seasonal and multi-year fluctuations in rodent numbers. The first is based on food availability (Batzli 1992, Jędrzejewski & Jędrzejewska 1996, Turchin & Batzli 2001), and the second on food quality (Holišová 1971, Tast & Kalela 1971, Hansson 1987, Batzli 1992, Jędrzejewska & Jędrzejewski 1998).

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The first hypothesis assumes that inhibited reproduction and decrease in rodent numbers observed in autumn and winter (in most years) is a direct result of limited food availability. Only in mast years, when food availability remarkably increases, is there high survival rate and continuation of reproduction in autumn and even in winter (Jensen 1982, Pucek et al. 1993, Hansson et al. 2000, Verhagen et al. 2000). The hypothesis of food quality explains the autumn and winter decline in rodent numbers with gradual deterioration of food quality, mainly of herbaceous plants (Holišová 1971, Hansson 1987, Jędrzejewska & Jędrzejewski 1998). In mast years, the increase in abundance of high-quality food, such as seeds of broad-leaved trees, prevents a decrease in rodent numbers (Górecki & Gębczyńska 1962, Drożdż 1968, Jensen 1982). Many authors combine these hypotheses assuming that both quality and quantity of food determine the population status and fluctuations of rodent numbers in the forests of Central and Northern Europe (Jensen 1982, Laine & Henttonen 1987, Hörnfeldt et al. 1986).

The aim of our study was to assess, in a laboratory experiment conducted in autumn, the effects of three diets differing in quality on food consumption, body mass, locomotor activity, and enzymatic activity in the bank vole *Clethrionomys glareolus* (Schreber, 1780), herbivorous-omnivorous species (Hansson 1971), common in forests throughout Europe. The results have been compared with the published data on a similar experiment conducted in spring (Wereszczyńska & Nowakowski 2004), and their implications for the wild-living populations have been discussed.

Material and Methods

Experimental bank voles ($n = 12$) were born in captivity and entered the experiment at the age of 2.5 months, with no prior breeding. They were descendants of wild-living voles captured in a mixed forest Sekuła near Siedlce (mid-eastern Poland, 52°09'N, 22°15'E). All experimental individuals were in good condition (average body mass was 20.75 ± 2 g). In captivity, they were fed standard mouse pellets, carrot, apple, sunflower seeds, and oats. During 10 days preceding the experiment they were habituated to a natural diet – herbs and acorns found at that time in the Sekuła forest. To keep the animals fit, we still supplemented the natural diet with mouse pellets. The Sekuła forest was dominated by Scots pine (*Pinus silvestris*) with an admixture of oak; the scattered undergrowth was formed by rowan (*Sorbus aucuparia*), blackberry (*Rubus* sp.), bird cherry (*Padus avium*), hazel (*Corylus avellana*), and alder buckthorn (*Frangula alnus*). Perennial plants dominated in the ground flora. No data about population density of bank voles in Sekuła forests are available. Other studies conducted in Polish temperate forests showed that bank voles show seasonal population dynamics with no multiannual cycles, and their autumn densities are usually within limits of 10–100 individuals/ha (Andrzejewski 1963, Goszczyński 1977, Jędrzejewski & Jędrzejewska 1993).

During the experiment the bank voles were kept singly in glass terraria 20 x 35 x 40 cm. They were provided with water and nest boxes lined with shredded paper towels. A metal netting of 5-mm mesh was mounted 5 cm above the bottom to collect crumbled remains of food. Running wheels for rodents (of 12-cm diameter) were also fixed in terraria and equipped with electronic rotation counters recording the distance covered and time of activity. The experiment was conducted under laboratory conditions (natural photoperiod, temperature $19 \pm 1^\circ\text{C}$) in 19–29 September 2001 and in 11–17 October 2001. Between the two stages (30 September – 10 October 2001), during a compensatory (control) period, all animals were fed a mixed diet.

During the experiment, bank voles were kept on three types of diet:

(1) Herb diet – plants most abundant in the forest ground level during the experiment and preferred by wild-living bank voles (D r o Ź d Ź 1966, G ę b c z y ń s k a 1976): *Mycelis muralis*, *Oxalis acetosella*, *Viola* sp., *Fragaria vesca*, *Majanthemum bifolium*, *Geum urbanum*, *Luzula pilosa*, *Vaccinium myrtillus*, *Impatiens parviflora*. We collected and provided the animals with whole plants including their underground parts. Every second day we gave the voles 10 g (fresh mass) of each herb species listed above (90 g in total). During the October stage of the experiment, *M. bifolium* and *I. parviflora* disappeared from the forest. Therefore, the animals were provided with 12.9 g (fresh mass) of the remaining herb species (also 90 g in total).

(2) Acorn diet – only acorns, randomly collected under different oak trees. Every second day 20 g of acorns were given to the animals.

(3) Control diet – *ad libitum* all herbs and acorns, mouse pellets, oats, sunflower seeds, apple, and carrot.

The bank voles were divided into two groups, six individuals in each (3 females and 3 males). Group I in September was provided exclusively with herb diet and group II only with acorn diet. In October, the diets were switched, so that animals from group I were given acorn diet while those from group II – herb diet. Between the two stages of the experiment, the compensation (control) stage was assigned (11 days, all experimental animals were kept on the control diet) in order to equilibrate differences in their condition and body mass. This compensation period served as control – mobility and body mass of all experimental animals were evaluated. Such an experimental design was chosen to avoid bias that may have resulted from individual differences in body mass, metabolism, and mobility of the animals, if three different groups had been compared.

During each addition of food all non-consumed remains were collected and then dried at 50 °C (remains of herbs for 2 days, of acorns for 4 days). Dried food remains were weighed with 0.01 g accuracy. At the beginning of each stage a sample of herbs and acorns (100 g of a dry mass from each species) was dried and weighed the same way as the food remains. In these samples, we evaluated the dry/wet mass ratio for each plant species, in order to calculate the amount of dry plant mass consumed by the bank voles.

The animals were weighed every 5 days. Records from the running wheel counters were read daily. The mobility of the bank voles was estimated based on the distance they ran in wheels, and the average and maximum daily speeds. Because of the experimental arrangement (the same individuals used in both stages) the activities of detoxification enzymes were measured only once, at the end of the second stage. Levels of cytochrome P-450 (O m u r a & S a t o 1964a,b) and glutathione transferases (L i n d r o t h 1989, L e s z c z y ń s k i & D i x o n 1992) in the microsome fraction were measured in livers of animals from both experimental groups (4 individuals from each group). The controls were 4 individuals from the laboratory colony group starved for 48 hours (according to O m u r a & S a t o 1964a,b). The animals were subjected to euthanasia by dislocation of neck vertebrae (according to prescriptions concerning laboratory animals' euthanasia in *Laboratory Animals 1997, 31: 1–32*).

In the first stage of the experiment carried out in September, one animal fed herb diet died on the 7th day, so for some calculations the sample size was lower. The dead animal was replaced with another one, from the laboratory group, at the beginning of compensatory period.

The results of autumn experiment were compared with that conducted in spring (March and April 2002) using the same experimental set-up (W e r e s z c z y ń s k a & N o w a k o w s k i 2004).

Results

Food consumption and body mass in autumn

During the experiment, bank voles consumed, on average 3.36 and 5.82 g of herb (dry mass, groups I and II, respectively) and 2.13 and 1.74 g of acorn per day (Table 1). Bank voles kept on both herb and acorn diet lost weight during both stages of the experiment (Table 2). With the herb diet in September this decrease averaged 2.5% of the initial body mass per day of experiment, and during the October series it was 1.6% per day. With the acorn diet the body mass of bank voles fell 1.4% and 0.85% per day, respectively (Table 2). In October, the condition of the animals fed with the herbs deteriorated rapidly after the 5th day of the experiment. Piloerection and unsteady walking was observed, and on the 7th day one animal was found dead. For that reason the experiment was terminated. In the compensation period, the body weight loss of bank voles from both experimental groups stopped, and even an increase was observed (0.50 and 0.64% of initial body mass per day; Table 2).

Daily rates of body mass changes in rodents on the same diet did not differ between groups I and II, but both groups pooled differed significantly when compared among diet types (herbs versus acorn, $P = 0.007$; compensation vs. herbs, $P < 0.0005$; and compensation vs. acorn, $P < 0.0005$; Mann-Whitney U-test).

Table 1. Daily food consumption by bank voles *Clethrionomys glareolus* (dry mass of herbs or acorn, g/day), mean \pm SE, in the autumn experiment ($n = 6$ individuals in each group). Samples marked by the same letters (a-a, ..., d-d) differ statistically from each other (ie. a from a, b from b etc.) at $P < 0.01$ (Mann-Whitney U-test).

Experimental group	Daily food consumption (g/day), mean \pm SE	
	Herbs	Acorns
Group I	3.36 \pm 0.13 ^{a,b,c}	2.13 \pm 0.26 ^{b,d}
Group II	5.82 \pm 0.10 ^{a,d}	1.74 \pm 0.17 ^c

Table 2. Body mass change, mean \pm SE, in absolute measures (g) and daily rate of change (g/day and g/day as percent of initial body mass) in bank voles kept on various diets.

Diet	Body mass (g)		Body mass change	
	First day	Last day	Grams/day	Percent daily change
Experimental group I				
Herbs	22.4 \pm 0.7	16.8 \pm 0.4	-0.56 \pm 0.06	-2.48 \pm 0.20
Compensation	16.8 \pm 0.4	17.8 \pm 1.3	0.09 \pm 0.08	0.50 \pm 0.46
Acorn	20.7 \pm 1.0	17.8 \pm 0.6	-0.30 \pm 0.06	-1.40 \pm 0.25
Experimental group II				
Acorn	18.5 \pm 1.3	17.3 \pm 0.3	-0.16 \pm 0.05	-0.85 \pm 0.26
Compensation	17.7 \pm 0.6	19.0 \pm 0.9	0.11 \pm 0.06	0.64 \pm 0.35
Herb	19.0 \pm 0.9	15.8 \pm 1.3	-0.31 \pm 0.07	-1.61 \pm 0.34

Locomotor activity and level of detoxification enzymes

Both in September and October, the bank voles from the groups fed with herbs were more mobile (as measured by the mean daily distance crossed by an individual in a running wheel) than those fed with acorns (Table 3). During the compensation period on control diet the

locomotor activity of all bank voles from both groups was significantly lower than their activity while on herb or acorn diet.

The animals from both experimental groups showed an increased level of liver detoxification enzymes. In both measurements the levels of cytochrome P-450 and the activity of glutathione transferases were higher in the bank voles fed with the herbs (Table 4). In this group the level of cytochrome P-450 was 2.7 times higher than in the control group and the activity of glutathione transferases was 2.3 times higher. In the bank voles kept on the acorn diet, this increase was respectively 2.0-fold for the level of cytochrome P-450 and 1.7-fold for the activity of glutathione transferases (Table 4).

Table 3. Locomotor activity of bank voles (distance covered daily in a running wheel) kept on various diets ($n = 6$ voles in each group). Statistical differences among rodents on various diets (groups I and II pooled due to lack of between-group differences): herbs versus acorn, $P = 0.001$; compensation vs. herbs, $P < 0.0005$; and compensation vs. acorn, $P = 0.001$ (Mann-Whitney U-test).

Experimental group	Locomotor activity (km/day), mean \pm SE		
	Herb	Compensation	Acorn
Group I	7.19 \pm 2.50	0.84 \pm 0.21	2.07 \pm 0.37
Group II	8.53 \pm 1.70	0.93 \pm 0.37	3.63 \pm 0.81

Table 4. Average level of detoxification enzymes in bank vole liver ($n = 4$ voles pooled in each group).

Detoxification enzyme	Control animals	Acorn-fed animals	Herb-fed animals
Cytochrome P-450 (nM cyt P-450/mg of protein)	0.887	1.826	2.419
Glutathione transferases (mM CDNB/mg of protein/min)	0.957	1.663	2.212

Discussion

The type of food provided during the autumn experiment had a distinct influence on locomotor activity, body mass, and the level of liver detoxification enzymes in the bank voles. The increased activity may occur as a reaction to various stress factors in laboratory rodents (Moraska & Flešner 2001), and has been observed also during food deprivation experiments in golden hamsters and rats (Benke et al. 1995, Masatoshi et al. 2001). Because behavioural changes accompanied diet alterations, we may exclude habituation or individual preferences of our experimental animals as possible causes of the observed differences in their locomotor activity. During the compensation period of feeding with the control diet the activity was at a similarly low level in both groups, and after the shift of diet from herbs or acorns, the activity of voles increased considerably. The increase, however, was higher on the herb diet, compared to the acorn diet. The increase in activity was accompanied by a decrease in body mass, despite higher food consumption. This indicates that the increase in locomotor activity might have been a stress response to inadequate diet, and a considerable decrease in activity during the compensatory stage might have been related to a recovery from stress (shift to well-balanced control diet). According to this interpretation, the herb diet would have caused higher discomfort than the acorn diet. That possibility is confirmed by

greater decrease in body mass on herb diet, compared to the acorn diet, and no decrease on the control diet. We may exclude that body mass dropped due to insufficient feeding since in both diets a surplus of food was supplied and the animals used only a part (27–44%) of the food provided. Under experimental conditions 6 to 20 g of the fresh plant mass per 24 hours per one bank vole is recommended (G ó r e c k i & G ę b c z y ń s k a 1962, D r o ń d ń 1968). During our experiment, 45 g of the fresh mass of plants or 12.5 g of acorns per 24 hours *per capita* was supplied.

The results of autumn experiment considerably differed from those obtained in March–April 2002 (W e r e s z c z y ń s k a & N o w a k o w s k i 2004). In that experiment, bank voles that were fed exclusively the fully developed herbs, showed good condition as their body mass increased (Fig. 1), and locomotor activity was low. In spring, condition of the animals fed acorns was poor, their body mass decreased (Fig. 1), and activity was much higher. These results show that herbal diet is adequate for bank voles at the beginning of the vegetation season, while in autumn its nutritional quality rapidly decreases (G r o d z i ń s k i 1961, H o l i š o v á 1971, J e n s e n 1982).

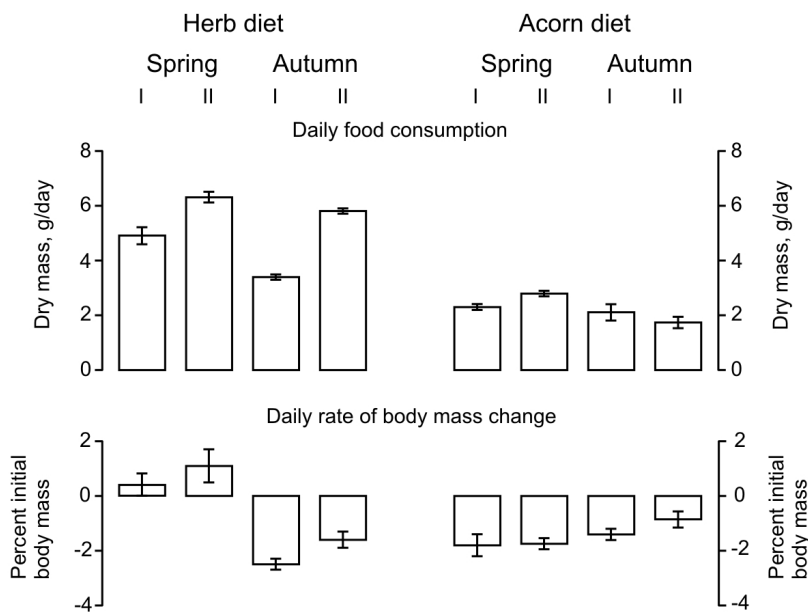


Fig. 1. Comparison of daily food consumption (grams of dry mass/day) and daily rates of body mass change (grams/day as percent of initial body mass) in bank voles experimentally fed herbs and acorns in spring (recalculated from W e r e s z c z y ń s k a & N o w a k o w s k i 2004) and autumn (this paper). I, II – experimental groups of voles. Bars are means \pm SE.

Thus, it can be assumed that the loss of body mass observed in the bank voles was the effect of a low quality of natural food in autumn, in particular of herbs. Their nutritive value is known to decrease distinctly between September and November (G r o d z i ń s k i 1961, J e n s e n 1982). The autumnal deterioration of herbs' quality is related mainly to their lower digestibility (e.g. due to higher content of fibre; D r o ń d ń 1968), decrease in the protein content (J e n s e n 1982), and increase in the level of secondary compounds (e.g. phenols, L a i n e & H e n t t o n e n 1987). H a m m o n d & W u n d e r (1991) and O w l

& Batzli (1998) observed increased food consumption by two vole species kept on a high-fibre, less digestible diet.

The two-fold increase in activity of liver detoxification enzymes indicates a high level of xenobiotics in food. They include alkaloids, terpenes, phenols, and coumarins that may disturb food digestion and absorption in voles (Marquis & Batzli 1989, Plesner Jensen & Doncaster 1999). Hansson (1991) observed that in autumn rodents consumed more tree bark, which he associated with its higher content of sodium, the element needed in processes of detoxification of secondary metabolites of plants.

Acorns are regarded as higher quality food (Drożdż 1968) in comparison with herbaceous plants, mainly due to greater calorific value and low fibre content. However, acorns may have considerable amounts of tannins, which have negative, antinutritional effects on rodents (Shimada & Saitoh 2003). As shown by the results of our autumn experiment, bank voles fed the acorn diet lost weight more slowly compared to those fed herbs (at only a slight increase in food consumption), showed lower level of locomotor activity (related to stress), and of liver detoxification enzymes. On the other hand, in spring, the overwintered acorns were markedly less valuable (bigger decline of body mass observed, see Fig. 1) than fresh acorns in autumn. Also pure acorn diet was worse compared to well-balanced control diet.

How can the apparent discrepancy be reconciled between the experimental data (weight decline and stress of bank voles fed acorns) and the field studies (good winter survival and increase in numbers after a mast year)? Recent studies on Japanese wood mouse *Apodemus speciosus* evidenced that mice could mitigate the negative effects of acorn tannins through acclimation mediated by the induced physiological countermeasures (Shimada et al. 2004). They included the increase in secretion of the tannin-binding salivary proteins and higher abundance of the tannase-producing enterobacteria *Streptococcus* and *Lactobacillus* (Shimada et al. 2006). Similar mechanisms can also operate in bank voles, but since our experimental animals were not fully acclimated to acorn tannins, we observed moderate loss of their body mass. However, under natural conditions bank voles are obviously able to successfully cope with detrimental effects of tannins in *Quercus robur* acorns, which – compared to several other species of North American, Asian, and European oaks – are among the most palatable for consumers due to their low tannin content and relatively high metabolizable energy (Shimada & Saitoh 2006).

Our experiment was conducted in autumn when in the natural environment the number of bank voles decreases and reproduction is inhibited (Aulak 1973, Hansson et al. 2000), even if the standing crop of potential vegetal food is still great (Grodziński 1961, Górecki & Gębczyńska 1962, Drożdż 1966, Zemanek 1972, Aulak 1973, Gębczyńska 1976, Jensen 1982). According to various estimates, the use of the potential food by forest rodents in the Central Europe ranges from as low as 0.4% to 16.5% of the net production or the calorific value of the available food (Grodziński 1961, Górecki & Gębczyńska 1962, Aulak 1973). This shows that the amount of potential food cannot be a direct limiting factor to the population growth. However, our experiment has shown that much of the herbaceous food available in autumn is of poor quality. The results of spring experiment (Wereszczyńska & Nowakowski 2004) were strikingly different: bank vole that fed with fully developed herbs were in good condition and increased their body mass. It suggests that availability of high-quality vegetal food is conducive to rapid spring and summer increase of bank vole numbers observed in wild-living populations. Seasonal variation in quality of vegetal food can also explain

differences in growth rates of the spring, summer, and autumn cohorts of bank voles in the wild (Zejda 1971).

Numerous experiments have shown that addition of an “extra food“ to ecosystems in autumn results in increased survival and reproduction of rodent populations, and in consequence, in their growth in numbers (Andrzejewski 1975, Bujalska 1975, Hansen & Batzli 1979, Banach 1986, Löfgren et al. 1996). In those experiments (in most cases conducted on bank vole populations), as a rule, a high-quality artificial food has been supplied such as oats, sunflower seeds, mouse pellets; Andrzejewski 1975, Löfgren et al. 1996, Eccard & Ylönen 2001). Therefore, our results show that in the food addition experiments not only the quantity but also the quality of food was manipulated.

In natural environment, bank voles do not consume just one type of vegetal food and can enrich their diet to some extent with high-quality animal food (Holišová 1971, Gębczyńska 1976, 1983), therefore, they do not suffer such dramatic reductions in weight and, consecutively, in survival. Nonetheless, our experiment suggests that poor quality of herbs in late autumn and winter may be the main cause of the seasonal density decline of this species.

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