British Journal of Environment & Climate Change
6(1): 43-52, 2016, Article no.BJECC.2016.004
ISSN: 2231–4784

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Cascade Effect of Climate Warming: Snow Duration - Vole Population Dynamics - Biodiversity

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Authors' contributions

This work was carried out in collaboration between the authors. Author JG designed the study and supervised the data collection and analysis, wrote and revised the manuscript. Author EJ had a significant share in the data collection and analysis, provided valuable suggestions for the study design and prepared all the figures. Both authors approved the final manuscript.

Article Information

DOI:10.9734/BJECC/2016/25313

Original Research Article

Received 2nd January 2016
Accepted 16th March 2016
Published 29th March 2016

ABSTRACT

Several recent reports have presented evidence indicating a change in arvicolid rodent dynamics from high-amplitude density cycles to acyclic fluctuations at relatively low level. The data come mostly from Northern Europe (>60° N) and indicate that the change is caused by climate warming, most pronounced in the winter. In this report we present data showing similar changes in the dynamics of two vole species, *Microtus oeconomus* and *M. arvalis*, in open habitats of Poland (<54°N) over last 25 y. Fairly regular fluctuations observed until early 1990s, subsequently changed to become more erratic. We tested which winter weather factors were most important for successful overwintering of *M. oeconomus* in Białowieża over 12 years, and how those factors changed over the last half-century according to the data from the local meteorological station. Finally, we demonstrate that the fall in the abundance of small game over the last 20 years has been linked to the decline of vole abundance.

Keywords: Biodiversity; climate change; fading rodent cycles; snow cover; winter survival; voles.

1. INTRODUCTION

In the last decade, several reports on arvicolid rodent population ecology have presented robust evidence indicating a change in lemming and vole population dynamics from regular high-amplitude density oscillations, known as population cycles, to acyclic fluctuations with a

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prevailing seasonal component and relatively low densities in “peak years” ([1] for a review). The majority of the data come from studies focused on the arctic region of Europe (above 60° N) or the hemi-arctic zone of Norwegian mountains [2,3,4,5], where the population cycles used to be most regular and were they started to collapse in the mid-1980s. More recently, similar changes in the population dynamics of voles have been reported also from the temperate regions of Europe [6,7,8].

The majority of studies have concluded that the fading of multiannual cycles is caused by climate warming, that is most pronounced in the winter season, which has led to dramatic increases in the frequency of deep winter declines linked to changes in snow cover. The importance of snow cover for the cyclic dynamics of vole populations was first recognized 30 years ago by Hansson and Henttonen [9]. There are several views regarding the most critical changes in snow cover parameters that are the main ecological factors responsible for increased winter mortality and collapsing vole population cycles. Among the underlying factors, the shortening of the winter season resulting in a decreased duration of snow cover is thought to be important. Voles become exposed to predation for longer periods [6,10,11], especially by generalist predators [4,3]. Other authors point towards detrimental changes in the snow structure. Although the snow cover in northern Europe is still deep and long-lasting, the snowpack becomes interspaced with ice crusts due to the effect of winter temperature fluctuations, which makes it too hard [5]. Increased snow hardness, especially at the base of the snowpack, precludes the formation of the subnivean space [12,13], which is a basic microhabitat of wintering voles. Well formed subnivean space provides the conditions necessary for successful winter survival, and spring abundances at the level required for cyclic peak densities, by ensuring access to food, facilitating escape from subnivean predators, and providing thermal isolation and good aeration of burrows [14,15].

Local mammalian and avian predators depend heavily on a repeatable influx of rodent biomass, adapting their reproduction to the episodes of lavish food supply in peak years [16,17,18]. It is predicted that collapsing population cycles and the decline in vole numbers will significantly affect local predator communities by decreasing the survival of predators specializing in rodents and by causing population declines in alternative prey species. Indeed, some of these events have already been observed, especially in northern communities [4,19,5].

In this report we examine the impact of recent climate warming on the dynamics of vole populations in Poland:

1. We present data indicating that similar changes in vole population dynamics have occurred south of 60° N, in open habitats of Poland (49°-54°N). While density oscillations were always less regular here than at more northern latitudes, certain vole species produced cyclic peaks of high abundance in some regions, but recently these peaks have faded.
2. Accepting the hypothesis on the effect of winter conditions on vole dynamics, we test which winter climate factors have been most important for successful over-wintering of the root vole *Microtus oeconomus* population in the open marshland of Białowieża Forest studied over 12 years.
3. Using long-term data provided by the meteorological station of Białowieża National Park, we analyze how important winter weather factors, specifically the characteristics of snow cover, have changed over the last 50 or so years (since 1960).
4. Finally, we show that in temperate regions (in Poland), a decline in small game abundance has occurred over the last 20 years, which supports the “black scenario” for local biodiversity due to vanishing high peak numbers in vole population dynamics.

2. MATERIALS AND METHODS

2.1 Winter Weather Data

The winter weather characteristics in Białowieża National Park employed in this study are based on long-term data on the mean daily temperature and snow cover depth recorded by the local meteorological station. A number of parameters were calculated for each winter season (November 1 – March 31): (1) the mean temperature and snow cover depth; (2) the number of days with snow cover of any depth, and of at least 5 and 10 cm depth (assuming that only snow cover above a minimum depth is meaningful for rodent survival); (3) the “sum of frost” measured as the sum of temperatures below zero and used as an indicator of the winter severity; and (4) the duration of the thermal winter, defined as the number of days between the first and the last day with a mean negative temperature.

For the purposes of this study, the records for 48 winters (1960/1-2007/8) were divided into four periods of 12 years each [1960/1- 1971/2, 1972/3-1983/4, 1984/5-1995/6, 1996/7-2007/8; hereafter the year of the start of a cold season (November) will be used to represent the whole season], and for each of these four periods, mean values of the aforementioned weather parameters were calculated and statistically compared for the assessment of long-term winter climate change.

Over the last 12 years, we have carried out a study of the *Microtus oeconomus* population in a sedgeland habitat of Białowieża Primeval Forest (see below). During this period, the annual values of the climatic factors were used to evaluate correlations between winter weather conditions and root vole population performance.

2.2 Vole Density Assessments

The population of *M. oeconomus* inhabiting open sedgeland in the Narewka river valley in Białowieża Primeval Forest was investigated between 1996-2008 on a 1- hectare plot using the CMR (catch-mark-release) method. Voles were trapped three times a year (May, July, September) in 100 live traps arranged in a 10 x 10 m grid. The vole density was estimated for each trapping session using the MNA method (Minimum Number known to be Alive – [20]). r More information on the site and methods employed is given in [21,22,23]. In this report, the annual vole abundances are represented by autumn vole densities. The number of overwintered individuals present in the population in May is taken as a measure of successful winter survival and as the predictor of the population growth rate in the following summer.

Data on the root vole density in the same sedgeland and adjacent open habitats of Białowieża were earlier collected by other autors [24]. As a proxy for vole density, they used an index of the number of individuals caught per 100 trap-nights. By combining their data with those of the present study it was possible to follow the root vole population dynamics over 23 years.

Data for another species, the common vole *Microtus arvalis*, come from long-term monitoring carried out in Poland until 1992 by regional plant pest control agencies [25]. Vole densities were assessed by a "short-cut" method: the number of reopened vole burrows per hectare. For the purposes of this study, data from western Poland were used, where population cycles were the most regular and peak densities the highest. This monitoring was extended in part of the same region (Obra river valley) in the years 1993-2000 [26]. The combined data from these two sources were used here to illustrate changes in common vole population dynamics over 25 years.

2.3 Small Game Abundance

Data on harvest levels of several small game species in years 1991-2007 for the whole country, provided by the Polish Hunting Association [27], were employed here as an indication of the abundances of these species in Poland.

3. RESULTS

The population dynamics of two vole species, *M. oeconomus* and *M. arvalis*, exhibited marked changes in the pattern of density fluctuation over the period under study. Population cycles, fairly regular until the late 1980s or early 1990s, subsequently changed to become more erratic fluctuations, that over the next ten years never reached the maximum density levels recorded earlier (Fig. 1). Since the disappearance of regular cycles in northern Europe has been attributed to frequent deep winter declines, resulting in low vole densities in spring, we tested the hypothesis that the spring number of overwintering individuals depends on certain characteristics of winter weather and tried to identify the most significant contributory factors. For this purpose, our 12-year data on the number of overwintering *M. oeconomus* individuals in the Białowieża population under investigation (dependent variable) was related to data on winter weather in the preceding cold season derived from local meteorological records (see METHODS). A strong significant multiple correlation ($R^2 = 69.0\%$, $p = 0.02$) was found for the following independent variables: duration of snow cover over 5 cm deep (Sn5), combined with "sum of frost" ($-\sum T < 0°C$) and duration of the thermal winter (N_{days}). The equation of the fitted model was $N_{voles} = 34.3 + 0.145 \times Sn5 - 0.023 \times (-\sum T < 0°C) - 0.235_{*} \times N_{days}$. The significance level was $p<0.05$ for all of these independent variables

(Table 1). AIC analysis revealed that this was the optimal model, with the lowest AIC_c among the set of considered competing models. Thus, all the parameters used in the multiple correlation might be regarded as important predictors for the number of winter survivors (Table 1).

The hypothesis that global warming has significantly changed winter conditions (and in consequence may have affected vole population dynamics) was tested by examining the long-term meteorological records of Białowieża National Park for changes in basic climatic parameters and those shown to have a significant effect on the abundance of overwintered voles in the spring (Fig. 2). All of the examined parameters indicated a gradual increase in the mildness of winters over the last half-century. Mean temperatures and those below zero (expressed as “sum of frost”) have become significantly warmer, while snow cover depth and duration have decreased. Specifically, the duration of deep snow cover has declined more steeply than that of snow cover *per se*. The decline in the occurrence of snow deeper than 5 cm between all four of the 12-year periods examined, was significant, while for any snow cover, only the first and the last periods differed significantly (results of statistical analysis on Fig. 2). Around fifty years ago (1960-1971), snow cover was present for, on average, 97 out of the 150 days of the winter season (65%), and for most of this time it was deeper than 5 cm. In the recent period (1996-2007), the ground was covered with snow for, on average, half of the winter season (77 days), but deeper snow cover lasted only for one third of this time. The only long-term winter characteristic that remained relatively stable (yet varied considerably within shorter intervals) was the duration of the thermal winter (Fig. 2).

Finally, we examined published data on changes in the harvest level of several species of small game over the last 17 years in order to verify the predictions that declining vole densities affect other species that may serve as alternative prey for local predators (Fig. 3). The harvest level is considered here to be a reliable index of countrywide population densities. The brown hare *Lepus europaeus*, partridge *Perdix perdix*, pheasant *Phasianus colchicus* and muskrat *Ondatr azibethicus* are common alternative prey for small and medium-sized carnivores and for raptors of open habitats in Poland. Our analysis revealed that since the beginning of the 1990s the numbers of these prey species have fallen steadily in parallel with the decline in common voles [significant Pearson’s correlation between numbers of *M. arvalis* (as on Fig. 1) and the joint small game abundances for years 1991-2000: $r = 0.672$, $p = 0.033$; see also *r* and *p* for each of the small game species considered separately – Fig. 3].

Table 1. Winter weather variables as predictors of the number of winter survivors (dependent variable) in the population of *M. oeconomus* in the following spring. Multiple regression model and AIC statistics

Independent variables	Mean (SE)	Partial correlation		df	AICc	Δ AICc
		t	*P*			
Snow≥ 5 cm (Sn5)	58.58 (8.92)	3.15	0.014			
Sum of frost ($-\sum T< 0°C$)	334.78 (45.26)	-2.37	0.045			
Thermal winter (N_{days})	129.91 (3.32)	-2.53	0.035			
Selected model v. competing models						
Sn5 x $-\sum T< 0°C$ x N_{days}				8	148.81	0
Sn5 x N_{days}				9	234.87	86.06
$-\sum T< 0°C$ x N_{days}				9	283.99	135.18
N_{days}				9	289.75	140.95
Sn5				10	319.02	169.21
$-\sum T< 0°C$				10	383.67	234.86

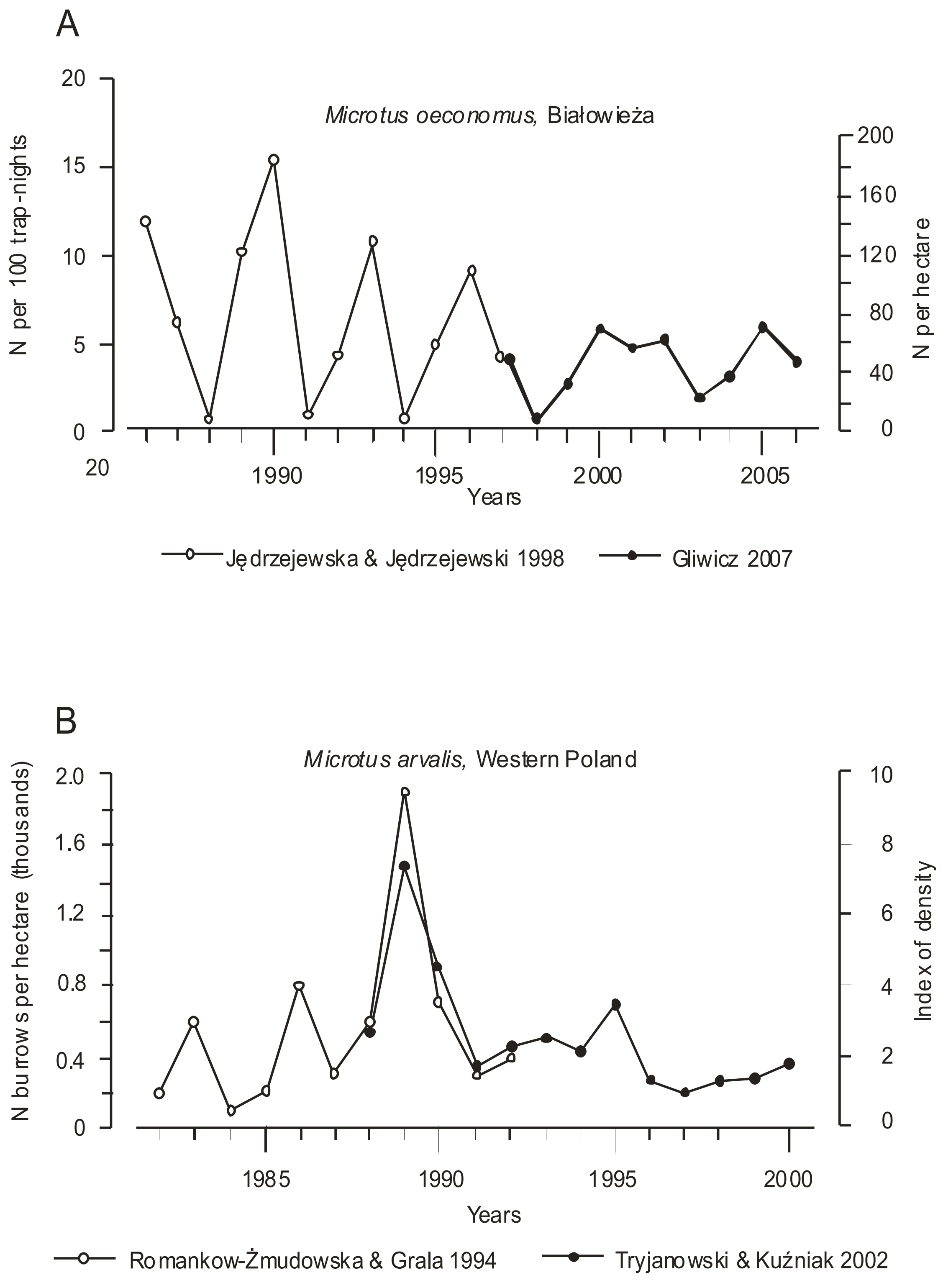

Fig. 1. Long-term population dynamics of two *Microtus* species in Poland. The combined data from two sources are plotted on both graphs

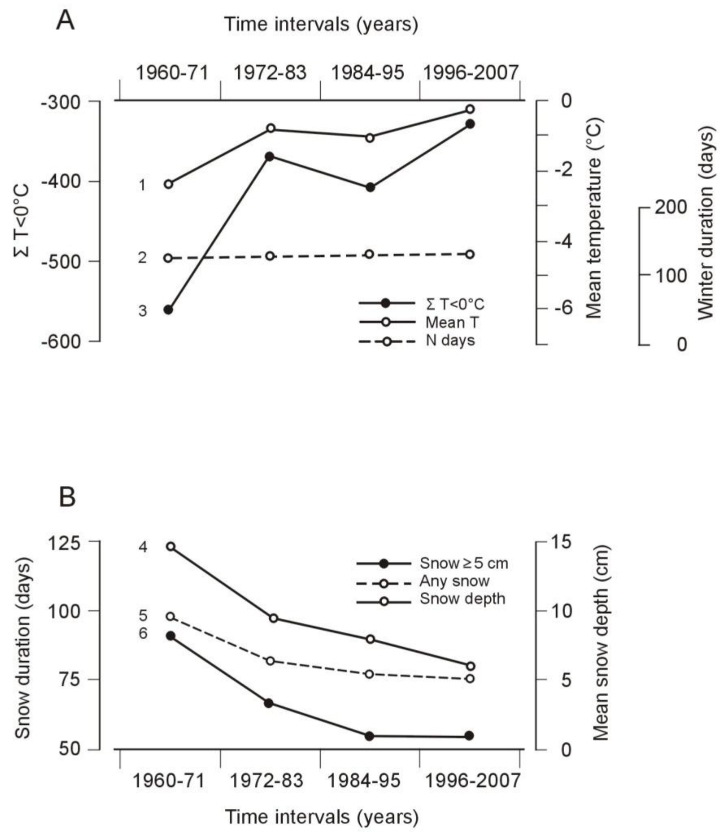

Fig. 2. Long-term winter condition changes based on temperature and snow cover recordings made at the meteorological station of Białowieża National Park. Statistical significance of the differences in the mean values for the four time intervals, as assessed by ANOVA: F = 2.94, *P* = 0.045 for curve 1; F = 44.57, *P*< 0.001 for curve 3; F = 2.80, *P* = 0.05 for curve 4; F = 3.43, *P* = 0.025 for curve 5. For curve 6, t-test: (1960-71 *v*. 1996-2007) t = 2.09, *P* = 0.048. For curve 2 - differences not significant

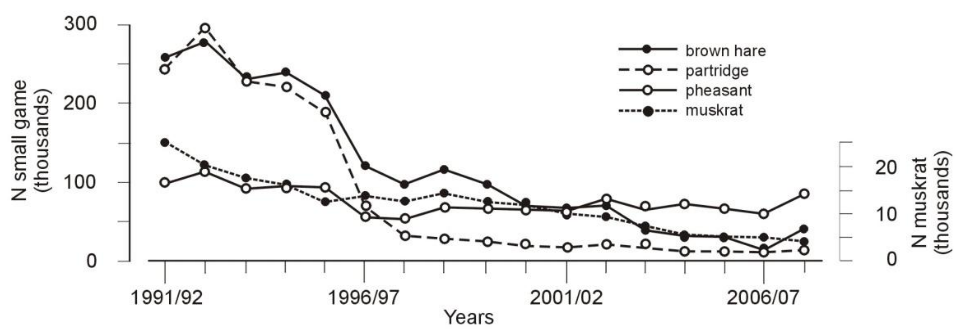

Fig. 3. Population dynamics of four small game species in Poland, expressed as harvest level in the hunting seasons of years 1991/1992-2006/2007. Data obtained from the Polish Hunting Association (after Kamieniarz and Panek 2008). Changes in the abundance of the basic small game species correlate significantly with changes in the common vole densities in years 1991-2000. Results of Pearson's correlation for log densities: hare *v.* vole - r = 0.622, *P* = 0.055; partridge *v.* vole - r = 0.664, *P* = 0.036; pheasant *v.* vole - r = 0.7756, *P* = 0.011; muskrat *v.* vole - not significant

4. DISCUSSION

The results of this study provide evidence that changes in the pattern of population dynamics of arvicolid rodents, first reported by Fennoscandian ecologists, are more widespread than previously thought and have occurred in regions situated below the latitude of 54° N. Before 1990, vole population density fluctuations in the Polish countryside were not universally cyclic [e.g.28], although many local populations of *M. arvalis* regularly underwent oscillations with s-index value much higher than 0.5 [minimum proposed by Henttonen et al. [29] as a criterion of cyclic changes] and with a frequency of 3-5 years [30]. In addition, fluctuations of *M. oeconomus* in open habitats of Białowieża, monitored before the mid-1990s, were of high amplitude and regularity with an s-index value of 0.45 [31]. Thus, the pattern of vole population density fluctuations was previously sufficiently distinct and regular for the much more erratic nature of their dynamics in recent years to be readily recognized. Furthermore, their numbers during the massive outbreaks/peak years of the past often exceeded 500 voles per hectare, and sometimes even 700-1000, especially in common vole populations [32]. Such levels have never been matched in the last 20 years. The change from fairly regular to random fluctuations and from high to much lower peak densities occurred several years earlier in the common vole (western Poland) than in the root vole (eastern Poland). This was probably because, in the generally milder western part of the country, the effect of climate warming more rapidly reached a level that impaired the winter survival of voles. A similar change in population density patterns were recorded for the field vole *M. agrestis* in central Europe [8], but the data necessary to confirm this for Poland are not available. On the other hand, we anticipate less obvious changes in the abundance of forest rodents, especially the bank vole, because the decline in depth and duration of the snow cover in forests is more moderate due to the forest microclimate, and the multiannual dynamics of the bank vole, especially in the zone of deciduous forests, seems to be more food-dependent and less predator-dependent [33,34].

The significant correlations between the number of winter survivors and the indices describing winter severity and snow conditions are in agreement with the results of recent studies [e.g.12,5,11]. We chose the number of survivors (rather than winter survival rate) as the dependent variable for several reasons. First, spring abundance of voles correlates positively with the summer population growth rate and the autumn abundance in the same year, while it does not depend on the autumn population density of the previous year. This was true in the case of the studied root vole population (unpublished data) and in other arvicoline populations of the arctic and temperate zones [5]. Second, for the occurrence of high peaks in cyclic populations and for massive outbreaks in non-cyclic ones, the increase in numbers must be continuous for two growing seasons, so that the high autumn density of the first season is well preserved at the beginning of the second season. If too few individuals survive the winter, high peaks/outbreaks will not occur. Therefore, winter conditions that negatively affect spring abundance (adverse winter hypothesis) over several years seem to be sufficient to cause dampened density oscillations and collapsing vole population cycles. Moreover, some authors suggest that repeatedly low vole abundance in successive spring seasons negatively affects population growth and dynamics of specialist predators (small mustelids) and destroys the pattern of prey-predator interactions that are considered to be the driving force of cyclic vole dynamics [4,1].

Of the three variables found to jointly determine (though indirectly) the abundance of winter survivors, the most significant was snow cover measured by a combined index of depth and duration (number of days with snow cover over 5 cm). The long-term records of snow cover in the eastern part of Poland indicated that the overall duration of snow cover was only weakly correlated with the duration of cover deep enough to be meaningful for rodent survival. Notably, this latter parameter has undergone a much more significant decline in recent years. Although it might be expected that voles prefer snow cover much deeper than the threshold set in our calculation, a depth of 10 cm or more was such a rare event in the last period of the study (in 1996/7-2007/8 mean snow depth was 6 cm – Fig. 2) that its beneficial effect on voles could not be established. In summary, our findings support the suggestions that shortening of the period with snow cover is the main factor in the decrease of spring densities at lower latitudes (< 55° N), and in consequence has the greatest influence on changing the population dynamics of voles. In addition we demonstrate the importance of a minimum depth of snow cover below which the presence of snow has little impact on survival. As suggested by Korslund& Steen [12] and Kausrud et al. [5] an appropriate structure of the snow layer in direct contact with the ground surface may also be important, although this is probably less significant (e.g. for food acquisition) in regions with generally thin and short-lasting snow cover.

The changes in the patterns of vole dynamics and the long-term decline in vole abundance have important implications for biodiversity. Since in the most of European ecosystems voles are the main prey for avian and mammalian predators, both specialists and generalists, the decline in the vole availability may affect many other species. The specialist predators, whose reproductive success depends on vole abundance, especially in spring, may dramatically decline in numbers. In Fennoscandia, long term monitoring data show such a decline in populations of several owls and in the arctic fox *Alopex lagopus* [4,35]; in the temperate zone, the Montagu'e harrier *Circus pygargus* may become strongly affected [36]. Decline in the diversity of many small and medium-sized herbivores can also be expected as an indirect effect of generalist predators switching from voles to alternative food resources like rabbits, hares and galliform birds. In Scandinavia, the recent significant decrease in populations of the mountain hare *Lepus timidus* and grouse (Tetraonidae) are believed to result from increased predation pressure [4].

In this paper we have presented an indirect evidence that shows the similar effect of climate change on species diversity in farmland areas in central Europe. The declining abundance of small game, i.e. brown hares, partridges and pheasants, indicated by data supplied by Polish hunters suggested an increasing impact of predators on these species over the last 15-20 years. Since the winters have become milder and the snow cover thinner, these potential prey, active on the snow surface, would be expected to have easier access to food resources and improved survival [37]. However, their numbers declined in parallel with vole numbers. This suggests a cause-effect relationship between decreased availability of the main prey species (voles) and increased demand by predators for an alternative food source (small game). In particular, the decrease in the frequency and level of outbreaks of *M. arvalis* might have a significant impact on the abundance of hare, partridge and pheasant because they share the same farmland habitat, and in absence of voles they become the major components of the diet of common predators [16]. A similar impact of changing patterns of *M. oeconomus* density on the numbers of other potential prey species is expected in more natural open habitats such as wetlands and meadows supporting a high diversity of birds and mammals. Further data are required to confirm this speculation.

5. CONCLUSIONS

- There is an evidence for much more erratic nature of vole population dynamics in the temperate zone regions in the last two decades.
- Adverse winter conditions (thin and short-lasting snow cover) that negatively affect spring abundance of voles are indicated as a cause for dampened vole density oscillations.
- An indirect effect of predators switching from the declining main prey (voles) to alternative food resources like rabbits, hares and galliform birds may strongly affect species diversity of field and grassland habitats.

ACKNOWLEDGEMENTS

We are grateful to the staff of Białowieża National Park and the Mammal Research Institute PAS for logistic help and for providing long-term meteorological data. MichałŻmihorski help us with AIC analysis. Our research on the root vole population was supported by grants from the Polish Science Foundation KBN/MNSW no. 6P04F 03615, 3P04F 04322 and 2P04F 03930.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

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