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Seasonality shapes the amplitude of vole population dynamics rather than generalist predators

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Seasonality has been suggested as a necessary factor for the initiation of vole population cycles in Fennoscandia. This has been well described for a latitudinal gradient. Here, we used an elevational gradient as a proxy for winter length to study how the length of the winter season correlates with the amplitude of bank vole *Myodes glareolus* population cycles. In addition, we studied whether the small mammalian generalist predator community present locally could explain any elevational effects. We estimated the population size of 30 local bank vole populations. We found a strong effect of elevation on the amplitude of the population cycle with local populations at around 800 m elevation having 1.5 times greater densities than populations in the valley (ca 300 m elevation). A univariate model with elevation as predictor for amplitude was twice as likely to be the best model than models including generalist predators. Our results fit well with the theories of a positive effect of winter length on the amplitude of vole population cycles in Fennoscandia, irrespective of whether the seasonal effect corresponds to a latitudinal or elevational gradient. The mechanisms may be limited resources during winter rather than generalist predators.

Keywords: density dependence, myodes, population cycles, predator community, red fox

Introduction

Periodic fluctuations in the size of small mammal populations (i.e. population cycles) are common in northern ecosystems (Finerty 1980, Krebs 1996, Myers 2018). These fluctuations tend to have a greater amplitude with increasing latitude. Such a relation is even found in other organisms such as grouse, hares and forest insects (Ims et al. 2008, Myers 2018). In small mammals, increasing amplitude of population fluctuations are associated with a longer winter season (Hanson and Henttonen 1985, 1988) and stronger delayed density-dependence related to winter predation by specialist predators (Stenseth et al. 2003). At the other end of the latitudinal gradient, stronger direct density-dependence occurs due to the presence of a larger number of generalist predators further south (Hanson and Henttonen 1985, Bjørnstad et al. 1995, Ims et al. 2008, Henden et al. 2009).

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Empirically-based modelling studies have confirmed that seasonality is a driver of the dynamics of cyclic populations, with density-dependent regulation occurring in winter (Stenseth et al. 2003). Generally, these results show that longer winters are associated with longer cycles and greater amplitudes (Stenseth et al. 2003, Lambin et al. 2006). These studies describe stronger interspecific competition during winter and greater intraspecific competition in both summer and winter at higher latitudes. While seasonal effects have primarily been used to explain the latitudinal gradient in the dynamics of small rodents, Strann et al. (2002) suggested similar effects for variations in the dynamics of the cycles along a coastal–continental gradient.

The mechanisms underlying the seasonality hypothesis remain unclear, but a high density-dependence during winter is expected if resources are limited (Hansen et al. 1999a). Another obvious mechanism is the connection between seasonality and community processes such as predation along the north–south gradient. Similar mechanisms may also be expected along an elevational gradient as generalist predator densities (especially the red fox *Vulpes vulpes*) tend to be higher in valleys close to human activities (Salek et al. 2014, Walton et al. 2017). Snow cover and condition also vary with elevation, with less stable winters in the valleys causing periodic melting and icing on the ground which limits access to resources such as nests and conspecifics for thermoregulation, due to reduced mobility under the snow. Predation from generalist predators like the red fox is also expected to decrease with increasing snow cover (Hansson and Henttonen 1988, Lindström and Hörnfeldt 1994).

In a recent review, Myers (2018) concluded that one of the remaining mysteries of population cycles is the variation in amplitudes. Here we used an elevational gradient as a proxy for variations in the winter season to study how the amplitude of bank vole *Myodes glareolus* populations correlate with seasonality. We monitored 30 local vole populations during two peaks and one low phase along an elevational gradient ranging from 260 m to 801 m a.s.l. Populations at the highest elevation attained snow cover earlier, and permanent snow cover lasted longer than at low elevations. The difference was approximately two months longer snow cover at 800 m than at 260 m.

We tested the seasonality hypothesis empirically, expecting greater amplitudes in the population cycles at high than at low elevation. We also tested whether seasonality, described by the elevation proxy, or the small predator community best described the amplitude variations.

Methods

Study area

The study was conducted in the boreal forest of Stor-Elvdal municipality, southeast Norway (61°N, 11°E, Fig. 1). The area has a relatively continental winter climate (Boonstra et al. 2016) with vegetation dominated by Norway spruce *Picea abies* and Scots pine *Pinus sylvestris* at low and medium elevations, and by mountain birch *Betula pubescens* and Norway spruce at higher elevations. The forest ground vegetation layer is dominated by bilberry *Vaccinium myrtillus*, mosses e.g. *Pleurozium schreberi* and lichens, e.g. *Cladonia rangiferina*. The average winter length (number of days with mean temperature below 0°C) during the study period was at the nearest weather stations 2.5 times longer at 930 m a.s.l. (Venebu), and 1.5 times longer at 672 m a.s.l. (Drevsjø) compared to 257 m a.s.l. (Evenstad) (eKlima 2019).

Trapping plots

The bank vole is a small arvicoline rodent, found primarily in the mature forests of Europe (Myllymäki 1977). We haphazardly selected 30 bilberry–spruce forest sites suitable for bank voles along forest roads to establish an elevation gradient in presumed good habitat for bank voles. The mean distance

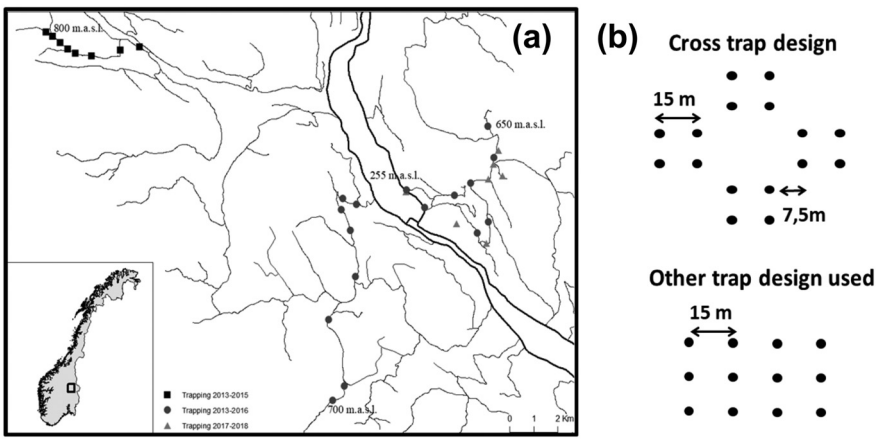

Figure 1. (a) The location of the trapping plots in the total study area. The black thick lines surrounding the label '255 m a.s.l.' indicate main roads in the valley bottom. Elevation is expressed as m above sea level. (b) Trapping plot design. The top panel shows the main, cross-shaped design with 16 traps, and the bottom panel the alternative design used when the main design did not encompass any suitable vole habitat, with 12 traps.

between plots was 1037 m, and minimum 500 m. At each of the 30 sites one trapping plots was established at 5–10 m from the forest roads (see Johnsen et al. 2017 for more details about field procedures). For logistical reasons, all plots could not be trapped every year and the number of trapped plots ranged from 24 to 6 (Table 1).

Trapping plots ranged from 250 to 801 m a.s.l. in a total area of ca 200 km^2. However, due to lower trapping effort in 2017 and 2018 (Table 1), the highest elevation was then 650 m a.s.l. Traps were allocated within the plots in a cross-shaped design of 60 × 60 m (Fig. 1; Ehrich et al. 2009). Each plot consisted of 16 Ugglan Special live traps. The cross design was chosen to maximise the area covered with a limited number of traps. If the cross design did not fit within the suitable habitat in a plot, we used trapping lines with a total 9, 10 or 12 traps, each 15 m apart. This adjusted trapping design covered approximately the same total trapping area (ca 0.6 ha) as the cross design. Traps were placed close to vole runways, dead trees or potential holes to increase the probability of catching voles. We avoided anthills, ant paths or areas with potential exposure to sun or water, to increase the survival probability of trapped individuals.

Field procedures

We monitored the plots every June and August (primary session; see Table 1 for details about trapping frequencies) during the years 2013–2018. Trap checking took place over three days with two checks per day, morning and evening (secondary trapping occasions). Traps were baited with carrots and oats, and activated 12 h before the first trap check. Traps were checked four to six times per session (Table 1). On the final check, we removed any remaining bait to avoid the supplementation of food and we left the traps open, i.e. deactivated, until the next trapping session.

We marked each new individual weighing more than 10 g by injecting a small passive integrated transponder (PIT) tag (7 mm length) into the subcutis. For each capture, we recorded identity, trap location, sex, sexual maturity and we weighed the trapped animals to the nearest gram.

Table 1. Trapping history. Number of trapping plots used, the number of times the traps were checked per session/month (secondary occasions) and total number of captures per month.

Year	Month	No. trapping plots	No. secondary trap occasions	Total number of captures
2013	June	24	5	72
	August	24	6	707
2014	June	24	6	497
	August	24	6	961
2015	June	24	6	11
	August	24	6	11
2016	June	16	6	3
	August	16	6	19
2017	June	6	5	23
	August	6	5	81
2018	June	6	5	42
	August	7	5	57

Density estimates

Each plot was assumed to have an independent local population. Population size was estimated as the minimum number of animals known to be alive (MNA; Krebs 1966) from trapping data. An individual was defined as present in the study area at a primary trapping session if it was caught at least once during the secondary occasions. In addition, an individual was assumed to be alive and present in the trapping plot at primary session t if it had been caught before during primary session $t-1$, and subsequently during primary session $t+1$. MNA of the local populations was calculated over time from the estimated individual capture histories. When an animal was found dead in the trap it was counted as present in the trapping station, but the life history ended at that point, with no possibility of surviving and affecting the number of individuals in the next trapping session.

The trapping plots covered ca 0.6 ha. We obtained an approximate estimate of local density by multiplying the population-specific MNA by 1/(0.6 × 0.6) ha. We did not correct population size estimated by the MNA for differences in capture probabilities as this was impossible for populations with very low densities. Mean capture probability, estimated from the number of individuals observed at a primary trapping session t divided by the MNA at session t, is normally high during the summer season (0.94 ± 0.01 SE) (Aars and Ims 2002).

Season was defined as summer from June to August trapping, and winter from August to June. Trapping twice a year (spring and fall), is a common way to create time series of voles and lemmings. Hence, the population density was estimated at the end of the winter in June, and at the end of summer in August. Amplitude was estimated per plot by using the maximum difference between maximum and minimum monthly estimate of MNA.

We applied generalised linear mixed models with population ID as a random factor in all models and carried out all statistical analyses using the package glmmTMBR in R ver. 3.5.2 software (Brooks et al. 2017, <www.r-project.org>).

Small predator community

We estimated track frequencies of generalist predators red fox and pine marten, *Martes martes*, by snow tracking along 2.95 km (SD = 0.5) transect lines in January for the period from 2003 to 2014. The transect lines were part of a nationwide monitoring program for Eurasian lynx *Lynx lynx* and were based on voluntarily work from members of the Hedmark Chapter of the Norwegian Association of Hunters and Anglers (Tovmo and Brøseth 2011). The transect line density was three (SE = 4) lines per 100 km^2. Of a total of 621 different lines, 281–484 lines were surveyed annually during favourable snow conditions, i.e. 2 ± 5 days after snowfall (see Breisjøberget et al. 2018 for more details). We used estimates of track frequencies, i.e. the number of tracks per km divided by the number of days since last snowfall, from 19 transect lines allocated between 300 m and 800 m a.s.l. and within 20 km south and north of the vole trapping plots.

Table 2. The most parsimonious Poisson regression models selected for the response variable minimum number of animals known to be alive per ha. All other models ΔAIC >50.

Model	AIC	ΔAIC
Elevation × Season + Elevation × Year + Season × Year	1008.5	0.0
Elevation × Season × Year	1009.4	0.9
Elevation × Year + Season × Year	1010.4	1.9

We used two estimates of predator abundance: fox tracks, and the sum of fox and marten tracks.

Data deposition

Data are available through Figshare digital repository <www.figshare.com>: doi: 10.6084/m9.figshare.8293535, doi: 10.6084/m9.figshare.8293937 and on request.

Results

The population trajectories showed that yearly and seasonal variations in the minimum number of animals alive in each population correlated with elevation as a continuous variable (Table 2). We categorised plots into two: 15 low elevation plots < 550 m and 15 high elevation plots > 350 m (Fig. 2). The highest peak population densities occurred in fall 2014, with up to 125 animals per ha in some of the high elevation populations. Low elevation populations had less than 100 animals per ha at the peak of 2014. The minimum densities in both low and high elevation populations were <2.2 animals per ha and did not differ between high and low elevations (Table 3). Peak population densities were 1.5 times greater in high elevation than low elevation populations (Table 3).

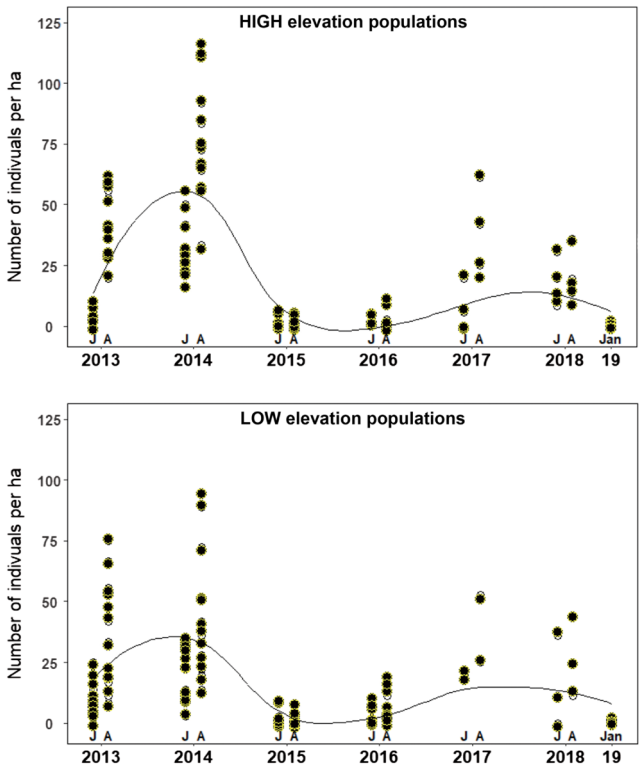

Figure 2. Trajectories of bank vole densities of each population (animals ha^{-1}), based on the minimum number of individuals known to be alive per ha. We have split the populations into 15 at low (250–532 m a.s.l.) and 15 at high (564–801 m a.s.l.) elevations. The smoothed line is based on the means for each month. We added January 2019 for illustrative purposes.

Table 3. Mean amplitude (animals ha^{-1} ± SE) of population cycles estimated as the difference between the maximum and minimum monthly estimates of population size for each population. We have split the populations into 15 at low (250–532 m a.s.l.) and 15 at high (564–801 m a.s.l.) elevation. Statistics (F, p) compare high and low elevation populations.

	Number of individuals			
	High elevation	Low elevation	$F_{1,28}$	p
Amplitude	68.3 ± 7.9	44.9 ± 6.2	10.76	0.003
Minimum	1.7 ± 1.0	2.2 ± 1.4	0.1	0.754
Maximum	70.0 ± 7.6	46.1 ± 6.2	5.89	0.022

There was a strong positive correlation between the amplitude and elevation ($r^2 = 0.28$, slope = 0.09 ± 0.03 (SE), $F_{1,28} = 10.76$, $p = 0.003$; Fig. 3). The indices of fox and generalist predators were highly correlated ($r > 0.99$), and both predator indices were also correlated negatively with elevation ($r = -0.98$). Hence, elevation and generalist predators were highly confounded. According to AIC weights, the univariate model with elevation as the predictor of amplitude was twice as likely to be the best model than the models including generalist predators (Table 4, Fig. 4).

Discussion

Our results confirmed our expectations that winter length was positively associated with the amplitude of vole population cycles. A two-month longer winter season resulted in

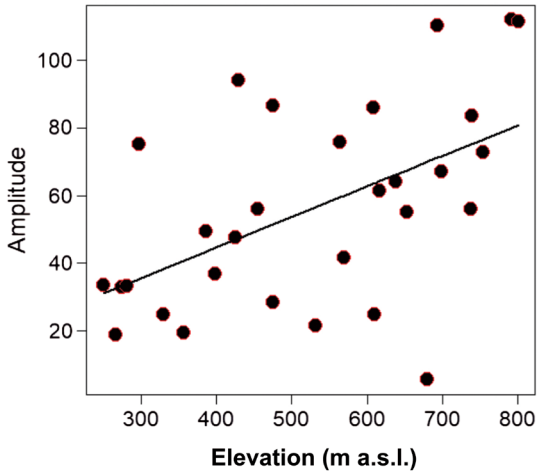

Figure 3. The regression between amplitude (no. of animals ha^{-1}) and elevation. Each symbol is one population.

Table 4. AIC information criteria for various models including elevation and generalist predators as predictors for amplitude (wAIC = AIC weight).

Predictor	Slope ± SE	AIC	ΔAIC	wAIC
Elevation	0.09 ± 0.03	283.9	0	0.41
Elevation + Generalists	0.20 ± 0.15	285.3	1.4	0.20
	95.98 ± 125.6			
Generalists	−71.44 ± 23.72	285.3	1.4	0.20
Fox	−87.31 ± 29.28	285.4	1.5	0.19

a 1.5-fold greater cycle amplitude of the local population fluctuations over the six-year study period. This was mainly due to the higher maximum densities at high elevations in the first peak (year 2014) in the time series. Profound temporal variation in cycle amplitude is a common characteristic in rodent populations (Kleiven et al. 2018, Soininen et al. 2018). Also, the fact that fewer plots with a lower altitude range were trapped in 2018 may have contributed to the lower amplitude of the second peak of the time series. Hence, the seasonality effect is elevational as well as latitudinal. As far as we know, we have for the first time tested directly whether the community of small generalist predators is part of the seasonality effect. Obviously, the small mammal community is completely confounded with elevation and season and it may be impossible to falsify the predation hypothesis completely. Furthermore, we cannot exclude the possibility of an elevational variation in predation impact due to a functional response rather than a numerical response of the predators. However, our results demonstrate that seasonality alone as a predictor of amplitude is twice as likely to be the best model, compared to models including generalist predators.

Seasonality is important for population cycles to occur (Stenseth et al. 2003), although this assumption is not supported by cyclic vole populations in agricultural areas in southwest France (Lambin et al. 2006), it seems robust at least for more natural boreal and arctic ecosystems. Empirically-based modelling studies based on time series from Fennoscandia have shown the significance of seasonality as a driver of the dynamics of cyclic populations showing strong density-dependence in winter (Bjørnstad et al. 1995, Hansen et al. 1999a, b, Kleiven et al. 2018). These studies describe strong interspecific competition during winter and high intraspecific competition in both summer and winter.

High density-dependence during winter is expected if resources are limited (Hansen et al. 1999a). Indeed, several studies of the winter ecology of cyclic vole populations confirm the significance of food resources during winter for winter survival (Ylönen and Viitala 1991, Schweiger and Boutin 1995, Eccard and Ylönen 2001, Huitu et al. 2003, 2007, Boonstra and Krebs 2006, Johnsen et al. 2017, Soininen et al. 2018, but see also Yoccoz et al. 2001). Food availability influences the bank vole social system (Ostfeld 1990), and overwintering groups have been reported to operate on high-quality patches with potentially high survival (Ylönen and Viitala 1991, Sundell et al. 2012).

Other resources than food may be limited during winter. For instance, Korslund and Steen (2006) found that survival of tundra voles *Microtus oeconomus* increased with increasing space availability in the subnivean area. Similar results show that snow depth could increase the summer density of brown lemmings *Lemmus trimucronatus*, affecting the amplitude and possibly the periodicity of the cycle (Bilodeau et al. 2013). Reid and Krebs (1996) found that shallow winter snow appeared to be a strong limiting factor in the population growth of collared lemmings *Dicrostonyx kilangmiutak*, and that the density of winter nests in voles and lemmings increased with snow depth (Reid et al. 2012). Finally, Ylönen and Viitala (1985) found that bank voles aggregated in areas with brush-vegetation

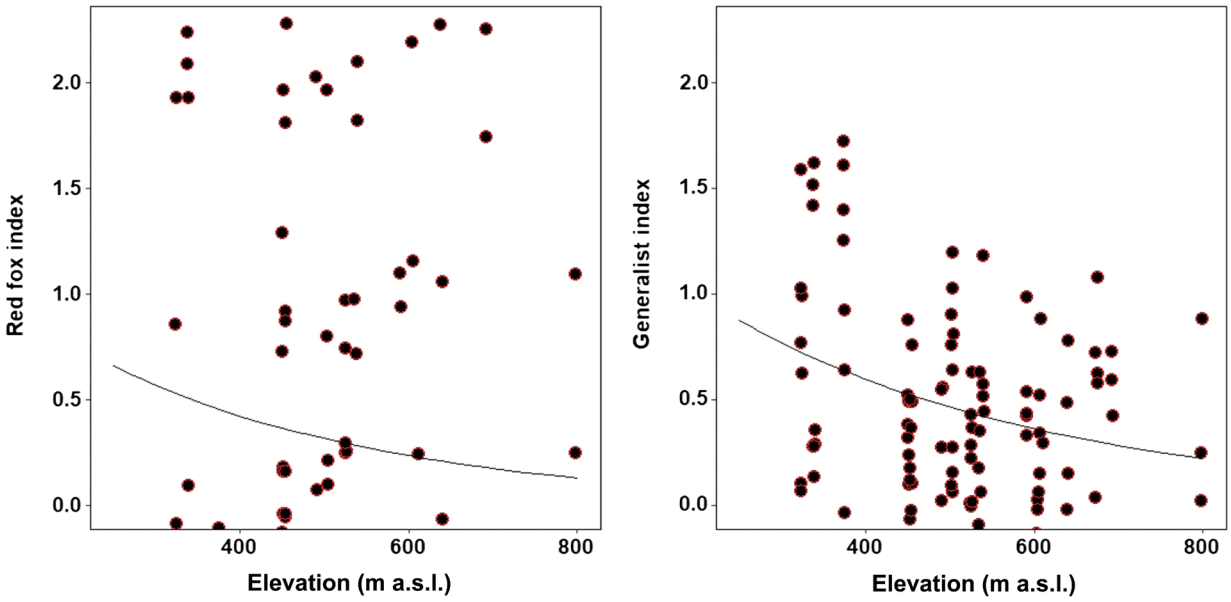

Figure 4. Correlations between indexed of generalist predators and amplitude.

before winter, which were also the areas with thickest snow cover during winter (see also Hambäck et al. 2002).

Winter aggregations benefit from a high level of social interactions (Ylönen and Viitala 1991) which allow high reproduction at the onset of the breeding season in spring (Andreassen et al. 2013, Hansen et al. 2013, Rémy 2013, Radchuk et al. 2016). This may give rise to high population growth rates in summer and consequently greater cycle amplitudes. It is to be noted that the described resources could be interacting with other factors and be used to minimise the direct causes of mortality such as predation or diseases during winter.

In contrast, populations at low elevation may be more vulnerable to unstable mild winter weather that reduces habitat availability and quality, with variable snow cover, due to repeated thawing and freezing phases at ground level (Aars and Ims 2002, Stien et al. 2012, Bilodeau et al. 2013, Hansen et al. 2013). This may limit access to food resources and shelter while increasing exposure to mammalian and avian predators and to lower critical temperatures (Hansson and Henttonen 1985, Aars and Ims 2002, Hoset et al. 2009, Haapakoski and Ylönen 2013). Breeding during winter is a characteristic of increasing vole populations (Krebs and Myers 1974). This may be restricted by weather conditions and some studies suggest that the timing of ice and snow melt in spring might be the most critical factor, as it is the spring population that initiates the peak phase of the population cycles (Aars and Ims 2002, Korslund and Steen 2006, Kausrud et al. 2008, Hoset et al. 2009, Ims et al. 2011, Cornulier et al. 2013, Haapakoski and Ylönen 2013, Fauteaux et al. 2015). Still, more knowledge is needed on small rodent winter ecology, and winter breeding is poorly understood (Krebs 1993, Aars and Ims 2002).

In conclusion, seasonality is an important factor in shaping the dynamics of cyclic vole and lemming populations. The effect may be seen as an intrinsic characteristic of cyclic vole populations. However, more probable the effect is connected to winter resource availability and inter- and/or intraspecific density-dependence. It may be empirically impossible to untangle the many confounding factors of the small mammal community, elevation and season. In a theoretical modelling approach Tyson and Lutscher (2016) found that even a small change in season length would have large effects on a simple predator–prey system. In this study the modelled predator behaved as specialist predator during the winter and a generalist during the summer. Thus, to elucidate to what extent predators act as a decisive mechanism connected to seasonality may thus require more detailed data than were available in the present study. Still we have been able to show that the abundance of generalist predators were not the best predictor of variation in cycle amplitude of a rodent species in boreal forest.

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Author contributions – All authors contributed developing the design of the study and commented on the various versions of the manuscript. HPA analysed the data and wrote the first draft of the manuscript. KJ, BJ and MN did all fieldwork. MO was responsible for the data on generalist predators.

Permits – The fieldwork was conducted in accordance with the regulations for animal experiments at the university with permission from landowners, the Norwegian Environment Agency and Norwegian Food Safety Authority (FOTS ID 5525 and ID 13908).

References

Aars, J. and Ims, R. A. 2002. Intrinsic and climatic determinants of population demography: the winter dynamics of tundra voles. – Ecology 83: 3449–3456.

Andreassen, H. P. et al. 2013. New views on how population–intrinsic and community–extrinsic processes interact during the vole population cycles. – Oikos 122: 507–515.

Bilodeau, F. et al. 2013. The effect of snow cover on lemming population cycles in the Canadian High Arctic. – Oecologia 172: 1007–1016.

Bjørnstad, O. et al. 1995. A geographic gradient in small rodent density fluctuations: a statistical modelling approach. – Proc. R. Soc. B 262: 127–133.

Boonstra, R. and Krebs, C. J. 2006. Population limitation of the northern red-backed vole in the boreal forests of northern Canada. – J. Anim. Ecol. 75: 1269–1284.

Boonstra, R. et al. 2016. Why do the boreal forest of ecosystems of northwestern Europe differ from those of western North America? – Bioscience 66: 722–734.

Breisjøberget, J. I. et al. 2018. The alternative prey hypothesis revisited: still valid for willow ptarmigan population dynamics. – PLoS One 13: e0197289.

Brooks, M. E. et al. 2017. GlmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. – R J. 9: 378–400.

Cornulier, T. et al. 2013. Europe-wide dampening of population cycles in keystone herbivores. – Science 340: 63–66.

Eccard, J. A. and Ylönen, H. 2001. Initiation of breeding after winter in bank voles: effects of food and population density. – Can. J. Zool. 79: 1743–1753.

Ehrich, D. et al. 2009. Multi-annual density fluctuations and habitat size enhance genetic variability in two northern voles. – Oikos 118: 1441–1452.

eKlima 2019. Norwegian meteorological institute – eklima. – Freely available online: <http://sharki.oslo.dnmi.no/>, accessed 14 06 2019.

Fauteux, D. et al. 2015. Seasonal demography of a cyclic lemming population in the Canadian Arctic. – J. Anim. Ecol. 84: 1412–1422.

Finerty, J. P. 1980. The population ecology of cycles in small mammals: mathematical theory and biological fact. – Yale Univ. Press.

Hambäck, P. A. et al. 2002. Winter herbivory by voles during a population peak: the importance of plant quality. – Ecography 25: 74–80.

Hansen, T. F. et al. 1999a. Multiannual vole cycles and population regulation during long winters: an analysis of seasonal density dependence. – Am. Nat. 154: 129–139.
Hansen, T. F. et al. 1999b. Interspecific and intraspecific competition as causes of direct and delayed density dependence in a fluctuating vole population. – Proc. Natl Acad. Sci. USA 96: 986–991.
Hansen, B. B. et al. 2013. Climate events synchronize the dynamics of a resident vertebrate community in the high arctic. – Science 339: 313–315.
Hansson, L. and Henttonen, H. 1985. Gradients in density variations of small rodents: the importance of latitude and snow cover. – Oecologia 67: 394–402.
Hansson, L. and Henttonen, H. 1988. Rodent dynamics as community processes. – Trends Ecol. Evol. 3: 195–200.
Haapakoski, M. and Ylönen, H. 2013. Snow events fragmentation effects and food determines overwintering success in ground-dwelling voles. – Ecol. Res. 28: 307–315.
Henden, J. A. et al. 2009. Nonstationary spatio–temporal small rodent dynamics: evidence from long-term Norwegian fox bounty data. – J. Anim. Ecol. 78: 636–645.
Hoset, K. S. et al. 2009. Demographic responses to a mild winter in enclosed vole populations. – Popul. Ecol. 51: 279–288.
Huitu, O. et al. 2003. Winter food supply limits growth of northern vole populations in the absence of predation. – Ecology 84: 2108–2118.
Huitu, O. et al. 2007. Phase dependence in winter physiological condition of cyclic voles. – Oikos 116: 565–577.
Ims, R. A. et al. 2008. Collapsing population cycles. – Trends Ecol. Evol. 23: 79–86.
Ims, R. A. et al. 2011. Determinants of lemming outbreaks. – Proc. Natl Acad. Sci. USA 108: 1970–1974.
Johnsen, K. et al. 2017. Surviving winter: food, but not habitat, prevents crashes in cyclic vole populations. – Ecol. Evol. 2016: 1–10.
Kausrud, K. L. et al. 2008. Linking climate change to lemming cycles. – Nature 456: 93–97.
Kleiven, E. F. et al. 2018. Seasonal difference in temporal transferability of an ecological model: near-term predictions of lemming outbreak abundance. – Sci. Rep. 8: 15252.
Korslund, L. and Steen, H. 2006. Small rodent winter survival: snow conditions limit access to food resources. – J. Anim. Ecol. 75: 156–166.
Krebs, C. J. 1966. Demographic changes in fluctuating populations of *Microtus californicus.* – Ecol. Monogr. 36: 239–273.
Krebs, C. J. 1993. Are lemmings large Microtus or small reindeer? A review of lemmings after 25 years and recommendations for future work. – In: Stenseth, N. C. and Ims, R. A. (eds), The biology of lemmings. Academic Press, pp. 247–260.
Krebs, C. J. 1996. Population cycles revisited. – J. Mammal. 77: 8–24.
Krebs, C. J. and Myers, J. H. 1974. Population cycles in small mammals. – Adv. Ecol. Res. 8: 267–399.
Lambin, X. et al. 2006. Vole population cycles in northern and southern Europe: is there a need for different explanations for single pattern? – J. Anim. Ecol. 75: 340–349.
Lindström, E. R. and Hörnfeldt, B. 1994. Vole cycles, snow depth and fox predation. – Oikos 70: 156–160.
Myers, J. H. 2018. Population cycles, generalists, exceptions and remining mysteries. – Proc. R. Soc. B 285: 20172841.
Myllymäki, A. 1977: Interactions between the field vole *Microtus agrestis* and its microtine competitors in central-Scandinavian populations. – Oikos 29: 570–580.
Ostfeld, R. S. 1990. The ecology of territoriality in small mammals. – Trends Ecol. Evol. 5: 411.
Radchuk, V. et al. 2016. From individuals to population cycles: the role of extrinsic and intrinsic factors in rodent populations. – Ecology 97: 720–732.
Reid, D. G. and Krebs, C. J. 1996. Limitations to collared lemming population growth in winter. – Can. J. Zool. 74: 1284–1291.
Reid, D. G. et al. 2012. Lemming winter habitat choice: a snow-fencing experiment. – Oecologia 168: 935–946.
Rémy, A. et al. 2013. Food distribution influences social organization and population growth in a small rodent. – Behav. Ecol. 24: 832–841.
Salek, M. et al. 2014. Changes in home range sizes and population densities of carnivore species along the natural to urban habitat gradient. – Mamm. Rev. 45: 1–14.
Soininen, E. M. et al. 2018. Transferability of biotic interactions: temporal consistency of arctic plant–rodent relationships is poor. – Ecol. Evol. 2018: 1–15.
Strann, K. B. et al. 2002. Is the heart of Fennoscandian rodent cycle still beating? A 14-year study of small mammals and Tengmalm's owls in northern Norway. – Ecography 25: 81–87.
Stenseth, N. C. et al. 2003. Seasonality, density dependence and population cycles in Hokkaido voles. – Proc. Natl Acad. Sci. USA 100: 11478–11483.
Stien, A. et al. 2012. Congruent responses to weather variability in high arctic herbivores. – Biol. Lett. 8: 1002–1005.
Sundell, J. et al. 2012. Spatio–temporal patterns of habitat use in voles and shrews modified by density, season and predators. – J. Anim. Ecol. 81: 747–755.
Schweiger, S. and Boutin, S. 1995. The effects of winter food addition on the population dynamics of *Clethrionomys rutilus*. – Can. J. Zool. 73: 419–426.
Tovmo, M. and Brøseth, H. 2011. Lynx monitoring in selected areas 2011. – NINA Report 750, Norwegian Institute for Nature Research, Trondheim, Norway.
Tyson, R. and Lutscher, F. 2016. Data from: seasonally varying predation behaviour and climate shifts are predicted to affect predator–prey cycles. – American Naturalist, Dryad Digital Repository <http://doi:10.5061/dryad.f2mk6>.
Walton, Z. et al. 2017. Variation in home range size of red foxes *Vulpes vulpes* along a gradient of productivity and human landscape alteration. – PLoS One 12: e0175291.
Ylönen, H. and Viitala, J. 1985. Social organization of an enclosed winter population of the bank vole *Clethrionomys glareolus*. – Ann. Zool. Fenn. 22: 353–358.
Ylönen, H. and Viitala, J. 1991. Social overwintering and food distribution in the bank vole *Clethrionomys glareolus*. – Ecography 14: 131–137.
Yoccoz, N. G. et al. 2001. Effects of food addition on the seasonal density-dependent structure of bank vole *Clethrionomys glareolus* populations. – J. Anim. Ecol. 70: 713–720.