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Possible impact of winter conditions and summer temperature on bank vole (*Myodes glareolus*) population fluctuations in Central Norway

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In recent decades, population fluctuations of microtine rodents have frequently faded out in parts of northern Europe, possibly because of climate change. Weather events may affect the rodents directly, but also indirectly, by acting on factors that generate population fluctuations. However, few studies have addressed the latter aspect. A species well suited for such a study is the bank vole (*Myodes glareolus*), which usually increases in number after a year with high seed production of bilberry (*Vaccinium myrtillus*). We analysed two snap-trapping time series of bank vole from Central Norway. When controlling for the impact of seed production of bilberry and Norway spruce (*Picea abies*), the number of bank voles trapped in the low-altitude area was negatively related to a summer temperature index of the two previous years, possibly because of the impact of temperature on the nutritional status of food plants. In the area situated at the highest altitude, there was a negative relationship with the winter NAO-index and a positive relationship with a snow depth index. Wet and mild winters are assumed to give unfavourable snow conditions, with alternating thawing and freezing, sometimes also creating an ice-layer at ground level, whereas a sufficient thick snow cover protects the rodents in periods with critical low temperatures. We conclude that an understanding of the ultimate cause of population fluctuations is needed to reveal the disturbing effects of weather events or other factors.

KEY WORDS: *Vaccinium*, *Myodes*, winter conditions, summer temperature, snow, vole fluctuations.

INTRODUCTION

Regular 3–4-year fluctuations in number are a characteristic of many microtine rodent populations at higher altitudes and latitudes in the northern hemisphere. There has, however, been a period with less regular fluctuations in many rodent populations

from the late 1980s to the early 2000s, a phenomenon possibly related to climate change (Cornulier et al. 2013). Weather events may interrupt the population dynamic by affecting small rodents directly (see below), but also indirectly, by affecting the factors that generate population fluctuations (White 2011). However, most attempts of linking changes in rodent population dynamics to changes in climate suffer from a lack of knowledge about the ultimate factors.

A common vole species in South Norway is the bank vole (*Myodes glareolus*). In contrast to *Microtus*-voles and lemming (*Lemmus lemmus*), bank voles do usually not reproduce in winter in Norway. Population peaks are usually observed in autumn 1 year after a peak in the seed crop of bilberry *Vaccinium myrtillus* (Selås 2020; Selås et al. 2021), which is an important food plant in winter (Hansson & Larsson 1978; Hansson 1985). Sympatric populations of the wood mouse (*Apodemus sylvaticus*), which eat berries but not bilberry plants, are not affected (Selås 2020). Hence, the berry–vole relationship, known also from other countries (Laine & Henttonen 1983; Krebs et al. 2010), is best explained by the plant stress hypothesis, which states that indigestive plant proteins, acting as feeding deterrents, are transformed to free amino acids during the process of flowering and berry ripening (White 1984, 1993). The subsequent increase in protein digestibility makes more plant biomass suitable as food and provides a temporal increase in the carrying capacity for herbivores that feed on bilberry plants.

It has been suggested that the multiannual variation in bilberry reproduction is caused by fluctuations in vole numbers, and not vice versa (Laine & Henttonen 1983). However, this hypothesis is not in accordance with patterns observed in southern Norway, where most bank vole peaks have occurred 1 year after a peak in berry production, regardless of the number of years between berry peaks (Selås 2020). Here, vole grazing appears to have minor impact on bilberry reproduction, which is well explained by weather variables acting during key stage of the flowering cycle (Selås et al. 2015).

Also, the irregular production of Norway spruce (*Picea abies*) cones may give an increase in bank vole numbers (Selås 2020), but then as a direct result of the seeds, which are frequently eaten by bank voles (Myllymäki & Paasikallio 1972; Ellingsen et al. 2017). This is equivalent to the effect of masting of some broadleaved deciduous trees at lower latitudes (Reil et al. 2015; Flowerdew et al. 2017). Because information about seed production of bilberry and Norway spruce is often available, time series on bank vole abundance are well suited to evaluate the impact of factors that may affect the cause of the population fluctuations, i.e., the nutritional status of bilberry plants, as well as weather factors that may affect the animals directly.

Among potential candidates for the disruption of regular vole fluctuations, the most obvious direct factor is high mortality due to unfavourable winter conditions. For instance, freezing temperatures in periods without an isolating snow cover may be detrimental for small mammals (Reid & Krebs 1996; McCafferty et al. 2003). However, the main focus for temporal absence of vole and lemming population peaks in Fennoscandia has been on alternating thawing and freezing in mild winters (e.g., Aars & Ims 2002; Korslund & Steen 2006; Kausrud et al. 2008). Such conditions might sometimes create an ice layer at ground level covering large areas, making food plants and shelter unavailable, but this happens infrequently.

Rodent population peaks have "faded out" also in areas of northern Europe that did not have permanent snow cover in winter (Cornulier et al. 2013). In Finland, the dynamics of vole populations during 1970–2011 correlated better with the growing

season than with winter snow conditions (Korpela et al. 2013). Increased summer temperatures may also explain the dampening fluctuation of a field vole (*Microtus agrestis*) population in the Czech Republic (Gouveia et al. 2015). High temperatures are beneficial for plants not only because of increased photosynthesis activity, but also because of increased mineralisation, which increases the access to nutrients (nitrogen and phosphorus) in the soil. Plants should thus be able to store more carbohydrates and proteins in the years prior to a high-seed production, and consequently be less exhausted afterwards, in areas or periods with high summer temperatures and long-growing seasons (White 2011; Selås et al. 2019). If the level of constitutional defence thus remains at a higher level, or the plants are able to rebuild this defence faster, high temperatures will be negative for the herbivore.

In this paper we use snap-trapping data from two areas in Central Norway (Sørensen et al. 2020) to analyse for effects of winter conditions and previous summer temperatures on the population dynamic of bank vole, while controlling for the effect of bilberry and spruce seed production in the previous year. The study areas are situated at different altitudes, and are both covered by forests of different age classes. The relationships with bilberry and spruce seed production were expected to be strongest in old forests, where the bilberry is most abundant, and where most trees are of reproductive age. The effect of unfavourable winter conditions was predicted to be strongest at high altitudes. Negative effects of warm summers, on the other hand, were predicted to be most visible in the lowland.

MATERIALS AND METHODS

Study areas

The two study areas are located in the municipalities Lierne (North boreal forest zone, 64.40°N, 13.82°E, 525 m elevation) and Steinkjer (Boreal forest zone, 64.01°N, 11.58°E, < 100 m elevation) in former Nord-Trøndelag County, Central Norway (Fig. 1). The most common vegetation type is bilberry-spruce forest. In Nord-Trøndelag, old mature stands of this forest type are usually dominated by spruce and bilberry (Hofsten et al. 2017). Other common species are downy birch (*Betula pubescens*), lingonberry (*Vaccinium vitis-idaea*), crowberry (*Empetrum nigrum*), and mosses (mainly *Pleurozium schreberi* and *Hylocomium splendens*). In early successional stages, the bilberry is usually less common, due to competition from grasses, in particular wavy hair-grass (*Deschampsia flexuosa*).

The bank vole is usually most common in old forest stands, because of higher availability of bilberry plants (Gorini et al. 2011; Wegge & Rolstad 2018). Here, bilberry biomass – shoots and bark – never appear to be a limiting factor for voles in winter, unless the ground is covered by ice. In both areas, snap trapping was conducted both in young and old forests, see below. A description of the vegetation type, based on units for vegetation mapping in Norway (Fremstad & Elven 1987), was made within a radius of approximately 2.5 m for each trap site.

In Lierne, the old forests stands selected for snap trapping were dominated by 50–250 years old spruce trees of approximately 20-m height. The proportion of traps situated in bilberry-spruce forest (vegetation type A4) was 84%. The remaining 16% were situated in nutritious poor wet spruce forest (vegetation type E2), where bilberry, cloudberry (*Rubus chamaemorus*), wood horsetail (*Equisetum sylvaticum*) and mosses (*Sphagnum* spp. and *Polytrichum* spp.) were the most common plants in the field layer. The young forest stands selected were dominated by 25–60 years old trees, either spruce (80%) or birch (20%), with height 2–15 m. Here, 44% of the traps were situated in bilberry-spruce forest (vegetation type A4) and 46% in nutritious rich bogs (vegetation type M1), with spruce, birch, willow (*Salix* spp.) and mainly grass and herbs in the

Fig. 1. — Map of Norway showing the location of the two study areas.

field layer. The remaining 10% were situated in nutritious rich ground water areas (vegetation type N2), dominated by willow, mosses and herbs.

In Steinkjer, the old forest stands used were dominated by approximately 100 years old spruce trees, with height 20–25 m, intermixed with birch and sometimes also with Scots pine (*Pinus silvestris*). Because this area is an old seabed with clay sediments, there were in general more herbs and fewer mosses than in Lierne. Most traps were situated in bilberry-spruce forests (vegetation type A4), but 3% were located in nutritious-rich wet forest (vegetation type E4), dominated by spruce, birch, willow, herbs and grasses. The young forests were dominated by 2–15 years old spruce trees, 1–5 m height. Here, 96% of the traps were situated in bilberry-spruce forests (vegetation type A4), and 4% in nutritious rich wet forest (vegetation type E4). The coverage of bilberry was in general lower in young forests in Steinkjer than in young forests in Lierne.

Snap trapping of small rodents

Small rodents were trapped by use of snap traps (type Rapp) baited with raw potato. We corrected the number of trap nights by subtracting 0.5 trap night for each released trap

without catch, and for each trap with capture of another species. In Lierne, 100 traps were set out for 1–2 nights 1–3 times each year during 1988–2021, usually 50 in old forest and 50 in young forest. In each habitat, traps were placed ca 5 m apart, along a line transect of 250 m. Because of the limited number of trap nights, we did not distinguish between young and old forest in the analyses, but we distinguished between early summer (June–July) and autumn (August–October). Bank voles were not trapped in early summer 1992, 1993, 1996, 1997, 2000, 2001 and 2003, and not in autumn 1991, 1994 and 1995. The mean annual number of corrected trap nights was 252 (range 96–398) in early summer and 225 (range 49–391) in autumn.

In Steinkjer, trapping was conducted only in autumn (early or mid September), except from the last 2 years. During 1996–2017, traps were put out for 2 nights at 30–60 sites, situated 25 m apart, and with five traps at each site. The five traps were arranged in a circle, with one trap in the centre, and one in each direction, 2 m from the centre. In most years, 50% of the trapping was conducted in old forest, the remaining in young forests (including clear-cuts). In 2018–2021, the same trapping protocol as in Lierne was used. For the entire study period, the annual mean number of corrected trap nights was 207 (range 146–385) in old forest and 210 (136–572) in young forests.

Bilberry indices

A bilberry index for Nord-Trøndelag was obtained by searching for bilberry production reports from this region in local, regional and national newspapers, available at the National Library of Norway. Because bilberry harvesting is popular in Norway, newspapers commonly give reports about the berry production, based on different sources, such as foresters, berry companies and experienced bilberry pickers. The mean annual number of newspaper reports found was 4.6 (range 2–9). Ten persons (age 38–61 years), not living in the region but familiar with bilberry harvesting and terms commonly used for descriptions of berry crops, were then asked to score the annual berry production based on these reports. The interviewed people were one associate professor, one with a master's degree in biology, one with a master's degree in forestry, four with a master's degree in nature conservation, one presently studying biology, and two field ornithologists.

The following scale for annual berry production was used: 1 = very poor, 2 = poor, below average, 3 = average or normal, 4 = good, above average and 5 = very good. We used the mean of the assessments of the 10 interviewed persons to calculate a bilberry index. Due to marked variations in annual seed production, the method has turned out to be appropriate for revealing peak years, which are often (but not always) common for larger regions (Selås 2019; Selås et al. 2021). However, we have an altitude difference of about 450–500 m between our two study areas, which in some years might have created important differences.

Spruce seeds

Information about seed crops of Norway spruce was taken mainly from annual reports from the Norwegian Forest Seed Centre (www.skogfroverket.no), but supplemented with newspaper interviews of staff at the Seed Centre and local or regional forest authorities or managers. There was a good flowering of Norway spruce in Nord-Trøndelag in 1992, 1995, 1998, 2006 and 2015. However, only in 2006, summer temperatures were high enough for sufficient seed ripening (mean June–September temperature 14.8 °C at Værnes meteorological station; eKlima.no). This autumn, the germination rate was at least 95%, even at higher altitudes. For the four other years (June-September temperatures 12.1–13.5 °C), the germination rate in Nord-Trøndelag was too low for large-scale commercially spruce seed collecting. For instance, it was reported to be only 4% in 1995. Hence, we used a categorical spruce seed index with value 1 for 2006 and value 0 for other years.

Summer temperatures

We used the mean temperature in June–September of the two previous years, provided by the Norwegian Meteorological Institute (eKlima.no), as an index of previous summer tempera-ture, assumed to affect bilberry plants. Previous studies from southern parts of Norway suggest that there is a negative relationship between this variable and the autumn population levels of both bank vole and forest grouse (Selås et al. 2011; Selås 2019).

The temperature data used are from Værnes (12 m altitude) in Stjørdal municipality, because there were no closer continuous temperature measurements available. Mean tempera-tures will be higher at Værnes than in our study areas, but the annual fluctuations are very similar. For years with temperature data from Lierne during 1986–2020, there was a highly significant correlation with temperature data from Værnes ($P < 0.0001$) for each of the months used (June: $r = 0.92$, $n = 29$; July: $r = 0.95$, $n = 29$; August: $r = 0.95$, $n = 30$; September: $r = 0.92$, $n = 29$). The same was true for temperature data from Steinkjer 1994–2020 (June: $r = 0.99$, $n = 22$; July: $r = 0.99$, $n = 24$; August: $r = 0.98$, $n = 24$; September: $r = 0.97$, $n = 24$).

Winter conditions

We used two indices assumed to reflect winter severity. As a proxy for snow conditions, we used the NAO-index for December–March (National Center for Atmospheric Research Staff 2021), which has turned out to be a better predictor for many ecological processes than local weather variables (Hallett et al. 2004). Negative NAO values reflect dry and cold winters, whereas positive values reflect wet and mild winters, assumed to be negative for voles because of alter-nating thawing and freezing (Hörnfeldt 2004; Solonen & Ahola 2010).

Also lack of a sufficient thick snow cover may be negative for small rodents. We therefore used the lowest mean snow depth in January, February or March as an independent variable in the analyses. All mean snow depths above 50 cm were truncated to 50 cm, because above this level, temperatures at the ground will remain close to 0 C regardless of air temperatures (Algaard 1976).

For Lierne, snow data were available from the meteorological station Holand (433 m altitude) for the period 1989–2019 and from Sandvika (420 m altitude) for 2020 and 2021. Although we lacked snow data from 1988, there is no doubt that the snow cover was far above 50 cm throughout the period January–March in Lierne this snow-rich winter (first author's diary notes). For Steinkjer, we used snow data from the meteorological station Utgård (50 m elevation). All snow data were provided by the Norwegian Meteorological Institute (eKlima.no).

In the high-altitude area Lierne, snow depths are positively correlated with the NAO-index, whereas in Steinkjer, there is a negative relationship, because much of the precipitation here is rain in winters with high NAO values. When snow depths above 50 cm were truncated to 50 cm, the relationship between the NAO-index and the snow index used for Lierne was not significant ($r = 0.25$, $P = 0.161$), whereas for Steinkjer, where monthly mean snow depths usually did not exceed 50 cm, there still was a significant correlation ($r = - 0.48$, $P = 0.014$).

Statistical analyses

We tested for cyclicity in the bank vole series (number trapped per 100 trap nights) and explanatory variables by use of spectral density. We thereafter used the annual number of bank voles trapped as response variables in generalised linear models (GLM) with Poisson distribution and log link, and with the log-transformed number of trap nights as offset. For each model, the degree of overdispersion was estimated in a post-model fit, and then controlled for by including an overdispersion parameter, estimated by Pearson's chi-square divided by the degrees of freedom.

The explanatory variables were the trapping index of the previous autumn (number per 100 corrected trap nights), bilberry and spruce seed indices of the previous year, mean summer temperature of the two previous years, lowest mean snow depth in January, February or March, and the winter NAO-index. For Lierne, the analyses of the number of bank voles trapped in autumn were also conducted with the trapping index from early summer as predictor, reducing the time series to 25 years. Any significant relationships with previous summer temperatures were followed up by path analyses, in order to separate direct and indirect impacts.

To obtain comparable parameter estimates in the multiple models, all continuous explanatory variables were scaled before analyses. There were no significant positive autocorrelations in the residuals of any of the multiple models. The software used was JMP®Pro 15.0.0 (SAS Institute, Cary, North Carolina, USA).

RESULTS

The only significant correlations between explanatory variables were the negative relationship between the NAO-index and the snow depth index used for Steinkjer (see Materials and Methods), and an artificial negative relationship between the NAO-index and the bilberry index of the previous year ($r = -0.48$, $P = 0.013$). There was a tendency for a 3.4-year cycle in the bilberry index (Fisher's Kappa = 4.68, $P = 0.089$). This cyclicity was significant from 1997 onwards (Kappa = 5.65, $P = 0.008$).

In Lierne, the proportion of bank voles trapped in old and young forest in early summer was 72.8 and 27.2%, respectively ($n = 453$). Corresponding values for the number trapped in autumn were 63.4 and 36.6% ($n = 1043$). In Steinkjer, 50.4% were trapped in old forest and 49.6% in young forest ($n = 1213$). In both study areas, there was a considerable annual fluctuation in the number trapped per 100 corrected trap nights (Fig. 2). There were no significant cycles in autumn trapping indices for the entire study period, but there was a significant 3.4-cycle from 1998 onwards in old forest in Steinkjer (Kappa = 5.25, $P = 0.017$), and from 2001 onwards in Lierne (Kappa = 5.35, $P = 0.010$).

In Lierne, there was a significant correlation between trapping indices in early summer and autumn ($r = 0.82$, $P < 0.001$). The autumn trapping index from Lierne was also significantly correlated with the autumn trapping index from old forest in Steinkjer ($r = 0.70$, $P < 0.001$), but not with the autumn trapping index from young forest in Steinkjer ($r = 0.28$, $P = 0.161$). Trapping indices from the two forest age classes in Steinkjer were significantly correlated ($r = 0.64$, $P < 0.001$).

Most bank vole population peaks were observed after a year with a high bilberry index (Fig. 2). There was a significant relationship between the bilberry index of the previous year and the log-transformed trapping index of bank vole both in early summer and autumn in Lierne, and in old and young forest in Steinkjer (Fig. 3). For the number trapped in old forest in Steinkjer, the bilberry index was a better predictor in univariate GLM tests ($\chi^2 = 13.31$) than the population index from young forest ($\chi^2 = 8.30$).

In Lierne, both the trapping index of the previous autumn, the bilberry and spruce seed indices of the previous year, and the two winter condition indices contributed to explain the number of bank voles trapped in early summer (Table 1). For the number trapped in autumn, there was a significant relationship with the bilberry and spruce seed indices of the previous year both in Lierne and in old forest in Steinkjer, and a marginally non-significant relationship in young forest in Steinkjer (Table 1). The NAO-index contributed significantly in Lierne, and the previous
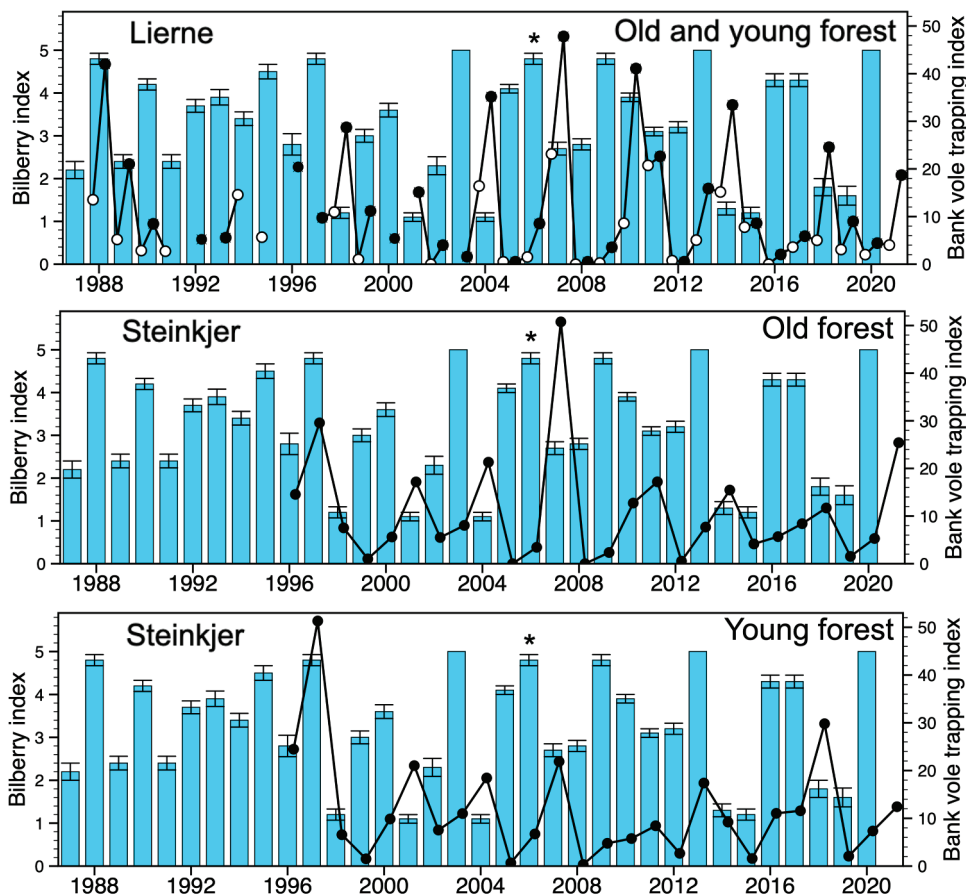
Fig. 2. — Number of bank voles trapped per 100 trap nights in early summer (open symbols) in Lierne and autumn (filled symbols) in Lierne and Steinkjer, Central Norway, in relation to seed crops of bilberry (bars wit SE). The only year with a heavy production of Norway spruce seeds is marked with an asterisk.

summer temperature in young forest in Steinkjer, and marginally non-significantly in old forest in Steinkjer (Table 1). The trapping index of the previous autumn did not contribute significantly in any of the two study areas, but in Lierne, there was a significant relationship with the number trapped in early summer ($P < 0.001$). The only other significant predictor in the latter model was the bilberry index of the previous year ($\chi^2 = 7.95$, $P = 0.005$).

If all analyses were performed without the bilberry and spruce seed indices as predictors, the only significant result for the weather variables was a negative relationship between the number of bank voles trapped and previous summer temperatures in young forest in Steinkjer ($\chi^2 = 5.47$, $P = 0.019$). In a linear regression model with the log-transformed trapping index as response, the relationship was nearly significant (Fig. 4). In a path analysis for the merged data from young and old forest in Steinkjer, where 2007 was omitted due to the impact of spruce seeds, there were no indirect
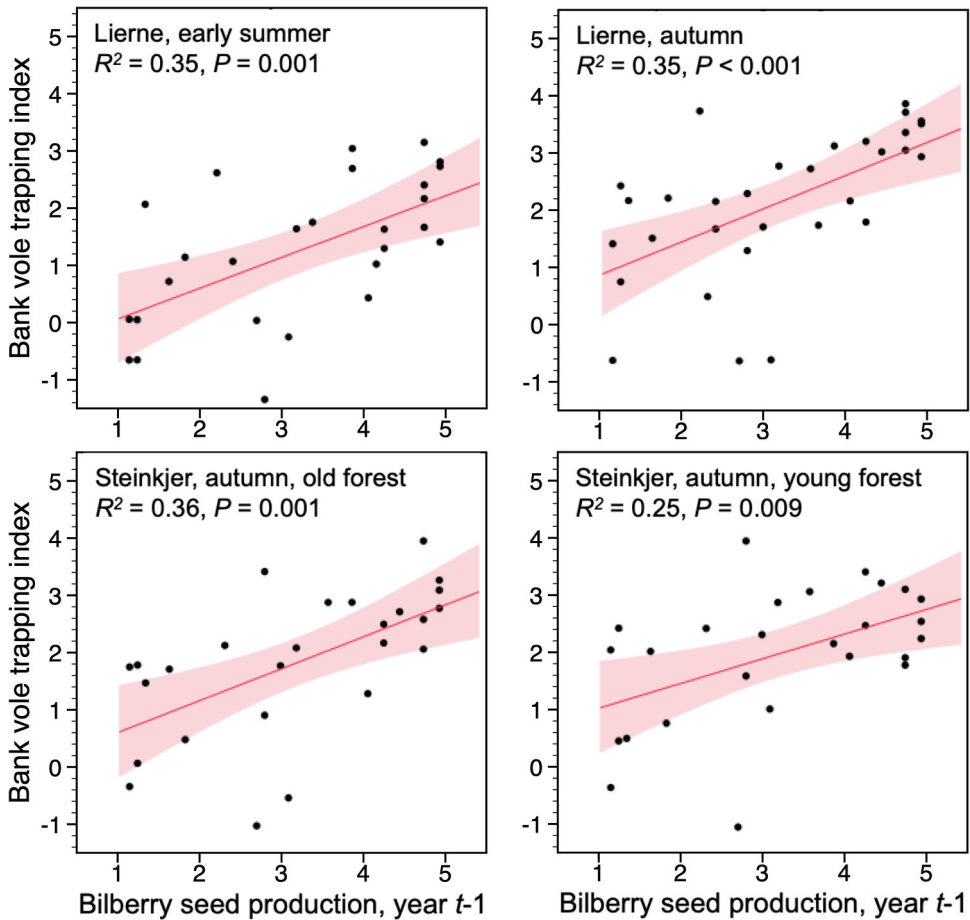
Fig. 3. — The log-transformed number of bank voles trapped per 100 trap nights in Lierne and Steinkjer, Central Norway, plotted against the bilberry index of the previous year. Shaded areas reflect 95% confidence intervals for the regression lines.

effects of previous summer temperatures through berry production or the trapping index of the previous year (Fig. 5).

DISCUSSION

In both study areas, there was a positive correlation between the number of bank voles trapped in autumn and the bilberry index, with a 1-year time lag. Some recent population peaks were common for large parts of Norway and Sweden, such as 2007, 2010 and 2014 (Ecke et al. 2017; Ecke & Hörnfeldt 2018; Framstad & Eide 2020; Selås et al. 2021), and they could all be related to high production of bilberries in the preceding year. In Lierne, there was a positive relationship with bilberries also when the trapping index in early summer was accounted for. This is in accordance with a 20-

Table 1.

Results from GLM models (Poisson distribution and log link, corrected for overdispersion) with the number of bank voles trapped year t as response variable, and the log-transformed number of trap nights as offset. Possible explanatory variables were standardised indices of the trapping index of the previous autumn, bilberry production, spruce seed production, mean June–September temperature, the PC-based December–March NAO-index and the lowest mean snow depth in January, February or March (0–50 cm). Only variables with $P < 0.1$ were included in the models.

Explanatory variable	Estimate	SE	df	χ^2	P
Lierne, early summer, old and young forest, 1989–2021, n = 25					
Intercept	0.522	0.290	1		
Autumn population index, t-1	0.393	0.140	1	7.25	0.007
Bilberries, t-1	0.790	0.203	1	18.86	< 0.001
Spruce Seeds, t-1	0.689	0.259	1	5.89	0.015
Winter NAO, t	− 0.366	0.145	1	6.06	0.014
Lowest snow depth, t	0.350	0.185	1	4.14	0.042
Lierne, autumn, old and young forest, 1988–2021, n = 31					
Intercept	1.513	0.205	1		
Bilberries, t-1	0.486	0.155	1	10.37	0.001
Spruce Seeds, t-1	0.615	0.188	1	9.33	0.002
Winter NAO, t	− 0.213	0.121	1	3.15	0.076
Steinkjer, autumn, old forest, 1996–2021, n = 26					
Intercept	1.270	1.191	1		
Bilberries, t-1	0.587	0.166	1	14.32	< 0.001
Spruce Seeds, t-1	0.826	0.167	1	21.57	< 0.001
Summer temperature, t-1 + t-2	− 0.267	0.140	1	3.62	0.057
Steinkjer, autumn, young forest, 1996–2021, n = 26					
Intercept	1.154	0.265	1		
Bilberries, t-1	0.310	0.168	1	3.59	0.058
Spruce Seeds, t-1	0.536	0.266	1	3.35	0.067
Summer temperature, t-1 + t-2	− 0.468	0.148	1	9.88	0.002

year snap trapping study from southern Norway (Selås 2020), and suggests that there is a delayed positive effect of a high berry crop not only during winter, but also during the succeeding breeding season. Also, the spruce seed index was a significant predictor for the annual number of bank voles trapped in Steinkjer and Lierne, confirming the importance of food for the population level of this rodent species.

The berry production was not estimated at local levels, but in most years, evaluations from different municipalities in Nord-Trøndelag were rather similar. However, newspaper reports do not always reflect the situation at higher altitudes, where adverse weather events more often interrupt flowering and seed ripening. Anyway, as this possible source of error is unlikely to increase the correlation with the number of voles
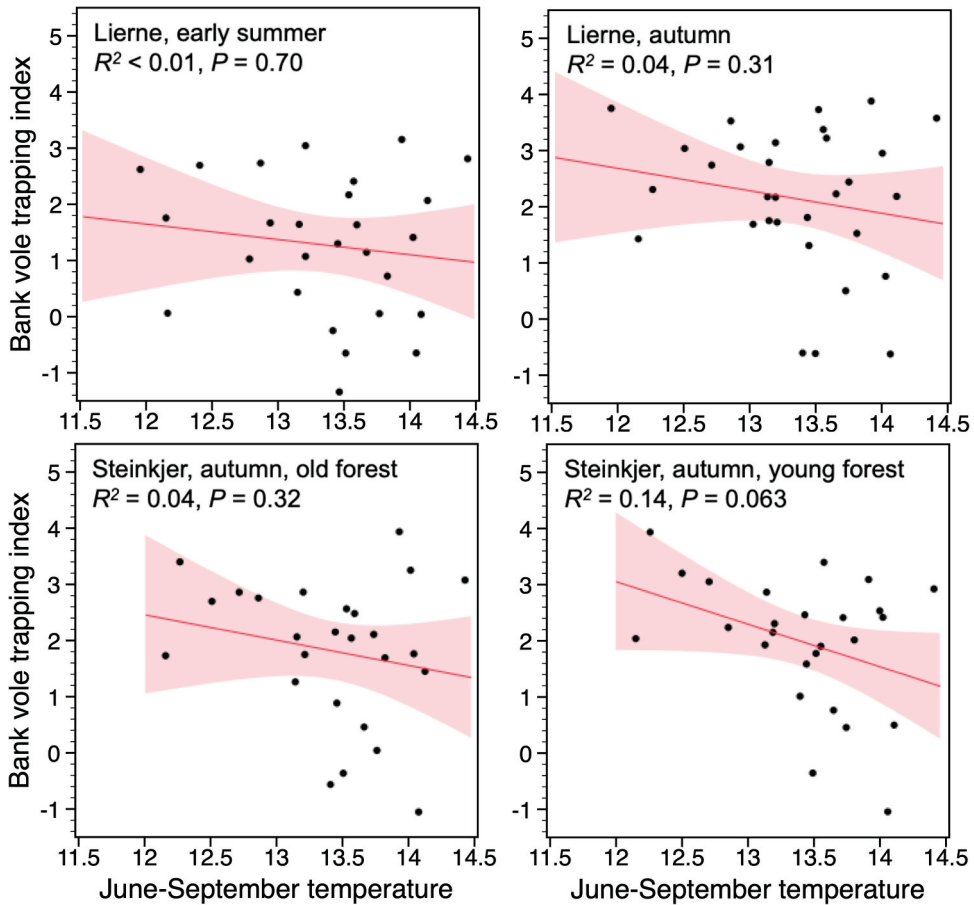
Fig. 4. — The log-transformed number of bank voles trapped per 100 trap nights in Lierne and Steinkjer, Central Norway, plotted against the mean temperature in June–September of the 2 previous years. Shaded areas reflect 95% confidence intervals for the regression lines.

trapped, our approach could be regarded as conservative. The production of spruce seed is usually synchronised over large areas, and the peak in 2006 was common to most part of Central and South-eastern Norway (Timmermann 2007).

There also was a negative relationship between vole number in young forest in Steinkjer, and June–September temperatures of the two previous years. According to the path analysis, this was not due to impacts of temperature on berry production or vole abundance in the previous year. Low temperatures in May and early June reduce the activity of pollinating insects, but there is only a minor time overlap between the flowering period and the defined summer period (June–September). In summer, low temperatures may delay or even prevent berry ripening, but this happens mainly at higher altitudes, and usually not in Steinkjer. Neither did summer temperatures appear to have a significant direct impact on bank vole abundance, which most likely was limited by food quality.
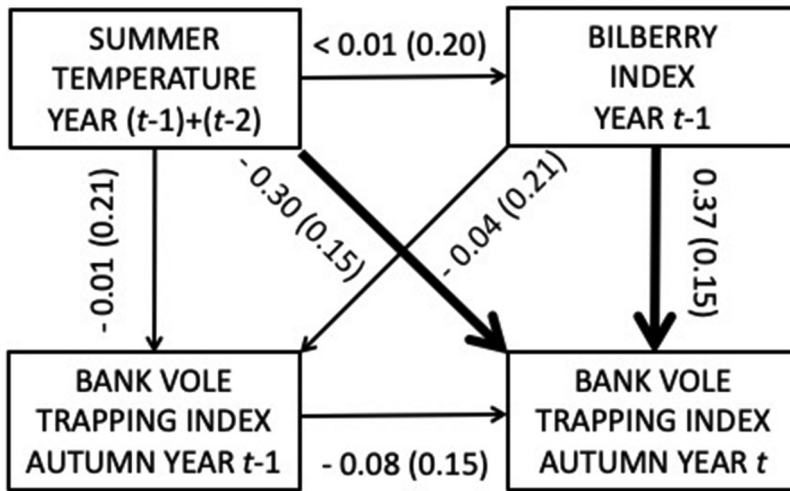
Fig. 5. — Path analysis diagram for some factors that may affect autumn population levels of bank vole in Steinkjer, year *t*. The values given are path coefficients with SE in brackets. Thick arrows indicate significant relationships.

It seems to be a general pattern not only for the bank vole, but also for other herbivore species, that the amplitude of population fluctuations decreases with increasing temperature (e.g., Johnson et al. 2010; Yan et al. 2013; Gouveia et al. 2015; Andreassen et al. 2020). One possible reason is that low summer temperatures have a negative effect on food plants, by delaying the restitution of the constitutional defence, and thus a positive effect on herbivore performance. However, since low summer temperatures are usually related to low atmospheric pressure, a not mutually excluding hypothesis is that higher surface fluxes of galactic cosmic ray muons in periods with low atmospheric pressure (De Mendonca et al. 2013) act as an additional plant stress factor (Selås 2014).

In particular in the low-altitude area Steinkjer, some of the deviations from the expected bilberry-vole relationship could be linked to previous summer temperatures. Despite a high bilberry index in 1997, there was no bank vole population peak in 1998. In 1997, June–September temperature at Værnes was 14.8 °C, which was among the highest recorded during the period 1994–2020 (mean 13.5 C), and together with 2006 the highest for a year with high berry production.

Two marked population peaks, Lierne 1988 and Steinkjer 1997, occurred despite an intermediate bilberry index in the previous year. In 1986 and 1987, the mean June–September temperature at Værnes was 12.1 and 11.8 °C, respectively. This was the lowest for two succeeding years during the entire study period. In some other parts of South Norway, there was a good production of bilberries in 1987 (Selås et al. 2021). It is possible then that bilberry plants started to invest in a high seed production also in Nord-Trøndelag, but failed because of low summer temperatures. Hence, a sufficient increase in protein digestibility to generate a bank vole population peak may have taken place.

Also prior to the bank vole peak in Steinkjer in 1997, there were 2 years with rather low mean June–September temperatures, 12.1 C in 1995 and 12.4 C in 1996 at

Værnes, which is the second lowest for 2 succeeding years during 1996–2020. Diary notes of the first author suggest that the bilberry production, at least locally, may have been better in 1996 than indicated by our bilberry index. However, the bank vole population peak in Steinkjer appeared to be particularly high in young forest, where the bilberry plant is less abundant. It is possible then that some other factors were especially favourable this year. Also, the number of field vole, which is most common in young forest, peaked in 1997, but the number was not exceptionally high.

We found significant relationships with the NAO-index and snow depth only for the number of bank voles trapped in the high-altitude area Lierne. It is possible that temperatures less often reached critical low levels in snow-poor winters in the lowland, and that frequent lack of snow in mild winters made the NAO-index less suitable as an index of snow conditions here. It is difficult to measure the impact of snow conditions on vole populations, and the NAO-index may not be a very good proxy for this factor (Kausrud et al. 2008). Nonetheless, there seems to be consensus regarding the significance of winter conditions for the performance of small rodents (e.g., Erlinge et al. 2011; Haapakoski & Ylönen 2013).

From the 1980s onwards, several ecologists concluded that regular population fluctuations of small rodents are likely to be caused by small mustelids (e.g., Hansson & Henttonen 1988; Gilg et al. 2006, but see Graham & Lambin 2002; Lambin et al. 2006). Predators may certainly affect prey numbers, and thus dampen or enhance herbivore population fluctuations, depending on type of predator (specialist or generalist) and the availability of alternative prey, but predation cannot explain the well-documented relationship between berry production and *Myodes*-voles. The fact that different rodent species often fluctuate in synchrony could be a result of synchronising effects of weather on flowering and seed production of some influential plant species. Not only dwarf shrubs, but also some sedges and grasses, utilised by *Microtus*-voles and lemmings, show large inter-annual variations in seed production. However, there are also several examples of asynchronous fluctuations in rodent communities (Hörnfeldt 1994; Krebs et al. 2019; Framstad & Eide 2020), of which some could be linked to events of asynchronous flowering of important plant species (Selås 2020).

There has been less interest for hypotheses that link rodent cycles to forage quality, possibly because early studies of relationships between plants and rodents gave ambiguous results (e.g., Hansson 1979; Andersson & Jonasson 1986; Laine & Henttonen 1987). Studies on the impact of forage quality have most often focused on grazing-induced plant defence (e.g., Lindroth & Batzli 1986; Seldal et al. 1994; Massey et al. 2008), but in contrast to the plant stress hypothesis, this mechanism cannot explain the spatial synchrony in rodent cycles (Selås et al. 2021). The reproduction of bilberry and other perennial plants is synchronised by large-scaled atmospheric events, which are usually acting over large areas. Of particular interest is air pressure during the period of flower bud induction in June, which in South-Norway has showed a significant 3.3 – 3.4-year fluctuation (Selås 2016). Unfortunately, the plant stress hypothesis is apparently not well known or understood, as it was actually ignored in three recent reviews papers on herbivore population cycles (Myers 2018; Oli 2019; Andreassen et al. 2021).

The relationships between bank vole population dynamic and weather variables reported here would hardly been revealed without indices of bilberries and spruce seeds as covariates. Based on these relationships, we predict less regular rodent fluctuations if temperatures continue to rise, partly because of more frequent occurrence of unfavourable winter conditions, and partly because of stronger constitutional

defence throughout the flowering cycle of plants. Monitoring studies of small mammal communities should also consider annual variations in reproduction of important food plants, as this may make it easier to reveal possible impacts of summer temperatures and winter conditions.

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No potential conflict of interest was reported by the author(s).

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