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# Small rodent winter survival: snow conditions limit access to food resources

LARS KORSLUND and HARALD STEEN
*Program for Experimental Behavioural and Population Ecological Research, Department of Biology, University of Oslo, Norway*

## Summary

**1.** In Fennoscandia during winter small rodents spend most of their time in the subnivean space, between the snow cover and the ground. The subnivean space is probably not a uniform habitat, but broken into accessible and inaccessible patches by ice covering the vegetation. This might reduce access to otherwise available food resources.
**2.** To test whether ice formations reduce access to food and thus limit winter survival of small rodents, we conducted an experiment where we increased subnivean space by adding corrugated aluminium sheets on the ground before onset of winter. The sheets prevented ice formation, thus mimicking natural occurring subnivean space, and providing more room for animals living in the subnivean space to forage.
**3.** During the experiment 142 *Microtus oeconomus* were passive induced transponder (PIT)-tagged, and a system consisting of fixed tube-shaped antennas and PIT-tag readers were used to provide data to analyse winter survival and individual subnivean space use. The extent of winter grazing was measured after snow melt by examining percentage area grazed.
**4.** The treatment resulted in increased survival which corresponded well with significantly higher space use and more grazing under the sheets.
**5.** Females showed a positive correlation between probability of survival and body mass while no such effect was observed in males.
**6.** The results suggest that the snow cover reduces survival in winter by physically enclosing the vegetation in ice and thus reducing access to otherwise available food resources. The amount of ice and its configuration might vary between years due to changing weather patterns. Our results offer a mechanistic explanation for variations in winter survival and suggest incorporating climate variables in future small rodent models.
**7.** Directional and long-term changes in climate might result in increased ice formation in the subnivean system. Such deterioration may lead to reduced winter survival and act by stabilizing population dynamics and dampening vole cyclicity.

*Key-words*: experiment, *Microtus*, PIT-tag, population dynamics, subnivean.

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## Introduction

Understanding small rodent population cycles requires knowledge about what initiates the population decline and what other factors are involved in driving the population to extreme lows. During winter severe subnivean conditions prevent photosynthetic activity (Tieszen 1974; Kappen 1993; Hamerlynck & Smith 1994) and plant growth (Eurola, Kyllönen & Laine 1984), and small rodents most probably have a fixed amount of low-quality food available throughout the winter (Hanski *et al*. 1993). The lack of food resource replenishment necessarily makes winter carrying capacity lower than in summer. Therefore, a healthy small rodent population might thrive and increase in an area during summer but the lower winter carrying capacity cannot support the same population size during the following winter, and a decline is the result. Such a

Correspondence: Lars Korslund, EBE, Department of Biology, University of Oslo, PO Box 1066 Blindern, 0316 Oslo, Norway. Tel: + 47 22854645; Fax: + 47 22854605; E-mail: lars.korslund@bio.uio.no

decline would result in a higher predator–prey ratio in spring, a situation that would drive the population down further (Pearson 1966; Fitzgerald 1977; Goszczynski 1977; Korpimäki, Norrdahl & Rinta-Jaskari 1991; Hanski & Korpimäki 1995). The limited amount of food resources during winter should make the overwinter survival dependent on food availability.

In winter the temperature gradient within a snow cover, between the cold surface air and the relatively warmer ground, causes water vapour to migrate upwards (Pruitt 1984; Marchand 1996). This process results in the formation of a stratum of fragile and loosely arranged snow crystals at the base of the snow cover called the subnivean space. In winter small rodents spend most of their time here, where they can find refuge from the harsh elements and most predators, and gain access to food (Fuller 1967; Pruitt 1984). The nature of the stratum facilitates movement and exploration of new areas for feeding (Marchand 1996), but the subnivean space is probably not continuous. In the 1960s and 1970s E. Østbye and colleagues measured snow conditions in alpine Norway every winter with a special focus on the subnivean space. They found that it was not a uniform habitat but was broken into accessible and inaccessible patches by ice covering the ground (Østbye personal communication). The presence of ice might reduce the amount of plant biomass available to small rodents (Hanski *et al.* 1993), and ultimately reduce carrying capacity to extremely low levels. The ice may also be responsible for the razor sharp boundaries between ungrazed and winter-grazed vegetation patches observed after snow melt (personal observation). Models have shown that inclusion of seasonal change in carrying capacity greatly enhances the ability to mimic cyclic population dynamics in voles (Hanski *et al.* 1993; Hanski & Korpimäki 1995) and time-series analysis has further shown that density-dependent regulation of population growth during winter appears to be important to produce multi-annual cycles (Hansen, Stenseth & Henttonen 1999). Therefore, ice may well explain the existence of ungrazed patches, and it will reduce the winter carrying capacity to even lower levels than those dictated by just the lack of plant growth.

Studies show that natural populations of voles can experience shortage of food during the winter in peak years (Hansson 2002) and in experiments vole populations under predator-free conditions crash due to overgrazing (Krebs, Keller & Tamarin 1969; Krebs *et al.* 1973; Klemola *et al.* 2000; Klemola, Norrdahl & Korpimäki 2000). Another experiment using food supplementation during winter has shown that winter food supply limits vole population growth and winter survival in the absence of predation (Huitu *et al.* 2003). These results, however, do not distinguish between population densities being reduced by initial food shortage caused by summer and autumn overgrazing (Bergeron & Jodoin 1995), and the carrying capacity being reduced by snow cover limiting access to otherwise abundant food resources.

For arvicoline rodents (voles and lemmings) there exists several biogeographical gradients in amplitude and degree of cyclicity: Fennoscandia (Henttonen, McGuire & Hansson 1985; Hanski *et al.* 1993; Bjørnstad, Falck & Stenseth 1995), Hokkaido, Japan (Bjørnstad *et al.* 1996; Stenseth, Bjørnstad & Falck 1996; Stenseth, Bjørnstad & Saitoh 1996; Saitoh, Stenseth & Bjørnstad 1998) and central Europe (Tkadlec & Stenseth 2001), and these gradients seem to follow a seasonality gradient (Tkadlec & Stenseth 2001). Within the Fennoscandian gradient, cycles is found primarily north of 60° N (Hansson 1971; Hansson & Henttonen 1985, 1988; Turchin 1993; Bjørnstad *et al.* 1995), and this has been explained by the long-lasting snow cover protecting small rodents from generalist predators, thus facilitating overwinter survival (Erlinge *et al.* 1983, 1984; Hansson & Henttonen 1985; Lindström & Hörnfeldt 1994; Hansson 2002). However, the snow will, most probably, also reduce the food access, and such strengthening of density dependence can also destabilize the dynamics (Hassell 1975; Hassell, Lawton & May 1976; May 1979).

The aim of this study was to assess experimentally how winter food availability and vole survival is affected by the extent of the subnivean space. We hypothesized that the properties of the snow cover reduces winter food availability and that the amount of available subnivean space limits vole space use and thus overwinter survival. Such factors limiting survival might also limit body mass growth. To test for this we ran a replicated field experiment where we increased artificially the amount of subnivean space by placing a network of corrugated aluminium sheets on the ground prior to the onset of winter. Our predictions were that the increased subnivean space would lead to higher individual space use together with increased grazing, a consequent increase in small rodent winter survival and a positive effect on body mass.

## Methods

### STUDY AREA AND EXPERIMENTAL DESIGN

The experiment took place at Finse (60°36′ N, 7°30′ E), south Norway, 1300–1400 m a.s.l in the low- and mid-alpine zones. The area is dominated by heath vegetation with large proportions of sheep fescue (*Festuca ovina* Linnaeus) and matgrass (*Nardus stricta* Linnaeus) (Dahl 1986; Fremstad 1997). Both Norwegian lemming (*Lemmus lemmus* Linnaeus) and root vole (*Microtus oeconomus* Pallas) live naturally in the area. The climate is alpine with cool summers and relatively mild winters, with high precipitation year-round and heavy snow cover lasting from late September to mid-June.

Four trapping grids (40 × 40 m, 100–500 m apart) were established in September 2002 on sites chosen to minimize differences in vegetation and topography. The grids were open and migration was allowed. All grids were equipped with 16 permanent trap stations in a 4 × 4 grid with 10-m spacing. Each trap station consisted of a 20 × 40 cm extendable stainless steel trap chimney (Schmid 1981) with lid and open base, marked with a stick. The trap chimney provided easy access from above for the trapper and from below for the animals. Each chimney was equipped with one Ugglan (Grahnab, Marieholm, Sweden) live trap and an isolating lid of 10-cm-thick Styrofoam, to make the internal temperature of the chimney subnivean-like. Close to the chimney a tube-shaped single coil passive induced transponder (PIT)-tag antenna was placed in an existing runway. Each antenna was covered by a sheet of corrugated aluminium, which prevented snow drift from blocking access, and the antenna cable was attached to a pole extending above the snow level. Encounters of PIT-tagged animals during an encounter session were recorded by attaching a Trovan® LID665 OEM PIT-tag decoder (EID Aalten BV, Aalten, the Netherlands) to the antenna.

The two treatment grids were manipulated by a network of 1-m-wide, 0·5-mm-thick corrugated aluminium sheeting connecting all trap stations. The sheets probably increased the total amount of subnivean space and prevented formations of compact snow and ice on the ground, and the specific configuration was chosen to counteract the subnivean fragmentation and increase movement. The total area covered by these sheets was 240 m$^2$, equivalent to 15% of the grid. The sheets were placed directly on the ground but the natural ruggedness of the terrain entailed that only parts of the sheets were actually in contact with the ground. This, in addition to the corrugated profile of the sheets, provided space for small rodents to move underneath.

To ensure comparable population densities in all grids and densities similar to that observed at the onset of winter in peak years, we chose to introduce animals. Prior to the experiment, during 5 days in mid-January 2003, trapping with snap-traps was carried out to remove resident animals; 0, 7, 5 and 0 *M. oeconomus* were removed from the control grids (1 and 3) and treatment grids (2 and 4), respectively (Fig. 1). Immediately after trapping, laboratory-bred *M. oeconomus* were introduced into each grid. The animals were offspring of adults trapped locally the previous summer and bred in the laboratory, and all had been kept separated by sex to prevent onset of reproduction. All animals introduced were born late during the previous autumn, but at varying dates so that the age and size composition of the groups was comparable to that of animals entering the winter. One week prior to introduction the animals were tagged with an 11 × 2 mm ID 100 A PIT-tag (EID Aalten BV) subcutaneously. The presence of the tag was confirmed just prior to introduction. A group of 25–26 animals, with an even sex ratio, were introduced into the four centre trap chimneys of each grid. Another 9–11 animals were introduced into each grid in April.

Temperature loggers were placed out on different places within each grid before onset of winter, logging ground surface temperature throughout the winter. A

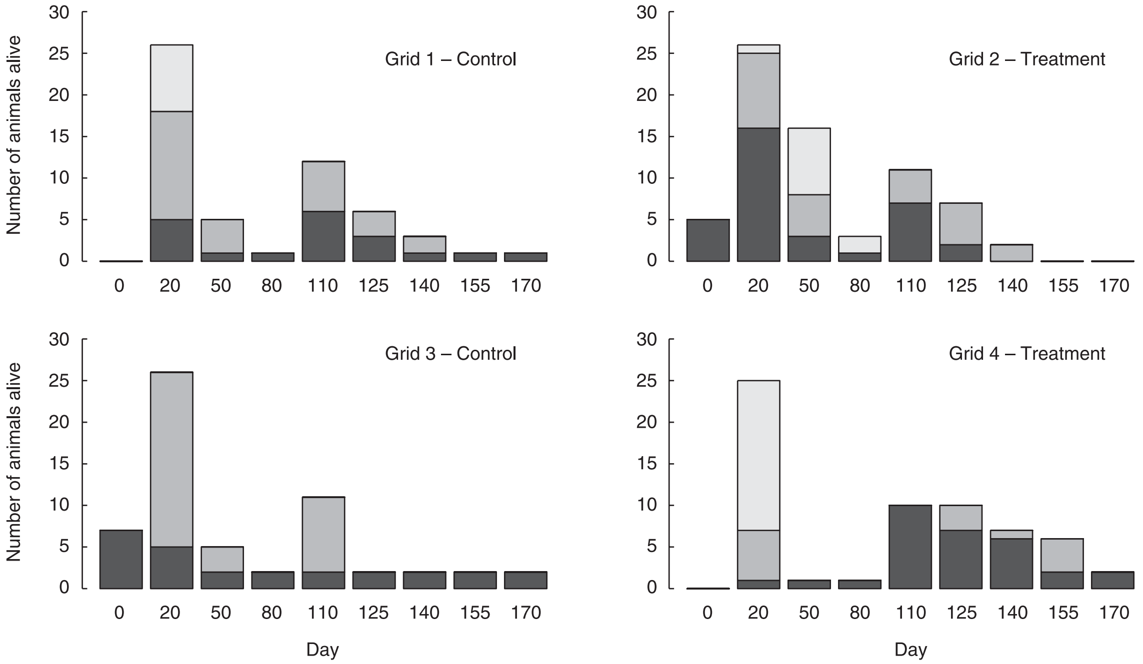

**Fig. 1.** Number of animals recorded alive within each grid during each trap session. The *x*-axis shows each session's temporal position as days after 1 January. At day 0 the bar represents number of animals present prior to the experiment. The total height of a bar corresponds to the number of animals alive. The dark grey section of a bar represents animals that survived until the next session (equal to the total height of the bar to its right). The medium grey section represents animals that did not survive until the next session, categorized as dead due to food limitation, and animals whose tags were not recovered. The light grey section represents animals that were killed by stoat and thus did not survive until the next session. The population density was not significantly different between treatment and control grids (LRT: $\chi^2 = 2{\cdot}2$, d.f. = 1, $P < 0{\cdot}14$).

visual inspection of the data gave the date of snow melt, which was defined as the first day after winter in which the ground surface temperature started to oscillate throughout the day (due to the disappearance of the insulating properties of the snow cover).

### DATA COLLECTION

Vole populations were monitored during 8-day encounter sessions once every month from January to April and bi-weekly from April to mid-June. Each encounter session was divided into two parts. During one half, the PIT-tag system was used, and during the other 4 days we live-trapped when weather conditions permitted. The Ugglan traps were baited with oat and carrot and checked once every 12 h. All animals trapped were identified, sexed and weighed and their reproductive status was determined. The use of PIT-tag monitoring ensured high-quality data for survival analysis, despite severe weather conditions making access to the experimental area impossible at times.

Immediately after snow melt, grazing damage was recorded. Within each grid 48 1-$m^2$ squares were sampled: one at random points on each of the 24 longitudinal and latitudinal 10-m lines between the trap stations [i.e. covered by aluminium sheets ('online') within treatment grids] and another 24 at random points outside these lines ('offline'). Hence both covered and uncovered vegetation were sampled in the treatment grids, and the equivalent locations were sampled in the control grids. Each 1-$m^2$ sample was divided into 100 10 × 10 cm squares and the number of squares showing signs of grazing was recorded providing an estimate of grazing intensity.

Parts of the mortality throughout the winter were suspected to be caused by stoat (*Mustela erminea* Linnaeus) as we occasionally observed faeces and tracks. Raven (*Corvus corax* Linneus), the only avian predator in the area in winter, was rarely observed, and we did not see any indication of other predators during the experiment. This minimal presence of alternative predators, in addition to a snow cover 1–2 m thick and limited vole activity on top of the snow, suggests that stoat was the main predator in the system. Because our hypothesis and predictions assumed no predation mortality we attempted to establish each individual's cause of death by searching the grids and surroundings for PIT-tags after snow melt. At the grids in which we had observed obvious signs of stoat throughout the winter, abandoned stoat nests were discovered on the ground. Because stoats have a strong tendency to cache prey (King 1989), a vole killed by a stoat (and necessarily its PIT-tag) would most probably end up in its nest. Therefore, we defined the voles whose PIT-tag was recovered in such a nest as killed by a mustelid. All voles whose tags were found elsewhere were categorized as dead due to food limitation if no obvious signs of predation indicated otherwise (Steen 1995; Steen *et al*. 1997). The remaining animals, whose tags were not recovered, were included in the survival analysis.

### SURVIVAL MODELLING AND DATA ANALYSIS

Apparent survival (called 'survival' in the following) and the recapture probability ('recapture' refers to the encounter of an animal by means of PIT-tag monitoring and live trapping) of the different populations were estimated in standard open population Cormack–Jolly–Seber models (Lebreton *et al*. 1992) implemented in program MARK 3·2 (White & Burnham 1999). As our focus was to establish how snow affects overwinter survival through food availability, all animals killed by a predator were censored at the last occasion they were known to be alive. Model selection was carried out according to Lebreton *et al*. (1992) and based on $AIC_c$ (the modified Akaike's information criterion). A goodness-of-fit (GOF) test was carried out on the global model, $\Phi_{g+s+t+(g*s*t)}\ p_{g+s+t+(g*s*t)}$ [both survival ($\Phi$) and recapture ($p$) probabilities dependent on treatment ($g$), sex($s$) and time($t$)] using RELEASE (Burnham *et al*. 1987) in MARK. The test was not significant suggesting that the fit of the model was acceptable (tests 2 and 3, RELEASE: $\chi^2 = 6{\cdot}83$, d.f. = 7, $P = 0{\cdot}45$). The recapture probability of animals within the treatment grids was equal to 1; hence this was fixed to 1 in all models in the model selection to increase detection-probability. In contrast, for the control animals recapture probability was < 1 and thus estimated in all models.

The number of recorded animals within each grid during each trap session was used to test for differences in population densities. The data were treated as repeated measurements, assuming Poisson distributed errors, and any differences of number of animals between treatment and control grids were analysed by means of generalized linear mixed models (Pinheiro & Bates 2000). The models were fitted with a change in intercept in April to account for the introduction of a second cohort.

Because live trapping was irregular, owing to unfavourable weather conditions, few animals were caught. The data on change in body mass were therefore scarce and this prevented testing the difference between treatment and control. However, it was possible to analyse difference in body mass between sexes, and a linear regression explaining the variation was modelled using the statistical package R (Venables & Smith 2002).

The winter grazing pattern was very patchy and many of the samples had no grazing, resulting in a high proportion of zeros in the data. Therefore the data were heavily over-dispersed and an assumption of a binomial error distribution was not met. Generalized linear models were employed to examine the frequency of grazing. Due to the over-dispersion, quasi-likelihood methods (Venables & Ripley 2002) were used to estimate parameters and their standard errors in R (Venables & Smith 2002).

To detect any difference in space use we counted the number of trap stations visited by each individual based on PIT-tag data. These count data were analysed by means of generalized linear models in R (Venables & Smith 2002) assuming Poisson distributed errors when estimating parameters and standard errors.

**Table 1.** Survival (Φ) models tested. All models except the global are based on constant recapture probability with treatment recapture fixed to 1 ($p_{g\_T=1}$). Group effect (control vs. treatment) is abbreviated *g*; difference between cohorts, *c*2; time effect, *t*; effect of sex, *s* and mass as an individual covariate, *m*. Mass in the second order; $m^2$ is used to test for a normalizing effect on survival

| Model no. | Model | No. of parameters | Deviance | AIC$_c$ |
|---|---|---|---|---|
| Cohort models | | | | |
| **1** | $\Phi_{g+c2+t+s+m+(s*m)}$ | 11 | 225·3 | 248·9 |
| **2** | $\Phi_{g+c2+t}$ | 8 | 233·7 | 250·5 |
| **3** | $\Phi_{g+c2+t+m}$ | 9 | 231·7 | 250·7 |
| **4** | $\Phi_{g+c2+t+s+m+m^2+(s*m)}$ | 12 | 225·1 | 250·9 |
| **5** | $\Phi_{g+c2+t+m+m^2}$ | 10 | 229·9 | 251·1 |
| **6** | $\Phi_{g+c2+t+s+m}$ | 10 | 230·0 | 251·2 |
| **7** | $\Phi_{g+c2+t+s}$ | 9 | 232·8 | 251·8 |
| **8** | $\Phi_{g+c2+t+m+m^2}$ | 11 | 228·8 | 252·3 |
| **9** | $\Phi_{g+c2+t+s+m+(g*m)}$ | 11 | 228·9 | 252·4 |
| **10** | $\Phi_{g+c2+t+(g*t)}$ | 11 | 228·9 | 252·4 |
| **11** | $\Phi_{g+c2+t+s+m+m^2+(s*m)+(s*m^2)}$ | 13 | 224·4 | 252·5 |
| **12** | $\Phi_{g+c2+t+(g*c2*t)}$ | 10 | 231·6 | 252·8 |
| **13** | $\Phi_{g+c2+t+s+m+(g*s*m)}$ | 13 | 224·8 | 252·9 |
| **14** | $\Phi_{c2+t}$ | 7 | 242·8 | 257·4 |
| **15** | $\Phi_{g+c2}$ | 4 | 264·5 | 272·8 |
| **16** | $\Phi_{g+c2+(g*c2)}$ | 5 | 262·9 | 273·2 |
| **17** | $\Phi_{g+c2+s}$ | 5 | 263·9 | 274·2 |
| **18** | $\Phi_{g+c2+s+(c2*s)}$ | 6 | 262·7 | 275·2 |
| General models | | | | |
| **19** | $\Phi_{g+t}$ | 8 | 261·1 | 277·9 |
| **20** | $\Phi_{g}$ | 3 | 271·9 | 278·0 |
| **21** | $\Phi$ | 2 | 274·2 | 278·3 |
| **22** | $\Phi_{g+t+s}$ | 9 | 259·8 | 278·9 |
| **23** | $\Phi_{g+s}$ | 4 | 270·9 | 279·2 |
| **24** | $\Phi_{g+t+s+(g*t*s)}$ | 13 | 251·9 | 280·0 |
| **25** | $\Phi_{g+s+(g*s)}$ | 5 | 270·2 | 280·5 |
| **26** | $\Phi_{g+t+s+(g*s)}$ | 10 | 259·4 | 280·7 |
| **27** | $\Phi_{g+t+(g*t)}$ | 15 | 252·6 | 285·4 |
| **28** | $\Phi_{g+t+s+(g*t*s)}$ | 28 | 233·3 | 299·6 |
| Global | $\Phi_{g+t+s+(g*t*s)}$ | 53 | 220·1 | 369·1 |

## Results

### SURVIVAL

The models that included differences in recapture between treatments were supported, but there was no support for including time or sex dependency in the recapture models. As mentioned, the recapture probability was fixed to 1 for the treatment animals ($p_{g\_T=1}$), and the control recapture probability of the best model was estimated to be 0·73 ± 0·09 (all parameter estimates are presented ± SE).

A selected set of appropriate models testing the effect of the following factors: treatment, time, sex, body mass and introduction cohort (*c*2), and interactions, where applied to the data (all models are presented in Table 1). As a result model 1; $\Phi_{g+c2+t+s+m+(s*m)}$ $p_{g\_T=1}$ was selected the best. This model included effects of treatment, introduction cohort, time and an interaction between mass and sex. Although this model was the best, several other models came close and it was obvious that several factors explained the variation. To account for model selection uncertainty we present survival estimates by model averaging (White, Burnham & Anderson 2001). Figure 2 shows model-averaged survival estimates for the seven time intervals (based on all models tested). Treatment populations had overall higher monthly survival than did control populations. The higher survival of females was not prominent and the additive effect of sex was included in model 1 due to the significant sex–mass interaction.

From period 3 and onwards survival was 100% for the animals remaining from introduction 1. Due to predation, population decline during the first 2 months was larger than indicated by the estimated survival. Thus estimates of the last five periods are based on the animals that escaped the bottleneck of the first 2 months and managed to establish in the area (one and one animals on the control grids, and three and one animals on the treatment grids, respectively, Fig. 1). For the second introduction cohort the survival in periods 4–7 fluctuated with time and was lower than that of the established animals from the first cohort.

The interaction between sex and body mass was clear (Fig. 3). While body mass had almost no effect on male survival, female survival increased rapidly with

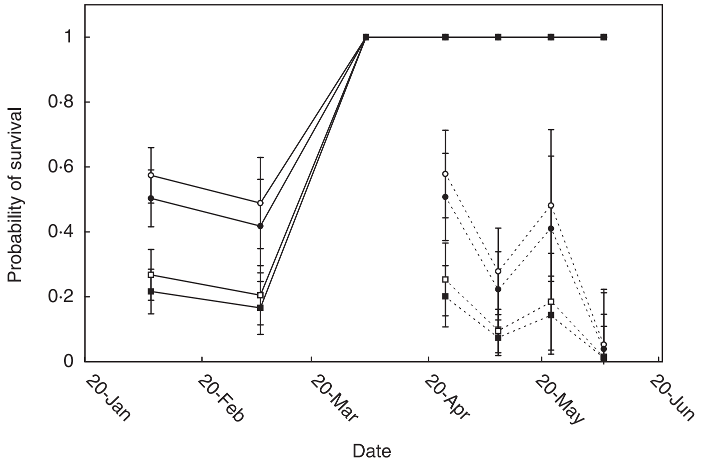

**Fig. 2.** Estimated monthly survival ± SE (model averages) for the seven time intervals. Circles represent treatment populations and squares represent controls. Solid and dotted lines represents the first and second cohort, respectively. Open symbols represent females and closed symbols represent males.

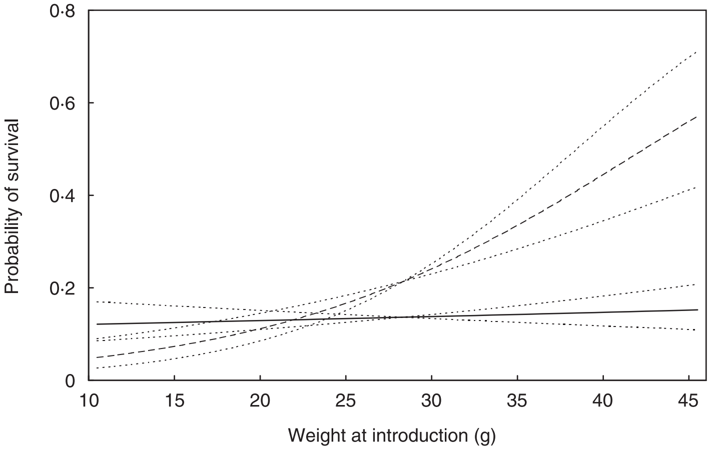

**Fig. 3.** Estimated monthly survival of males and females as an effect of introduction body mass (cohort 2, period 6 used as an example). Solid line represents males and dashed line represents females. Dotted lines show standard errors. The estimated effect of body mass on survival (on the logit-scale) was 0·08 ± 0·24 and 1·02 ± 0·40 (mean ± SE) for males and females, respectively. This corresponds to a 44% increase in survival probability of a female increasing from 25 to 30 g. The equivalent change for a male is 3%.

body mass. A female with an initial weight of 30 g had 44% higher probability of survival compared to a female weighing 25 g. The equivalent difference for males was 3%.

### POPULATION DENSITY

There were no significant differences in population density between the treatment and control grids (LRT: $\chi^2 = 2{\cdot}24$, d.f. = 1, $P < 0{\cdot}14$). Figure 1 shows the number of animals present within each grid at each trap session during the whole experiment, and the number of animals living within the grids prior to the experiment. The figure also provides detailed information regarding mortality causes. There were obvious losses due to stoat predation in both treatment grids and in one of the control grids, but the proportion of killed animals was higher in both treatment grids than in the control grid.

### SPACE USE

There was a significant difference in individual space use between treatment and control (LRT: $\chi^2 = 18{\cdot}6$, d.f. = 1, $P < 0{\cdot}0001$) (Fig. 4). Mean number of trap stations visited was almost twice as high among individuals at the treatment grids compared to the control grids (3·57 ± 0·24 and 1·97 ± 0·28, respectively).

### BODY MASS

There was a negative relationship between body mass at introduction and body mass change during the first 30 days after introduction (Fig. 5). A linear regression model including introduction body mass and sex explained the variation in body mass change most effectively ($R^2 = 0{\cdot}84$, $n = 23$, $P < 0{\cdot}0001$). Large individuals of both sexes lost weight, while small individuals gained weight. The increase in body mass was

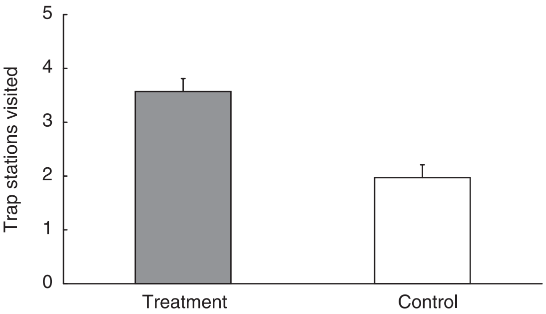

**Fig. 4.** Estimated individual space use for root voles in treatment and control grids. The mean number of trap stations visited (± SE) was almost twice as high among individuals on the treatment grids compared to individuals at the control grids (3·57 ± 0·24 and 1·97 ± 0·28, respectively). This difference was significant (LRT: $\chi^2$ = 18·6, d.f. = 1, $P$ < 0·0001).

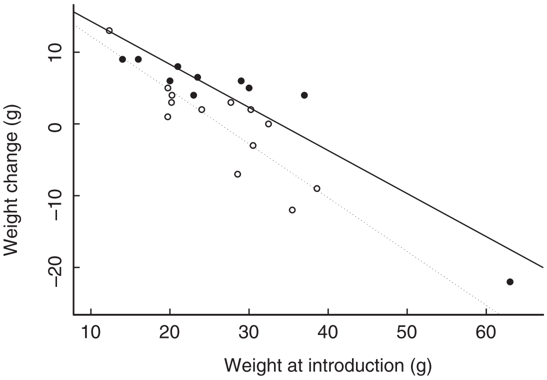

**Fig. 5.** Change in body mass during the first 30 days after introduction as an effect of body mass at introduction. Open circles represent females and closed circles represent males. The solid line represents the least squares fit of males ($y$ = 20·3 – 0·60$x$) and the dotted line the equivalent of females ($y$ = 19.8 – 0.75$x$) ($R^2$ = 0·82, $n$ = 22, $P$ < 0·0001).

especially strong among males, of which only one of 10 individuals lost weight.

### GRAZING

We found that the model explaining the variation in grazing intensity most effectively included: difference between treatment and control (LRT: $\chi^2$ = 20·5, d.f. = 1, $P$ < 0·5), difference between 'online' and 'offline' (LRT: $\chi^2$ = 516·5, d.f. = 1, $P$ < 0·001) and their interaction (LRT: $\chi^2$ = 1065·8, d.f. = 1, $P$ < 0·0001). The significant interaction suggests a difference in frequency of grazing between covered (0·45 ± 0·044) and uncovered (0·10 ± 0·027) areas within the treatment grids and no difference within control grids (0·22 ± 0·037 and 0·28 ± 0·041, respectively) (Fig. 6). The overall grazing in the control grids was intermediate between covered and uncovered areas in the treatment grids, resulting in no significant difference between treatment and control. However, treatment was still included in the model due to the significant interaction.

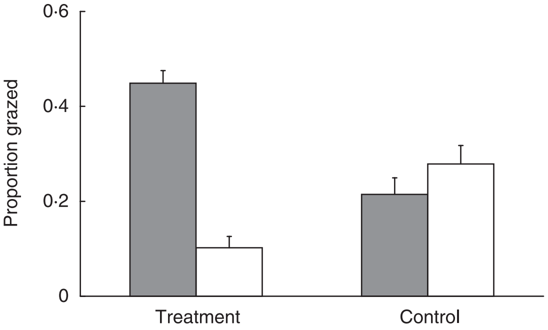

**Fig. 6.** Proportion grazed (± SE) as an effect of treatment and position within grid ($n$ = 190). Dark grey columns represent samples from under the sheets on the treatment grids and on the equivalent locations, between trap stations, on control grids ('online'). White columns represent samples taken at other random locations within the grids ('offline'). There was a significant difference between 'on-' and 'offline' within the treatment grids but not within the control grids (LRT: $\chi^2$ = 1065·8, d.f. = 1, $P$ < 0·0001).

## Discussion

Our objective was to assess whether the snow cover limits the access to subnivean food by physically enclosing patches of vegetation resources and if this reduces winter survival. By adding a network of corrugated aluminium sheets on the ground before onset of winter we obtained a way to counteract this possible detrimental effect. We expected that the corrugated profile of the sheets would create space mimicking the natural occurring subnivean space, thus giving the root voles access to more natural forage. The results support our hypotheses regarding survival and space use as animals living within the treatment grids survived better, had higher space use and grazed larger areas. The larger areas grazed underneath the sheets and the higher space use indicates that the physical properties of the snow cover limits access within the subnivean environment. The hypothesis regarding limitations in body mass change could not be tested due to few data points.

It can be argued that the size of the trapping grids was small compared to the distances root voles are known to move during summer (Steen 1994). However, we found it necessary to ensure high enough recapture probabilities and this was only possible by minimizing the distance between trap stations, thus limiting grid size. Increasing the grid size would also reduce comparability owing to the highly variable vegetation and topography. From the 103 animals introduced in January we documented that more than 70% never left the grid, and this indicates that the animals stayed mainly in the area, even though the grids were not fenced to stop migration. Therefore, we believe that the grid size chosen was reasonable.

The animals whose tags were not recovered either died within the grid without this being recorded, or they managed to leave. Any migrations were probably motivated by food limitation, and migrating animals probably had higher mortality, as observed among dispersers during summer (Steen 1994) Thus any difference in emigration between treatments might have effected the results of the survival analysis, as all animals not recovered were included in the analysis. However, there was no significant difference in proportion of tags not recovered between treatment and control grids (LRT: $\chi^2 = 2{\cdot}12$, d.f. = 1, $P < 0{\cdot}15$). Predation on possible migrating animals might have affected the general level of estimated survival but not the difference between treatments. Therefore, including non-recovered animals in the analysis should not affect our main conclusions.

To introduce animals into the subnivean space might seem an unnatural situation. The quality of the subnivean environment is probably enhanced by resident animals maintaining runways as the snow cover is forming, and animals introduced through a stable snow cover in January might be exposed to a subnivean environment of poorer quality. However, basing the experiment on naturally occurring animals would be too risky. We wanted to stress food limitation similar to 'peak years', and the population density in the area was obviously too low to provide high enough and equal densities of natural occurring animals in all grids (Fig. 1). To introduce animals earlier was not found suitable either. In an experiment, in which field voles (*M. agrestis* Linnaeus) were transplanted between open systems in the absence of snow, only about a third of the introduced animals was ever recaptured (Ergon, Lambin & Stenseth 2001). This loss of animals was due probably both to mortality and emigration. We believe an introduction of animals before onset of winter would be almost useless due to the surroundings acting as a sink, and we deliberately chose to study a non-enclosed system to avoid unnatural snowdrifts forming around fences. Introduction into the subnivean obviously involved moving around on the top of the snow cover, and initiating this process before the snow cover was stable enough to carry a man wearing snow shoes would probably do more harm to the subnivean space (Schmid 1981) than would the lack of resident animals. The low rate of movement within the control grids (Fig. 4) might be a direct effect of unmaintained subnivean environment, but even with seven naturally occurring animals living within one control grid and none within the other (Fig. 1), no significant difference in space use between these two grids was detected ($2{\cdot}03 \pm 0{\cdot}25$ and $1{\cdot}33 \pm 0{\cdot}66$ for grid 1 and grid 3, respectively). As far as we know there exists no information indicating whether this observed rate of movement under the snow cover is unnaturally low or is actually representative for the overwinter situation experienced by small rodents in alpine habitats.

The survival modelling revealed that monthly winter survival of *M. oeconomus* was limited by the subnivean fragmentation. Animals from the treatment grids had monthly survival probabilities two times higher than control animals during the 2 first months after introduction (Fig. 2). Natural mortality during these 2 months, in addition to loss due to predation, reduced the population sizes of the first introduction cohort to one to three animals in each grid. These population densities seemed well below carrying capacity at treatment as well as control grids because these few animals remained alive for the rest of the winter, and a further introduction of a second cohort did not appear to reduce their survival. These densities were also well below the highest densities of naturally occurring animals observed by trapping prior to the experiment.

While the survival probabilities of the established animals from introduction cohort 1 were stable at 100%, survival of the animals from the second cohort varied with time. The first period of low survival, during the first half of May (Fig. 2), can be explained possibly by extreme subnivean conditions. Large amounts of water were observed in the subnivean space at this time (up to a third of the trap chimneys in the grids were flooded) and it is likely that the presence of water reduced survival indirectly by reducing the amount of available subnivean space and possibly also directly by drowning of animals. Aars & Ims (2002) found a negative correlation between winter survival rates and mean winter temperature, a relationship they ascribed to melting and freezing of vole habitats. Other studies have also suggested similar phenomena effecting vole survival (Merritt & Merritt 1978; Boonstra & Rodd 1983). The proportion of the subnivean space that is inaccessible due to water is likely to vary between years due to climatic variation, but periods of such low survival, especially as low as in the control populations, even if temporary, would greatly reduce the probability of an individual surviving the whole winter by acting as a temporal bottleneck.

The second drop in survival, during the first half of June (Fig. 2), coincides with snow melt. The disappearance of snow is likely to be associated with the onset of dispersal (Boonstra & Rodd 1983), a situation that would be interpreted as a decrease in survival as we cannot account for permanent emigration. In addition, due to more available space individuals would, by pure chance, be less likely to pass through the antennas. Such a reduction in capture probability would result in reduced survival estimates in models already constraining capture probability as constant. Another possibility explaining the sudden drop in survival could be increased predation due to the lack of protecting snow and the return of migratory birds of prey.

The higher survival probability of animals living within treatment grids should entail higher population densities here compared to the control grids. This, however, was not the case (Fig. 1). The population densities were not significantly different, and this seems to be due to a higher predation pressure within the treatment grids counteracting the effect of higher survival. In the survival analysis, mortality due to predation was censored out and thus the population densities at the treatment grids were lower than what the survival estimates should dictate. Predation was the main reason to introduce a second cohort of animals in April (Steen & Korslund, in preparation).

The majority of small mammals experience weight loss during winter (Iverson & Turner 1974; Hansson 1990; Hansson 1991; Aars & Ims 2002), and our observations support these findings. An optimal intermediate size (26·3 and 33·8 g for females and males, respectively; Fig. 5) is apparent from the negative correlation between weight at introduction and weight change. However, in males the negative correlation was caused by extreme weight loss of one large male (–22 g), while all other males increased in body mass. Removing this outlier would result in negligible negative effects of large body mass among males. This is supported by the male survival function (Fig. 3), which indicates no effect of size on survival. On the other hand, we cannot exclude the possibility that this large male displayed a true survival trade-off between body mass at introduction and body mass change, as such large males do occur in the population at the onset of winter. One could expect a negative correlation between change in body mass and initial body mass due to the variation in body mass (Blomquist 1977), producing a spurious effect. However, the variation seems constant and the regression is based equally on positive and negative weight changes on opposite sides of the intermediate values. The results also confirm earlier findings (Aars & Ims 2002), and hence we find the observed relationship between body mass at introduction and change in body mass to be credible.

Survival was correlated positively with introduction body mass among females but constant among males (Fig. 3). The positive effect among females seems to contradict earlier results on *M. oeconomus* presented by Aars & Ims (2002), in which, in both sexes, individuals of intermediate sizes had the highest survival probabilities. However, the negative effect of size in that experiment was caused mainly by low survival of post-reproductive individuals (Aars & Ims 2002), whereas we used only non-reproductive animals. None the less, our heaviest females were considerably larger than the optimal size (25 g) determined by Aars & Ims (2002), apparently without experiencing any detrimental effect on survival. Perhaps winter survival is not only a function of size but also of reproductive history, where non-reproductive individuals have an initially higher probability of survival. The weight loss in winter is believed to be due partly to it being hard to sustain the required energy intake (Iverson & Turner 1974; Stenseth 1978; Hansson 1990; Hansson 1992), and this contradicts the high survival of heavy females we observed. However, if both small and large individuals must adjust their size to survive, both extremes must undergo a critical phase of adjustment. It is possible that the cost of weight adjustment is higher for small individuals than for large ones and that this cost compromises survival.

We expected two related effects of grazing due to our treatment: a direct effect underneath the sheets and a more widespread effect resulting in higher grazing on the whole grid. The direct effect of artificial subnivean space was obvious. Under the sheets the level of grazing was higher than on any other parts of the grids, both treatment and control. Within the treatment grids the difference was more than fourfold between covered and uncovered areas and the difference between covered areas on the treatment grids and the equivalent areas on the control grid was twofold. This suggests that the sheets prevented the snow from blocking access to otherwise inaccessible vegetation. As expected, there was no significant difference within the control grids, but the overall grazing here was higher than expected and thus the overall effect on grazing was not significant between treatments. This is mainly an effect of heavy grazing on grid 3 (0·39 ± 0·05, compared to 0·11 ± 0·03 on the other control grid). Here the terrain was more rugged and this seems to increase the possibility of movement and hence grazing in the consequent depressions (personal observation). The relatively high number of animals living within this grid prior to January (Fig. 1) has probably also contributed to increase the grazing, and we cannot guarantee that one or several animals managed to escape the removal and thus contributed to the grazing. However, no such untagged animals were live-trapped after the introduction.

Prior to the introduction there were animals living on one of the treatment grids as well (Fig. 1). These animals most probably had the same effect on the existing vegetation as on grid 3. Here, however, the space use of animals, and thus the grazing, might have been concentrated underneath the sheets, especially early in winter when such sheets may act as a refuge, and this may have contributed to the large difference within the grid. However, the same relative within-grid pattern of grazing was also seen on the other treatment grid and here no pre-experimental animals were detected.

Models including a reduction in carrying capacity in winter can mimic cyclic population dynamics in voles more effectively (Hanski *et al.* 1993; Hanski & Korpimäki 1995), and density-dependent regulation of population growth during winter appears to be an important element in production of multi-annual cycles (Hansen *et al.* 1999). Our study suggests that the reduced carrying capacity during winter is caused by the physical properties of the snow cover and the consequent fragmentation of the subnivean space. This is additional to an already reduced food quality due to the lack of vegetation replenishment during winter. Because the process creating the subnivean space is highly dependent on climatic factors, such as temperature (Pruitt 1984; Marchand 1996), winter climate may have a considerable effect on the population dynamics of small rodents. Long-term changes in climate may lead to a permanent aggravation of the subnivean conditions and lead most probably to a further decrease of winter carrying capacity. Erlinge *et al.* (1983, 1984) has shown how high winter predation can outweigh the summer production of vole populations. We expect that more severe subnivean conditions will lead to higher winter mortality, and this might have an effect similar to winter predation, resulting in a stabilization of population dynamics and a dampening of vole cyclisity.

## Conclusion

The higher level of grazing underneath the sheets and the higher space use within the treatment grids supports our hypothesis that snow cover limits access to natural forage during winter. We also estimated higher survival in the populations inhabiting the treatment grids, and we find it plausible that this was the direct effect of greater food availability under the sheets. However, due to high within-treatment variation we cannot tell whether or not the individual food intake was higher in the treatment populations. The higher survival of treatment animals did not result in a corresponding higher population density due to an equalizing effect of predation. Snow cover apparently reduces survival by physically enclosing the ground and vegetation by ice, impermeable to small rodents, reducing access to otherwise available food resources. With this process in mind, winter food resources may be overgrazed although, after snowmelt, food seems to be abundant. Including seasonal differences in carrying capacity in models has proved useful when trying to explain cyclic population dynamics, and here we present results that contribute to elucidate this mechanism. To our knowledge, this is the first time anyone has carried out experiments testing the mechanisms involved regarding small rodents' access to natural occurring food resources under snow.

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