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Demographic responses to a mild winter in enclosed vole populations

Katrine S. Hoset · Jean-François Le Galliard · Gry Gundersen

Abstract Mild winter weather causing snow to melt and ice to accumulate on the ground has been proposed to cause the decreased survival of individuals, and less pronounced cyclicity, of small rodent populations in Fennoscandia. However, detailed data linking ice accumulation to decreased winter survival is lacking. We live-trapped and monitored with passive integrated transponders enclosed populations of root voles (*Microtus oeconomus*) exposed to different amounts of ice accumulation through a mild winter. We studied how social behaviour and survival responded to snow melt and ice accumulation. Voles avoided ground ice by moving their home ranges, thus increasing home range overlap in enclosed populations experiencing more extensive ice cover. Winter survival was not affected by the amount of ice accumulation, and was only slightly reduced during ice formation in early winter. The lowest survival rates were found at the onset of snow melt in early spring. These results suggest that ice accumulation does not cause lower survival during mild winters, probably because plastic social behaviour enables root voles to reduce the negative effects of varying winter weather on survival. The mechanisms for lower survival during mild winters may operate during spring and be related to spring floods or increased susceptibility to predators.

Keywords Home range overlap · Ice accumulation · *Microtus oeconomus* · Social behaviour · Winter survival

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Introduction

In recent years the regular and conspicuous density cycles of some rodent populations in Fennoscandia and in Northern England have become less pronounced (Steen et al. 1996; Hansson 1999; Henttonen 2000; Bierman et al. 2006), partly because the amplitudes of the density variations have reduced in size (Bierman et al. 2006). The changes in the amplitude of population fluctuations in these areas coincided with dramatic changes in winter demography, most notably accentuated winter declines and reduced strength of the delayed density dependence during the winter (Henttonen 2000; Strann et al. 2002; Hörnfeldt 2004; Bierman et al. 2006). The processes that may explain these marked temporal changes are poorly understood (Aars and Ims 2002; Hörnfeldt 2004), and may vary between populations and species living in different ecological systems. One explanation, intended for Fennoscandian conditions with high snow cover during winter,

refers to an increasing frequency of mild winters due to steadily warmer climatic conditions (Hörnfeldt 2004). In Sweden, for example, snow establishes later and melts earlier, and fluctuations in snow depth and winter temperatures lead to repeated thaw and freeze episodes, causing severe ice formation on the ground (Hörnfeldt 2004). These conditions could lead to increased predation risk, increased energetic costs due to thermoregulation, and reduced availability of food and hiding places (Hörnfeldt 2004). In Northern England, vole dynamics have also been found to correlate with decreasing length of permanent snow cover, even though the total duration of snow cover is much shorter (Bierman et al. 2006).

Prevailing winter climatic conditions may be important for the winter survival and reproduction of many small rodents (Hansson 1984; Aars and Ims 2002). Warmer and more unstable winter conditions might lead to less snow and higher frequencies of ice formation on the ground, thereby making more food resources unavailable (Korslund and Steen 2006) and increasing the probability of avian or mammalian predation (Hansson and Henttonen 1985; Hörnfeldt 2004). Insulating effects of snow diminish as snow cover reduces, thus increasing exposure to temperatures of below zero (Marchand 1996). In addition, milder climatic conditions could be associated with longer growth seasons for plants and therefore might lead to weaker trophic interactions between rodents and their food resources (Ergon et al. 2004; Bierman et al. 2006). Unfortunately, very few studies have tried to establish which factors could be critical for winter demography, and—if they are—at what time these factors affect winter demography. It is well known that the apparent survival of many small rodents is higher during winter than summer, while winter reproduction remains rare (e.g., Merritt and Merritt 1978; Yoccoz and Mesnager 1998; Aars and Ims 2002). Although some winter reproduction can occur when densities are low and/or food availability high, population growth still remains negative (e.g., Tast and Kaikusalo 1976; Hansson 1984; Tast 1984; Norrdahl and Korpimäki 2002). Furthermore, there are some indications that both autumn freeze and spring thaw may be critical to small mammal survival (e.g., Merritt and Merritt 1978).

The postulated direct effects of winter climate on the winter demography of small rodents could be dampened by adaptations that enable these species to cope with stochastic, unpredictable variations in seasonally changing environments. Small rodents in general are considered to be very plastic in their social behaviour, activity patterns, as well as in their growth and reproductive efforts (Madison 1990; Ims 1997; Tkadlec and Zejda 1998). Plasticity in these behavioural and life history traits may help reduce mortality when weather conditions deteriorate. For example, winter conditions can be associated with

huddling behaviours (West and Dublin 1984), increased tolerance for other individuals (Madison 1984; West and Dublin 1984), and lower body mass or reproductive effort (Iverson and Turner 1974). Still, very little is known about the social behaviours of small rodents that live under snow and how their social behaviours may respond to temporal changes in climatic conditions during winter. In a study involving four different winters and experimental enclosures situated in an agricultural terrain with permanent snow cover during winter (southeast Norway), Aars and Ims (2002) showed that winter survival of root voles (*Microtus oeconomus*) decreased when the number of days with mean temperature above 0°C during winter increased. They suggested that ice formation on the ground could be a plausible mechanism for their observed pattern, but could not rule out alternative explanations such as flooding during spring thaw or differential avian predation, and could not link mortality to any specific period of the winter. Korslund and Steen (2006) also showed that increased connectivity under the snow increased the survival probability of root voles in the absence of predation. Here, we study how differential ice formation on the ground may impact survival, social behaviour and space use of root voles more specifically.

During one mild winter weather spell in southeast Norway, we observed contrasting ice formation on the ground in six experimental populations of root voles. We took advantage of these contrasts to examine the potential demographic effects of ice formation in a quasi-experimental manner. We collected detailed demographic data throughout the winter to reach a far greater mechanistic understanding of individual responses than in previous studies. We predicted that root voles could respond to ice accumulation by decreasing home range size without experiencing any changes in home range overlap with other individuals. Alternatively, voles could move their home range without changing the size, in which case overlap between neighbouring home ranges should increase. These responses in space use and social behaviour could be followed by changes in winter survival. If ice formation itself affects survival, we expect winter survival to depend on the amount of ice accumulation. If snow melt or ice on the ground in winter increase exposure to free water or predators, we expect to find an overall negative effect of ice presence on survival.

Methods

Study site and general procedures

We monitored six populations of root voles established in enclosures during summer from October 2004 to April 2005 at Evenstad Research Station, Southeast Norway

(250 m a.s.l., 61°25′N, 11°04′E, Fig. 1). Each main population had access to a habitat patch (46 × 27 m) of meadow vegetation situated in each of six available enclosures (50 × 50 m). The habitat patch was situated two meters from each of three enclosure edges and confined on the fourth side by a semipermeable chicken-wire fence situated 1 m from the habitat patch. This chicken-wire fence only allowed individuals smaller than ca. 30 g to access smaller available patches on the other side of the fence (set up for a parallel summer experiment, see Fig. 1). However, when snow accumulated next to the fence, animals had the opportunity to move out of the main habitat area by climbing. We trapped the neighbouring areas during the regular trapping sessions throughout the winter to keep track of how many animals escaped the patch. Most individuals chose to stay in the source population, while a total of 24 of 221 animals moved to the small habitat patches between November and April (unpublished trapping data). In each habitat patch, 42 Ugglan live traps (Grahnab, Marieholm, Sweden) were distributed in seven rows (7.5 m apart) with six traps (5 m apart) in each row. Every second trap was equipped with tube-shaped single coil antennae for PIT-tag (passive integrated transponder) monitoring that were attached to Trovan® LID665 OEM PIT-tag decoders (EID Aalten BV, Aalten, Holland) during monitoring. Each custom-made antenna consisted of a
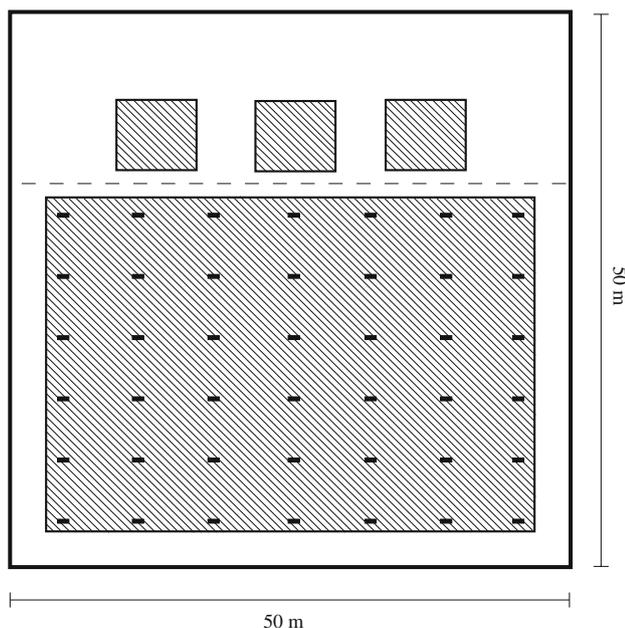
plastic tube (20 × 4 cm) and the antennae were placed on the ground along the runways to maximize recording rates (Korslund and Steen 2006). Each time a tagged vole passed through an antenna, the data logger recorded PIT-tag ID, date and time.

Founder animals used in the study originated from a laboratory population, so all individuals present in the population during the winter were either lab-bred F0 individuals, or first- or second-generation field-born individuals. At the release of individuals in May 2004, three populations were initiated at high density (approximately 80 individuals per ha) and three at low density (approximately 40 individuals per ha). Populations were allowed to develop freely during the summer, and by the middle of October we obtained a new distribution of three "high-density" (approximately 135 individuals per ha) and three "low-density" (approximately 70 individuals per ha) populations (see Table 1). We tracked populations by live trapping every third week from 14 October to 18 April, and by PIT-tag monitoring in two periods. Each PIT-tag monitoring period lasted for three consecutive days and was conducted in three populations at the same time. Monitoring occurred on 10–16 December 2004 and 11–18 January 2005 (hereafter referred to as PIT-tag sessions 1 and 2, respectively). All individuals and newborn individuals caught during trapping sessions were equipped with PIT tags (Trovan©). At the last trapping session in April, we removed all of the animals were still alive.

Winter climatic data were obtained from nearby meteorological stations [see Appendix S1 in the "Electronic supplementary material" (ESM) for more details]. We also obtained data on snow depth and snow melt from the snow map data set produced by The Norwegian Meteorological Institute (MET) and The Norwegian Water Resources and Energy Directorate (NVE). At the end of December 2004, temperatures started to rise and caused ice formation in the

Fig. 1 Schematic description of the experimental system. At one end of each enclosure (50 × 50 m) a large habitat patch of tall grass (46 × 27 m) was separated from small habitat patches by a semipermeable chicken-wire fence (*dashed line*) that only allowed individuals weighing less than ca. 30 g to move. The *black marks* show the distribution of live traps. Habitat patches are represented by *hatched areas*

Table 1 Summary of the enclosure system and experiment

Enclosure number	Density	Age structure	Winter recruits	Ice cover (% of available area)
1	60	0.83	30	43
2	80	0.38	20	17
3	70	0.43	26	47
4	140	0.36	49	49
5	110	0.45	45	18
6	160	0.44	35	14

Information on the density (individuals per ha) and age structure (proportion of adult individuals) in enclosures at the start of the study period, the total number of winter recruits in each enclosure, and the amount of ice cover on the ground in each enclosure is provided. At the start of the study, enclosure 3 had a low density and enclosure 5 had a relatively high density. From the third trapping session, enclosure 3 had a high density and enclosure 5 had a low density

habitat patches, clearly separating enclosures into two groups characterized by a high (around 45%, three replicates) or a low (around 15%, three replicates) amount of ice cover (see Table 1 and next section for calculation of ice cover). There was also a difference in the distribution of ice between the two groups, with ice being patchier in the low ice cover enclosures. These differences in ice cover were due to small differences in topography between enclosures. We were able to record the effect of ice formation on the spatial organization of the populations, as PIT-tag session 1 occurred before the ice started to accumulate, and session 2 occurred after.

Space use and ice cover estimations

We calculated home range sizes and the ice cover in the enclosures by kernel estimation using the Animal Movement 2.0 extension for Arc View 3.3 (Hooge and Eichenlaub 2000). For the home range estimates, we used enclosure-specific smoothing parameters found by including all point locations in each enclosure in both PIT-tag sessions, and calculated them by least squared cross-validation (LSCV; mean number of observations per individual per plot is 20.37) in order to restrict the amount of overestimation of home ranges due to small sample sizes (Seaman and Powell 1996; Seaman et al. 1999). We also subtracted any home range area that fell outside the habitat patch to ensure that individual home range estimates did not extend outside enclosure fences. To estimate the extent of ice cover in each enclosure, we photographed each square defined by four trap stations in every enclosure (at an angle approximately 1.5 m above the ground) at the start of the last PIT-tag monitoring (i.e., as ice accumulation reached its maximum). From the photographs, we divided the area into approximately 1×1 m squares and recorded whether the square was covered in ice or not. The area covered with ice was then estimated by kernel estimation in Arc View. To apply similar smoothing parameters to all estimates of ice cover in order to allow comparisons between enclosures, and to restrict overestimation as much as possible, we calculated a common smoothing parameter by LSCV on the jointed data on ice cover from all enclosures.

We estimated the proportion of each home range in PIT-tag session 2 (post ice period) that overlapped with the ice-covered area; hereafter named "observed overlap with ice-covered area". We also mapped the ice-covered area on the pre-ice home ranges from session 1 to estimate how much of that home range would have been covered in ice if the home range had not shifted; hereafter named "potential overlap with ice-covered area". The measurement of the potential overlap with ice cover was important to control for individual variation in risk exposure to ice, due to

differences in home range location prior to ice formation for example. We compared the observed and potential overlap with ice-covered area estimates to test the assumption that home ranges changed in a manner that reduced contact with ice.

Overlap between home ranges was calculated as the mean proportion of the home range of each individual that overlapped with all other individuals in the population in both PIT-tag sessions, and was expressed as the proportion of the total home range of each individual. Movement of home ranges from PIT-tag session 1 to session 2 was estimated as the geometric mean distance between the centres of individual home ranges in the respective PIT-tag sessions. This is a crude measurement; however, it more accurately described the movement direction than any other possibilities we had available (such as the mean distance between core areas between sessions).

Statistical analyses

In all analyses of space use, we only used data on individuals surviving from PIT-tag sessions 1–2. Home range size (50%), total overlap with neighbouring home ranges, and overlap with the ice-covered area was analysed using mixed effects models (Pinheiro and Bates 2000) chosen by a forward selection procedure in R (R Core Development Team 2005). In the analyses of home range size and overlap with ice cover, we built models to test effects of PIT-tag session, density, a factor describing the amount of ice cover (high and low), sex, age class (adult and juvenile), and recruitment rate (estimated as the number of new individuals in the populations divided by the total density). Home range size was included as an additional fixed effect in analyses of overlap with ice cover. Based on an initial evaluation of the data (Pinheiro and Bates 2000), we assigned enclosure identity as a random effect on density without an effect on intercept. In the analyses of home range overlap, we tested the effects of the same factors with a random effect of enclosure identity on both density and the intercept. Since there was no difference in home range overlap between enclosures with high and low amounts of ice cover before ice formation, we pooled the fixed factors PIT-tag session and amount of ice cover into a single factor with three levels (PIT-tag session 1 with no ice, PIT-tag session 2 with high ice, and PIT-tag session 2 with low ice) to ease visualization of the results. Home range data were log-transformed, while overlap data were arcsine-transformed during analyses to ensure that standard assumptions of normality and homogeneity were met. Data on log-transformed movement distances were further analyzed using linear models since no random variation among enclosures was found. In this case, variables included as possible explanatory factors were sex, age class, density,

a factor describing the amount of ice cover (high and low), 50% home range size, the proportion of the home range covered with ice, and the area available to each individual.

We analyzed effects of ice formation on immediate recruitment rates (proportion of new individuals in the population between PIT-tag sessions) by generalized linear regression with binomial errors and a logit link. We checked for differences between PIT-tag sessions and between enclosures with high and low ice cover. We also analyzed effects of ice formation on short-term survival ($n = 58$), long-term survival ($n = 81$) and temporal variation in survival ($n = 220$). First, short-term survival due to ice was measured to find out how ice accumulation itself affected the immediate survival probability of voles. This was considered the survival from PIT-tag session 1 (just prior to ice formation) to session 2 (just after ice formation), analysed using a GLM procedure with binomial error terms in R. We tested the effects of the potential overlap with ice-covered area, sex, age, density and enclosure. Second, long-term survival was analysed by estimating the overall survival from November to April of those individuals known to be alive in November. This analysis was done to determine how the amount of ice affected overwinter survival and to compare our survival estimates with those of Aars and Ims (2002). In addition to the enclosure level of ice, we controlled for the effects of age and body mass. Both analyses assumed that all voles were equally trappable during the winter, which was confirmed since we had very high capture probabilities (personal observation) using PIT tags (short-term survival) and when we removed all individuals in April by live trapping (long-term survival).

Third, we analyzed temporal variation in winter survival from October 2004 to April 2005 using standard open population Cormack–Jolly–Seber (CJS) models in Program Mark 5.0 based on live trapping data (White and Burnham 1999). The CJS model was run on pooled data from all enclosures to help determine potential causes of mortality. This analysis included all individuals entering and leaving the populations throughout the study, and the CJS model allowed independent estimation of apparent survival (Φ) and recapture probabilities (P). Since the study area was open, a change in apparent survival includes both permanent dispersal events and death events. Model selection was based on a small sample correction of Akaike's information criterion (Burnham and Anderson 2002). We performed a goodness-of-fit test on the global model Φ_{s*a*t} P_{s*a*t}, where both apparent survival and recapture probability depended on sex (s), age class (a, adult or juvenile, where juveniles are defined as individuals weighing less than 25 g that are not reproductively active), and time (t). using the RELEASE program in MARK (Burnham et al. 1987). The goodness-of-fit tests suggested some

overdispersion in the model (tests 2 and 3 combined, $\chi^2 = 44.47$, $df = 33$, $P = 0.086$) due to different effects of marking on future survival between groups (i.e., violation of test 3: $\chi^2 = 38.53$, $df = 27$, $P = 0.070$). This was an effect of juvenile females that were already marked as being slightly less likely to be seen again on later occasions compared to newly marked juvenile females. The violation was not strong and we decided to apply a ĉ correction of 2.46 on the AICc values (QAICc; Burnham and Anderson 2002) to accommodate this violation. The model selection procedure for survival was relatively robust against variation in ĉ such that the best model of survival remained the same with or without correction. We used QAICc to select the best possible models following the methodology of Lebreton et al. (1992); see Table S2 in the ESM for a list of candidate models. In a first step, we searched for the most suitable model of recapture rates according to gender, age and time. This minimum adequate model based on QAICc was then used to search for the best model describing survival rates according to gender, age, and time, plus the additional effects of density and amount of ice cover in each enclosure. Next, we used this best model of survival to test the additional effects of climate variables (mean temperature, variation in mean temperatures, presence of ice, snow depth, and amount of melted snow) to see if any of these climate parameters could explain the observed temporal variation in survival.

Results

Space use

The observed proportion of the 50% home range that was inside the ice-covered area in each enclosure after ice formation was significantly smaller than the potential overlap with the ice-covered area ($F_{1,78} = 19.967$, $P < 0.001$; see Table 2 for values of space use parameters). Additionally, the observed overlap with ice-covered area increased with density ($F_{1,78} = 6.528$, $P = 0.013$) and home range size ($F_{1,78} = 6.123$, $P = 0.016$). According to the best model, 50% kernel estimates of home range size only depended on density, with a negative relationship between home range size and density ($1 + \log(3.757 - 0.026[\text{density}])$; $F_{1,80} = 8.008$, $P = 0.006$), and thus did not change between PIT-tag sessions.

Geometric movements of individual home range centres between PIT-tag sessions 1 and 2 were lower in enclosures with low amounts of ice cover than in enclosures with high amounts of ice cover ($\log(2.114 - 0.522[\text{low ice}])$; $F_{1,29} = 5.935$, $P = 0.021$). Total overlap differed according to session and amount of ice cover in session 2 ($F_{2,78} = 18.198$, $P < 0.001$), and decreased nonsignificantly

Table 2 Observed mean $\pm$ SE of home range estimates (m^2, 50% kernel estimates), proportion of the home range that is located within the distribution of ice cover (proportion cover of 50% home range), and total overlap (given as proportions of 50% home range) in sessions 10 and 12

	PIT-tag session 1	PIT-tag session 2	
		High ice	Low ice
Home range 50%	33.5 $\pm$ 2.7	34.0 $\pm$ 3.0	26.1 $\pm$ 3.4
Proportion ice cover	0.33 $\pm$ 0.04[a]	0.14 $\pm$ 0.06[b]	0.14 $\pm$ 0.04[b]
Total overlap	0.09 $\pm$ 0.02[a]	0.37 $\pm$ 0.06[b]	0.08 $\pm$ 0.02[a]
Geometric movement		9.5 $\pm$ 1.3[a]	6.0 $\pm$ 1.1[b]
Recruitment rate	0.44 $\pm$ 0.04[a]	0.55 $\pm$ 0.12[a]	0.44 $\pm$ 0.10[a]

The observed mean $\pm$ SE movement distance (in metres) of home ranges from sessions 10 to 12 are given for populations with high and low ice cover. Recruitment rate is given for enclosures with high and low ice cover both before and after ice accumulation due to inherent differences in recruitment rate between these plots

Significant differences between values according to modelling are indicated by different superscript letters, where [a] differs from [b]
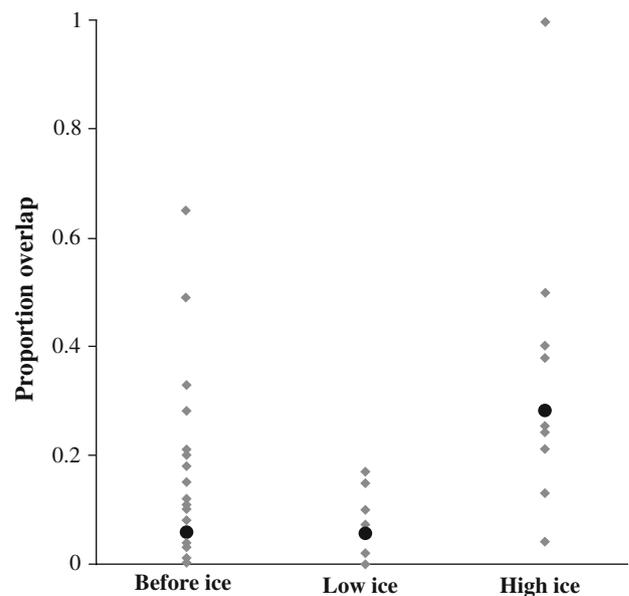

Fig. 2 Model estimates (*black circles*) and observed values (*grey diamonds*) of the mean proportion of individual home ranges that overlap with any neighbour's home range before the ice appeared and in enclosures with low and high ice cover after ice appeared

with increasing recruitment ($F_{1,78} = 0.568$, $P = 0.454$). Overlap between home ranges was lowest in session 1 and in the low ice enclosures in session 2, and highest in the high ice enclosures in session 2 ($0.01 \times \sin(0.029 + 0.029$[high ice session 2] $- 0.003$[low ice session 2] $- 0.005$[recruitment]); see Fig. 2).

Recruitment and survival

Recruitment rate did not differ between PIT-tag sessions, or between enclosures with differences in ice cover (estimated proportion of recruits in each population: 0.36 [CI: 0.28, 0.45], effect of session: $\chi^2 = 0.197$, $df = 1$, $n = 11$, $P = 0.657$; effect of ice: $\chi^2 = 0.064$, $df = 1$, $P = 0.800$). Most individuals were recruited to the populations before February; only 15 of the 205 individuals were recruited between February and April. Short-term survival probability between PIT-tag sessions did not depend on sex, age class, density, and proportion of home range covered with ice ($\chi^2 = 0.984$, $df = 1$, $n = 58$, $P = 0.321$) or enclosure. Short-term survival probability was estimated to be 0.63 ± 0.269 SE (i.e., monthly survival probability for this period is approximately 0.84). When analysing the long-term winter survival probability of individuals from the start of November until April, the best model showed that overwinter survival only depended on sex ($\chi^2 = 9.662$, $df = 1$, $n = 81$, $P = 0.002$), but was not dependent on body mass, age class, or amount of ice cover (effect of ice $\chi^2 = 0.256$, $df = 1$, $n = 81$, $P = 0.613$). Females survived 12 times better than males (female 0.24 ± 0.03 SE, male 0.02 ± 0.004 SE).

The patterns found in the analyses of temporal variation in winter survival also provided no evidence that ice cover on the ground influenced survival (see Table S2 in the ESM for an overview of the competing models). The best model of the probability of recapture showed that adults had higher recapture rate than juveniles (adults 0.96 ± 0.03 SE, juveniles 0.81 ± 0.05 SE), while there was no difference between sexes. The best model of apparent survival rate before constraining models according to climatic variables included age, time and density. The best overall model replaced time with mean temperature and presence of ice cover irrespective of amount of ice, and also included an interaction between age and presence of ice cover (Table 3). The best model did not include any effect of the amount of ice, although the difference in QAICc between the best model and a model including amount of ice was small (ΔQAICc = 1.4, see Table S2 in ESM). However, the model estimates remain the same with or without the inclusion of an effect of the amount of ice, and the effect of the amount of ice was not different from 0 ($\beta = 0.84 \pm 1.07$ SE, CI: [-1.27, 2.94]). According to this best overall model, adults survived better than juveniles before December 8 (see Fig. 3), and after this date adults and juveniles had equal apparent survival probabilities. Apparent survival of adults increased slightly from October to the middle of December, and was marginally reduced from the time of ice accumulation to the middle of February. Juvenile apparent survival increased steeply from the start of the study until the start of January.

Table 3 Effects of age, presence of ice, mean temperature and population density on three-weekly winter survival probabilities

Factors	Estimate	Standard error	95% CI
Intercept	0.67	0.78	−0.86 to 2.19
Age	−3.49	0.72	−4.91 to −2.07
Presence of ice	−1.02	0.74	−2.47 to 0.44
Mean temperature	−0.17	0.05	−0.27 to −0.07
Density	0.13	0.05	0.03 to 0.22
Age × ice	2.62	0.86	0.95 to 4.30

Parameter estimates with standard error and 95% confidence intervals were obtained from the best mark–recapture model linking factors with winter survival (see Table S2 in the ESM for the list of models and model deviances). Estimates are given on the logit scale
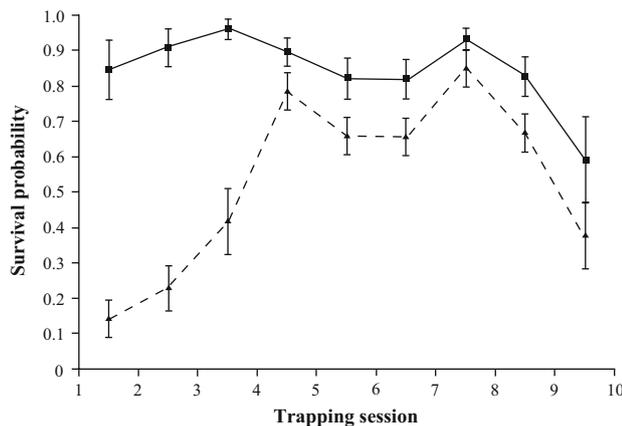

Fig. 3 Estimates of apparent survival probabilities of root voles between trapping sessions from mid-October 2004 to mid-April 2005 from the best model obtained from the program MARK. Adult survival is represented by *solid line*, and juvenile survival by *dashed line*. The dates of the trapping sessions are: *1*, October 14; *2*, November 1; *3*, November 23; *4*, December 8; *5*, January 4; *6*, January 26; *7*, February 14; *8*, March 7; *9*, April 1; *10*, April 18

Then juveniles followed a similar reduction in apparent survival during ice accumulation as adults, before it dropped from the start of spring (Fig. 3).

Discussion

In this study, we took advantage of contrasted ice formation on the ground across population replicates to examine the potential relationship between ice cover and demography in a quasi-experimental setting. Our comparison involved two levels of ice formation during the very same winter and similar populations with respect to vegetation and demographic characteristics. Hence, any demographic difference between these two treatments can be more strongly attributed to amount of ice formation than if we had conducted a correlative study involving several winters differing in many other variables (e.g., snow depth). Our

study also gives detailed information on space use and survival throughout the winter, and therefore a greater mechanistic understanding of how voles responded to ice formation during the winter than in previous studies. According to our results, ice accumulation during mild winters had limited impact on winter survival of voles, although their social and spatial behaviours changed according to the accumulation of ice. As predicted, home range overlap of root voles and the geometric movement of home range centres were affected by the amount of ice accumulated in enclosures. The mild weather episode during the midwinter was associated with slightly reduced survival irrespective of the amount of ice cover, but the most critical period for vole survival in our enclosures was the spring time, associated with snow melting and onset of reproduction.

The overlap between individual home ranges in the high ice cover enclosures was almost five times as high as in the low ice cover enclosures (Fig. 2), but home range overlap of individuals was equal in the enclosures before ice appeared and in low ice cover enclosures after ice appeared. This change in overlap could not be explained by changes in home range size, as the 50% kernel estimates did not change between observation sessions. Instead, geometric movement of home range centres from sessions 1 to 2 was higher in enclosures with high ice cover. These results imply that voles responded to the appearance of ice by moving their home ranges away from the ice-covered areas without reducing home range size. It then follows that individuals are forced together in smaller areas and overlap with each other more in enclosures where ice cover is high. The difference in behaviour between high and low ice cover plots shows the plasticity that root voles exhibit in their social behaviour during the winter season, as reported in other small rodent species during the summer season (Madison 1990; Ostfeld and Klosterman 1990). In general, this plasticity of the social system may enable root voles to respond to deteriorating winter conditions by changing their space use, providing ice-free space is available (Hoset et al. 2008). However, if most of the habitat areas are covered with ice, voles cannot avoid ice accumulation, and effects of ice formation on survival rate would be elicited (see Merritt and Merritt 1978; Boonstra and Rodd 1983).

Contrary to the marked changes in space use caused by the melting of snow and ice formation on the ground, our survival analyses suggest no apparent effects of ice formation on winter survival. The survival probability from before to immediately after ice formation did not change with the amount of ice accumulated. Similarly, the amount of ice accumulated did not affect overall winter survival. On the other hand, the three-weekly survival estimates for the winter suggest that the mild-climate period during the

midwinter had a weak delayed effect on winter survival, since survival was marginally lower shortly after the time of ice accumulation (Fig. 3). The slight delayed effect of the mild weather conditions could result from differences in thermoregulation costs, food availability, melting of the snow cover, or exposure to avian predators rather than ice formation on the ground. Effects of food depletion and energetic costs of thermoregulation would probably accumulate over time rather than affect survival immediately. Avian predation would also be independent of the amount of ice cover, which fits our results.

Why did we not find any effects of ice accumulation on winter survival? One possibility is that ice accumulation does not directly affect winter survival. Instead, ice accumulation may have indirect effects on survival during spring by either amplifying the effects of snow melting and flooding, or by reducing cover that protect against predators. Previous evidence for an effect of ice accumulation on the survival of voles in mild winters comes from correlative data where there is no possibility of linking mortality to any particular mechanism (Aars and Ims 2002). Another possibility, since we only have data from one mild winter, is that the voles were in a particularly good condition this year, which may have increased their ability to cope with harsh environmental conditions such as extensive ice formation on the ground. During the winter, we had 17 days with a mean temperature of above 0°C and a mean winter temperature of −5.6°C, and the mean winter survival probability across sex was 0.12 [0.05, 0.19]. Comparable winters in Aars and Ims' (2002) study (years 1994 and 1997 in their Fig. 3) showed a survival probability of ca. 0.02 [0.01, 0.05]. This suggests, together with the relatively high recruitment rate for the winter season, that our overwintering populations experienced good conditions (see discussion on winter conditions below) compared to those in Aars and Ims' (2002) study. Alternatively, the absence of detectable demographic effects of ice accumulation could be attributed to the potentially smaller range of variation and sample size than in previous comparative studies involving several study years. None of the experimental enclosures exhibited more ice cover than 50% of the habitat area, and more extensive ice cover may have caused substantial mortality in these enclosures. However, we lack the data on ice cover in natural habitats inhabited by small mammals in Fennoscandia required to judge the relevant range of variation in ice cover for these species.

The lowest survival probabilities occurred during spring thaw, indicating that the main mechanism causing low survival in mild winters operates during this time period. High spring mortality has repeatedly been reported in vole species under a range of environmental conditions (Krebs 1966; Krebs and Boonstra 1978; Boonstra and Rodd 1983; Taitt and Krebs 1983). A number of hypotheses have been proposed to explain this pattern. Food limitation can be important if there is scramble competition for food resources in winter. The food resources will then be depleted by the end of the winter, which causes mortality to increase (Klemola et al. 2000; Huitu et al. 2003). It is also possible that voles are more accessible for generalist predators, as the sheltering snow cover disappears during spring thaw (Hansson and Henttonen 1985; Korpimäki 1986; Hörnfeldt 2004). Furthermore, in many vole species, individuals start to disperse in spring after becoming sexually mature in order to find new available habitats with less competition (Lambin and Krebs 1991; Crespin et al. 2002), and males in particular may experience increased mortality due to higher levels of aggressive contact between reproductively active individuals (Krebs and Boonstra 1978; Boonstra and Rodd 1983; Taitt and Krebs 1983). In our populations, spring survival was low despite the fact that individuals were enclosed and had few dispersal opportunities. Thus, breeding dispersal cannot explain the spring reduction in survival in this study. As our vole populations experienced good winter conditions (see further discussion of this below), we suggest two possible explanations for the observed reduction in spring survival. Firstly, voles could experience higher mortality because avian predators gained access to the voles as the snow melted and disappeared in spring (Hörnfeldt 2004). Because of the simultaneous onset of reproduction, the voles also moved more and would therefore be more vulnerable to avian predation (Koivunen et al. 1996). Secondly, the survival probability of voles could have decreased due to an increase in aggressive encounters between individuals at the onset of reproduction, as indicated in many North American vole populations (Krebs and Boonstra 1978; Boonstra and Rodd 1983; Taitt and Krebs 1983; Lambin and Krebs 1991).

Quite surprisingly, survival was also positively related to density. Higher densities may also affect survival positively by increasing the number of runways kept free from snow and ice. This would then increase food availability, which is important for winter survival (Korslund and Steen 2006). It is also possible that aggregation into groups at higher densities increased survival through better thermoregulation (West and Dublin 1984). Thermoregulation in small rodents does indeed demand high energy output during winter (Jackson et al. 2001), and root voles have high thermoregulatory and living costs and must therefore reduce individual energy expenditure to resist the cold (Wang and Wang 1996 and references therein). Aggregation of root voles into family units are common at high density during the summer (e.g., Andreassen and Ims 1998), but the aggregation observed in this winter study still requires further investigation (Hoset et al. 2008). It has been suggested that winter aggregations are possible

because reproduction ceases and individuals become more tolerant towards each other (West and Dublin 1984). However, we observed reproduction in our study, and it has repeatedly been reported that root voles breed in winter when circumstances allow them to (Tast and Kaikusalo 1976; Tast 1984). Still, we found that root voles remain highly sociable in winter (Hoset et al. 2008 and this study). It is possible that the higher local population density caused by the coverage of large parts of the enclosures with ice and spells of low ambient temperatures in the absence of an insulating snow pack was more important in shaping the intraspecific space use in root voles.

The high winter survival rates and the occurrence of winter reproduction in our study, as judged by the recruitment of new individuals throughout the winter (Table 2), suggest that the voles were in good physical condition. The animals may therefore have been able to withstand the unexpected ice accumulation well. Good physical condition in winter suggests favourable food availability, as voles survive better during winter when food availability is high (Huitu et al. 2003), and voles are known to adjust their body mass to environmental conditions (Ergon et al. 2001; Ergon et al. 2004). Good winter conditions may also explain why we did not find an effect of body mass on survival, as reported from this site by Aars and Ims (2002). A possible alternative explanation for the good body condition could be that traps were baited during trapping, thus providing food throughout the winter. However, we used low-quality crushed oats as bait, and oats alone are not known to initiate winter breeding (Batzli 1983; Prevot-Julliard et al. 1999).

We conclude that the combination of no effect of ice accumulation on survival during ice accumulation, no effect of the amount of ice accumulated on the overall winter survival, and a constantly high survival rate throughout the winter despite the ice accumulation event suggests that ice formation on the ground does not explain low winter survival in mild winters. On the contrary, the mechanisms causing higher mortality in mild winters might operate in the transition from winter to spring. Therefore, accumulation of ice caused by mild winter weather cannot cause the reduction in vole winter survival that is thought to be the main reason for the decline in the amplitude of vole population cycles in Fennoscandia (e.g., Henttonen 2000; Strann et al. 2002; Hörnfeldt 2004; Bierman et al. 2006). Even though survival was not affected by ice formation, voles showed behavioural changes consistent with a response to the changed environment. We suggest that the plastic social system of root voles minimises the effect of environmental changes due to (for example) ice accumulation in winter, and that individuals were in good physical condition and were able to cope with adverse climatic conditions. Even though our study shows that winter climatic changes itself may not necessarily affect the winter survival of small rodents, we need to collect similar data to that described above over several winters in order to determine how important body condition is relative to behavioural plasticity in shaping winter survival patterns.

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