

The effects of winter climate and intrinsic factors on survival of cyclic vole populations in southeastern Norway

Kaja Johnsen*, Olivier Devineau & Harry P. Andreassen

*Inland Norway University of Applied Sciences, Faculty of Applied Ecology, Agricultural Science and Biotechnology, Campus Evenstad, NO-2480 Koppang, Norway (*corresponding author's e-mail: kaja.johnsen@inn.no)*

Received 6 Feb. 2018, final version received 8 May 2018, accepted 8 May 2018

Johnsen, K., Devineau, O. & Andreassen, H. P. 2018: The effects of winter climate and intrinsic factors on survival of cyclic vole populations in southeastern Norway. — *Ann. Zool. Fennici* 55: 173–185.

Changes in winter climate is a possible explanation for dampened population cycles in voles. For voles living in the subnivean space for several months of the year, we may expect that winter conditions affect survival. We examined the effect of different winter climate descriptors (snow depth, subnivean temperature, snow crust) and different intrinsic factors (sex, age, physiology, behaviour estimated as the longest distance travelled between traps) on winter survival of bank voles *Myodes glareolus* in southeastern Norway by live-trapping voles monthly along elevation gradients. We tested whether winter conditions alone (winter hypothesis), intrinsic factors alone (intrinsic hypothesis), or winter conditions in combination with age and sex were more important for winter survival of voles (multiple factor hypothesis). Our results do not support the winter hypothesis as there were no relations between winter survival and snow depth, snow crust and subnivean temperature. We found strongest support for the intrinsic hypothesis, where the distance travelled was positively correlated with survival. We hypothesize that this behavioural descriptor is related to food resources and their importance during winter, where an increased activity range (distance travelled between traps) increase the access to food resources.

Introduction

Vole populations in Fennoscandia fluctuate regularly with peaks every 3–4 years, predominantly in highly seasonal environments, north of 60°N (Hansson & Henttonen 1985, Bjørnstad *et al.* 1995). These multi-annual population cycles substantially impact the functioning of ecosystems (Cornulier *et al.* 2013), because small rodents represent an important food resource for preda-

tors, and because they affect the nutrient and vegetation dynamics through their feeding behaviour (Pastor & Naiman 1992, Jędrzejewski *et al.* 1993, Sirotnak & Huntly 2000, Bakker *et al.* 2004). However, during recent decades, the vole cycles dampened and the high peaks disappeared (Ims *et al.* 2008). Low winter survival caused by climate change was proposed as a possible explanation for the dampening of the vole cycles (Aars & Ims 2002, Hömfeldt 2004, Kausrud *et al.* 2008).

In the seasonal environments of northern Fennoscandia, vole populations experience rapid growth during a short reproductive summer season, and a long population decline in winter. Voles can breed in winter, but only when they have access to ample food resources (Smyth 1966, Eccard & Ylönen 2001). As voles spend most of winter in the subnivean space, i.e., between the snow cover and the ground, conditions under the snow are therefore crucial for winter survival. The most critical periods for winter survival are in autumn, before the ground is covered with snow, and in spring, when the snow melts, as well as during milder periods in winter when conditions are least stable (Fuller *et al.* 1969, Aars & Ims 2002, Hoset *et al.* 2009).

A predicted consequence of global warming are warmer and wetter winters (IPCC 2013) with frequent melting-freezing events. Such conditions can cause icing on the ground or the formation of snow-crust layers (Aars & Ims 2002). Ice-covered ground limits access to food below the ice, and it limits movement within the subnivean space because the space becomes fragmented into accessible and inaccessible patches (Korslund & Steen 2006). As suggested by Mysterud (2016), snow crust may also prevent movement and restrict access to the surface of the snow.

Besides the subnivean conditions the properties of the snow are also important. Indeed, snow cover provides insulation and maintains a stable subnivean temperature of around 0 °C. A deep snow cover also provides protection against mammalian generalist predators (Lindström & Hörnfeldt 1994) and avian predators (Sonerud 1986). Deeper snow positively affects overwinter survival in the northern red-backed vole *Myodes rutilus* (Boonstra & Krebs 2006). In arctic lemmings (*Lemmus* and *Dicrostonyx*), snow depth is positively linked to winter habitat selection and population growth rate (Reid & Krebs 1996, Reid *et al.* 2012).

Winter conditions may thus be an important determinant of vole winter survival. In addition, age- and sex-specific variations in spacing and movement behaviours (Andreassen & Ims 2001, Andreassen *et al.* 2013) may result in individual-dependent vulnerability to intraspecific competition, predation and diseases, as well as access to

food. It has also been shown that small mammals adjust their body mass to a physiological optimum during winter (Iverson & Turner 1974, Merritt & Merritt 1978, Hansson 1990, 1991). For species with sexual size dimorphism this may result in higher winter survival of the smaller sex (Aars & Ims 2002). Both behavioural and physiological factors may interact with winter conditions to cause variations in survival rates of animals in different age and sex categories. This in turn leads to changes in the age and sex compositions of the population during the phases of the population cycle (cf. Getz *et al.* 2007, Inchausti *et al.* 2009, Andreassen *et al.* 2013). Hence, it is important to evaluate the effects of intrinsic factors on winter survival, such as physiology or behaviour that can be inherent to the population, or age and sex that are under an influence of winter conditions, or effects of extrinsic factors such as food or predation.

For this study, we live-trapped 14 bank-vole (*Myodes glareolus*) populations monthly along two elevation gradients. We monitored those populations for two consecutive winters in 2013–2015, including a complete population crash during the 2014/2015 winter. We used body mass as a physiological descriptor, and the maximum distance travelled between traps during a trapping session as a behavioural descriptor indicating activity. We considered three hypotheses: Winter survival of voles depends on (1) winter conditions only (winter hypothesis), (2) the interaction between winter conditions and age and/or sex (i.e., driven by an interaction between winter conditions and intrinsic and/or extrinsic factors) (multiple-factor winter hypothesis); or (3) intrinsic factors only (i.e. driven by sex, age, behavioural and/or physiological descriptors) (intrinsic hypothesis).

Material and methods

Study area

The study was carried out in typical boreal forest in the Stor-Elvdal municipality, south-eastern Norway (61.4°N, 11.1°E). Vegetation in the area is dominated by Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*), with bil-

berry (*Vaccinium myrtillus*) in the field layer and mosses (e.g. *Pleurozium schreberi*) in the ground layer. The climate is continental with relatively dry weather, large diurnal variation in temperature, warm summers and cold winters (Boonstra *et al.* 2016). Snow cover normally lasts from December to April.

This region experienced dampened voles and lemming cycles with no high population peaks between the mid-1980 and 2007 (Hörnfeldt 2004), when cyclic behaviour returned. Peaks were recorded in the summers of 2011 and 2014 (Johnsen *et al.* 2017, and unpubl. data from the Inland Norway University of Applied Sciences).

Trapping procedure

Trapping was carried out along two transects at elevations between 280 and 750 m a.s.l. Each transect consisted of 7 grids (14 grids in total), separated by at least 500 m. Voles were caught within 60 × 60 m trapping grids, each consisting of 16 Ugglan multiple capture live traps (Granab, Sweden) arranged in a cross pattern (Fig. 1a). An alternative layout was used for three grids which were adjusted to encompass suitable habitats (Fig. 1b). Grids were located in a typical bank vole habitat, which would ideally be mature forest with areas dominated by bilberry in the field layer (Myllymäki 1977, Gorini *et al.* 2011).

The traps were placed along runways or close to holes with potential vole activity, so that they were part of the runway system when not activated. Each trap was covered with a 30 × 30 × 40 cm floorless, plywood box to prevent the trap from being covered by snow. Location of each trap was marked with a stick and a ribbon in the closest tree, which were kept fixed throughout the study.

Traps were activated once a month (primary sessions) and checked in the morning and evening for three consecutive days (i.e., six secondary occasions per session), from December to May in 2013/2014 and 2014/2015. During January–April 2014, some traps-days were lost due to either extreme cold (below −20 °C) or heavy snow concealing the traps. Overall mortality due to trapping was low (mortality rate ± SE for

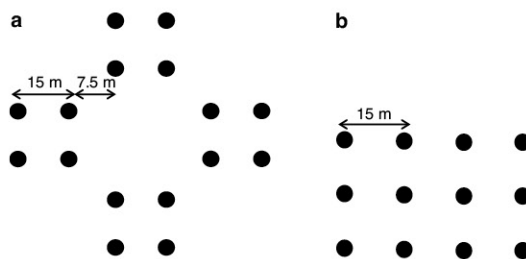


Fig. 1. Trapping-grid design. (a) Main cross-shaped design with 16 traps ($n = 11$), and (b) alternative design with 12 traps used when the cross-shaped design did not include suitable habitats ($n = 3$).

recaptured individuals in winter 2013/2014 = 0.016 ± 0.006 , and in winter 2013/2014 = 0.032 ± 0.023). Activated traps were baited with oats and carrots, and supplemented with sawdust to keep the voles warm. The captured voles were individually marked with pit-tags (1.25×7 mm ID-100VB Nano Transponder), sexed, weighed to the nearest 1 g, and checked for reproductive status (mature if open vagina or scrotal testicles). We used a basic LID-560 Pocket Reader (Trovan[®]) to read the tags.

Climate variables

Once a month, i.e. during the primary trapping session, in every trapping grid we recorded the snow depth to the nearest 1 cm, and the presence/absence of snow-crust layers. Snow crust was a resistant layer anywhere between the top and the bottom of the snow pack. We also recorded presence/absence of ground ice. However, during those two winters we never observed contiguous hard ice covering the ground (i.e., ice cover patches were always less than 2 mm thick and less than 0.5 m^2). Therefore, we did not include this variable in our analysis. We used a temperature logger (HOBO U23 Pro V2) to measure the subnivean temperature every 6 hours in 10 grids.

Data analysis

The second winter of our study corresponded to a decline/low phase in the vole population cycle. Very few individuals were captured in each trap-

ping grid during this period, which prevented the use of capture–recapture methods to analyse the data at the grid level. A grid-level analysis was important for assessing the effect of the variation in winter condition descriptors. We estimated monthly winter survival by considering an individual to have survived when it was present during one primary session and known to be alive during the next session. Hence, the survival estimates did not take into account variations in capture probability and dispersal/migration, and therefore cannot be considered estimates of true survival, but rather of persistence in the grid.

Our focus was to study winter conditions independent of year, phase of the population cycle or primary trapping session (i.e. month). Capture–mark–recapture studies of voles often show a temporal effect, i.e. an effect of year and primary trapping session (e.g. Crespin *et al.* 2002). This could be due to differences in trapping probability between primary trapping sessions, seasonal effects or other unknown factors. We modelled survival as a function of winter conditions and intrinsic factors, with a generalized linear mixed model using trapping grid and session as random effects. As we include session as a random effect, it means that we did not study the effect of climate and intrinsic factors as between-month but rather within-month variation.

We considered the following independent variables to explain individual monthly survival over winter; snow depth, presence/absence of snow-crust layers, subnivean temperature, sex, age (juvenile or adult), body mass (g) and maximum distance travelled between traps per primary trapping session. Further, we constructed models based on our three hypothesis: (1) winter hypothesis (cf. Appendix): model combinations with climate predictors, only additive effects; (2) multiple factor winter hypothesis: model combinations with climate, age and sex predictors, with interaction terms between climate and age/sex; and (3) intrinsic hypothesis: model combinations with only intrinsic predictors (age, sex, body mass and maximum distance travelled), with interaction term between age and sex.

We estimated Akaike's information criterion corrected for small sample sizes (AICc) when modelling survival. Because of high model

uncertainty, we used full model averaging across all candidate models (Symonds & Moussalli 2011). We carried out all statistical analyses using R (R Core Team 2016).

Results

Population and survival background

No populations of the trappable individuals went extinct during the 2013/2014 winter, whereas 13 out of 14 populations of the trappable individuals went extinct during the 2014/2015 winter (Fig. 2). The minimum number known to be alive decreased across the populations from December to January, and started to increase again from April to May in the 2013/2014 winter. The trend was same from December to January in the 2014/2015 winter, but there was no increase starting in April (Fig. 2). Survival was low in December, but high throughout the rest of the winter of 2013/2014. During the winter 2014/2015, survival started at the similar level for juveniles as in 2013/2014, and even increased from March to April, before it declined from April to May to the lowest survival that winter (Fig. 3). In the 2014/2015 winter, no adult females were recaptured after January, whereas an adult male immigrated into one of the populations in February but was not recaptured later.

Conditions in winter

The mean snow depth was 15 cm greater in 2013/2014 (mean snow depth = 53 cm) than in 2014/2015 (mean snow depth = 38 cm, $F_{1,153} = 9.33$, $p = 0.003$), and snow was deeper at higher elevation ($F_{1,153} = 12.76$, $p < 0.001$; Fig. 4). The mean snow depth was 24 ± 2 cm (mean \pm SE) already in December and increased to a minimum of 35 cm in January. There were no differences in mean subnivean temperatures between years ($F_{1,153} = 1.30$, $p = 0.26$) or elevations ($F_{1,153} = 1.50$, $p = 0.22$; Fig. 5). There were more trapping grids with snow crust in 2014/2015 than in 2013/2014 ($\chi^2_{1,158} = 4.1$, $p = 0.04$), but there was no difference among elevations ($\chi^2_{1,158} = 0.03$, $p = 0.9$; Table 1).

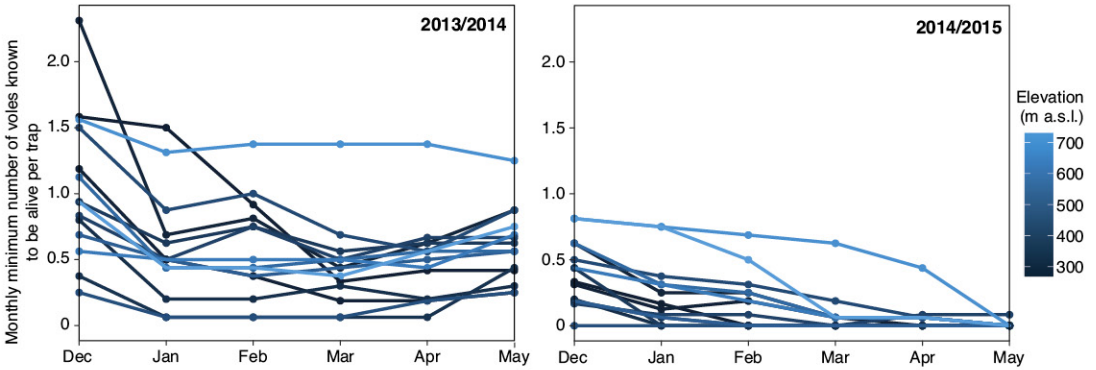


Fig. 2. Monthly minimum number of voles known to be alive per trap in trapping grids (represented by lines) during the two winters. Trapping grids are coloured according to their elevation.

Survival

Several models of survival were equally good, with 3 models $< 2\Delta AICc$ (cf. Appendix). When

we calculated the mean AICc weight across all models for each of the three hypotheses, we found that the models for intrinsic hypothesis received about 6 times more support than

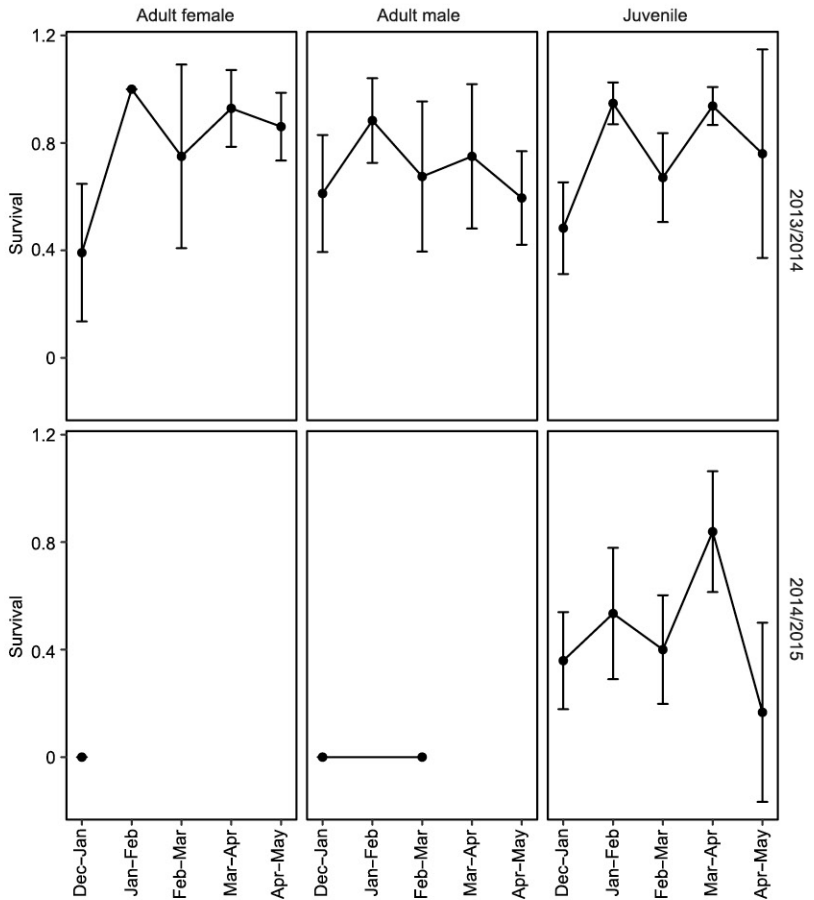


Fig. 3. Mean ($\pm 2SE$) monthly survival rates of juveniles, adult females and adult males during the two winters.

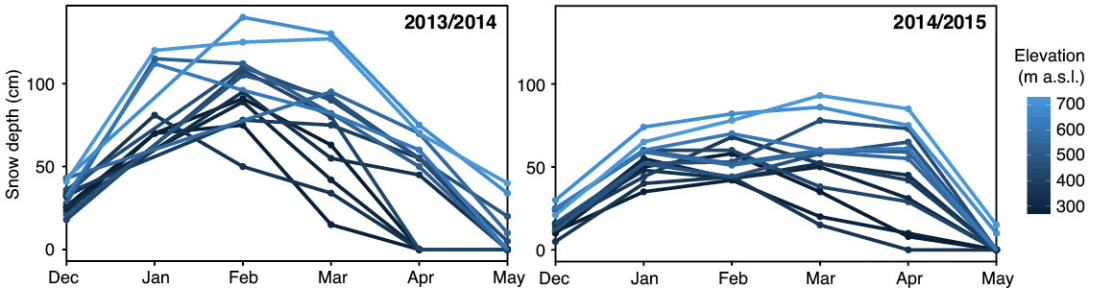


Fig. 4. Monthly snow depth (cm) in trapping grids (represented as lines) during the two winters. Trapping grids are coloured gradually according to their elevation.

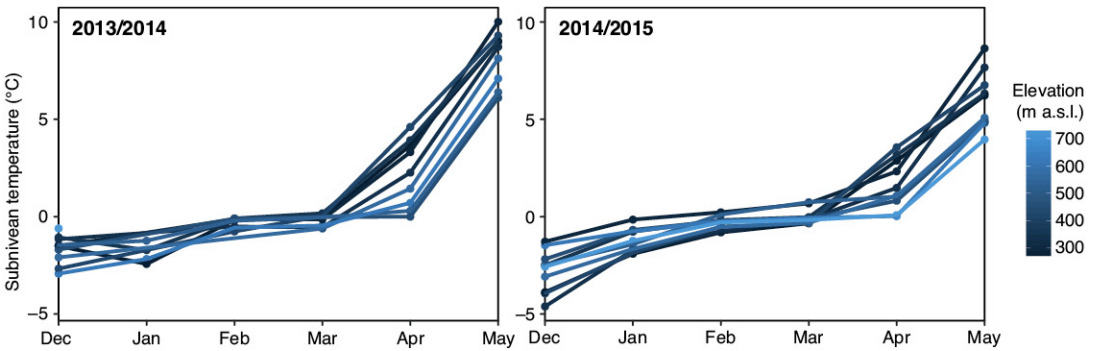


Fig. 5. Monthly mean subnivean temperature (°C) across trapping grids (represented as lines) through the two winters. Trapping grids are coloured gradually according to elevation (m a.s.l.).

models corresponding to the winter hypothesis, and about 145 times more support than the models for the multiple-factor winter hypothesis (Table 2).

Although there was no strong evidence for any particular model, both the model selection (Appendix) and estimates \pm SE obtained from full model averaging (Table 3) imply that the maximum distance travelled between traps was more strongly correlated with within-month survival than any other variables. Relationships between survival and maximum distance travelled between traps were linear and positive (cf. Fig. 6).

Table 1. Percentages of trapping grids with snow crust per month for the two winters.

	Dec	Jan	Feb	Mar	Apr	May
2013/2014	57	67	85	100	50	0
2014/2015	79	100	79	100	86	0

Discussion

Survival of the voles was lower in December than later in the season, and it coincided with the month with thin snow cover. This effect could be caused by December-specific unknown confounding factors, such as low trap probability, mortality due to physiological constraints in early winter or emigration behaviour. In our modelling we found no correlation between within-month variation in winter climatic conditions and survival, even though we compared bank vole populations across a wide range of survival rates (from stable to crashed winter population) and within-month variation in winter conditions. Instead, behaviour expressed as the maximum distance travelled between traps was

Table 2. Mean model weight per hypothesis.

Winter hypothesis (H1)	0.004
Multiple-factor winter hypothesis (H2)	0.0002
Intrinsic hypothesis(H3)	0.0258

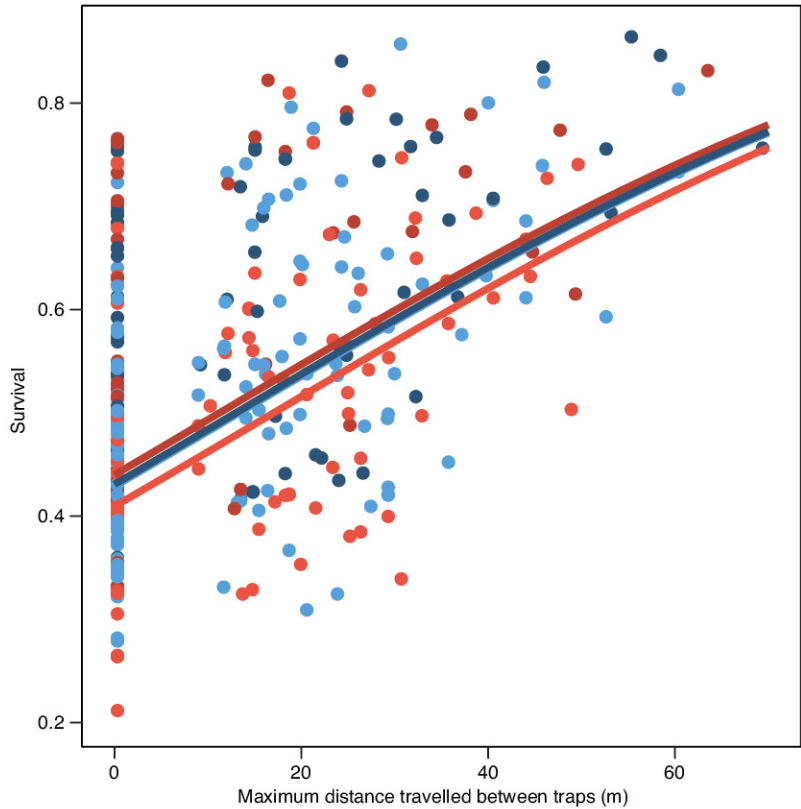


Fig. 6. Age and sex specific winter survival correlated with the maximum distance travelled between traps per individual within a trapping session, predicted from model averaging estimates. Red = females, blue = males; light colour shades = juveniles = dark colour shades: adults.

the best predictor of winter survival in bank voles, supporting the intrinsic hypothesis.

Two variables related to climatic conditions, snow depth and snow crust, differed between the two winters. The snow cover was deeper, and there was less snow crust during the first winter, when the vole populations survived well. However, these variables did not explain variation in survival. During our study, the subnivean temperatures remained stable, with no fluctuations between day and night, and there was no difference between years. The low variation in subnivean temperature may explain the lack of response, which may be due to the fact that in both years, snow depth reached > 20 cm, which corresponds to the maximum insulation capacity (Pruitt 1970). However, Whitney (1976) found that *Myodes* voles survived well when exposed to extreme subnivean temperatures (-30°C), with survival being even higher than for most summer periods. Also Fuller (1977) found no effect of subnivean temperatures on winter mortality in red-backed voles *Myodes gapperi*.

Most studies on how winter affects voles and lemmings compared autumn populations with spring ones (Reid & Krebs 1996, Aars & Ims

Table 3. Candidate model estimates explaining survival of bank voles; J = juvenile, M = male.

Variable	Estimate	SE
Intercept	-0.2424	1.3980
AgeJ	-0.1216	0.2998
TrapDistance	0.0209	0.0089
SexM	-0.0305	0.2777
AgeJ \times SexM	0.1136	0.3486
Bodymass	0.0228	0.1427
Bodymass ²	-0.0006	0.0039
Subnivean temperature	0.0029	0.0276
Snow depth	0	0.0012
Snow crust	-0.0102	0.0886
SexM \times snow crust	0.0002	0.0341
SexM \times snow depth	-0.0001	0.0014
SexM \times subnivean temperature	-0.0003	0.0107
AgeJ \times snow crust	-0.0005	0.0417
AgeJ \times snow depth	0	0.0006
AgeJ \times subnivean temperature	-0.0004	0.0135

2002, Bierman *et al.* 2006, Boonstra & Krebs 2006, Kausrud *et al.* 2008, Ims *et al.* 2011, Reid *et al.* 2012, Stien *et al.* 2012, Korpela *et al.* 2013, Bilodeau *et al.* 2013). Few studies, however, monitored populations continuously throughout winter (Whitney 1976, Martell & Fuller 1979, Korslund & Steen 2006, Hoset *et al.* 2009, Johnsen *et al.* 2017). During recent decades, the impact of winter climate on small-rodent survival has been reinforced by the detrimental effect of icing on the ground (Aars & Ims 2002, Korslund & Steen 2006, Kausrud *et al.* 2008, Hoset *et al.* 2009, Stien *et al.* 2012), and dampening rodent population cycles (Ims *et al.* 2008). Most of those studies focused on open alpine areas where freezing at the ground level is more frequent and thus there is a higher probability of icing than in a boreal forest. Martell and Fuller (1979) compared winter mortality of red-backed voles between tundra and taiga, and found that mortality was highest in tundra, and they hypothesised that the tundra populations were controlled by environmental factors, while taiga populations were controlled by resources. The fact that we never observed any ice on the ground during our study may be due to more stable climatic conditions inside the forest than in alpine areas where ice forms on the ground more easily. Few studies examined the effects of winter climatic variables on vole survival in forested areas. Contrary to the results obtained by Kausrud *et al.* (2008) in alpine areas, Korpela *et al.* (2013) found that milder winters had no effect on survival in boreal vole populations. Also Hoset *et al.* (2009) found no effect of ground icing on winter survival in enclosed populations of root voles *Microtus oeconomus*.

Of the intrinsic factors that we included in our models, only the maximum distance travelled between traps per individual within a primary session seemed to correlate with survival. This variable reflects activity, which in turn is related to resource availability and searching. The wider activity range voles have, the more resources they can access. It has been shown that if available food is of poor quality, home ranges of the voles grow in size (Bondrup-Nielsen & Karlsson 1985). It is likely that food quality and presumably quantity are lower in winter. Therefore, individuals which manage to expand their range when food

is scarce or of poor quality can survive better throughout winter. An additional explanation may be that the initially most fit individuals are able to move greater distances under the snow, as it is likely more energetically demanding to move under the snow. However, the only measure of animal body condition we had was body mass and it did not correlate with survival.

Many studies looking at survival from autumn to spring have shown that voles can adjust their body mass to a certain optimum to increase winter survival (Iverson & Turner 1974, Merritt & Merritt 1978, Hansson 1990, Aars & Ims 2002, Wan *et al.* 2014). We, however, could not find any correlation between monthly body mass and survival. Previous studies that have found an optimal winter body mass considered body mass in autumn as a determinant of survival until spring, while we studied monthly survival rates during the winter period with snow cover. This difference may explain why we did not find a body mass effect. In our study, individuals may have already begun adjusting their body mass prior snowfall in December, and those whose body mass deviated from the optimum, either too heavy or too light, would already have died before December.

We found no strong support for a sex- or age-specific variation in monthly survival. As seen in Fig. 3, there is a phase-dependent effect on survival when survival of adults is zero during the crash winter. This effect cannot be explained by within-month variations in winter conditions and/or intrinsic factors, and should be studied further. As voles adjust their body mass to a certain mean in winter, both sex and age classes are more physiologically similar during that period. In addition, as voles inhabit the subnivean area, avian predators cannot detect them unless they move on top of the snow. However, Aars and Ims (2002) and Hoset *et al.* (2009) found that winter survival of females as compared with that of males in enclosed populations of root voles was higher, which was explained by sexual size dimorphism with smaller females surviving better.

Winter climate may be important for vole survival in some years with mild or unstable winter climate (e.g. winters with highly fluctuating temperatures and little snow). A series of consecutive winters with low winter survival may then

dampen cycles, but we found no indication that winter climate was a driver of population cycles in forested areas or in itself affected survival. Food resources seem to be an important factor affecting winter survival in voles (as shown previously by e.g. Huitu *et al.* 2003, Haapakoski & Ylönen 2013, Johnsen *et al.* 2017), and the maximum distance travelled between traps may serve as a measure of resource searching or availability of food resources. Food resources may also be one of the phase-dependent factors affecting bank vole dynamics (Crespin *et al.* 2002). However, we need more studies of the winter ecology and behaviour of voles to fully understand the connections between social structure and movement patterns and winter survival. There is also a need for innovative techniques to study voles under the snow (Soininen *et al.* 2015).

References

- Aars, J. & Ims, R. A. 2002: Intrinsic and climatic determinants of population demography: the winter dynamics of tundra voles. — *Ecology* 83: 3449–3456.
- Andreassen, H. P., Glorvigen, P., Rémy, A. & Ims, R. A. 2013: New views on how population-intrinsic and community-extrinsic processes interact during the vole population cycles. — *Oikos* 122: 507–515.
- Andreassen, H. P. & Ims, R. A. 2001: Dispersal in patchy vole populations: role of patch configuration, density dependence, and demography. — *Ecology* 82: 2911–2926.
- Bakker, E. S., Olf, H., Boekhoff, M., Gleichman, J. M. & Berendse, F. 2004: Impact of herbivores on nitrogen cycling: contrasting effects of small and large species. — *Oecologia* 138: 91–101.
- Bierman, S., Fairbairn, J., Petty, S., Elston, D. A., Tidhar, D. & Lambin, X. 2006: Changes over time in the spatiotemporal dynamics of cyclic populations of field voles (*Microtus agrestis* L.). — *The American Naturalist* 167: 583–590.
- Bilodeau, F., Gauthier, G. & Berteaux D. 2013: The effect of snow cover on lemming population cycles in the Canadian High Arctic. — *Oecologia* 172: 1007–1016.
- Bjørnstad, O. N., Falck, W. & Stenseth, N. C. 1995: A geographic gradient in small rodent density fluctuations: a statistical modelling approach. — *Proceedings: Biological Sciences* 262: 127–133.
- Bondrup-Nielsen, S. & Karlsson, F. 1985: Movement and spatial patterns in populations of *Clethrionomys* species: A review. — *Annales Zoologici Fennici* 22: 385–392.
- Boonstra, R. & Krebs, C. J. 2006: Population limitation of the northern red-backed vole in the boreal forests of northern Canada. — *Journal of Animal Ecology* 75: 1269–1284.
- Boonstra, R., Andreassen, H. P., Boutin, S., Husek, J., Ims, R. A., Krebs, C., Skarpe, C. & Wabakken, P. 2016: Why do the boreal forest ecosystems of northwestern Europe differ from those of western North America? — *Bioscience* 66: 722–734.
- Cornulier, T., Yoccoz, N. G., Bretagnolle, V., Brommer, J. E., Butet, A. & Ecke, F. 2013: Europe-wide dampening of population cycles in keystone herbivores. — *Science* 340: 63–66.
- Crespin, L., Verhagen, R., Stenseth, N. C., Yoccoz, N. G., Prévot-Julliard, C. & Lebreton, J. D. 2002: Survival in fluctuating bank vole populations: Seasonal and yearly variations. — *Oikos* 98: 467–479.
- Eccard, J. A. & Ylönen, H. 2001: Initiation of breeding after winter in bank voles: Effects of food and population density. — *Canadian Journal of Zoology* 79: 1743–1753.
- Fuller, W. A. 1977: Demography of a subarctic population of *Clethrionomys gappari*: numbers and survival. — *Canadian Journal of Zoology* 55: 42–51.
- Fuller, W. A., Stebbins, L. L. & Dyke, G. R. 1969: Overwintering of small mammals near Great Slave Lake Northern Canada. — *Arctic* 22: 34–55.
- Getz, L. L., Oli, M. K., Hofmann, J. E. & McGuire, B. 2007: Demography of fluctuating prairie vole populations: comparison of demographic variables among phases of fluctuations. — *Acta Theriologica* 52: 291–298.
- Gorini, L., Linnell, J. D. C., Boitani, L., Hauptmann, U., Odden, M., Wegge, P. & Nilsen, E. B. 2011: Guild composition and habitat use of voles in 2 forest landscapes in south-eastern Norway. — *Integrative Zoology* 6: 299–310.
- Hansson, L. 1991: Regional and individual variation in body growth in winter of bank voles *Clethrionomys glareolus*. — *Acta Theriologica* 36: 357–362.
- Hansson, L. 1990: Ultimate factors in the winter weight depression of small mammals. — *Mammalia* 54: 397–404.
- Hansson, L. & Henttonen, H. 1985: Gradients in density variations of small rodents: the importance of latitude and snow cover. — *Oecologia* 67: 394–402.
- Hoset, K. S., Le Galliard, J. F. & Gundersen, G. 2009: Demographic responses to a mild winter in enclosed vole populations. — *Population Ecology* 51: 279–288.
- Huitu, O., Koivula, M., Korpimäki, E., Klemola, R. & Norrdahl, K. 2003: Winter food supply limits growth of northern vole populations in the absence of predation. — *Ecology* 84: 2108–2118.
- Hörnfeldt, B. 2004: Long-term decline in numbers of cyclic voles in boreal Sweden: Analysis and presentation of hypotheses. — *Oikos* 107: 376–392.
- Haapakoski, M. & Ylönen, H. 2013: Snow evens fragmentation effects and food determines overwintering success in ground-dwelling voles. — *Ecological Research* 28: 307–315.
- Ims, R. A., Henden, J.-A. & Killengreen, S. T. 2008: Collapsing population cycles. — *Trends in Ecology and Evolution* 23: 79–86.
- Ims, R. A., Yoccoz, N. G. & Killengreen, S. T. 2011: Determinants of lemming outbreaks. — *Proceedings of the National Academy of Sciences* 108: 1970–1974.

- Inchausti, P., Carslake, D., Attié, C. & Bretagnolle, V. 2009 Is there direct and delayed density dependent variation in population structure in a temperate European cyclic vole population? — *Oikos* 118: 1201–1211.
- IPCC 2013: *Climate change 2013: The physical science basis*. — Contribution of working group I to the fifth assessment report of the intergovernmental panel on climate change. Cambridge University Press, United Kingdom and New York, NY, USA.
- Iverson, S. L. & Turner, B. N. 1974: Winter weight dynamics in *Microtus pennsylvanicus*. — *Ecology* 55: 1030–1041.
- Johnsen, K., Boonstra, R., Boutin, S., Devineau, O., Krebs, C. & Andreassen, H. P. 2017: Surviving winter: Food, but not habitat structure, prevents crashes in cyclic vole populations. — *Ecology and Evolution* 7: 115–124.
- Jędrzejewski, W., Rychlik, L. & Jędrzejewska, B. 1993: Responses of bank voles to odours of seven species of predators: experimental data and their relevance to natural predator–vole relationships. — *Oikos* 68: 251–257.
- Kausrud, K. L., Mysterud, A., Steen, H., Vik, J. O., Østbye, E., Cazelles, B., Framstad, E., Eriksen, A. M., Mysterud, I., Solhøy, T. & Stenseth, N. C. 2008: Linking climate change to lemming cycles. — *Nature* 456: 93–97.
- Korpela, K., Delgado, M., Henttonen, H., Korpimäki, E., Koskela, E., Ovaskainen, O., Pietiäinen, H., Sundell, J., Yoccoz, N. G. & Huitu, O. 2013: Nonlinear effects of climate on boreal rodent dynamics: mild winters do not negate high-amplitude cycles. — *Global Change Biology* 19: 697–710.
- Korslund, L. & Steen, H. 2006: Small rodent winter survival: snow conditions limit access to food resources. — *Journal of Animal Ecology* 75: 156–166.
- Lindström, E. & Hörnfeldt, B. 1994: Vole cycles, snow depth and fox predation. — *Oikos* 70: 156–160.
- Martell, A. M. & Fuller, W. A. 1979: Comparative demography of *Clethrionomys rutilus* in taiga and tundra in the low Arctic. — *Canadian Journal of Zoology* 57: 2106–2120.
- Merritt, J. F. & Merritt, J. M. 1978: Population ecology and energy relationships of *Clethrionomys gapperi* in a Colorado subalpine forest. — *Journal of Mammalogy* 59: 576–598.
- Myllymäki, A. 1977: Interactions between the field vole *Microtus agrestis* and its microtine competitors in Central-Scandinavian populations. — *Oikos* 29: 570–580.
- Mysterud, I. 2016: Range extensions of some boreal owl species: comments on snow cover, ice crusts, and climate change. — *Arctic, Antarctic and Alpine Research* 48: 213–219.
- Pastor, J. & Naiman, R. J. 1992: Selective foraging and ecosystem processes in boreal forests. — *American Naturalist* 139: 690–705.
- Pruitt, W. O. J. 1970: Some ecological aspects of snow. — In: Pruitt, W. O. J. (eds.), *Ecology of the subarctic regions*: 83–89. Proceedings of the Helsinki Symposium, United Nations Educational, Scientific and Cultural Organization, Paris.
- R Core Team 2016: *R: a language and environment for statistical computing*. — R Foundation for Statistical Computing, Vienna, Austria.
- Reid, D. G., Bilodeau, F., Krebs, C. J., Gauthier, G., Kenny, A. J., Gilbert, B. S., Leung, M. C. Y., Duchesne, D. & Hofer, E. 2012: Lemming winter habitat choice: a snow-fencing experiment. — *Oecologia* 168: 935–946.
- Reid, D. G. & Krebs, C. J. 1996: Limitations to collared lemming population growth in winter. — *Canadian Journal of Zoology* 74: 1284–1291.
- Sirotnak, J. M. & Huntly, N. J. 2000: Direct and indirect effects of herbivores on nitrogen dynamics: voles in riparian areas. — *Ecology* 81: 78–87.
- Smyth, B. Y. M. 1966: Winter breeding in woodland mice, *Apodemus sylvaticus*, and voles, *Clethrionomys glareolus* and *Microtus agrestis*, near Oxford. — *Journal of Animal Ecology* 35: 471–485.
- Soininen, E. M., Jensvoll, I., Killengreen, S. T. & Ims, R. A. 2015: Under the snow: a new camera trap opens the white box of subnivean ecology. — *Remote Sensing in Ecology and Conservation* 1: 29–38.
- Sonerud, G. A. 1986: Effect of snow cover on seasonal changes in diet, habitat, and regional distribution of raptors that prey on small mammals in boreal zones of Fennoscandia. — *Holarctic Ecology* 9: 33–7.
- Stien, A., Ims, R. A., Albon, S. D., Fuglei, E., Irvine, R. J., Ropstad, E., Halvorsen, O., Langvatn, R., Loe, L. E., Veiberg, V. & Yoccoz, N. G. 2012: Congruent responses to weather variability in high arctic herbivores. — *Biology Letters* 8: 1002–1005.
- Symonds, M. R. E. & Moussalli, A. 2011: A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. — *Behavioral Ecology and Sociobiology* 65: 13–21.
- Wan, X., Zhang, X., Wang, G. & Chen, L. 2014: Optimal body weight of Brandt's voles for winter survival. — *Journal of Arid Environments* 103: 31–35.
- Whitney, P. 1976: Population ecology of two sympatric species of subarctic microtine rodents. — *Ecological Monographs* 46: 85–104.

