Influence of climatic factors on the population dynamics of small mammals (Rodentia, Soricomorpha) on the sites affected by windthrow in the High Tatra Mts

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Abstract

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Climatic factors and related changes of the temperature, humidity and sunshine demonstrably affect the population dynamics of small mammals. This complex influence gets more intense in the case of natural and anthropic disturbances which occurred in the forest ecosystems of the High Tatra Mts in 2014 (wind calamity) and in 2015 (forest fire). During the period of research in 2005–2015, we were observing successive changes in the species composition, abundance and spatio-temporal distribution of small mammals on the seven permanent research areas by using the CMR method. Besides the changes of selected habitat variables, we were also continually measuring values of meteorological elements (such as air and soil temperature, relative air and soil humidity, thickness and duration of snow cover). Statistical testing of the thickness and duration of snow cover proved significant influence of these factors on the population dynamics of small rodents (Rodentia) and shrews (Soricomorpha). Winters with a thicker snow cover and longer snow periods had a positive effect on the reproduction and surviving of both taxonomic groups in the subsequent vegetation season. We have discovered the positive correlation between the temperature and the quantity dynamics of dominant small rodents while shrews responded to higher temperatures with less spatio-temporal activity. Gradient analysis of the complex influence of measured meteorological elements proved species-specific differences in the responses of small mammals to the current and conditions of weather indicated by ecological requirements of plant species within a specific habitat.

Keywords

population dynamics, small mammals, snow cover, temperature

Introduction

Small ground dwelling mammals (Rodentia, Soricomorpha) are highly adaptable animals which can be found in all habitats ranging from the tropics to the polar regions (Hayward and Phillipson, 1979). They are an important part of food webs and an interacting element between vegetation and soil subsystems (Golley et al., 1975). Detailed information are available at present for several species on small mammals biology, autecology, population and communities organisational levels and functions in various, e.g. forest and grassland

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ecosystems (Barrett and Peles, 1999). This makes small mammals a suitable object for testing ecological hypothesis based on a landscape scale.

Changes of weather evidently influence population density, survival and growth of small herbivore rodents. Chen et al. (2015) reported nonlinear responses to several meteorological parameters, e.g. precipitation or air temperature. Population dynamic of small mammals is influenced also by the weather in previous winter, especially snow cover depth and number of days with snow cover. Mostly Russian authors, e.g. Formozov (1946, 1961) and Semyenov et al. (1958) studied survival rate of small mammals according to the snow parameters in past. Fuller et al. (1969) presented winter mortality as an important determination factor for the size of small mammals spring population. Several authors, e.g. Vickery and Bider (1981), Hansson (1987), Hansen et al. (1999), Stokes et al. (2001), Lima et al. (2002), Kalcounis-Rueppell et al. (2002), Vieira et al. (2010) studied the influence of climatic factors (temperature, humidity, snow cover) on population dynamics, diurnal activity, fecundity, survival rate or food behaviour of small mammals. In Slovakia, Hlôška and Saniga (2005) studied the influence of precipitation on diurnal activity of small mammals in supra-montane vegetation zone in the Malá Fatra Mts. Jurčovičová and Kozubová (2007) studied the influence of temperature and precipitation on small mammals diversity and density in the Nature Reserve Šúr in south-western Slovakia.

In area of the High Tatra Mts (Slovakia) had occurred considerable natural and anthropic disturbances in 2014 (wind calamity) and in 2015 (forest fire) which changed significantly character of local forest ecosystems. The main symptoms were that matured trees were almost completely destroyed and canopy closure was eliminated. Thus the aim of our paper was to test the following hypotheses in such specific habitat conditions: 1) Snow cover height and duration of snow cover influence reproductive activity and abundance of small mammals in the next breeding (vegetation) season; 2) Air temperature modifies ground surface activity of small mammals; 3) Population dynamics of species are changing according to the values of observed meteorological parameters (air temperature, soil temperature and moisture, precipitation) and microhabitat properties featured by site conditions and successional stage of vegetation.

Materials and methods

Study plots

The research was carried out in the Tatra Mountains from 2005 to 2015 on five research plots representing different intensity of natural disturbances and one reference undisturbed plot in larch-spruce forest. These six plots were located in the range of 925 to 1,260 m asl: NEX – Jamy, 49°09′37″N, 20°15´21″E, 1,100 m asl, forest stands affected by the wind calamity in year 2004, no management intervention (no processing of wind-thrown and broken trees, no forestation); EXT – Danielov dom, 49°07´13″N, 20°09´50″E, 1,260 m asl, forest stands affected by the wind calamity in 2004, treated by applying common forestry measures (wood mass removed, plot forested partly); REF – Smrekovec, 49°07´15″N, 20°06´26″E, 1,210 m asl, intact stands, so-called reference (control) plot; FIR 1A and FIR 3A – Tatranské Zruby, 49°07´49″N, 20°11´53″E and 49°08´02″N, 20°11´32″E, 1,025 and 1,100 m asl, two plots in forest stands affected by the calamity and later by a fire; CVL (Čierny vodný les) – Nový Smokovec, 49°08´06″N, 20°12´30″E, 1,015 m asl, forest stands affected by the wind calamity, water-holding measures applied; OVL (Oliverov vodný les) – Tatranská Lomnica, 49°10´20″N, 20°16´59″E, 925 m asl, forest stands affected by the wind calamity, water measures applied. On each trapping point we estimated habitat variables (altitude, orientation, inclination) and vegetation cover using phytocenological records. To characterise successional stages of study habitats, phytocenological mapping was performed during 2–4 vegetation seasons in each plot and Ellenberg's eco-indices were calculated.

Trapping of small mammals

So called quadrat method was used for small mammals captures. Research sites were of uniform size 75 × 75 meters, covering an area of 0.56 ha. Each capture campaign organized twice per year (in spring and in autumn) lasted three days and three nights. Thirty six Chmela-type traps were installed on each site on a regular mesh, distance 15 m. The trapped animals were marked and released (CMR method). Mixture of fish, nuts, oat, extruded water larvae and sunflower oil served as bait. The traps were checked several times during day. Coded ear marks for Rodentia and marking colour for Soricomorpha were used for marking the catches. After marking, on each trapped small mammal we estimated sex, sexual status, and approximate age. Trap effort was standardized for each site for each trapping sessions by dividing the number of captures by the number of nights that sites were open (Lentic, 2003). Standardized trap data (captures/plot/night) of individual abundance were used in all analyses.

Climatic data and analyses

Meteorological parameters (snow cover height and length, air temperature and humidity, soil temperature in 2005–2015) and abundance of dominant and eudominant species, as well as spatio-temporal distribution of sexually active females in small mammal populations were used for the analysis of weather impact on population dynamics. Snow depth (in cm) was measured at the meteorological station Tatranska Lomnica, 830 m asl by a snow stake. Air temperature (°C) and humidity (%) was measured at 200 cm height by the Hygroclip 2 (Rotronic, Switzerland) sensor as 60 min instant values. Soil temperature was measured in 8 cm depth by a termocouple Campbell 107 as 60 min instatnt value. All meteorological data were recorded and stored by the Campbell CR10x dataloger (Campbell Scientific, UK). Data matrix contained 1,603 rows and 46 columns. Contingency tables were used for classification, transformation a visualisation of data. Correlations were tested in statistical environment R (R Core Team, 2015). Direct gradient methods in CANOCO for Windows 4.5 and CanoDraw for Windows 4.14 (Cajo and Šmilauer, 2002) were applied in multidimensional analysis of ecological data.

Results

Small mammals community

During our study we trapped and marked 1,288 individuals from 14 species of small mammals. Three species were eudominant, one species was dominant, one species was subdominant and the largest number of species (nine) had subrecendent proportion. An overview of species composition, abundance, diversity and equitability of small mammals are shown in Table 1. Five species had euconstant proportion; *Apodemus flavicollis*, *Clethrionomys glareolus*, *Microtus agrestis*, *Sorex araneus* and *Sorex minutus*. Also five species were classified as accessory species; *Apodemus sylvaticus*, *Arvicola amphibius*, *Micromys minutus*, *Microtus arvalis*, *Neomys fodiens*. Four species in the sample had accidental proportion; *Apodemus agrarius*, *Muscardinus avellanarius*, *Neomys anomalus* and *Sicista betulina*.

Table 1. Number of individuals, number of species, species diversity (H´), equitability ($E_{1/D}$), relative abundance (D) and frequency (K) of small mammals on six research plots during 2005–2015 (list of mammal species is arranged alphabetically)

Species / research plot	CVL	EXT	FIR1A	FIR3A	NEX	OVL	REF	n	D (%)	K (%)
Apodemus agrarius	–	–	–	–	5	–	–	5	0.39	14.29
Apodemus flavicollis	34	15	56	22	13	23	10	173	13.43	100.00
Apodemus sylvaticus	–	1	2	–	–	–	–	3	0.23	28.57
Arvicola amphibius	1	–	–	–	–	2	–	3	0.23	28.57
Clethrionomys glareolus	91	76	66	93	131	100	122	679	52.72	100.00
Micromys minutus	–	–	–	1	2	–	–	3	0.23	28.57
Microtus agrestis	14	22	18	14	5	19	1	93	7.22	100.00
Microtus arvalis	1	–	–	2	–	–	–	3	0.23	28.57
Muscardinus avellanarius	–	–	5	–	–	–	–	5	0.39	14.29
Neomys anomalus	–	–	–	–	–	1	–	1	0.08	14.29
Neomys fodiens	4	–	–	–	–	3	–	7	0.54	28.57
Sicista betulina	–	1	–	–	–	–	–	1	0.08	14.29
Sorex araneus	40	59	63	24	24	62	8	28	21.74	100.00
Sorex minutus	8	6	2	4	4	7	1	32	2.48	100.00
Number of individuals	193	180	212	160	184	217	142	1,288		
Number of species	8	7	7	7	7	8	5	14		
Diversity index (H´)	2.083	1.969	2.108	1.824	1.476	2.026	0.792	1.961		
Equitability ($E_{1/D}$)	0.412	0.463	0.543	0.368	0.269	0.398	0.268	0.205		

Variability of climatic factors

According to the meteorological observation in Tatranská Lomnica (830 m asl) the average snow cover height varied in the range of 1.0 cm (winter 2014/15) to 19.9 cm (winter 2005/06) in the study period 2005–2015. The trend of snow cover height was declining (r^2 = 0.63) with slight increase in the winters of 2012/13 and 2013/14. Duration of snow cover above 1 cm ranged from 54 days (winter 2014/15) to 134 days (winter

2005/06). The trend of snow cover days was less evident than snow height (r^2 = 0.29) but also declining. Snow cover lasting more than 100 days occurred five times during the study period (Fig. 1). Average snow cover above 8 cm was found during only four winter seasons (2005/06, 2006/07, 2012/13 and 2013/14; Fig.1). During the catches, air temperature ranged from 1.2 to 28.6 °C, relative air humidity varied from 45 to 100% and soil temperature varied in the range of 7.5 to 28.2 °C. The average values of meteorological parameters are shown in Table 2. Differences in the air and soil temperature, respectively, were significant among the sites (Kruskal-Wallis ANOVA, air: χ^2 = 54.5, df = 6, $P < 0.001$; soil: χ^2 = 187.2, df = 4, $P < 0.001$) as well among the years (air: χ^2 = 382.6, df = 7, $P < 0.001$; χ^2 = 180.9, df = 7, $P < 0.001$).

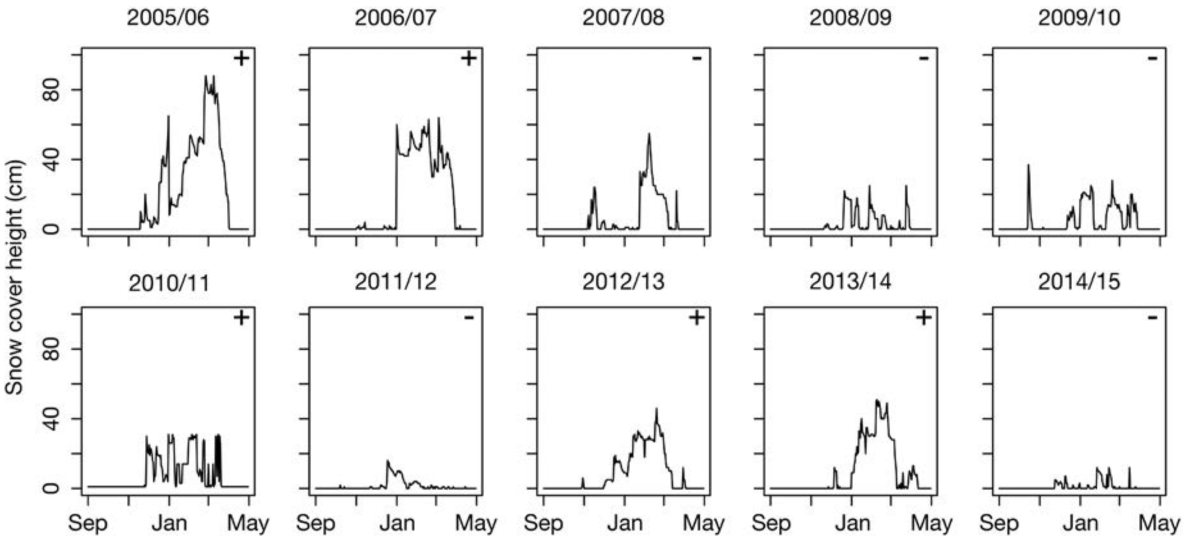

Fig. 1. The winters with snow cover above 100 days and average height above 8 cm (+) and winters with snow cover below 100 days and average height below 8 cm (–) as measured in Tatranská Lomnica (830 m asl).

Table 2. Average air temperature, humidity and soil temperature on research plots during 2005–2015

Variable / research plot	CVL	EXT	FIR1A	FIR3A	NEX	OVL	REF
Air temperature (°C)	13.34	12.72	10.97	9.84	12.30	13.67	10.88
Relative air huminidy (%)	80.26	72.76	69.28	73.36	82.96	82.24	75.23
Soil temperature in16 cm (°C)	15.86	14.25	14.47	13.99	10.42	–	–

Influence of snow cover on small mammals

Abundance of small rodents (Rodentia) increased significantly after long lasting and snow rich winters. Variable winter weather or winters with discontinued snow cover caused statistically significant population decline (one-sample t-test, t = 3.9, df = 10, P = 0.002; Fig. 2a). Number of individuals after the winters with sufficiently deep and long duration of snow cover ranged from 8.3 to 16.1 captures per sites and nights. Number of individuals during breeding seasons following poor snow winters ranged from 2.8 to 6.3 captures per sites and nights. We found significant fluctuation changes also in Soricomorpha population (t = 4.513, df = 8, P = 0.001, Fig. 2b). Population size increased during breeding seasons that followed winters rich on snow. The catches increased from 0.9 captures per sites and nights in 2006 up to 4.9 in 2007. Whereas average snow cover height was 18.9 cm and its duration was 134 days in winter 2005/06 and 16.0 cm and 108 days in winter 2006/07.

The snow cover height and duration determined also species richness of small mammals. While species number varied between three and seven after snow poor winters, after snow rich winters increased up to six and nine species. The difference was significant (one-sample t-test, t = 10.6, df = 10, $P < 0.001$).

Continuous snow cover significantly increased proportion of sexually active male and female individuals in local Rodentia populations. On the contrary, snow poor winter with warm and rainy weather negatively influenced reproduction capacity. In 2007 breeding season, proportion of sexually active individuals was

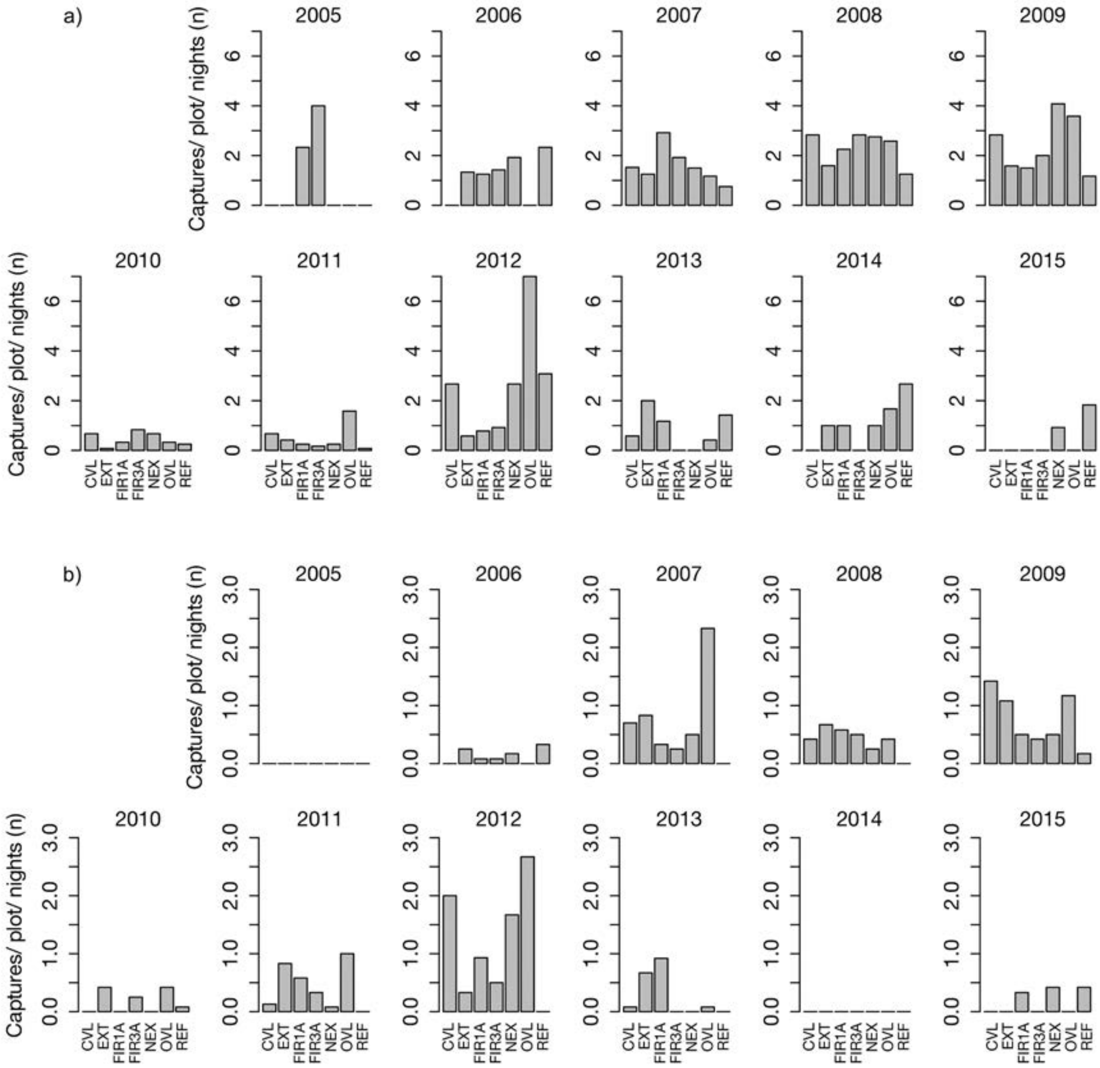

Fig. 2. Fluctuation in numbers of individuals of a) rodents and b) shrews trapped as six study plots during breeding seasons 2005–2015. Snow cover height and its duration in winters preceding breeding seasons see in Fig. 1.

significantly higher after winter with deeper and longer duration of snow cover ($\chi^2 = 25.9$, df = 2, $P < 0.001$), slight decline was observed in 2008 and 2009. High portion of the individuals in reproductive age was recorded again in summer 2011 after snow rich winter 2010/11 ($\chi^2 = 13.8$, df = 1, $P = 0.001$). Notable decline in numbers of sexually active individuals of both sexes of rodents were recorded after mild winters 2007/08 and 2011/12 (Fig. 3). The differences in ratio between sexually active and inactive individuals induced by previous winter characteristics are bigger in shrews than in rodents populations (Fig. 3).

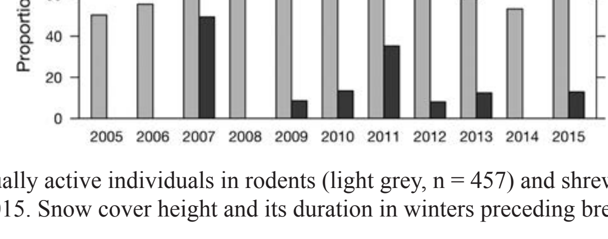

Fig. 3. Relative ratio of sexually active individuals in rodents (light grey, n = 457) and shrews (dark grey, n = 320) during breeding seasons 2005–2015. Snow cover height and its duration in winters preceding breeding seasons see in Fig. 1.

We did not find significant correlations neither between number of individuals and snow height (rodents, r = 0.34; shrews, r = –0.43; $P > 0.05$) nor between number of individuals and duration of snow cover (rodents, r = 0.13; shrews, r = –0.12; $P > 0.05$) in both groups of small mammals (Fig. 4).

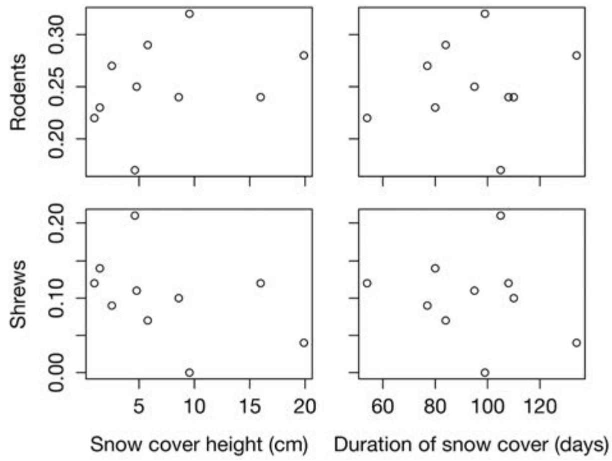

Fig. 4. Relations between snow cover height, snow cover duration and the numbers of rodents and shrews (captures/ plot/ night) in the next growing seasons.

Temperature and dominant species of small mammals

We tested the hypothesis on differences in surface activity of dominant small mammals induced by temperature. Significant differences in temperature tolerance were found in three species, for the air temperature (Kruskal-Wallis ANOVA, $\chi^2 = 8.8$, df = 2, $P = 0.013$), as well as for the soil temperature ($\chi^2 = 70.2$, df = 3, $P < 0.001$). During catches, the average air temperature with maximum surface activity of *A. flavicollis* was 13.0 °C and soil temperature was 14.8 °C. Species *C. glareolus* was the most active at the air temperature of 12.3 °C and soil temperature of 11.9 °C and activity of *S. araneus* culminated at 13.1 °C and 13.3 °C respectively.

Climatic gradients and distribution of small mammals

Effects of four climatic variables (soil moisture, soil temperature, air temperature and precipitation) were explained in RDA analysis. The first ordinary axis was identified by level of natural disturbance (wind in 2004) as well as anthropogenic disturbance (fire in 2005). Second ordinary axis explained the moisture gradient. Successional changes induced by windstorm took place on the five study plots (REF, NEX, EXT, OVL, CVL), whereas two similar plots (FIR1A and FIR3A) were affected by fire in early stage of succession. The order along the moisture gradient was as follows: REF, FIR1A, FIR3A, NEX, EXT, OVL, CVL. The numbers of *N. fodiens*, *S. minutus*, *C. glareolus* and *M. agrestis* species correlated well with soil moisture. The number of *S. araneus* individuals increased with increasing air temperature. Species *A. flavicollis* positively reacted to increasing amount of precipitation (Fig. 5).

Spatiotemporal changes in the distribution and number of individuals in small mammals populations we assessed by phytocenological bio-indication of plot conditions using the Ellenberger's indicator values. The indicator values calculated for the study plots and years are shown in Table 3. Soil moisture gradient positively correlated with the number of *A. agrarius*, *N. fodiens* and *S. araneus* individuals. An increase of population size we observed in *A. flavicollis* species along pH and soil nitrogen gradients. Species *C. glareolus* showed elevated affinity to increasing continentality of microhabitats (Fig. 6). The values of Ellenberg's indices have changed according to successional stage of vegetation and determined both spatial and temporal dynamic of small mammals communities.

Discussion

Presented results documented some influence of the snow height and duration of snow cover on abundance of small rodents, proportion of sexually active individuals, and population growth. These demographic and population parameters correlated well with long-lasting and snow reach winters. Contrary to that, these population variables were negatively influenced by preceding winters with low snow cover, short or

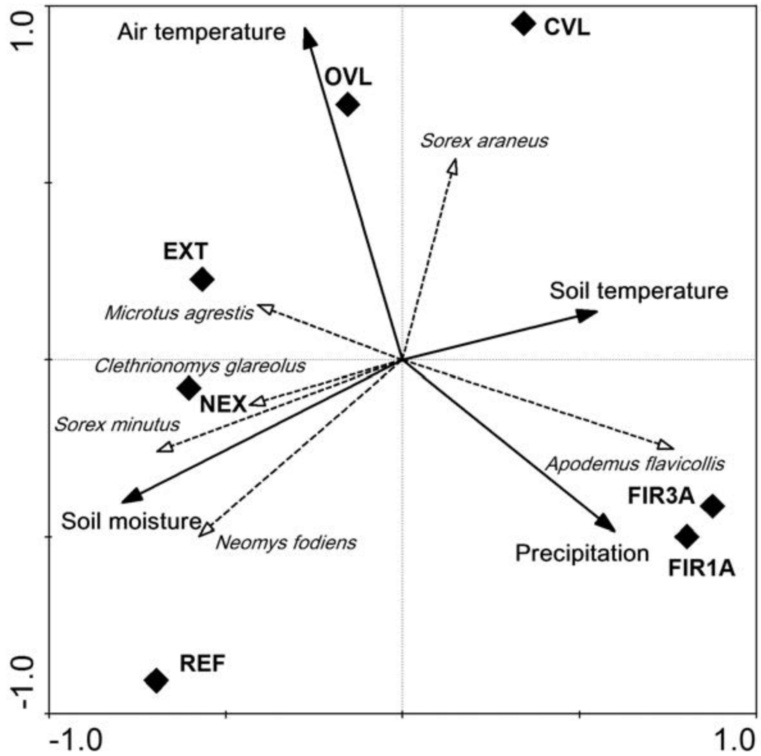

Fig. 5. Results of RDA analysis on species abundance and environmental data (meteorological characteristics) in study plots. First canonical axis explains 28.4% and second 16.7% from the whole data variability.

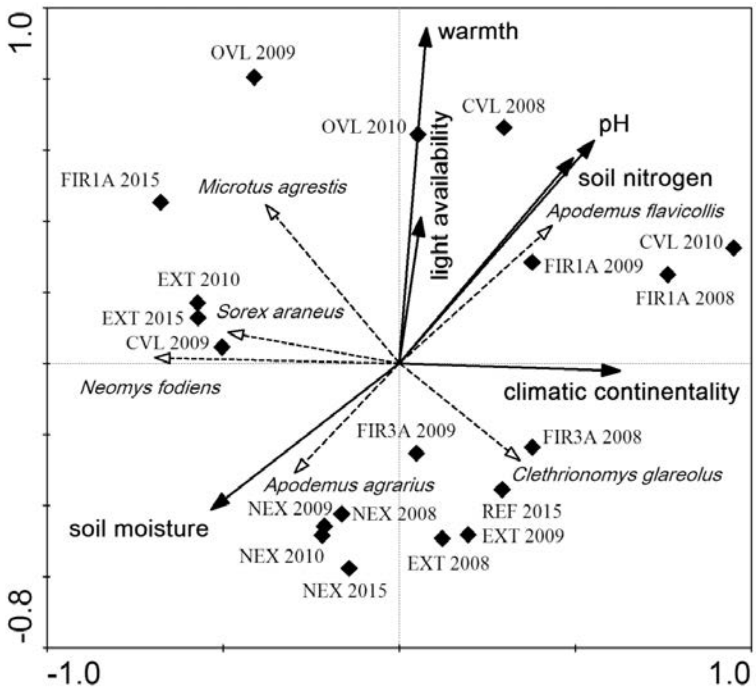

Fig. 6. Results of RDA analysis on species abundance and environmental data (Ellenberg's eco-indices) in study plots. First canonic axis explains 47.8% and second 11.1% from the whole data variability.

interrupted snow coverage periods. In shrews populations, the negative influence of high and long-lasting and positive effect of low and discontinuous snow-cover were observed.

Table 3. Ellenberg's eco-indices of six study plots counted on the basis of the phytocoenological indication of the plant species. Values are averaged from 2–4 vegetation seasons in each plot.

Plot	CVL	EXT	FIR1A	FIR3A	NEX	OVL	REF
Light	6.24	5.62	6.76	6.85	5.92	6.02	4.93
Warmth	4.57	4.16	4.36	4.07	4.02	4.63	4.05
Continentality	4.01	4.21	4.25	4.31	3.77	4.07	4.33
Humidity	5.77	5.83	5.39	5.45	6.21	5.72	5.54
pH	4.24	2.59	3.80	3.68	2.47	3.34	2.41
Nitrogen	5.08	3.67	5.56	5.46	3.44	4.51	3.41

Fuller et al. (1969) stated the influence of microclimate factors during winter (especially snow height and duration) on small mammals mortality and spring reproduction size in his several years long study. High mortality of small mammals during winters with limited snow cover reported several Russian authors (e.g. Formozov, 1946, 1961; Kirikov, 1946; Semyenov et al., 1958). Ilenko and Zubchaninova (1963) reported home range changes and sexual ratio changes in *C. glareolus* and *A. sylvaticus* species induced by height and duration in snow cover. Our study demonstrated that the winter periods with continuous snow cover significantly increased the ratio of sexually active individuals in rodents population. Mild winters with missing snow cover and warm weather had opposite influence on reproduction capacity. Similar changes were observed in the ratio between sexually active and inactive individuals in local population of Soricomorpha. Spottiswoode and Saino (2010) reported possible influence of environmental changes on sexual behaviour. The influence of climate changes on sexually specific mortality presented also Møller (2012).

Winter season weather in the Tatra Mts foothills is changing in the last decades as a response to global climate changes. In long term run, natural disturbances and perturbations caused by climate variability significantly modify species richness and abundance of small mammals. Blois et al. (2010) predicted changes in species diversity by increase of ubiquist species in local populations. In their comparative study has been suggested that increase of the air temperature above the value which small mammals had been exposed during their evolutionary traits might stimulate disintegration of native populations and invasion of alien species. According to our study, the influence of ambient temperature determined by the air and soil temperature plays significant role on the diurnal activity of small mammals. Vieira et al. (2010) studied the influence of ambient temperature and precipitation on the small mammals diurnal activity and reported positive correlation between activity with ambient temperature under elevated relative air humidity. However, under low air moisture the correlation between animal activity and ambient temperature was negative. Based on our results we conclude that besides body size, the biorhythm and spatial activity is mostly driven by ambient temperature and moisture (Lovegrove, 2003). Also Bronson (2009) found that mammals with smaller body were more sensitive to the environmental factors such as temperature and precipitation.

Multidimensional analysis of our data (abundance and ecological distribution of small mammals according to the selected climate parameters) confirmed significant influence of measurable climate gradients on the number and distribution of small mammal individuals. We found the site conditions (indicated by plant communities) as reliable indicator of favourable microhabitats for distinguished small mammal species. Thus such environmental gradients could be generally understood as important endogenous components of their ecological niches (Forman and Godron, 1986).

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