INLAND NORWAY
UNIVERSITY
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PhD Thesis

Seasonal- and phase-dependent effects on vole population dynamics

PhD In Applied Ecology

2018

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Preface

I did not know a lot about voles before I started this PhD. Many people associate voles with pests and do not like them. I did not really like or dislike them before. Now, I think they are the cutest (bank voles of course) most fascinating creatures. When people outside the field of ecology asked me which species I studied, and I answered "klatremus" (bank vole), they just laughed until they understood that I actually was serious. They toughed I just made a joke about Klatremus from Hakkebakkeskogen (a Norwegian story for children about a vole called Klatremus).

First of all, I would like to thank my main supervisor, **Harry P. Andreassen**. I am very grateful that you have been my supervisor. Your support, patience and help has been incredible. You are always so positive and helpful. No matter if you are laughing with me or of me, you cheer me up. Thanks for your great ideas.

My co-supervisor **Olivier Devineau**, you are so patient! I am so grateful that you supported me during my roller coaster in R. Thank you for helping me with the most stupid questions. You have saved me over and over again.

Thanks to all the field workers helping me collecting my data. I could not have done it without you. A special thank you to **Barbara Joncour**, **Thomas Vogler** and my fellow PhD-student **David Carricondo Sánchez**. Not all the days and evenings we were running around in the forest looking for traps were that fun – in rain, 1.5 meters of snow or sun. Now I miss it!

I have to thank **Lasse Asmyhr** for all the discussions, both academic and non-academic (read dogs and hunting), in the BEcoDyn-office. I enjoyed our three years sharing the same office.

I would also like to thank all fellow PhD-students here at Evenstad, both current and past. It has been great working in this PhD-environment, sharing laughter and complains. I especially thank **Cyril Milleret** for discussions (many about skiing though), and your statistical support (what is it about these French people and statistics?)

The environment at Campus Evenstad has been great for doing a PhD. I really enjoy being a part of this society. I have to thank all of the "coffee-people" for making my day start with laughter almost every day. Especially **Elisabeth**, **Ragnhild** and **Mona** for making a normal sometimes PhD-day sunny, my, at times therapists, and friends. There are so many people I could have

mentioned that has contributed to a great working environment, but the list is too long to acknowledge you all. Thanks to all colleges at Evenstad.

Thomas, the love of my life. Thanks for taking care of me and supporting me.

Thanks to **Mocca**, **Tine** and **Vilja** for making sure that I frequently got some fresh air and exercise.

Og til slutt, takk til **mamma** og **pappa** som har lært meg å bli glad i naturen og dens goder, og som alltid har støtta meg på alle måter de kan.

Table of content

Sammendrag (Norwegian summary)

Populasjonssykluser hos smågnagere er en viktig komponent i det boreale barskogsøkosystemet på de nordlige breddegrader. Mange hypoteser har blitt beskrevet for å forsøke å forklare disse sykliske svingningene, men predasjon, mattilgang og muligens intrinsiske faktorer dominerer som forklarende faktorer. Disse regelmessige svingningene med høye amplituder har imidlertid blitt borte i løpet av de senere tiår, noe som mest trolig vil ha konsekvenser for økosystemet. Lav vinteroverlevelse forårsaket av klimaforandringer er foreslått som en forklaring for at de høye amplitudene ble borte. Det er derfor viktig å forstå hvilke faktorer som bidrar til endringer mellom sesonger og faser på populasjonsdynamikken. I denne avhandlingen presenterer jeg et detaljert studie av klatremus *Myodes glareolus* hvor jeg følger populasjoner månedlig gjennom mer enn to år. Hovedmålet var å studere vinterpopulasjoner for å få mer kunnskap om grunnleggende mekanismer som forårsaker smågnagersykluser og hvorfor de høye amplitudene ble borte. Jeg studerte hvorvidt klimaforhold om vinteren (snødybde, temperatur under snøen og skare) hadde en effekt på vinteroverlevelse, eller om adferd (maksimal avstand forflyttet mellom feller, brukt som mål på aktivitetsområde) og/eller fysiologiske (kroppsvekt) faktorer var mer viktig. Jeg fant ingen sammenheng mellom vinteroverlevelse og klimaforhold, men jeg fant en positiv sammenheng mellom vinteroverlevelse og aktivitetsområde, som betyr at overlevelsen øker ved lenger avstand de beveger seg. Jeg foreslo en hypotese om at aktivitetsområde var relatert til mat og viktigheten av mat om vinteren, noe som betyr at individer som klarte å bevege seg mer under snøen hadde større mattilgang. Viktigheten av mat om vinteren ble også bekreftet ved et eksperiment hvor tilleggsfôring gjennom vinteren forhindret et krasj i populasjonen. Jeg fant også bevis for territoriell adferd hos voksne hunner om vinteren, noe som også indikerer viktigheten av mat om vinteren, siden mat trolig er hovedgrunnen til at hunner forsvarte territorier utenfor ynglesesongen. Resultater viser også at en optimal kroppsvekt i oktober er viktig for vinteroverlevelse, siden individer som var for tunge eller for lette i forhold til et visst optimalt vektintervall ikke overlevde vinteren. I tillegg viser jeg at sosial adferd hos voksne hunner er viktig i den stigende fasen av syklusen, der jeg fant en større grad av overlappende leveområder i den stigende fasen sammenlignet med krasjfasen. For å konkludere: Vinterklima kan være viktig i noen særlige vintre med mildt og ustabilt klima, men jeg fant ingen indikasjoner for at vinterklima var en driver av populasjonssyklusene. Jeg fant mer støtte for viktigheten av mat for vinteroverlevelsen, og dens bidrag til å forme populasjonssykluser hos klatremus.

Abstract

Vole population cycles are a major force driving boreal ecosystem dynamics in northern latitudes. Many hypotheses has been described to explain these cycles, but high predation, low food availability and possibly intrinsic factors predominate. However, these regular fluctuations with high amplitudes has dampened during the recent decades, causing unknown effects for the ecosystem. Low winter survival induced by climate change has been proposed as a possible explanation for dampening of the vole cycles. Understanding factors that contribute to the seasonal- and phase-dependent effect on population dynamics is therefore important. In this thesis, I present a detailed study of bank voles *Myodes glareolus* as I followed populations monthly throughout more than two years. The overall aim was to study winter populations to get a better knowledge of the mechanisms underlying vole population cycles and the dampening of amplitudes. I studied whether winter climate conditions (i.e. snow depth, subnivean temperatures and snow crust) had an effect on winter survival, or if behavioural (maximum distance moved between traps, as a descriptor of activity range) and/or physiological (body mass) conditions were more important. I found no correlation between winter survival and winter climate conditions. However, I found a positive correlation between winter survival and activity range, i.e. the survival increased with longer distances voles moved in winter. I hypothesised that activity range was related to food resources and their importance during winter, meaning that individuals that were able to move more in the subnivean space could access more resources. The importance of food during winter was confirmed by an experiment where supplemental feeding during winter prevented a population crash. I also found evidence for territorial behaviour in adult females during winter, again indicating the significance of food resources during winter, as food may be the main reason why females would defend territories during the non-breeding season. My results also show that an optimal body mass in October is important for winter survival, as individuals that were too heavy or too light according to an optimal body mass range did not survive the winter. Additionally, I show that social behaviour in adult females is important in the increase phase of the cycle, as I found a higher degree of overlap in home ranges in increase phase compared to crash phase. To conclude: Winter climate may be important in some particular years with mild or unstable winter climate, but I found no indication that winter climate was a driver of the population cycles. However, I found support for food resources playing a significant role for winter survival, hence contributing to forming population cycles in bank voles.

Keywords:

Behaviour, climate, feeding experiment, *Myodes glareolus*, physiology, population dynamics, sociality, winter

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List of papers

This thesis is based on following original papers and manuscripts.

Paper I:

Johnsen K., Devineau O., and Andreassen H. P. The role of winter climate and intrinsic factors on survival of cyclic vole populations in south-eastern Norway. *Annales Zoologici Fennici,* 55: 173-185

Paper II:

Johnsen K., Boonstra R., Boutin S., Devineau O., Krebs C., and Andreassen H. P. (2017). Surviving winter: Food, but not habitat structure, prevents crashes in cyclic vole popultions. *Ecology and Evolution,* 7(1): 115-124

Paper III:

Johnsen K., Devineau O., and Andreassen H. P. Phase- and season-dependent social behavior in cyclic vole populations. *Manuscript*.

1. Introduction

1.1 Population ecology

A population is a group of individuals of the same species that inhabit a given area at the same time (Rockwood 2009a). In population ecology we want to know which factors are most important for controlling abundance, growth rate and distributions of populations in space and time. It is important to know these factors to improve management and conservation of populations. Turchin (2003a) proposed to divide population dynamics into three main categories; (I) exponential growth, (II) population self-limitation and (III) consumer-resource oscillations. In the first case (I) populations will grow exponentially as long as the environment for all individuals in the population remains constant (Turchin 2001). The environment refers to all factors that can affect vital rates of individuals (e.g. resources, density/crowding, abiotic factors). This means that exponential growth is density-independent. The best example of exponential growth is the human population that has continuously grown since around 1650. The second case of population dynamics (II) refers to that population growth cannot go on forever (Turchin 2003a). This assumes that the population at one point encounters a limiting resource (e.g. food, water, nest sites, space), and the growth is density-dependent. Logistic population growth is an example in this category when population growth ceases when the population reaches the carrying capacity of the environment (Rockwood 2009b). The third case of population dynamics (III) suggests that trophic interactions are the key function in driving population oscillations (Turchin 2003a). These oscillations are controlled by density dependence. If the density dependent factors are very strong, it can lead to chaotic population dynamics. However, if there is a time-lag before the negative feedback mechanisms initiates, we get a delayed density dependence that can lead to cyclic population dynamics. (Rockwood 2009b).

1.2 Population cycles

Multi-annual population cycles has puzzled scientists for decades (Elton 1924, 1942; Krebs and Myers 1974; Hörnfeldt 1978; Keith 1990; Small et al. 1993; Stenseth and Ims 1993; Kendall et al. 1998). Cyclic population dynamics are predictable multiannual fluctuations in density, consisting of regular periods with variable high amplitudes, and are regulated by delayed density dependent factors (Hörnfeldt 1994). Cyclicity occurs in a wide range of species and is most

common in mammals and birds (Kendall et al. 1998). These regular population fluctuations predominantly occur in highly seasonal environments in northern latitudes, where the period of the cycle for a given species has been shown to increase with latitude (Hansson and Henttonen 1985; Hanski et al. 1991; Bjørnstad et al. 1995). The most known studied cycles are possibly the snowshoe hare *Lepus americanus* cycles and the rodent (Arvicoline rodents) cycles. Snowshoe hare in North-America exhibits a 9- to 10 year population cycle (Krebs et al. 2014), whereas rodents in the Northern latitudes exhibit a 3-5 year population cycle (Sundell et al. 2013). Population cycles are characterized by a low, increase, peak and decrease/crash phase. In voles, the crash can be very abrupt, i.e. a rapid decrease in density, and it may occur during the breeding season (Stenseth and Ims 1993; Andreassen et al. 2013). However, population crashes are more often observed during winter and possibly the following spring/summer (Krebs and Myers 1974; Perrin 1979; Wiger 1979; Hansson and Henttonen 1985). Many hypotheses has been proposed to explain these cycles, but most often they have been associated to predation or food availability for both rodents and snowshoe hare, in addition to potential intrinsic factors (e.g. sociality and maternal effects, Keith 1990; Krebs et al. 1995, 2018; Krebs 1996; Andreassen et al. 2013; Myers 2018).

1.3 Intrinsic and extrinsic factors driving the population cycles

Several extrinsic factors have been proposed to contribute to the cyclic fluctuations in voles (e.g. predation and food). Predation has probably received most support as a driving mechanism for vole- and lemming cycles (Korpimäki and Krebs 1996; Hanski et al. 2001; Turchin and Hanski 2001; Turchin 2003b; Korpela et al. 2014). However, it has also been suggested that food, either the quantity or the quality, has a role in driving the cycles (Gilbert and Krebs 1981; Huitu et al. 2003; Krebs et al. 2010; Boonstra and Krebs 2012; Reynolds et al. 2012).

Several intrinsic factors have also been proposed as mechanisms contributing to cyclic fluctuations (e.g. behaviour and physiology). Social behaviour has been linked to many hypothesis explaining population cycles, often related to kin-selection and territorial behaviour (Charnov and Finerty 1980; Lambin and Krebs 1991; Krebs 1996). Furthermore, body mass has been assessed as an important factor, particularly related to winter survival, as voles adjust their body mass to a physical optimum during winter to increase their winter survival (Iverson and Turner 1974; Merritt and Merritt 1978; Hansson 1990; Aars and Ims 2002). Also, extrinsic and

intrinsic factors could interact to drive vole population cycles (Stenseth et al. 1996; Andreassen et al. 2013; Radchuk et al. 2016).

1.4 Dampening of cycles and the winter climate hypothesis

Multi-annual population cycles with regular high amplitude peaks in rodents have been described to fade out over the last decades (Ims et al. 2008). However, there seem to be variations in the strength and length of the dampening, indicating that dampening of high-amplitude peaks can be species- and/or area-specific (Strann et al. 2002; Hörnfeldt 2004; Huitu et al. 2007; Brommer et al. 2010; Korpela et al. 2013). It has been hypothesized that climate change is the decisive factor explaining the dampening of the cycles due to reduced winter survival (Hörnfeldt et al. 2005; Kausrud et al. 2008; Cornulier et al. 2013). With global warming, temperatures will rise and precipitation will increase (Stocker et al. 2013). For winter conditions, this means that there will be a shorter period with intact ground covered by snow, e.g. the autumn will last longer and the spring will arrive earlier. The winter precipitation is estimated to increase, but because of rising temperatures there will be more incidents of rainfall in place of snow during the winter (Jylhä et al. 2008). These melting-freezing events can lead to the formation of an ice layer on the ground, and alter the quality of the snow (Jylhä et al. 2008). In total, the winter climate will be more unstable and less predictable than previously. In Norway, the mean temperature in 2017 was 1.1 °C higher than the average temperature the last 30 years, and the precipitations were 120 % of the average precipitations the last 30 years (Meterologisk institutt 2018). For the winter season 2016/2017 only, temperatures were 3.7 °C above average temperature the last 30 years and precipitations were 140 % of the average precipitation the last 30 years (Meterologisk institutt 2017).

For voles living in the subnivean space, between the ground and the snow cover, for several months per year, the subnivean conditions are crucial for surviving the winter. Snow has several important qualities, such as providing the voles with thermal insulation and protection against generalist and avian predators (Sonerud 1986; Lindström and Hörnfeldt 1994). An ice cover on the ground which is anticipated during climate change, due to frequent thawing and freezing events, can deteriorate access to resources as the food would be encrusted in the ice, and ice prevent access to food by fragment the subnivean space into accessible and inaccessible parts (Aars and Ims 2002; Hörnfeldt 2004; Korslund and Steen 2006; Kausrud et al. 2008).

1.5 Winter ecology of small rodents

Seasonality has been described to be an essential part of the population cycles (Hansen et al. 1999; Taylor et al. 2013). Even though winter seem like an important season in the vole cycle (Hansen et al. 1999), most focus on small rodents has been in the breeding season. Here I summarize studies on winter ecology of small rodents in the Northern latitudes according to:

Body mass:

- It has been shown that small rodents have a physiological optimal winter body mass that is species specific.
    - Iverson and Turner (1974) found that meadow vole *Microtus pennsylvanicus* populations lost between 30 – 40 % of their mean body weight from August to February.
    - Wiger (1979) found that weights of male bank voles over winter were lowest in year of increase phase and highest in year of peak phase. Further they found that the late summer cohort of the population had highest winter survival.
    - Ylönen and Viitala (1985) found that winter weight in enclosed populations of bank voles reached its minimum in November/December, with differences between cohorts within the population.
    - Hansson (1990) found that the body weight for bank voles and field voles *Microtus agrestis* declined in winter, and that it was most prominent in smaller vole species, independent of autumn body weight or climate conditions.
    - Hansson (1992) found that body weights in laboratory field voles and bank voles were lower in winter than autumn.
    - Aars and Ims (2002) found that tundra voles *Microtus oeconomus* adjusted their body mass to a certain mean during winter.
- However, Aars and Ims (2002) have studied the association between body mass and survival showing that the tundra voles adjusted their winter body mass to increase survival. While Karlsson (1988) could not find that body mass in bank voles could be used to predict winter survival.

- Hansson (1992) found that reproduction was negatively correlated to winter weights, especially in bank voles.

Winter climate and snow conditions

- Kausrud et al. (2008) showed that changes in winter weather and snow conditions could affect the dynamic of lemmings in alpine areas, and they even predicted the observed absence of rodent peaks after 1994 with their models.
- Korslund and Steen (2006) found that survival of tundra voles increased with increasing space availability in the subnivean area.
- Perrin (1979) proposed that an extreme autumn climate with poor snow cover and low subnivean temperatures caused high mortality in red-backed voles *Myodes gapperi*, either directly, or indirectly by detriment to foraging or forage quality.
  - However, Whitney (1976) found that red-backed voles *Myodes rutilus* survived well under extreme winter conditions (subnivean temperatures at -30°C), actually even better than most summer periods.
  - Neither did Fuller (1977) find an association between winter mortality in red-backed voles (*M. gapperi)* and the severity of winter conditions.
- Several winter condition parameters have been associated with lemming species populations:
  - Bilodeau et al. (2013) found that snow depth could increase the summer density of brown lemmings *Lemmus trimucronatus*, affecting the amplitudes and possibly the periods of the cycle.
  - Reid and Krebs (1996) found that low autumn temperatures and shallow winter snow appeared to be strong limiting factors in population growth of collared lemmings *Dicrostonyx kilangmiutak*.
  - Reid et al. (2012) found that the density of winter nests in voles and lemmings increased with snow depth, indicating that snow depth is a determinant of winter habitat quality.
  - Similarly to the last reference, but for bank voles, Ylönen and Viitala (1985) found that bank voles aggregated in areas with brush-vegetation before winter, which were also the area with thickest snow cover during winter.

- In contrast: Korpela et al. (2013) found that population dynamics in voles (*Microtus* and *Myodes*) correlated more strongly with growing season than with winter climate conditions; milder winters did neither decrease winter growth rates nor dampen high-amplitude cycles.
- Hoset et al. (2009) did not find a correlation between winter survival in root voles and ice accumulation, concurrently they found that survival were lowest at the onset of snow melt in early spring.

Winter habitat

Except for the studies mentioned above on selection of nest sites with specific winter conditions there are few studies on winter habitat of voles. However, Karlsson (1988) found that bank voles preferred winter habitats with more rocks and Karlsson and Potapov (1998) found that overwintering bank voles selected the same locations for nest sites across a decade.

Behaviour

- Karlsson (1985) found that female bank voles had more overlapping home ranges than males in winter.
- Karlsson and Ås (1987) found that bank voles shared nests at low densities during winter, while they went in different directions for foraging, indicating the trade-off between advantages and disadvantages of nest sharing.
- Perrin (1981) found for red-backed vole (*M. gapperi)* that adult males were more aggressive than adult females during winter.
- Karlsson and Potapov (1998) found that bank vole males average home range size were positively correlated with snow depth in April, indicating that snow is favourable when travelling longer distances during breeding season.
- Korslund (2006) found that tundra voles displayed a synchronous free-running activity rhythm under the snow when subnivean fragmentation were decreased, and that the activity was evenly distributed during the 24-h day.

Food

- Boonstra and Krebs (2006) proposed that winter survival was the key factor limiting red-backed vole (*M. rutilus)* populations, as a function of food production during the previous summer.

- Martell and Fuller (1979) compared winter mortality in red-backed voles between tundra and taiga, and found highest mortality in tundra. They proposed that tundra populations are controlled by environmental factors while taiga populations are controlled by overexploitation of resources.

- Several experiments have been carried out to test the effect of food on vole populations during winter:
  - Eccard and Ylönen (2001) found that bank voles started breeding earlier in spring when they were fed with sunflower seeds during winter, compared to feeding naturally by spruce seeds.
  - Schweiger and Boutin (1995) found that winter food supply in red-backed voles (*M. rutilus*) only created high autumn densities in local patches, but were not able to create a peak in the population over a larger area.
  - Ylönen and Viitala (1991) showed that supplementary fed bank voles aggregated in groups during winter, and that the distribution of food affected the over-all winter distribution of voles.

- While most experiments have shown positive effects of winter feeding on vole populations, Huitu et al. (2003) managed to prevent a winter crash in field voles only if supplementary feeding was combined with the elimination of predation.

- Few observational studies exist from natural vole populations, but Huitu et al. (2007) found evidence for a deterioration in the physiological conditions in field voles and a depletion of winter food resources in the winter of decrease phase compared to the winter in increase phase.

Predation

- Haapakoski et al. (2012) found that predation risk, even without direct predation, delayed the initiation of breeding in bank voles compared to populations with supplementary feeding.

Breeding

- Aars and Ims (2002) found that tundra vole population changes over winter were density dependent (recruitment), while differences between winters were density-independent (climate).

- Ims et al. (2011) found that the steeper increase in Norwegian lemming *Lemmus lemmus* outbreaks compared to vole outbreaks were caused by breeding and population growth during winter in lemmings, while nonbreeding voles declined over winter.

2. Objectives

Global warming is happening and has become a true challenge for humankind and it will have a big impact on ecosystems. Small rodents are key species in the boreal forest. As small rodents form large resource pulses to the ecosystem in their peak phases (Ostfeld and Keesing 2000), little is known about what will happen in the ecosystem if these high amplitude cycles diminish. Climate change has been proposed to deteriorate winter conditions for voles, decreasing winter survival and consequently dampen amplitudes.

Much focus about the impact of winter climate conditions on voles has been on the level of amplitudes and between-winter survival, i.e. comparing fall and spring populations. However, to get a more detailed idea about the effect of winter climate conditions on vole population dynamics we need to study the within-winter survival. The overall aim of the present project was to study winter populations of bank voles in detail to get a better knowledge of the mechanisms underlying vole population cycles and the dampening of population amplitudes. I did this by observing natural populations of bank voles in elevation gradients (Fig. 1) used as a proxy for winter climate, and by performing experiments manipulating winter conditions for these natural populations.

More specifically, my objectives were:

1) To assess whether winter survival was associated with winter climate conditions, directly (through snow conditions and temperatures) or indirectly (through food resources and habitat), or if behavioural and/or physiological conditions are more important for winter survival (**Paper I, Paper II**).

2) To test Andreassen et al.'s (2013) multifactorial model (describing how interactions between social behaviour and extrinsic factors, e.g. predation, contribute to shape population dynamics) by studying how social behaviour changed with different seasons and phases of the cycle (**Paper III**).

Fig. 1. The picture is showing the elevation gradient from my study area, where it is clearly showing the difference in climatic conditions along the gradient.

3. Material and methods

3.1 Study animal

The bank vole is a small microtine rodent distributed across Europe from mature forests to reforestation areas and meadows (Myllymäki 1977; Mitchell-Jones et al. 1999). It is characterized by a relatively short life span (about one year) but high reproductive rate. In Fennoscandia, reproduction mainly occurs during the summer season from late May to September (Koivula et al. 2003). Bank voles are omnivorous, eating mainly seeds, berries, fungi, forbs, grass and some insects (Hansson 1985). While their winter diet in Fennoscandia is predominated by dwarf shrubs *Vaccinium* spp., it also includes fungi, lichens and some berries and seeds (Hansson and Larsson 1978). Hansson and Larsson (1978) found examples of decreasing amounts of seeds and berries in the diet of bank voles towards the crash phase. Females are territorial while male home ranges are large and overlap extensively (Mazurkiewicz 1971). Female territoriality is assumed to be a response to the spatial distribution, abundance and renewal of food resources (Ostfeld 1990).

3.2 Study area

The study was carried out in the boreal forests of Stor-Elvdal municipality in southeast Norway (61°N, 11°E) (Fig. 2) from June 2013 - Oktober 2016. These forests are dominated by Norway spruce *Picea abies* and Scots pine *Pinus sylvestris*, with bilberry *Vaccinium myrtillus* in the understory shrub layer, and mosses (*e.g. Pleurozium schreberi*) in the ground layer. The region has experienced dampened cycles and absence of peak in voles and lemmings since the mid 1980's (Hörnfeldt 2004). In 2007 the cycles returned, with summer peaks in 2007, 2011 and 2014 (Johnsen et al 2017, Hedmark University of Applied Sciences, unpublished data).
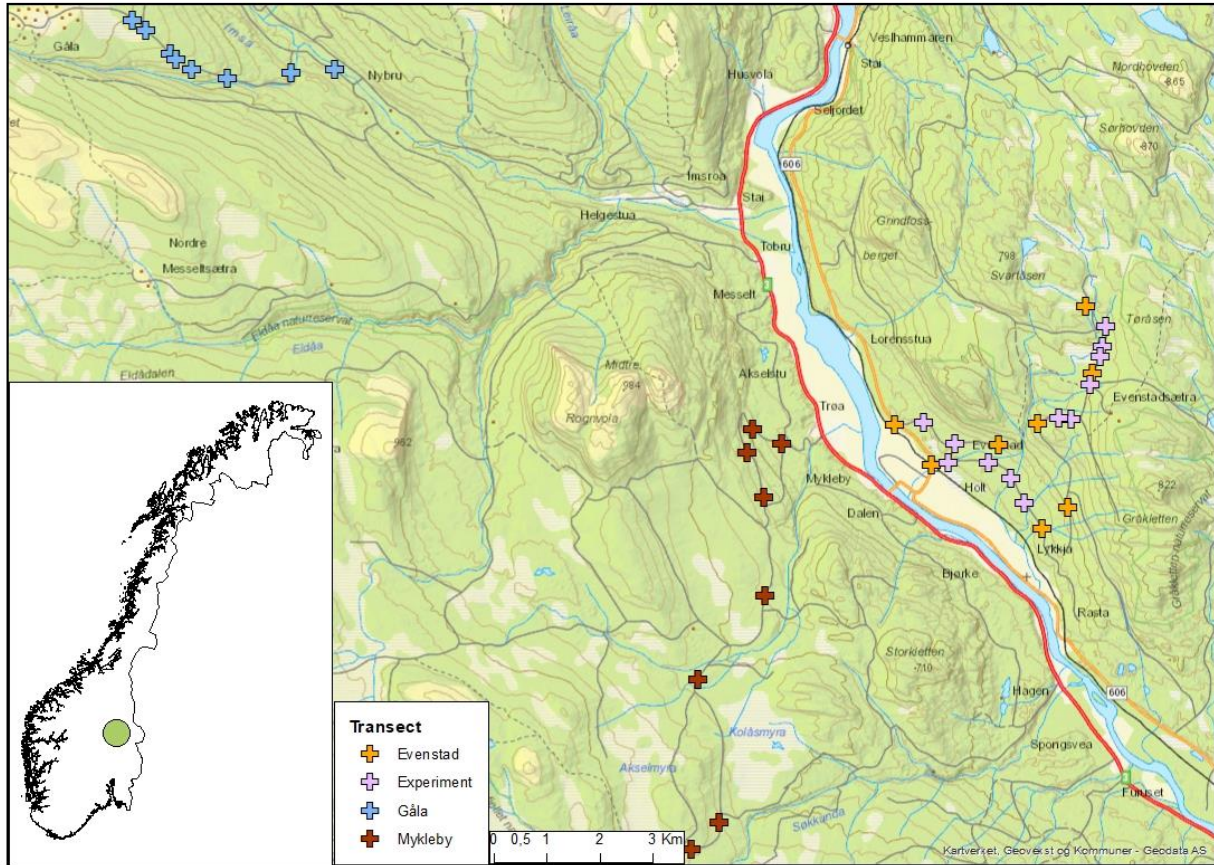
Fig. 2. The study area located in southeast Norway, presenting the trapping plots along the three elevation gradients.

3.3 Trapping procedure

Trapping was conducted in the three different regions Evenstad, Mykleby and Gåla. In every region there were 8 trapping grids distributed along an elevation gradient. Voles were caught on 60 m x 60 m grids consisting of 16 Ugglan multiple capture live traps (Granab, Sweden) arranged in a cross pattern (spacing between traps 15 meters) (Paper I, Paper II, Paper III), except for some grids where we adjusted the layout in order to encompass suitable habitat (Paper I, Paper II, Paper III). Grids were located in typical bank vole habitat, preferably in mature forest with areas dominated by bilberry in the understory shrub layer (Myllymäki 1977; Gorini et al. 2011), and near a forest road. We placed grids in all suitable forest habitat fragments along the road, but with a minimum of 500 m between grids.

To increase capture probabilities, traps were located close to a runway or a hole with potential vole activity within a 3 m radius from the predefined layout of traps (e.g. cross pattern). Trap locations were marked with a stick and a ribbon in the closest tree, and they remained fixed throughout the study. Traps were left at the capture site permanently so that voles could habituate to them and use them as part of their runway system when traps were not active. During a live-trapping session, traps were set in the evening of day 1, checked the next morning, and the next evening each day for 3 days (6 secondary trap occasions per session). Traps were baited with oats and carrots. Captured voles were individually marked with pit-tags (1.25x7 mm ID-100VB Nano Transponder), sexed, weighed to the nearest gram, 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.

3.4 Winter trapping

During winter each trap was covered with a 30 cm x 30 cm x 40 cm floorless plywood box to prevent the traps from being covered with snow. The boxes were removed in the spring when the snow melted around them. Traps were supplemented with sawdust for warmth. Only two of the regions were trapped during winter, and in January-April 2014, some trap-days were lost owing to either extreme cold (below -20 °C) or to heavy snow concealing the traps (Table 1).

3.5 Experimental design

Our experimental design assessed the impact of elevation, food, and habitat structure on vole survival and dynamics. The manipulations were duplicated at two elevations (Low elevation: 280-320 m.a.s.l., High elevation: 550-700 m.a.s.l.) to permit comparison of vole population performance under conditions that were expected to be more stable and less subject to temperature fluctuations and icing (high elevation), and less stable (low elevation). The Feeding experiment was designed to prevent winter food limitation and the Habitat manipulation consisted in creating an ice-free subnivean habitat structure. On the Feeding grids, we provided a mixture of 80% oats and 20% sunflower seeds *ad libitum* inside the trap boxes. Presence of food was checked every trapping session and food was added if necessary. We use a total of ca. 250 kg of seeds per winter. For the Habitat grids, we spread straw 20 cm thick over about 4 square meters centred on each of the trap boxes. Hence, each of the 16 trap stations on a grid received this amount of straw.

At each elevation, Control, Feeding, and Habitat grids were randomized along the forest roads. We had 8 Control grids at Low elevation and 6 at High elevation, and 3 Feeding grids and 3 Habitat grids at both elevations, making a total of 26 grids. Each year, both the Feeding and the Habitat manipulations were initiated in November and lasted until May, when the snow had melted enough to expose bare ground at both elevations. See Table 1 for full trapping history.

Table 1. Full trapping history.

Month and year	Transects	N grids	N secondary occasions
June13	3	24	15
July13	3	24	15
August13	3	24	18
September13	3	24	18
October13	2	16	12
November13	1	7	6
December13	2	14	12
January14	2	6	12
February14	2	13	6
March14	2	14	12
April14	2	14	12
May14	2	14	12
June14	3	24	12
July14	3	24	12
August14	3	24	12
October14	3	24	12
November14	3	24	12
December14	2	14	12
January15	2	14	12
February15	2	14	12
March15	2	14	12
April15	2	14	12
May15	2	14	12
June15	3	24	12
July15	3	24	12
August15	3	24	12
June16	2	16	12
August16	2	16	12
October16	2	16	12

3.6 Winter conditions

Temperature loggers (HOBO U23 Pro V2) were used to record subnivean temperature every 6 h in 10 grids: 5 at high elevation and 5 at low elevation. Snow depth (measured to the nearest cm), presence of snow crust layers, and presence of icing on the ground was determined once every trapping session in Control grids. Snow crust layer was assessed as the presence/absence of one or several snow crust layers. Icing on the ground was assessed visually as the presence/absence of ice on the ground.

3.7 Statistical analyses

3.7.1 Within-monthly survival at grid level (Paper I)

Due to a decline/low phase in the vole population cycle in our study period, few individuals were captured at a trapping grid level during winter. This prevented us from using capture-recapture analyses, as a grid level analysis was important to assess the variation in winter conditions descriptors. My focus was to study winter conditions independent of year, phase of the cycle or primary trapping session (i.e. an within-month variation). 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 included session as a random effect, it means that we do not study the effect of climate and intrinsic factors as between month variation, but rather within month variation.

3.7.2 Abundance and over-winter survival (Paper II)

We used the robust design approach to estimate abundance and survival with the capture-recapture data (Pollock 1982; Kendall 1999). The robust design approach assumes that the population is open between primary trapping sessions (i.e. from one month to the next), but closed within trapping sessions (i.e. secondary trapping occasions from one trap check to the next during a given trapping session). This allows the model to provide estimates for (monthly) true survival S and abundance N, as well as for capture/recapture (denoted p and c) and emigration/return (γ" and γ') probabilities.

3.7.3 Sociality (Paper III)

We estimated density (D) and sigma (σ) for each trapping grid and season using spatially explicit capture-recapture (SECR) models (Efford 2016). Parameter σ is the spatial scale of detection that describes the relationship between detection probability (g0) and the distance between a trap and an animal activity centre, and can be understood as a metric of home range size (Bogdziewicz et al. 2016; Efford et al. 2016). To estimate detection probability we used a half-normal detection function, and a spatial buffer on 50 meters. Model parameters (D, g0, σ) were set to be session dependent.

Efford et al. (2016) suggest to re-parameterize the models using k (the relationship between home range size and density, expressed as the degree of home range overlap), however we were not able to estimate k for adult females, due to too few captures. We therefore ran a linear regression between $\log(\sigma) = \log(k) + \beta \log(\sqrt{D})$ and density, and obtained residuals from the regressed model. We used these residuals as an index for home range overlap, where a negative value means that there were less home range overlap than expected by the density, and positive means that there was more home range overlap than expected by the density. We estimates home range overlap only among adult females as we were interested in changes in sociality in the territorial segment of the population.

4. Background results

4.1 Population background

A total of 1879 individuals were captured 9231 times during the period of our study. In the study period the populations experienced all the four different phases of a cycle; increase, peak, crash and low phase. Both the spring and summer of 2013 and 2014 had high population densities with a winter decrease in between. Hence, we have chosen to call the whole period from June 2013 until August 2014 for the *increase* phase peaking in August 2014, and the period from September 2014 as the *crash* phase of the cycle (Fig. 3). The crash phase in the populations occur during late fall and winter, where 13 out of 14 populations of the trappable individuals went extinct from December to May. The very sharp-pointed shape of the peak phase emphasize the importance of time in studies of small rodents, whereas a less frequent trapping effort could have shown a lower level of the amplitude.

Fig. 3. Minimum number known to be alive (MNKA) per trap from June 2013-October 2016.
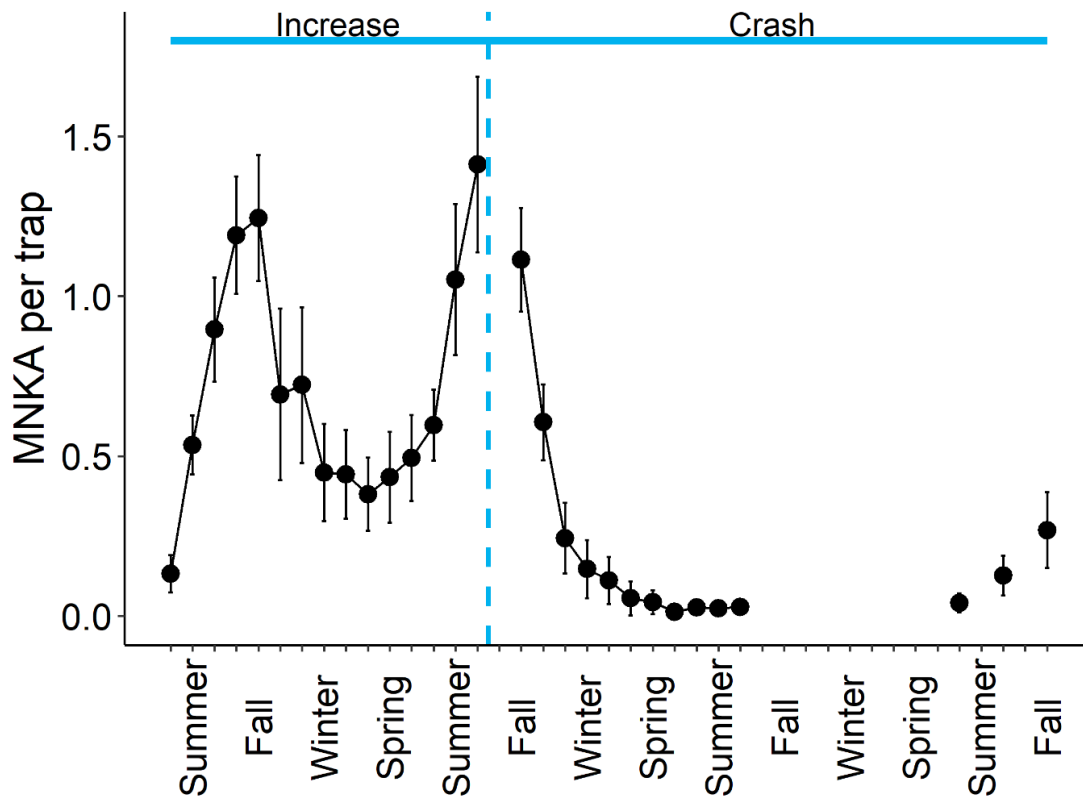
4.2 Background of winter conditions

Mean snow depth was 15 cm deeper in the winter of 2013/2014 than the winter of 2014/2015 (Fig. 4), and it was deeper at higher elevations as expected. There were more trapping grids with presence of snow crust in 2014/2015 than in 2013/2014, but no difference between elevations, as I might had expected due predicted difference in temperatures between elevations. There were no difference in subnivean temperature between years (Fig. 4) or elevations (Paper I), probably because snow depth reached >20 cm, which is considered the maximum insulation capacity (Pruitt 1970), both winters and all elevations.
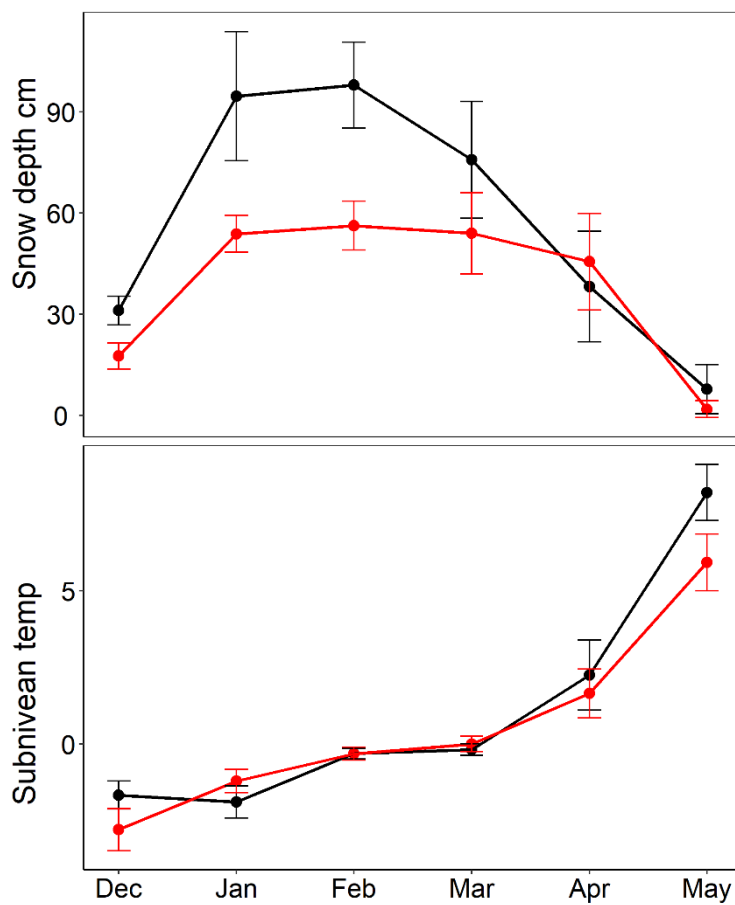

Fig. 4. Mean snow depth and mean subnivean temperature per month across the two winters of the study. Black circles and lines is the winter 2013/2014 and red circles and lines is the winter 2014/2015.

5. Results and discussion

5.1 Winter survival

5.1.1 Effects of climate and winter conditions

I could not find support for a correlation between winter climate conditions and within-winter survival (Paper I). Even though I compared populations across a wide variation in survival rates from a stable and a crash winter and an elevation gradient creating within-month variation in winter conditions. This could be due to the lack of severe winter conditions during the study period, e.g. there was no icing on the ground. However, neither Korpela et al. (2013) or Hoset et al. (2009) found an effect of milder winters on survival of vole populations.

As a matter of fact, I did not register any extensive icing on the ground during the two winters of the study. It could of course be due to no exceptional winter weather conditions during the study period, but I also started to question if it is possible to get these events of extensive icing on the ground in the forest. Most focus on icing on the ground has been either in alpine areas (Kausrud et al. 2008; Stien et al. 2012), or on agricultural or other grass fields (Aars et al. 1999; Korslund and Steen 2006), where the field layer is either almost absent or mostly consisted of plant species low in wood fiber that breaks easily. Most of these studies only use a climate index as a proxy for ground icing, and actually do not visually observe the ice.

5.1.2 Effect of food and habitat structure

Food supply, on the other hand, did affect winter survival of voles (Paper II). When comparing three experimental treatments: artificial habitat structure, supplementary feeding and control, over the two winters of 2013/2014 and 2014/2015, I found a positive effect of feeding on over-winter survival (Fig. 5). Survival in feeding populations were higher than control populations in both the increase winter and the crash winter. Actually, supplementary feeding prevented a winter crash. However, survival in the habitat populations did not differ from control populations in any of the winters. In this study I used elevation as a proxy for climate, where I compared two different elevations, and I found that winter survival was higher in high than low elevation populations. However, there were no interacting effect between elevation and year, indicating that the winter crash was not associated with climate.
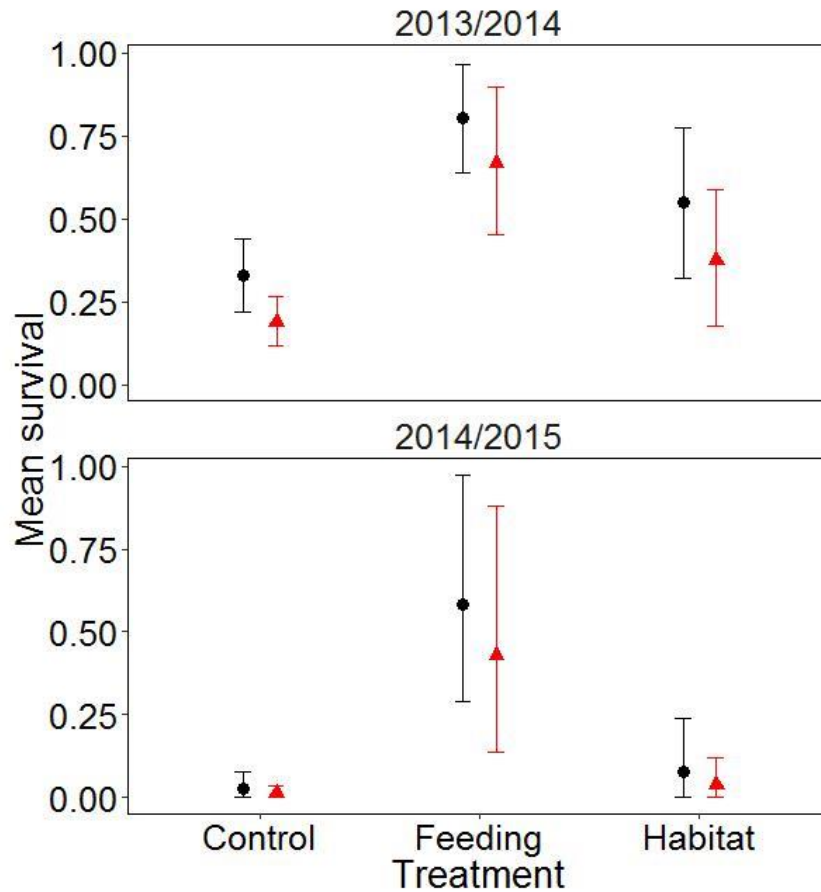
Fig. 5. Mean 6-month survival from December to May in the three treatments. Black circles and lines are high elevation grids and red triangles and lines are low elevation grids.

5.1.3 Effects of behaviour

I also found support for a correlation between activity range and within-winter survival, i.e. the longer maximum distance individuals moved between traps during a primary trapping session the higher their survival (Paper I). This result may also be connected to food resources, as a wider activity range will most likely provide access to more resources. Bondrup-Nielsen and Karlsson (1985) found that with poorer food quality voles expand their home ranges.

5.1.4 Effects of body mass

Both adults and juveniles survived the 2013/2014 winter well, while in the 2014/2015 winter all adults died and only some few juveniles survived the winter (Fig. 6). Although I did not find an association between monthly body mass and winter survival, I still hypothesize that it can play an

significant role for winter survival, as has been shown previously (Iverson and Turner 1974; Merritt and Merritt 1978; Hansson 1990; Aars and Ims 2002; Wan et al. 2014). In Paper II I analysed the monthly body mass from December to May. However in December, the individuals that were not able to adjust their body mass may already have died. I hypothesised that the fall body mass could be a better predictor for winter survival and studied the survival from October to March explained by body mass in October. During the winter of 2013/2014, it is obvious that bank voles have an optimal body mass to be physiologically able to survive the winter (Fig. 6). For juveniles this is between 14 and 20 g, while for adults this is between 17 and 22 g. Individuals with a body mass below or above this limits are not able to survive the winter, with a few exceptions (Fig. 6). In the crash phase winter of 2014/2015, there were very few adult individuals within the optimal body mass range, and no adult individuals that survived the winter (Fig. 6). However, very few juvenile individuals survived as well, even though there were many juveniles within the optimal body mass range in October (Fig. 6). A posteriori I hypothesised that the lack of adults in the crash winter could explain juvenile mortality, i.e. that the juveniles somehow are dependent of adults to survive the winter, for instance to access food resources. However, I did not find a correlation between juvenile winter survival and presence of adults.

Low adult survival in the crash phase could then be explained by adults being too large to physiologically being able to survive the winter. Large animals in the peak phase are commonly observed in cyclic vole populations and are often described as the Chitty effect (Oli 1999). The larger adults in the fall of 2014 before the crash compared to the previous fall may be explained by age. The last cohorts in summer 2014 did not mature sexually as they did in 2013, that is only 33 % of the adults on October 2014 were from late born cohorts, compared to 76 % in 2013 (Table 2). This could be explained by dispersal being inversely density dependent (Andreassen and Ims 2001), so at high densities (i.e. the peak summer of 2014) juvenile animals remained in their natal home range and became reproductively supressed due to lack of breeding space (Wolff 1997). Furthermore, Wiger (1979) found that in peak summers, bank voles terminated their breeding earlier, leading to the lack of the normally last born cohorts. This means that the adults in fall are older and larger before the crash than fall seasons in the increase phase. In addition, Wiger (1979) found that the latest summer cohorts survived winter best.
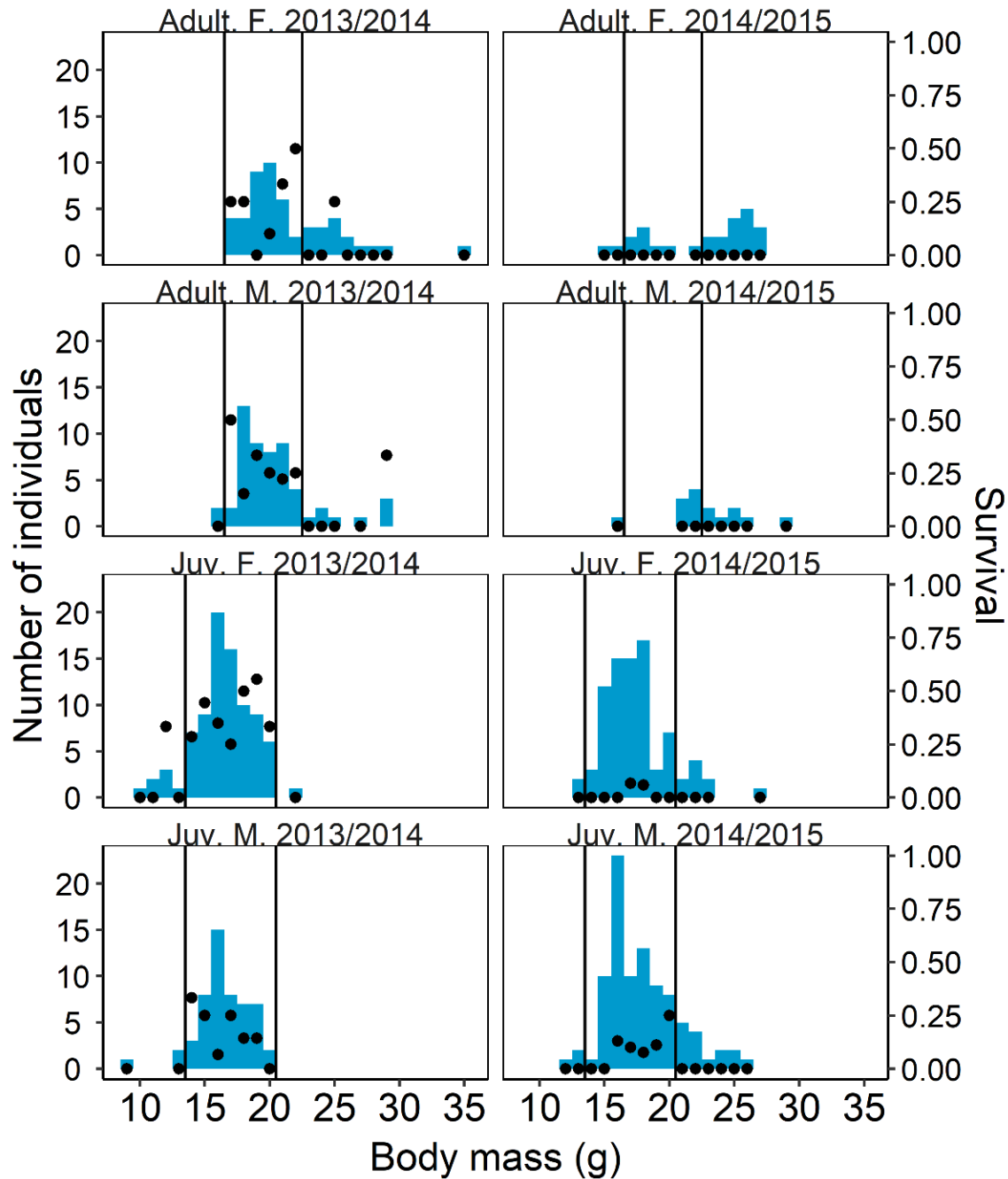
Fig. 6. Number of individuals across different body masses in October (blue bars), and their survival from October to March (black dots). The graph is divided into sex (F = female, M = male), age (juvenile, adult) and year.

Table 2. The percentage of adult individuals that were captured for the first time in two different cohort-categories, that were alive in October 2013 and October 2014. Early cohort is from January-July, while late cohort is from August-October.

	2013	**2014**
Late cohort	76	33
Early cohort	24	68

5.2 Phases and social behaviour

The degree of adult female home range overlap was highest in the first summer/fall of the increase phase of the cycle, i.e. in 2013, somewhat lower the second increase year and lowest during the crash phase in 2014 (Fig. 7). Female home range overlap correlates well with population growth rate, i.e. increasing degree of female home range overlap corresponds with higher population growth rates (Paper III). This positive correlation is possibly due to the fact that social behaviour, probably within kin-groups, may enhance reproductive success (Ylönen et al. 1990; Ylönen and Viitala 1991; Rémy et al. 2013). The positive correlation between social behaviour and growth rate has been shown previously, where the social behaviour was closely related to patchiness of resources (Rémy et al. 2013). However, towards the end of the second year in the increase phase, the female home range overlap decreased drastically, indicating that the social system was disrupted. I hypothesised that food resources could have been a factor disrupting the social system, after overexploitation during two high density summers. Bank voles have been found to lose weight and die when feeding on a green diet alone (Kostelecka-Myrcha and Myrcha 1964), indicating that they depend on specific food resources for growth and survival. Shortage of, for instance seeds, could force adult females to become more territorial in the crash phase (Ostfeld 1990). Another just as important factor, might be predation, where there is an increase in predation due to predators functional and numeric response (Sundell 2006), first removing the dominant males due to their risky movements (Haapakoski and Ylönen 2010). This can lead to infanticide that will reduce recruitment and population growth rate (Andreassen and Gundersen 2006), that will induce risky movements in adult females. I propose, as Andreassen et al. (2013), that intrinsic (sociality) and extrinsic (predation, food) factors interact in the different phases to shape multiannual population cycles.
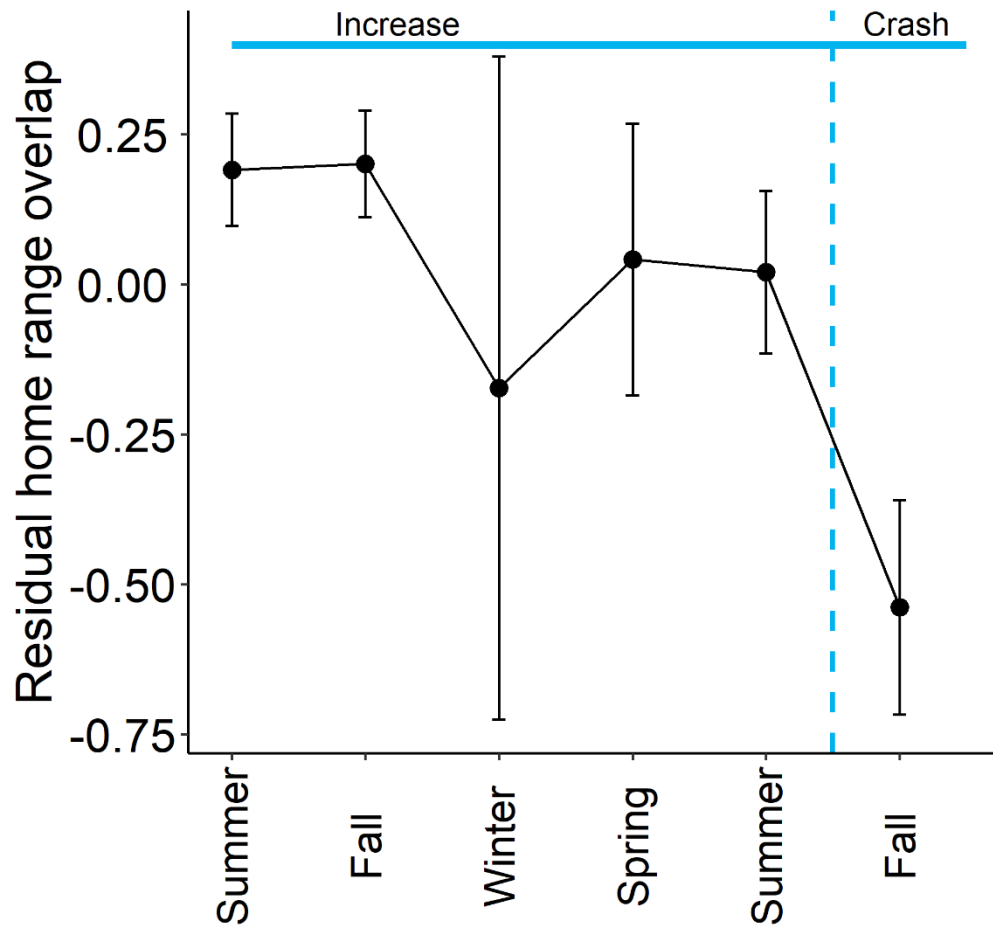
Fig. 7. Adult female home range overlap per three-month season, from June 2013 – November 2014.

6. Conclusions

I found no evidence that winter climate conditions played a significant role in driving the decrease in the amplitude of vole cycles or that vole population cycles in itself could be associated to winter conditions in the forests of central inland Norway. However, it does not mean that winter climate can not be an important factor in some winters with particular mild or unstable winter conditions, or in other habitats with higher probability for ground frost which limits the assimilation of melted snow. This could be in more open areas with less humus layer and sparse vegetation in the field layer (e.g. alpine areas and fields). Moreover, it can be discussed whether the amplitudes really were dampened in bank voles, which is the fundament of the climate hypothesis. But there is no doubt that the climate is, and will continue changing, most likely not improving the winter conditions for small rodents.

I show that low adult survival in the crash phase can be explained by adults being too large to physiologically being able to survive the winter. This may be connected to lack of food resources which seems to be the best explanation for low winter survival of juveniles in the crash phase. The significance of food during winter was confirmed in the experiment with supplemental feeding and the positive correlation between activity range and survival.

Social amicable individuals during the increase phase seems to be common in small rodents and may be one of the driving forces for the outbreaks of mice in the southern hemisphere and the increase phase of vole population cycles in the northern hemisphere. To what extent the collapse in social behaviour contributes to the crash phase or is a consequence of other factors driving the crash is more ambiguous.

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