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Conspicuous demographic and individual changes in a population of the common vole in a set-aside alfalfa field

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The termination of agricultural production in intensively managed fields leads to the succession of weed communities and to changes in the vegetation cover and food supply for animals. We studied a population of the common vole on a regularly managed alfalfa field in southern Moravia (Czech Republic) during two and a half consecutive years. When the field was set aside, the vegetation cover transformed significantly and we studied the same vole population for the next three years. Multi-annual variation in population size disappeared; maximal abundances decreased, and mean body size tended to be lower in the weed-filled habitat. We observed conspicuous seasonal patterns in the proportion of breeding females, sex ratio and in litter size variation; however these patterns did not depend on the field management regime. The set-aside field had a strong effect on vole population dynamics; however, other well-designed studies are needed to distinguish between the possible causal processes (immigration, natality or survival) of the observed changes.

Introduction

Many vole species exhibit pronounced multi-annual changes in population density, i.e. population cycles (Finerty 1980, Stenseth & Ims 1993). Hypotheses proposed to explain these changes focus on various exogenous and endogenous factors, such as predators (Hansson & Henttonen 1988, Hanski & Korpimäki 1995), the abundance (Lack 1954) or quality (Agrell *et al*. 1995) of food resources, or individual traits such as genotype (Chitty 1960, 1967) or age (Boonstra 1994, Tkadlec & Zejda 1998a). These factors are assumed to be involved in feedback mechanisms controlling vole population numbers.

Food availability is an extrinsic factor clearly limiting population growth; however, its role in cyclic dynamics is not evident. Experimental addition of food results in earlier maturation (Bujalska 1975), a longer reproductive period (Saitoh 1989), increased survival (Schweiger & Boutin 1995), a higher proportion of reproductively active animals (Desy & Thompson 1983), lower vulnerability of offspring to direct killing and/or detrimental effects from other females (Jonsson *et al*. 2002), and to higher population densities (Desy *et al*. 1990, Yoccoz *et al*. 2001). Vole populations that have succeeded in escaping regulation by predators are limited in growth by a lack of winter food (Huitu *et al*. 2003). Nev-

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ertheless, food addition was not able to prevent population decline after a peak (Henttonen *et al.* 1987, Stenseth & Ims 1993, Krebs 1996). Even though it is documented that vole populations at peak periods can cause considerable destruction of food resources (Stenseth & Ims 1993), food quantity is a limiting factor mainly for large mammals and only exceptionally is considered to have a function in causing population cycles in microtines (Turchin *et al.* 2000).

Food quality hypotheses have recently been reconsidered. Since the original work of Kalela (1962), other food quality hypotheses have been generated. It is frequently observed that small mammals are strongly selective when given a choice, and selected food plants are typically low in phenolics and fibre, and high in protein (Hambäck *et al.* 2002 and reference therein). Chemical compounds in the consumed plants (mainly phenolics) provide the necessary feedback mechanism for population regulation. Renewed food-based hypotheses include the role of some micronutrient requirements (Batzli 1986) as well as the effects of non-nutrient plant compounds such as hormone-like substances, alkaloids, and phenolics (Berger *et al.* 1977, Sanders *et al.* 1981, Haukioja 1980). These hypotheses are supported by a direct analysis of habitat carrying capacities, changes in diet composition, feeding experiments, and the analyses of nutritional parameters in the ingested food (review in Butet 1996).

The common vole, *Microtus arvalis* (Pallas, 1778) is the most numerous vole species in central Europe. The species is characterized by overlapping generations with a non-stable age structure (Jánová *et al.* 2003), multi-annual and seasonal density changes (Tkadlec & Stenseth 2001), rapid sexual development of females, which are capable of fertile mating at two weeks of age (Tkadlec & Krejčová 2001), and cohort specific reproductive tactics (E. Jánová unpubl. data). Recently, it has been found that food quality (Butet 1996) is associated with the occurrence of a population outbreak. It suggests that food supply can influence this species' population dynamics. As part of a larger research project exploring various demographic changes within fluctuating populations of the common vole in the agricultural landscape of southern Moravia (Czech Republic), we snap-trapped one population of this species during two 3-yr periods strikingly differing from each other in terms of habitat composition and food supply. Both parts of the study were performed in the same area. The change in vegetation cover was, thus, the most important factor that can influence changes in the population.

We compared individual and population parameters of the common vole and tested the hypothesis that food supply, in terms of a land-use change, does not influence population dynamics and structure of the natural population of this species. More specifically, we predicted that common voles in a suboptimal (i.e. weed-filled; Balmelli *et al.* 1999) habitat will exhibit changes in their population structure and dynamics. (i) A decrease in vegetative biomass and the quality of the food supply should lead to a decrease in mean vole density and the level of cyclicity (Cole & Batzli 1978, Huntly & Inouye 1987) therefore in a weed-filled habitat we expected a lower vole population density. (ii) Animals in suboptimal habitats should reach a lower body mass owing to a decrease in food quality and quantity (Cole & Batzli 1978, Adamczewska-Andrzejewska 1981). Hence we predicted that common voles in a suboptimal habitat should be smaller in size than in the cultivated alfalfa field with optimal food supply. (iii) The common vole population sex ratio varies consistently during the year with more males in winter and more females in summer and this pattern is caused by sex differences in recruitment (Bryja *et al.* 2005). During favourable conditions (i.e. in years with a high alfalfa production), we predicted more pronounced shifts towards female recruitment in the spring leading to a rapid population growth rate during the first half of the year. (iv) If reproduction in suboptimal habitats is lower and the reproductive season shorter (Cole & Batzli 1978), we expected a decreased proportion of breeding females in the weed-filled field at the beginning and at the end of reproduction. (v) If litter size increases during better conditions (Gustafsson *et al.* 1983), females living in more productive alfalfa fields should have larger litter sizes.

Material and methods

Habitat structure and food supply

The common vole population was studied in an alfalfa field near Drnholec in southern Moravia, Czech Republic (48°53´30´´N, 16°27´30´´E); the study plot was 500 × 900 m during the first three years (1996–1998), but after ploughing decreased to 200 × 900 m (2001–2003). During the first period, research was carried out in a newly established and intensively managed alfalfa field (hereafter called MAN), while during the second period (2001–2003) the same field was set aside (hereafter called ABA), and consequently its plant composition changed markedly (Heroldová *et al.* 2005). The study site was surrounded by crop fields where the main production was corn, barley, maize and sunflower. The study area was devoid of perennial vegetation that could be used by voles (Holišová 1959). Vegetation cover was sampled four times a year (March, May, July and October) by removing the above-ground biomass from randomly placed 0.5 × 0.5-m plots. Plot number varied according to vegetation cover heterogeneity (from 9 to 20 plots). Plants were clipped at the soil surface, divided into species and dried at 70 °C to a constant weight. As seeds are important food supplies for rodent species, seed biomass was evaluated separately according to Rychnovská (1987).

Population sampling

The vole population was sampled by regular monthly snap-trapping from May 1996 to September 1998 and from May 2001 to September 2003 (plus an additional trapping session in January 2001). Snap traps were baited with fried wicks (soaked in fat and flour) and exposed for one night at lines of 100 traps (usually three parallel lines). Traps within a line were placed 3 m apart. The trapping lines were placed in different localities in each season, yet the whole study plot was covered equally. No traps were closer than 50 m from the borders of the study field. The traps were inspected in the morning and all captured individuals were weighted, sexed, measured and dissected. In total, 1634 common voles were snap-trapped during the study. The reproductive state of females was identified as breeding (i.e. with recent placental scars on the uterus or with embryos) or non-breeding, and the number of embryos was recorded.

We assume that the removal of individuals from the population had no discernible effect on the common vole demography. If however it did, the influence on the population was constant for the entire experiment due to regular intervals between trapping and a constant (one night and relatively similar number of traps) and low capture effort. The probability of catching an individual at low densities is quite low and at some trapping times during the declining phase of the population, no individuals were captured. The assumption of a negligible influence of trapping on vole population dynamics is justified by the fact that population densities of the common vole regularly exceed 1000 individuals per hectare (Jánová *et al.* 2003). Changes in vole numbers were described by using the index of number of voles caught per 100 trap-nights (relative abundance; RA). In order to restore the original variation in the data that was presumably lost due to the "saturation effect", the index was transformed by assuming a random (Poisson) distribution of voles, i.e. transformed index = [–ln(1 – index/100)]100 (Caughley 1977).

Comparison of the numbers of predators and voles

The monitoring of slots and faeces of predators (carnivores) was done in 1996–1998 at the margins of the study field on soil and snow cover, but due to a relatively small density of predators it was not measured in the second period. The occurrence of predator faeces apparently has no direct effect on the density of voles (the highest number of faeces occurred in the spring while the highest vole density occurred in the autumn). From a sample of 84 specimens of faeces, 86.9% were from foxes (*Vulpes vulpes*), followed by 11.9% from martens (*Martes* sp.) and 1.1% from weasels (*Mustela* sp.). The least weasel (*Mustela nivalis*) was occasionally captured in life traps

(Ugglan type) in an adjacent study plot (alfalfa field), where the life-trapping of voles was performed. The numbers of captured weasels were low and had no apparent relation to the vole density (their captures were randomly distributed during the study period); we, therefore, did not analyze their numbers. Because of a high vegetation cover during the second study period and mainly a high stand of alfalfa during the first period, we did not analyse the direct effects of avian predators on the vole population, although the numbers of avian predators observed in the air were recorded for each trapping period.

The fox (*Vulpes vulpes*) seems to be one of the most important predators in our study site due to its high mobility, which provides foxes with hunting possibilities in the agrocenosis quite far from hedgerows (which constitute a refuge for predators). We used the yearly numbers of foxes killed in the 10 781 ha large hunting district of Doubrava, 20 km from the study site (Ingr 2006), for the analysis of the correlation between the numbers of foxes and voles. We calculated the average number of captured voles per 100 traps for the period of May–September for every year and the Kendall τ correlation coefficient between this index and yearly numbers of shot fox. This period was chosen because voles were present from May to September in all years investigated. We did not have data on the densities of other predators and assumed that the number of foxes is correlated with the densities of these other predators (Norrdahl & Korpimäki 2002c).

The effects of land-use changes on the common vole population

The effects of a changing food supply (i.e. vegetation cover) on the vole population was assessed by comparing both individual (body length and condition) and population (sex ratio, density, proportion of breeding females) parameters in the two study periods (MAN *vs*. ABA).

First, we analysed the effects of a change in land use on the animals' body length for both sexes and on the body condition of males. Body condition was calculated as the ratio between body weight (g) and body length (mm) — the higher the index, the stockier the individual (Norrdahl & Korpimäki 2002a). The body mass of females may be affected by pregnancy, so we did not calculate the index of body condition for females. We had to bear in mind the influence of year on body size due to the influence of cyclicity and inter-seasonal variability (Tkadlec & Zejda 1998a, Norrdahl & Korpimäki 2002a). The body size of males is larger than that of females (i.e. Niethammer & Krapp 1978, Tumur *et al*. 2005), so the sexes were analysed separately. Mean body size is highly variable throughout the year — parameters such as sex ratio (e.g. Oli 1999, Norrdahl & Korpimäki 2002b) or a changing age structure (Jánová *et al*. 2003) can affect results in a multifactorial analysis. Due to seasonal changes in body size and differences between the sexes, each season had to be analyzed for each year and sex separately. To increase sample sizes for statistical analyses, the data used in the body size and condition analyses were grouped over 3-month periods, i.e. spring (March, April, May), summer (June, July, August), autumn (September, October, November) and winter (December, January, February). For example, the winter of 1996 started in December 1996 and continued until February 1997. Only samples with more than ten individuals were used in the analyses of body condition. Data on body size during the spring and winter of 1996 and body condition of males in the spring of 2001 were not analysed due to the paucity of the data. In 2003 only the body size of females during the summer could be analysed. The effect of management (MAN *vs*. ABA) and year on the body parameters in each season was analysed using a nested analysis of variance designed (years nested in management). If year turned out to be statistically significant, a post hoc Tukey HSD test was used to determine where these differences were (Statistica, Statsoft 2000).

Second, we evaluated the effects of changed habitat conditions on the vole population structure, e.g., the population sex ratio and the proportion of breeding females in the population. Sex ratio in the population was calculated from the numbers of individual captured in snap traps. Capture probability of the common vole did not exhibit a consistent sex-dependent pattern in live traps (Bryja *et al*. 2005) and we expected a similar pattern in snap traps. We thus assumed that the sex ratio obtained directly from catches is a robust parameter and is a true reflection of the real population sex ratio. The analysis of variation in the sex ratio between years was not possible because sampling was complete only in two years (1997 and 2002). As sex ratio in the common vole population varies seasonally (Bryja *et al*. 2005), we divided the data into two-month samples. First, we compared differences in the sex ratio in each of the two-month periods between all years using a χ^2-test. Thereafter, we compared differences in the sex ratio between the ABA and MAN periods (numbers of males and females were lumped together for all years per management type), using a χ^2-test in the two-month period. The number of breeding and non breeding females in the breeding season was analysed separately for each year because the proportion of breeding females in a fluctuating population varies strongly between years according to the phase of the cycle (Tkadlec & Zejda 1998b, Norrdahl & Korpimäki 2002b). Subsequently we analysed the numbers of breeding females from the MAN and ABA periods by pooling their numbers as in the analysis of sex ratio. Owing to low sample sizes, we lumped together the animals from April to May, June and July; while August, September and October were analysed separately. The observed and expected numbers of breeding and non-breeding females were compared using a χ^2-test.

Third, land use could affect demographic parameters such as litter size or population growth rate. Litter size was determined from the number of embryos found in dissected pregnant females. The embryos of females from 1998 were excluded from the analysis due to a small sample size. Litter size varies during the reproductive season (Myllymäki 1977, Bryja 2000), therefore season (as the number of days from the beginning of the year) was used as a continuous predictor in a general linear model, where the effects of field management was tested. The population growth rate per week was calculated as the increase in RA between May and September (data were available for these months in each year) divided by the number of weeks in these periods. However, maximal abundance was sometimes gained earlier in the year, so we also calculated the maximal population growth rate per week from May to the trapping season when maximal abundance was observed. If a population decline appeared during the year, the maximal growth rate was estimated from the differences in RA in May and trapping action with the lowest RA; the maximal population growth describes the maximal decrease of density in this case.

Results

Habitat structure and food supply

In the first period of the study (MAN, 1996–1998), the available plant biomass consisted almost exclusively of cultivated alfalfa. Its dynamics during the course of the year was influenced by a regular harvesting and biomass decline steeply twice a year. During the vegetative period, a great amount of green diet was available to herbivores (mean = 193 g m^{-2} from March to October). Weedy species were presented in the field in low numbers mostly only in spring and autumn and reached a maximum of 14 g m^{-2} in October 1998 (Fig. 1).

In 2001 the alfalfa was six years old and the field was left aside. It was only mowed in July 2001 but the dry alfalfa biomass was left in the field. Weedy species rapidly colonised the field. The first dominant weeds in the autumn of 2001 were *Capsella bursa pastoris* and *Stellaria media*. An invasion of other annual weeds such as *Amaranthus* sp. or *Chenopodium* sp. started in the spring of 2002. These annual weeds soon dried up and produced seeds. In 2003 a high diversity of annual weeds was enriched by perennial species such as grasses (for details on plant succession *see* Heroldová *et al*. 2005) and in the autumn (October), all species produced as much as 200 g m^{-2} of seeds. With the succession of weeds, the biomass of alfalfa decreased (Fig. 1). During the vegetative part of the set-aside period (ABA, 2001–2003), the mean biomass of alfalfa was 66.6 g m^{-2}. In 2003, the mean biomass of alfalfa (from March to October) was only 8.9% of the total biomass.

The effects of land-use on vole dynamics

During the course of the study, the vole popula-

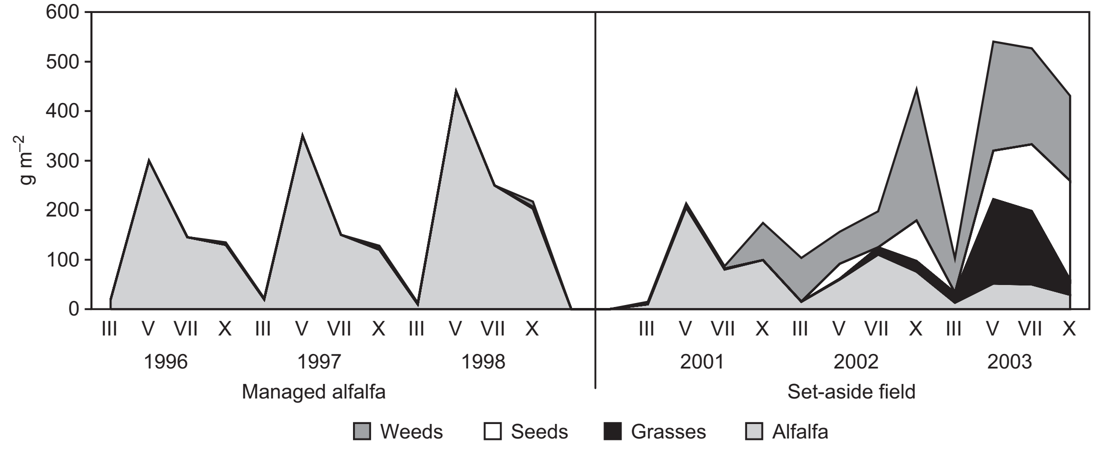

Fig. 1. Changes in dry plant biomass in the experimental field (g m^{-2}). Plant biomass was divided into four groups: alfalfa (green parts of the alfalfa), weeds (all herb weeds), seeds (all seeds), and grasses (green parts of grasses).

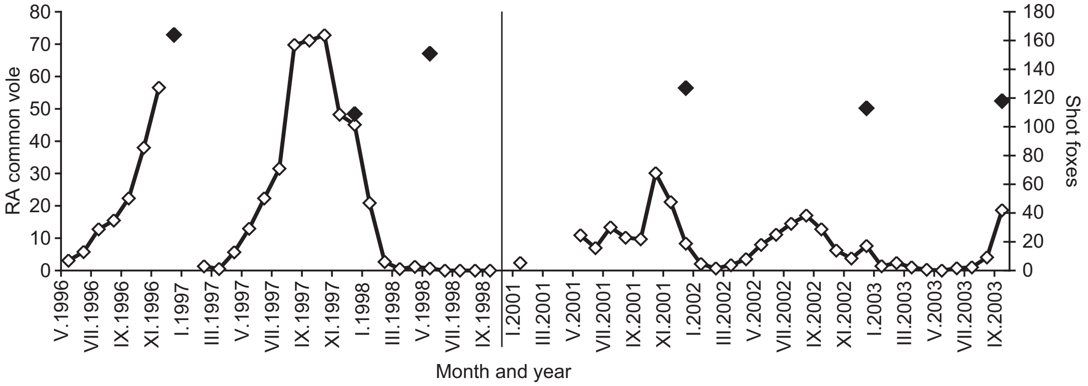

Fig. 2. Fluctuations in vole numbers represented as RA, i.e. the number of voles caught per 100 trap-nights recalculated for the saturation effect (empty diamonds). The yearly number of shot foxes in the hunting district is also indicated (black diamonds).

tion passed through large fluctuations in numbers (Fig. 2). Both intra- and inter-seasonal vole abundance variations were present in the MAN. Abundance increased from low spring densities to high densities in late summer and early autumn. Population density increased in 1996 (maximum RA = 56.5), peaked in 1997 (RA = 82), and a strong summer decline in density was observed in 1998 to almost zero. No individuals of the common vole were captured from June to September 1998. After abandoning the field in 2001, multi-annual changes disappeared; the population exhibited striking seasonal oscillations with almost zero densities in the spring and relatively high, but comparable, peak autumnal densities of 20–30 individuals per 100 trap-nights.

The correlation between predators and voles densities

The Kendall τ correlations between the average number of captured voles on 100 trap-nights and the numbers of shot foxes were non-significant (Kendall $\tau = -0.467$, $p = 0.188$), suggesting there is no direct effect of foxes on the mean annual density of the vole population.

The effects of habitat structure on individual and population parameters

Body size and condition

We analysed the effects of management and year on individual body size and condition. For both sexes, body length was smaller in the autumn of the ABA period. For males there were also marked decreases in body length during the winter and summer of the ABA period (Table 1). Furthermore male body condition was lower in the ABA than in the MAN in the summer, autumn and winter. The effect of year was significant for females in spring, summer and autumn and for males in spring body condition. This was caused by the large body size in the peak year 1997. On the contrary, smallest body sizes were, in most cases, found in 2002 (*see* Fig. 3).

Sex ratio

A decreasing proportion of males from winter to mid-summer and a subsequent increase in the autumn was a consistent pattern of the sex ratio variation during both periods of the study (Fig. 4). Negligible differences were detected in the sex ratio in May and June when fewer males in the MAN than in the ABA were observed ($\chi^2 = 3.447$, $p < 0.1$). This reversed in July and August when a higher proportion of males was observed during the MAN than the ABA period ($\chi^2 = 5.901$, $p < 0.05$). All differences disappeared in the autumn when the sex ratio became the same during both periods.

Reproductive activity

A higher proportion of breeding females was observed during April + May (Fig. 5) in the ABA than in the MAN period ($\chi^2 = 8.63$, $p < 0.05$), but only one year of each period was analysed (1997 and 2002). Generally, the proportion of breeding females in the MAN and ABA was similar in June and July, only in 2002 was breeding intensity higher than in any other year ($\chi^2 = 8.63$, $p < 0.05$). The proportion of breeding females in both periods was equivalent in August ($\chi^2 = 0.065$, $p > 0.1$), but again in September it increased in the MAN as compared with that in the ABA ($\chi^2 = 15.351$, $p < 0.001$) — in September the MAN period included data only from 1996. Also in October the proportion of breeding females in the MAN period was higher as compared with that in the ABA ($\chi^2 = 3.108$, $p < 0.1$) — only year 1997 could be analysed for the MAN period.

Litter size

In total, we obtained material from 434 litters. Litter size was slightly higher in the middle and lower at the beginning and the end of the reproduction season (GLZ; Wald statistic = 3.223, $p < 0.071$). Mean litter size was 6.15; maximal litter sizes were in June with a mean of 6.85 embryos

Table 1. The effects of management and year (nested within management; nested ANOVA) on the body size of males and females, and on the body condition of males. The spring data were analysed using one-way ANOVA becuase only two years (1997 and 2002) could be compared. Significant *p* values are set in boldface.

	Males				Females			
	Management		Year		Management		Year	
	F	*p*	*F*	*p*	*F*	*p*	*F*	*p*
Body length								
Spring	2.076	> 0.1	0.407	> 0.1	0.030	> 0.1	7.508	< **0.01**
Summer	12.772	< **0.01**	0.824	> 0.1	1.695	> 0.1	3.249	< **0.05**
Autumn	27.502	< **0.01**	0.672	> 0.1	19.10	< **0.01**	0.551	> 0.1
Winter	17.391	< **0.01**	1.672	> 0.1	15.99	< **0.01**	4.890	< **0.05**
Body condition								
Spring	1.499	> 0.1	4.010	< **0.1**				
Summer	14.062	< **0.01**	0.263	> 0.1				
Autumn	32.578	< **0.01**	1.529	> 0.1				
Winter	11.194	< **0.01**	0.210	> 0.1				

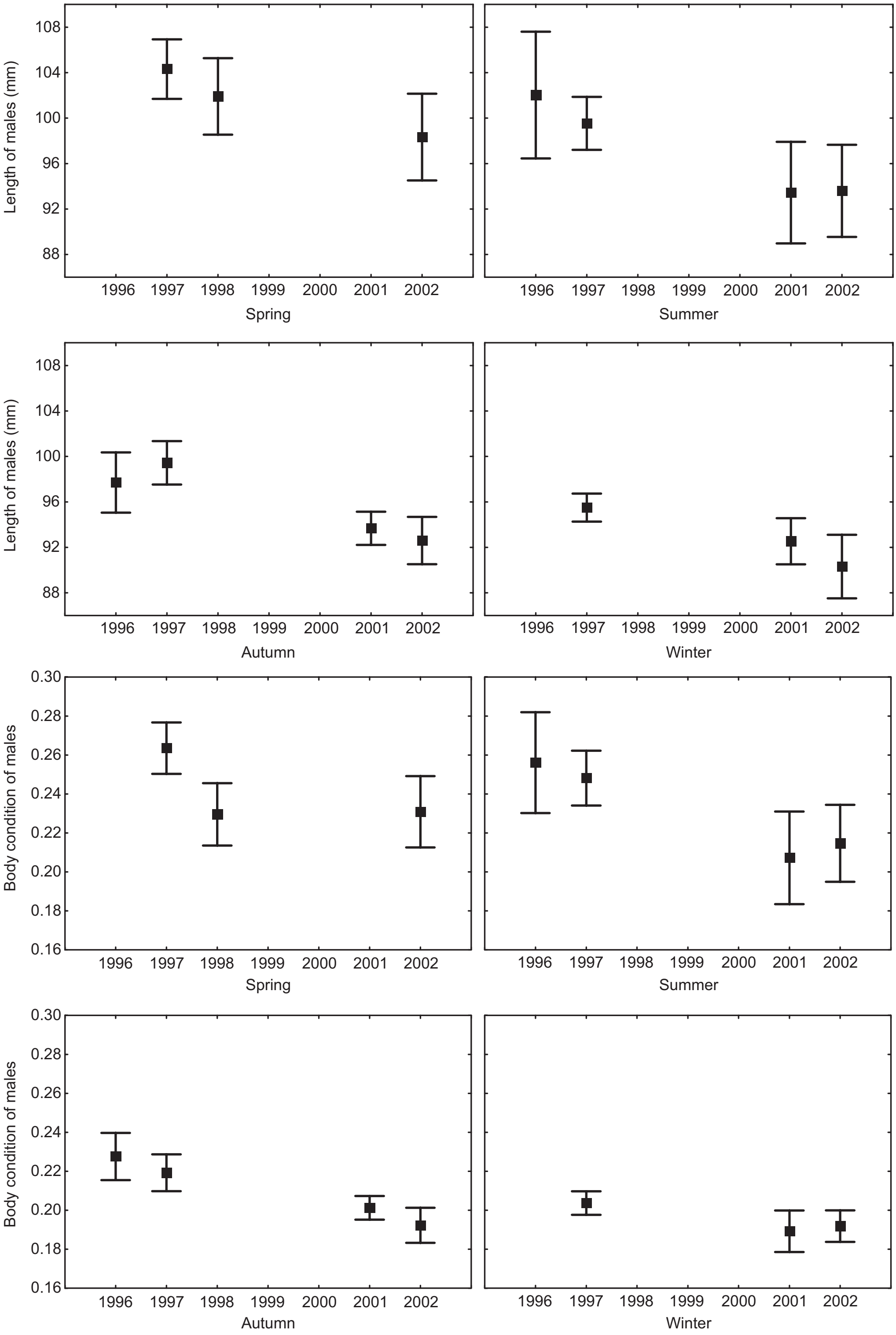

Fig. 3 (continued on the next page). Box-and-whisker plots of the body length (both sexes) and body condition (males only) of the common voles collected per season and year. Only seasons with more than 10 individuals were used to create the plots.

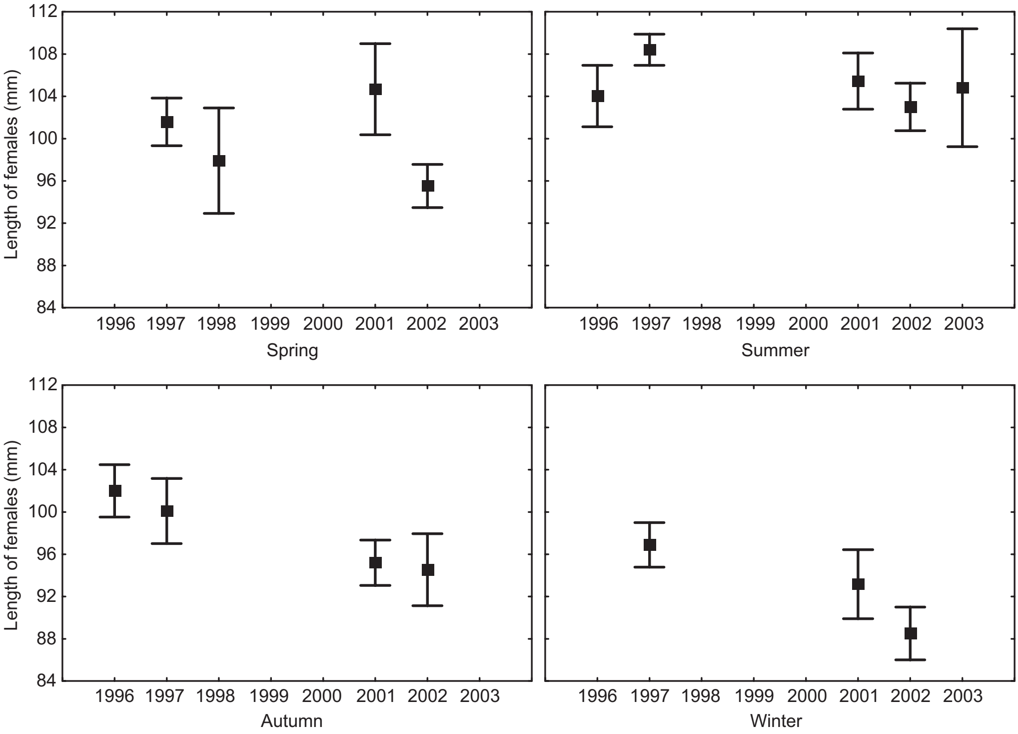

Fig. 3. Continued.

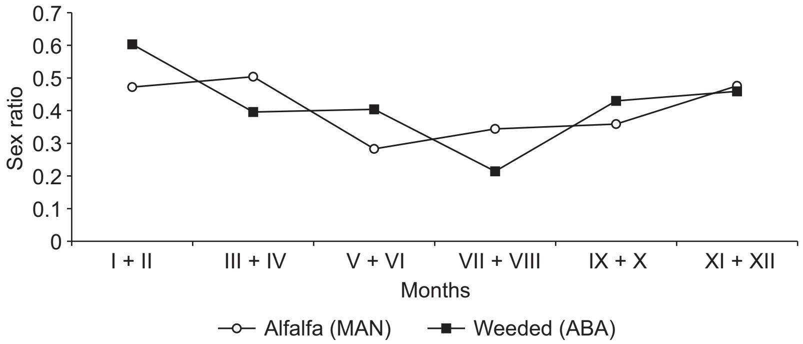

Fig. 4. Sex ratio variation during both sampling periods. The points represent the proportion of males collected in all years (MAN and ABA separately).

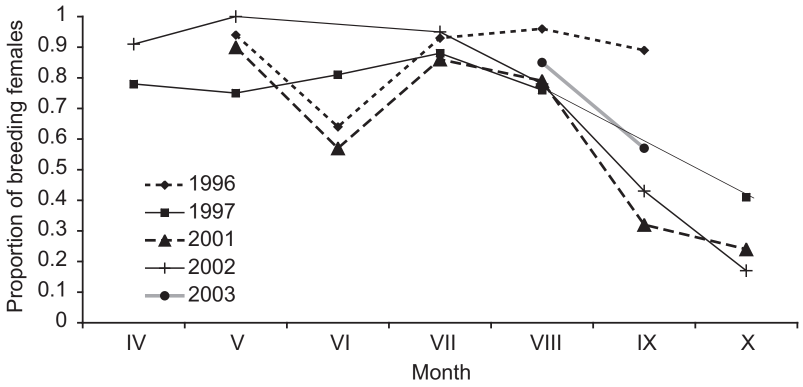

Fig. 5. Variation in the proportion of breeding females captured per month and year. Years were analysed separately due to the expected influence of cyclicity on the intensity of reproduction.

per female. Litter size did not differ between the MAN and ABA periods (GLZ; Wald statistic = 0.017, $p = 0.913$), and the interaction between management type and season was negligible (GLZ; Wald statistic = 0.021, $p > 0.1$).

Growth rate

Growth rate during the reproductive season was positive in every year except in 1998 when a strong summer decline was observed (Table 2). The highest population growth rate was in the peak year 1997 and much lower values were detected in the ABA. The negative growth rate in 2001 was caused by a higher RA in May than in September.

Discussion

We studied a population of the common vole in an alfalfa field within two 3-year periods. As the study was performed in the same locality, the two study periods were similar in local weather conditions (except for severe frost during the spring of 2003) and geomorphology (soil characteristics, elevation, etc.). The only conspicuous difference between the two periods was field management leading to pronounced differences in the plant community structure. Plant composition in the study plot significantly affected vegetation cover and other microhabitat properties leading to changes in the food supply for herbivores, including small rodents, and consequently to considerable changes in the structure of their community (Heroldová *et al*. 2005). More specifically, the proportion of seed-eating species (mainly pygmy-field mice) strikingly increased, while those preferring green parts of plants (common vole) decreased. The most numerous species in alfalfa fields is the common vole and the changes in habitat structure are expected to significantly affect their individual and population properties. In this study, we showed that in the set-aside field, the overall body size of voles decreased and that reproduction was reduced at the beginning and the end of the season as a consequence of changed environmental conditions. However, other demographic parameters, such as litter size and population sex ratio remained unchanged. The interpretation of our results should, however, be done with caution because of a lack of spatial replication.

Changes in vegetation cover and vole population dynamics

Intensively managed alfalfa was a very suitable crop plant for the common vole, providing sufficient green biomass in the vegetative season and roots and buts during winter. The vole population exhibited extreme inter- and intra-annual variation in abundance with a very high density in the peak year 1997. After the field was abandoned and the weeds succeeded alfalfa on the plot, vole population abundance decreased and the multi-annual fluctuations disappeared. Similar abundance changes were observed in the neighbouring area using life traps (*see* Bryja *et al*. 2005) and the results confirmed that 1996 is the year of increase and that oscillations disappeared after the regular cultivation of alfalfa had ceased. However, the borders between cyclic and non-cyclic populations are uncertain and longer observation periods are needed (Sandell *et al*. 1991, Krebs 1996). This is in accordance with findings that rodent populations in habitats with a low mean standing crop and cover of ground vegetation, low nutrient vegetation, successional vegetation or in sites where farmland outweighs grassland have reduced inter-seasonal fluctuations and lower peak densities (Jedrzejewski & Jedrzejewska 1996, Hansson 1999, Oksanen *et al*. 1999, Raoul 2001, Tumur *et al*. 2005).

Table 2. Vole population growth rate per week from May to September and from May to the trapping period with the highest (maximum) density.

	1996	1997	1998	2001	2002	2003
May–September	1.070	2.945	–0.015	–0.068	0.400	0.875
May–maximum	1.070	5.225	–0.40	0.828	0.400	0.875

Food availability is presumably the primary factor affecting small mammal population dynamics (Wilson *et al* 1993, Franois *et al*. 1997). Perennial crops such as alfalfa are known to be a very suitable habitat for the common vole (Spitz 1968, Heroldová *et al*. 2004). Voles prefer green parts of plants (Holišová 1959) that are produced almost throughout the vegetative period by alfalfa. During winter it supplies buds and roots. Moreover, the burrow networks of voles are well preserved in multi-annual perennial crops in the absence of yearly ploughing. Populations of voles living in habitats with predominantly alfalfa reach higher abundances than populations in habitats dominated by grasses or set-aside habitats (Cole & Batzli 1979, Markowski 1980) and abundance increases in habitats of higher food qualities (Rogers & Gorman 1995). During the first stage of our research (1996–1998) the vegetation cover was mostly alfalfa, which is the optimal diet for common voles (Holišová 1959, Balmelli *el al*. 1999) and very high abundances were observed.

During the second stage of this study (2001–2003) green biomass was abundant only in spring in the form of various green parts of weedy species and alfalfa. Very early in the summer, the dominant annual weed plants dried up producing seeds. The lower biomass of green plants during this period of the study correlated with a decrease in maximum vole density.

Alternative causes of changes in vole population dynamics

The abundance of predators, measured as the number of slots and faeces, was not high and the decrease in population densities does not seem to be caused by an increase in predation rate. The influence of food supply on vole demography is much stronger when vole densities are low or in the absence of predators (Huitu *et al*. 2003). It must be taken into consideration that voles were not the only dominant prey in the weed-filled field; the increasing number of mice (*Apodemus* sp.) in the weed-filled habitat (Heroldová *et al*. 2005) offers an alternative food source for predators. Changes in the number of predators are a consequence of a delayed density dependence on prey densities, and have a strong effect especially at low and moderate prey densities (i.e., Hanski & Korpimäki 1995, Jedrzejewski & Jedrzejewska 1996, Norrdahl & Korpimäki 2002c, Huitu *et al*. 2003), and is also dependent on vegetation cover. In addition, predation was neither sufficient nor necessary to drive the cyclic changes in some vole populations (Delattre 1984, Graham & Lambin 2002), yet the importance of predation in driving vole population cycles in central Europe is still unclear.

Population dynamics of the common vole after the phytocenological changes could not only be affected by changed trophic conditions but also by spatial and food competition with other rodent species. We observed that the abundance of pygmy field mice (*Apodemus microps*) increased significantly in the set-aside plot, a likely consequence of the high production of weed seeds (Heroldová *et al*. 2005). Unfortunately, no behavioural data on contest competition exist; however, we suppose that competition for resources exists. Food preferences of the common vole and the pygmy field mouse are different (Holišová 1959), but some food components can be shared by both species. Our snap-trapping experiment (unpubl. data) showed that some common vole burrows were used by pygmy field mice. A simple replacement of common voles by pygmy field mice was rejected, because the total number of small rodents in the study field rapidly decreased after the field had been set aside (Heroldová *et al*. 2005). Aggressive behaviour between mice and voles is not very common. For example, when a bank vole and strip field mouse meet, the contact results in an escape rather than in a fight (Kozakiewicz & Boniecki 1994). Compared to other *Apodemus* species, the pygmy field mouse is quite peaceful (Suchomelová & Frynta 2000) suggesting that the effect of pygmy field mice on vole density is not important.

We do not believe that vole emigration plays an important role in the demographic changes observed. The crops from adjacent fields were similar during all years of this study — corn, barley, maize and sunflower, which are not a preferred food source for the common vole (Holišová 1959), and we, therefore, assumed only a low rate of emigration during the short phase of green corn (May and June). Dispersal and home ranges of the common vole are quite small (Briner *at al*. 2005), therefore we assumed only random and occasional migrations between the study site and adjacent fields.

Another explanation of the disappearance of cyclicity and decreasing abundances in our study could be a more general pattern of vole population dynamics in a larger area, such as in the case of decreasing densities and diminishing fluctuations in Fennoscandia from the 1970s to the early 2000s (Hörnfeld 2004). However, regular monitoring of small mammal pests done twice a year in the region of our study confirmed the persistency of cyclicity during the 1990s and 2000s. Low (1996, 1998, 2003) median (1997, 2002) and high (2001) occurrences of the common vole in alfalfa were detected by the State Phytosanitary Administration in the whole region of southern Moravia (unpubl. data), suggesting that the relatively low density in 2001 observed in our study plot is mainly caused by changes in local conditions.

General weather patterns such as temperature and precipitation represented by the NAO index (North Atlantic Oscillation, Hurrell 1995) could affect the densities of small rodents. Yet the amount of biomass of the main food source of the common vole, such as alfalfa or perennial herbs (in the abandoned field), do not depend much on weather conditions. Data on the NAO index (available at http://www.cgd.ucar.edu/cas/jhurrell/indices.html) show that the winter NAO in the years 1996, 1997 and 2001 was negative, but in 1998, 2002 and 2003 it was positive. A positive NAO indicates warmer weather and better seed production and, consequently, higher vole densities in Scandinavia (Stenseth *et al*. 2002), however this simple prediction does not coincide with our data. A possible explanation is that the NAO index has a weak or no effect on weather conditions in central Europe, while its effect is stronger in northern and western Europe, Greenland and the east coast of Canada (Ottersen *et al*. 2001).

Changes in individual quality of voles

An individual's body size depends on the quality and quantity of the food supply (Cole & Batzli 1978, Adamczewska-Andrzejewska 1981). The abundances as well as body sizes of voles in our study decreased after changing from a well-digestive and full-year available alfalfa field to an annual and then perennial weed field. Male voles were smaller during the whole year after the change in agricultural management; the same pattern was observed in the autumn and winter in females. This pattern is usual in suboptimal habitats, such as pastures, with a higher proportion of grasses and lower densities of voles (Cole & Batzli 1979, Rogers & Gorman 1995), and is explained by better trophic conditions in alfalfa fields (Adamczewska-Andrzejewska 1981). Alternatively, smaller body sizes could be a consequence of the disappearance of cyclicity because individuals from the cyclic population have, on averages, larger body sizes than those from non-cyclic ones (Hansson 1985, Hansson & Jarrola 1989).

Larger body sizes and better body conditions of individuals as typical features of cyclic populations at peak densities (Chitty & Chitty 1960) have been regularly observed in many studies (Tkadlec & Zejda 1998a, Krebs 1996, Norrdahl & Korpimäki 2002a). We also observed a strikingly bigger body size and body condition in the peak year 1997 than in any of the other years. The body size of females in the spring of 2001 (the peak year in southern Moravia) was as high as in the peak year 1997 and their smaller mean body size in 2002 was comparable with that in the decline year 1998. This pattern was apparent and could indicate residual cyclicity of the population in the weed-filled habitat (*see* also Agrell *at al*. 1992).

We conclude that there are at least two possible causes of a decrease in vole body size in the weedy field. (1) The cyclic population in the managed alfalfa field exhibited a pronounced Chitty effect (Chitty & Chitty 1960), i.e. the occurrence of large animals in peak years. After the cycles had disappeared (either due to the changed phytocenological structure of the plot or due to climatic factors like the NAO or any other causes), the Chitty effect also disappeared and animals, on average, were smaller. (2) The changed vegetation structure and lower supply of suitable food directly affected individual development and the animals reached a lower body size as compared with that of animals living in the optimal habitat. This possibility is supported by considerable inter-annual variation in body size even after a change in habitat composition, which is a typical feature of biologically cyclic populations (Agrell *et al*. 1992, Krebs 1996).

Changes in vegetation cover and demographic parameters

The population sex ratio shifted towards a higher proportion of males before the reproductive season started, while females started to predominate from the time when young individuals (from the litters) become part of the active population. The proportion of males increased again during the second half of the reproductive season. This pattern was very similar in both periods of the study and seems to be typical for many species of voles and is caused by seasonal variation of both sex-dependent survival and recruitment (Bryja *et al*. 2005, Tumur *et al*. 2005). Even if this pattern is robust, it seems to be quantitatively affected by density with higher amplitudes of sex ratio variation in high-density years (Bryja *et al*. 2005). We thus assumed that seasonal variation of the population sex ratio will be less pronounced in suboptimal habitats with lower carrying capacities. However, we did not observe differences among sex ratios in the managed and weed-filled fields but we confirmed a robust seasonal pattern of vole population sex ratio oscillations.

We observed considerable variation in the proportion of breeding females, however we suppose it is a consequence of strong cyclicity of the population in the alfalfa field. The very high proportion of breeding females in the autumn of 1996 indicates a prolonged reproductive season in the year before peak population densities, which is typical for growing populations (Tkadlec & Zejda 1998a, Erlinge *et al*. 2000). The ratio of breeding females in the alfalfa field at the beginning of the reproductive season in the peak year was lower than in the weed-filled one. Although the relative proportion of breeding females was low in the alfalfa field, the absolute number was high and sufficient to produce great numbers of juveniles. The lower proportion of breeding individuals in the peak year could be because of a delayed age of maturation at high densities and a decreasing proportion of breeding females (Boonstra 1989, Tkadlec & Zejda 1998a, 1998b). Generally, however, better quality food (Ford & Pitelka 1984, Desy & Batzli 1989; Andreassen & Ims 1990) and a higher quantity of the food supply (Hansson 1983) result in an increase in the proportion of breeding females.

The nutrient content in food plants is an important factor in herbivore reproduction and a lower litter size is expected with lower quality food in most mammals (Cole & Batzli 1979, Batzli 1986). Seasonal variation in litter size was observed, with largest litters in the middle of the reproductive period. This could depend on photoperiod because large litter sizes were observed during prolonged light periods in laboratory conditions (Krejčová 1998). However, no effect of habitat type on litter size was found, which is in agreement with the published literature (Norrdahl & Korpimäki 2002b). Hence, lower densities in the abandoned field were probably not caused by smaller litter sizes. A lower intensity of reproduction (in terms of number of litters per season) or a higher mortality rate seems to be good candidate explanations for the observed changes in vole dynamics. However, causal factors leading to changes in vole demography after changes in agricultural management will need more specified experiments with controlled parameters such as the quality and quantity of food, and more precise estimates of emigration and recruitment. We did not find any differences in litter size, yet population growth rate in the alfalfa field was higher than in the set aside plot (according to Huitu *et al*. 2004, Steen *et al*. 2005). Changes in population growth rate might be related to increasing levels of immigration, survival and recruitment (Rogers & Gorman 1995).

In conclusion, a change in field management leads to changes in the vegetation cover and food supply that significantly influence the population dynamics of the common vole. The inter-year fluctuations disappeared and population growth rate, as well as maximal densities, decreased after the change in land-use and deterioration of the food supply. Individual body condition decreased with decreasing density. Since no changes in the proportion of breeding females, sex ratio or litter sizes were detected after a change in field management, alternative explanations for the observed changes in vole dynamics exist.

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