







ARTICLE

Abundance, predation, and habitat associations of lemming winter nests in northern Sweden

Jan Vigués¹  | Karin Norén¹  | Caitlin Wilkinson^{1,2}  |
Marianne Stoessel³  | Anders Angerbjörn¹  | Fredrik Dalerum^{1,4,5} 

¹Department of Zoology, Stockholm University, Stockholm, Sweden

²Department of Environmental Research and Monitoring, Swedish Museum of Natural History, Stockholm, Sweden

³Department of Physical Geography, Stockholm University, Stockholm, Sweden

⁴Biodiversity Research Institute (IMIB, UO-CSIC-PA), Spanish National Research Council, Research Building, Mieres Campus, Mieres, Spain

⁵Department of Zoology and Entomology, Mammal Research Institute, University of Pretoria, Hatfield, South Africa

Correspondence

Karin Norén
Email: karin.noren@zoologi.su.se

Funding information

EU Interreg; Fjällräven International AB; Naturvårdsverket, Grant/Award Number: 802-0199-18; Oscar and Lili Lamm Memorial Foundation, Grant/Award Number: FO2018-0022; World Wildlife Fund; EU Interreg Felles Nord II, Grant/Award Number: 20203530

Handling Editor: Alessio Mortelliti

Abstract

Spatially synchronous fluctuations of animal populations have profound ecological consequences, especially in northern latitudes. Spatially coupled fluctuations are often seen in small rodent populations, albeit with local and regional variations. While both resource limitation and predation influence rodent dynamics, their relative importance for generating spatial variation is less clear, particularly during winter. In this study, we quantify spatial variation in winter abundance of the Norwegian lemming (*Lemmus lemmus*) across three ecologically connected mountain areas in northern Sweden and evaluate whether the relative strength of bottom-up and top-down regulation influences such variation. Our data included observations of predated and nonpredated winter nests as well as environmental characteristics of nest locations and nest predation. While the direction of annual changes in lemming nest abundance was perfectly synchronized among the three areas, there were differences in nest abundance, potentially caused by contrasting amplitudes of temporal fluctuations in lemming winter populations. Mustelid predation was positively associated with decreasing lemming populations but did not differ in occurrence among the three areas. Lemming nests were predominantly observed in meadows, whereas areas prone to flooding and close to the tree line were underrepresented. Mustelid predation was most common close to the tree line, but not associated with geomorphological characteristics related to snow depth. We suggest that the observed differences in lemming winter abundances were caused by variations in the relative strength of bottom-up and top-down regulation in the three mountain areas. We encourage further studies evaluating how the relative strength of different processes influence local population regulation, and how such processes influence spatial variation in animal population dynamics at different spatial scales.

KEYWORDS

microtine rodents, Norwegian lemming, population cycles, population synchrony, spatial variation

This is an open access article under the terms of the [Creative Commons Attribution](https://creativecommons.org/licenses/by/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2022 The Authors. *Ecosphere* published by Wiley Periodicals LLC on behalf of The Ecological Society of America.

INTRODUCTION

Spatial synchrony in temporal fluctuations across geographically disjunct populations has long been of great interest to ecologists (Elton & Nicholson, 1942; Moran, 1953). Such coupled fluctuations have been observed in many diverse taxa (Liebhold et al., 2004) and may be caused by correlated climatic conditions (i.e., Moran effects) (Kendall et al., 2000; Moran, 1953; Ranta et al., 1997), trophic links between species (Ims & Andreassen, 2000; Ims & Steen, 1990; Stenseth et al., 1999), or dispersal processes (Holmes et al., 1994; Molofsky, 1994). The strength of spatial synchrony is likely to vary over space and time (Ranta et al., 1998; Sheppard et al., 2015) and may influence important population characteristics such as regional extinction rates (Engen, 2007; Engen et al., 2002; Heino et al., 1997) and fitness distributions across populations (Gaillard et al., 2000). While the specific factors influencing variations in the degree of synchrony are still poorly known (Jarillo et al., 2020; Walter et al., 2017), it is generally believed that combinations of different drivers are required for it to occur (Walter et al., 2017).

Understanding the factors behind these coupled fluctuations is particularly relevant at high latitudes, where seasonal variation in weather is more pronounced than in more southern areas (Hansson & Henttonen, 1998; Ims & Fuglei, 2005), and the climate is changing most rapidly (Ruckstuhl et al., 2008). Small rodents are keystone species in northern tundra environments (Ims & Fuglei, 2005; Krebs, 2011), and they often undergo dramatic cyclic fluctuations in population sizes (Ecke & Hörnfeldt, 2021; Elton, 1924; Krebs et al., 2002). The specific factors driving these cycles have long been debated (Chitty, 1960), with the two dominating hypotheses being food availability and predation (Korpimäki et al., 2004; Krebs, 2002, 2011; Prevedello et al., 2013). These cycles have historically shown a strong spatial synchrony, which has mainly been attributed to climatic conditions (Angerbjörn et al., 2001; Henden et al., 2009; Selås, 2016). However, since population dynamics of small rodents are greatly influenced by winter conditions (T. F. Hansen et al., 1999; B. B. Hansen et al., 2013; Hörnfeldt, 2004), climate warming may have profound effects on the spatial and temporal dynamics of small rodents in northern regions (Duchesne et al., 2011a; T. F. Hansen et al., 1999; Reid et al., 2012; Solonen, 2006).

In addition to environmental variability, trophic interactions may also influence the spatial synchrony of small rodent population dynamics (Hoset et al., 2014; Liebhold et al., 2004). Predation may cause local variations in such population dynamics as a response to spatial variation either in predator abundance or in realized

predation risk (Brown et al., 1999; Lima, 1998). Indirect risk effects may be further complicated by trade-offs between food availability and shelter (Brown & Kotler, 2004). Combined, indirect risk effects have been suggested to have stronger demographic consequences for prey populations rather than predation-related mortality (Creel & Christianson, 2008), although the generality of such claims has been questioned (Wirsing et al., 2021). However, both the spatial distribution of predators and the availability of potential predation refugia likely interact with environmental conditions in generating spatial variation in the population dynamics of prey.

The Norwegian lemming (*Lemmus lemmus*) is an ecologically important small rodent in the Fennoscandian mountains (Ims & Fuglei, 2005), which experiences 3- to 5-year-long demographic population cycles (Ecke & Hörnfeldt, 2021). Although these population cycles appear to be spatially as well as temporally coupled, both environmental factors and predation may cause local variations through density-dependent mechanisms (Le Vaillant et al., 2018; Morris, 1988). Small mustelids have been proposed as drivers for population fluctuations in northern rodents due to their narrow prey range and sedentary nature (Andersson & Erlinge, 1977; Hanski et al., 1991, 2001; Korpimäki & Krebs, 1996; Sittler, 1995). Two species of small mustelid are sympatric in northern Scandinavia: the stoat (*Mustela erminea*) and the least weasel (*Mustela nivalis*) (Stoessel et al., 2019). However, a recent study suggests that over 80% of the winter predation on lemmings is carried out by the least weasel (Vigués et al., 2021). Although resource constraints may impact lemming distribution and abundance during the winter months (Korslund & Steen, 2006; Le Vaillant et al., 2018), small mustelids are prone to cause disruptions to lemming winter demographics because they prey on lemmings throughout the winter (Sittler, 1995; Stoessel et al., 2019). Some species, such as the stoat, also show pronounced time lags in their numerical responses, which may further influence population dynamics (Gilg et al., 2006).

Like other lemming species (Maclean et al., 1974; Sittler, 1995), Norwegian lemmings build winter nests out of vegetation to serve as a refuge from extreme temperatures (referred to as lemming nests from here on). These nests are easily identifiable in the tundra and can be surveyed after snow melt to provide information on lemming winter abundance (Gilg et al., 2003; Krebs et al., 2012) and breeding activity (Duchesne et al., 2011b). Furthermore, lemmings are often predated on by small mustelids in the nests (Maclean et al., 1974). This leaves conspicuous traces within the nest allowing quantification of mustelid predation on lemmings during winter through nest surveys (Sittler, 1995; Vigués

et al., 2021). We will hereafter refer to nests where predation events have occurred as “predated” nests, although we acknowledge that it is not the nests themselves that have suffered the predation events. In addition, since lemming winter nests, including predated ones, are stationary objects, they can be used to assess habitat associations of lemming winter populations as well as habitat associations of mustelid winter predation on lemmings (hereafter referred to as “nest predation”) (Duchesne et al., 2011a).

In this study, we utilize lemming nest surveys to quantify spatial synchrony of lemming winter populations within a 1500-km² region of northern Sweden. We subdivided the region into three distinct mountain areas connected by treeless habitat so that lemming populations could be demographically connected (Figure 1), and quantified differences in lemming winter abundance between these three mountain areas. In addition, we quantified the intensity of mustelid winter predation on lemmings within each mountain area, as well as habitat associations between lemming nest locations and mustelid predation of lemming nests. Our objectives were to evaluate (1) spatial variation in lemming nest abundance in relation to contrasting phases of the lemming population cycle, (2) spatial variation in winter predation by mustelids in relation to contrasting phases of the lemming cycle, and (3) habitat associations of lemming nests and of nest predation in relation to contrasting phases of the lemming cycle. Due to the potential for demographic connectivity between the three

mountain areas, determined by the availability of treeless habitats connecting them, we predicted that lemmings would be demographically synchronized across the region, that there would be limited differences in lemming nest abundance between the three mountain areas within the region, and that the three mountain areas would experience similar levels of nest predation. We also expected that lemming winter nests would be predominantly found in habitats that protect them from harsh temperatures while providing good food availability, but that a lack of obvious predation refugia would result in limited habitat associations of nest predation.

MATERIALS AND METHODS

Study area

The study was carried out in the Vindelfjällen Nature Reserve, Västerbotten county in northern Sweden (67°00' N, 17°00' E). The reserve covers 5600 km² of land ranging from 500 to 1700 m above sea level (asl). The vegetation is dominated by mountain birch and coniferous forests at lower elevations, with tundra vegetation above the tree line, which occurs between 600 and 800 m asl. The tundra at lower elevations is characterized by the presence of fen and marshes, composed of sedges (*Carex* sp. and *Eriophorum scheuchzeri*) and graminoids (*Poa* sp. and *Pleuropogon sabiniei*) (Le Vaillant et al., 2018). At

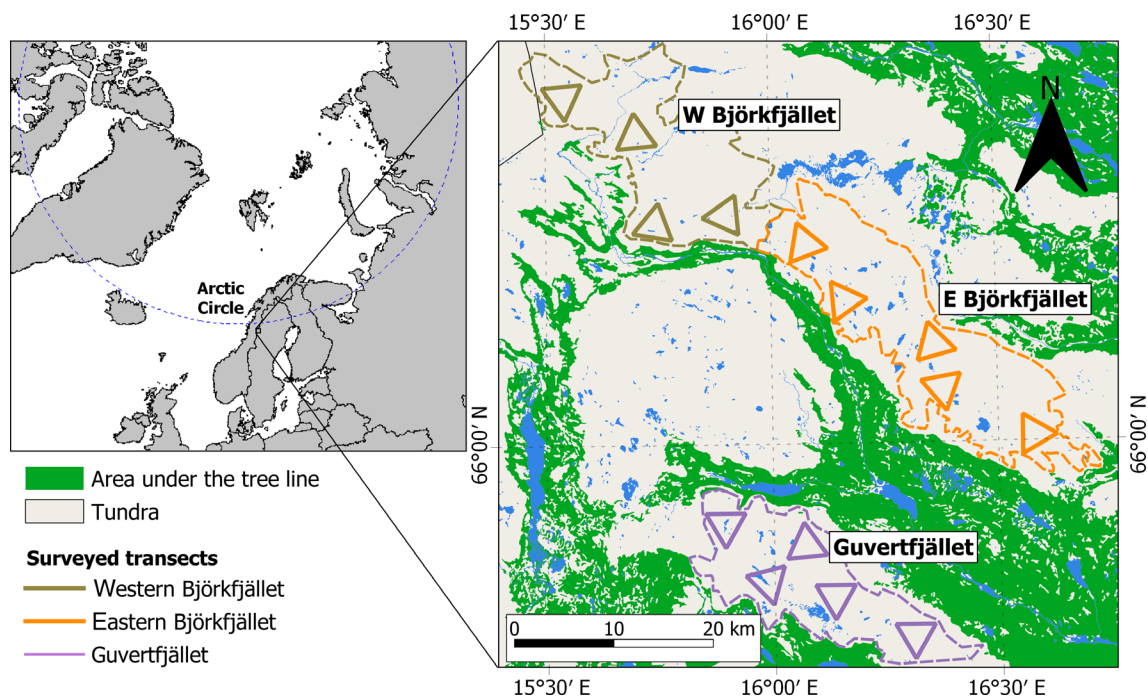


FIGURE 1 Location of the study region as well as the triangular transects used to survey lemming nests within three mountain areas in Vindelfjällen, northern Sweden.

higher elevations, the tundra is more mesic and is primarily comprised of heath vegetation, characterized by low-lying perennial herbs (*Saxifraga* sp., *Potentilla* sp., and *Ranunculus* sp.), low-growth woody plants (*Vaccinium myrtillus*, *Betula nana*, and *Salix* sp.), mosses, and lichens (Le Vaillant et al., 2018). Mean summer and winter temperatures range from 9 to -5°C , respectively (<https://www.smhi.se/data/meteorologi/temperatur>). The area has a mean annual precipitation of 1004 mm, much of which falls as snow. Average snow depth in the study area during February to April was 0.91 m during the years 2017–2019.

Lemming winter nest survey

Lemming winter nests were counted along 14 triangular transects, each consisting of three 4-km-long sides (wild-life triangles, Lindén, 1996). These transects were randomly placed within both wet and mesic tundra to ensure that they covered all major vegetation types. We divided the study region into three areas of approximately 250 km², according to potential geographical barriers such as forested valleys and rivers. The transects were divided among areas with five transects placed in eastern Björkfjället, four in western Björkfjället, and five in Guvertfjället (Figure 1). Lemming nests were counted in all areas during July 2015, 2017, 2018, 2019, and 2020, except for western Björkfjället where no counts were made in 2015 and 2017. Nest counts were done by one observer in 2015 and 2017 and a different observer from 2018 to 2020. Furthermore, sampling efforts differed between years, with the effective distances surveyed being 84 km in 2015, 62.5 km in 2017, 120 km in 2018, 132 km in 2019, and 116 km in 2020 (Table 1). Each nest position was recorded using a handheld GPS receiver

(Garmin eTrex 10 or GPSmap 64, Olathe, KS) with an approximate accuracy of 1 m. The perpendicular distance to the transect line was measured using measuring tape. Although we did not define a limited search strip width around each transect, more than half of the nests (59%) were observed 1 m or less from the transect line, 89% were observed within 5 m, and only 2% were observed further than 20 m (Appendix S1: Figure S1). Mustelid predation of nests was also recorded, based on a thin fur layer lining the inside of the nests, and other remains observed around the nest (Sittler, 1995). Following previous studies (Duchesne et al., 2011a; Schmidt et al., 2021; Sittler, 1995), we have here assumed that the locations of predated nests reflect the spatial distribution of mustelid winter predation. Only nests pertaining to the previous winter were counted. Although they are known to persist for more than 1 year (Duchesne et al., 2011a), old nests can be easily distinguished due to their flattened appearance with bleached and partially decomposed nest material (Maclean et al., 1974), and such nests were not counted. To evaluate habitat associations between nest site locations, absence points were placed at 1-km intervals along the transects. The survey was granted approval from the County Administration Board of Västerbotten (521-3191-2014 and 521-4640-2019).

Environmental variables

To evaluate habitat associations of lemming nests and of nest predation, we used a series of environmental variables related to winter availability of food and other essential resources, to microclimate (including snow depth), and to proximity of forested areas with potential predators and competitors. The environmental variables included vegetation type, normalized difference

TABLE 1 Number of observed lemming winter nests (N), number of nests with signs of predation events (N_{pred}), and distance walked during surveys (in kilometers) in western Björkfjället, eastern Björkfjället, and Guvertfjället, as well as a lemming trapping index (trapped lemmings—number of trapped lemmings per 1000 trap-nights) and estimated demographic phase for the years 2015–2020.

Year	Western Björkfjället			Eastern Björkfjället			Guvertfjället			Trapped lemmings	Demographic phase
	N	N_{pred}	Distance	N	N_{pred}	Distance	N	N_{pred}	Distance		
2015				100	14	48	99	9	36	0.5	Decrease
2016										0	Decrease
2017				0	0	36	0	0	27	0	Low
2018	55	4	48	17	1	36	13	1	36	0.2	Increase
2019	353	16	48	391	15	36	223	3	48	1.0	Increase
2020	34	3	41	40	8	36	103	12	39	0	Decrease

Note: No lemming winter nest surveys were done 2016. The lemming trapping index refers to spring trapping index from a concurrent small rodent survey in the region (Ecke & Hörnfeldt, 2021). The demographic phases were defined as: decrease, lemming trapping index lower than previous spring; low, lemming trapping index at zero as previous year; and increase, lemming trapping index higher than previous spring.

vegetation index (NDVI), distance to tree line, aspect and angle of the slope, and tangential and profile curvatures. Similar variables have previously been used to assess habitat use of lemmings during winter (Duchesne et al., 2011a, Schmidt et al., 2021). Digital data were obtained from the website of Lantmäteriet (the Swedish mapping, cadastral, and land registration authority; <https://www.lantmateriet.se/>). We used a digital vegetation layer to define vegetation types. Based on definitions in Carlsson et al. (1999), we grouped vegetation types into five categories: dry heath, fresh heath, grass heath, meadow, and fen. The heath vegetation was characterized by various dwarf shrubs, graminoids, and herbs such as *Saxifraga oppositifolia* and *Silene acaulis*. Meadows were characterized by more lush vegetation of tall-growing herbs such as *Stellaria nemorum*, *Silene dioica*, *Trollius europaeus*, and graminoids including *Juncus biglumis*, *Deschampsia alpina*, and *Carex lachenalii*. The fens were characterized by a substantial moss cover as well as various *Carex*, *Juncus*, and *Salix* species. We defined the tree line as the limit of forest vegetation types in the same digital vegetation layer as we used for vegetation types and calculated the shortest perpendicular distance between this identified tree line and each nest location or absence point. While we recognize that occasional isolated trees may have occurred above the tree line with this definition, we believe that it provides a robust estimate to the closest distance to forested habitats. To measure primary productivity, we used the same method developed and tested by Erlandsson et al. (2019), which consists of computing the NDVI equation (Tucker, 1979) on color infrared orthophotos with a 0.5-m spatial resolution (Denison et al., 1996; Erlandsson et al., 2019; Le Vaillant et al., 2018). This method has been used in previous studies in the area (Erlandsson et al., 2019; Le Vaillant et al., 2018; Stoessel et al., 2019). We obtained elevation from a digital elevation model (DEM) with a 2-m resolution. This DEM was also used to calculate slope (in degrees) and aspect (in degrees) as well as profile and tangential curvatures (per meter), using a 3 × 3 pixel neighborhood size. Profile and tangential curvatures describe the curvatures along the steepest slope and in the direction of the slope tangent, respectively. GIS processing was done in QGIS (version 3.10.12, <https://qgis.org>), using functions from the GRASS GIS 7.4.1 (GRASS Development Team, 2018) environment.

Demographic phases of the lemming population

Lemmings in the study area exhibit dramatic annual variations in population size (Ecke & Hörnfeldt, 2021). We

designated each winter as occurring during either a decrease, low, or increase phase of the regional lemming population. These demographic phases were based on a time series of annual trapping data carried out under the National Environmental Monitoring Program of Small Rodents (Ecke & Hörnfeldt, 2021, Table 1). Lemming nests counted during a year with decreasing lemming spring abundance compared to the previous spring were classified as having occurred during a decrease phase, whereas nests counted during a year with higher spring abundance compared to the previous spring were classified as having occurred during an increase phase. With these definitions, the years 2018 and 2019 represented the increase phase and 2015, 2016, and 2020 the decrease phase (Table 1). However, we did not conduct lemming winter nest surveys in 2016. Lemming abundance in 2017 was low but unchanged compared to the previous spring. We therefore defined this year as low phase and included it in abundance-related analyses despite the lack of observed lemming nests that summer.

Statistical analysis

We used a simple index based on pair-wise similarity in the direction of annual change to assess synchrony in lemming nest abundance, calculated as:

$$A = t_{ij} / (T - 1),$$

where t_{ij} is the number of time steps time series i and j moves in the same direction (i.e., no change, decrease, or increase), and T is the length of the time series (Buonaccorsi et al., 2001). The index A can take values from 0 (indicating total asynchrony) to 1 (indicating perfect synchrony). Due to an uneven number of sampled years in western Björkfället, we calculated pair-wise indices for each pair of areas rather than a joint index for the whole region.

We used generalized linear mixed models to evaluate differences between areas and demographic phases in lemming nest abundance and nest predation by mustelids. We used the number of counted lemming nests at each transect as well as the number of predated nests in relation to the total number of nests counted at each transect as response variables. We included mountain area (i.e., eastern Björkfället, western Björkfället, and Guvertfället), phase (i.e., increase or decrease phase), and their two-way interaction as fixed predictors, as well as year and individual triangle identity as random grouping variables. Considering that not all transects were fully completed, we added distance walked at each survey occasion as an offset for the model on abundance, effectively modeling nest abundance as a

rate of nests encountered per unit of distance surveyed. We also excluded the low phase from the nest predation model, since no nests were detected that year. The models were fitted using restricted maximum likelihood with a Poisson error distribution and a log link function for the model on abundance and a binomial error distribution and a logit link for the model on predation. No spatial autocorrelation was detected in the residuals from either model, based on Moran's I (abundance model $I = -0.04$, $Z = 0.36$, $p = 0.643$; predation model: $I = -0.04$, $Z = 0.42$, $p = 0.597$). We used estimated marginal means to evaluate pair-wise post hoc contrasts between areas within the decrease and increase phase adjusting the p values for multiple comparisons using the Tukey method (Lenth, 2021). We excluded the low phase for these post hoc contrasts since we did not observe any lemming nests during this phase. While we used raw lemming nest counts to evaluate spatial and temporal variation in lemming winter abundance, we have presented nest abundance as densities (number of nests per hectare ± 1 SE), estimated using distance sampling methodology, to facilitate interpretation and comparisons with other studies (Buckland et al., 2004). Details regarding fitting the detection function are outlined in Appendix S1: Figure S1. Considering we did not conduct a full nest count within specified areas, we did not deem it appropriate to analytically evaluate the structure of the spatial distribution of nests.

We also used generalized linear mixed models to evaluate habitat associations of lemming nest locations and of nest predation, and if such habitat associations differed between demographic phases. Location types, that is, nest or absence point or predated or nonpredated nest, were used as binary response variables. Demographic phase, all environmental variables, and all two-way interactions between demographic phase and the environmental variables were set as fixed predictors. In addition, three-way interactions between demographic phase, area, and an environmental variable were added if statistically significant (Appendix S1: Table S1), to enable specific evaluations of differences between phases within each area. For both the model on nest locations and on nest predation, sample year was added as a random factor. A spatial correlation structure using the Matern algorithm (Stein, 1999) was included for the model on nest locations, as it eliminated spatial autocorrelation among the residuals ($I < 0.01$, $Z = 0.89$, $p = 0.371$). We did not include this for the model on predated lemming nests since the residuals were not spatially correlated ($I = 0.01$, $Z = 0.99$, $p = 0.323$). Both models were fitted using a binomial error distribution and a logit link function. These models were restricted to data collected during 2015, 2018, 2019, and 2020, since no nests were found in 2017.

There was no collinearity among any of the environmental predictors ($R^2 < 0.22$, for all pairs of predictors). For all models, there were no signs of over- or under-dispersion, and visual inspection of standardized residuals did not suggest deviations from critical model assumptions.

All analyses were done in the statistical environment R (version 4.1.1, R Development Core Team, 2021), using the contributed packages distance (version 1.0.2, Miller et al., 2019), DHARMA (version 0.4.5, Hartig, 2022), emmeans (version 1.6.2-1, Lenth, 2021), lme4 (version 1.1-27, Bates et al., 2015), spaMM (version 3.7.34, Rousset & Ferdy, 2014), and spdep (version 1.1-7, Bivand & Wong, 2018).

RESULTS

Spatial variation in abundance and predation of lemming nests

A total of 1428 lemming nests were recorded during the study: 199 in 2015, 0 in 2017, 85 in 2018, 967 in 2019, and 177 in 2020. Of these, 23 had visible signs of predation on lemmings in 2015, 6 in 2018, 34 in 2019, and 23 in 2020 (Table 1).

The directions of annual changes in lemming nest abundances were perfectly synchronized between the three areas ($A = 1$ for all pair-wise comparisons, Figure 2a). However, there was a significant two-way interaction effect of area and demographic phase on lemming nest abundance ($\chi^2 = 119.16$, $df = 3$, $p < 0.001$). Guvertfjället had lower nest abundance than both eastern ($\beta = -0.97$, $SE_{\beta} = 0.20$, $p < 0.001$) and western Björkfjället ($\beta = -0.69$, $SE_{\beta} = 0.20$, $p = 0.007$) during the increase phase, but higher abundance during the decrease phase (eastern Björkfjället $\beta = 0.50$, $SE_{\beta} = 0.20$, $p = 0.076$; western Björkfjället $\beta = 0.92$, $SE_{\beta} = 0.30$, $p = 0.005$). There was no difference in lemming nest abundance between eastern and western Björkfjället (increase phase $\beta = 0.27$, $SE_{\beta} = 0.20$, $p = 0.470$; decrease phase $\beta = 0.42$, $SE_{\beta} = 0.30$, $p = 0.340$) (Figure 2b).

There was a higher proportion of predated nests during the decline phase than during the increase phase ($\beta = 1.57$, $SE_{\beta} = 0.39$, $p < 0.001$, Figure 2c), but no effect of area ($\chi^2 = 1.60$, $df = 2$, $p = 0.449$) nor an interaction between area and demographic phase of the lemming population ($\chi^2 = 2.94$, $df = 2$, $p = 0.230$).

Habitat associations of lemming nest locations

The only significant three-way interaction between mountain area, demographic phase, and environmental

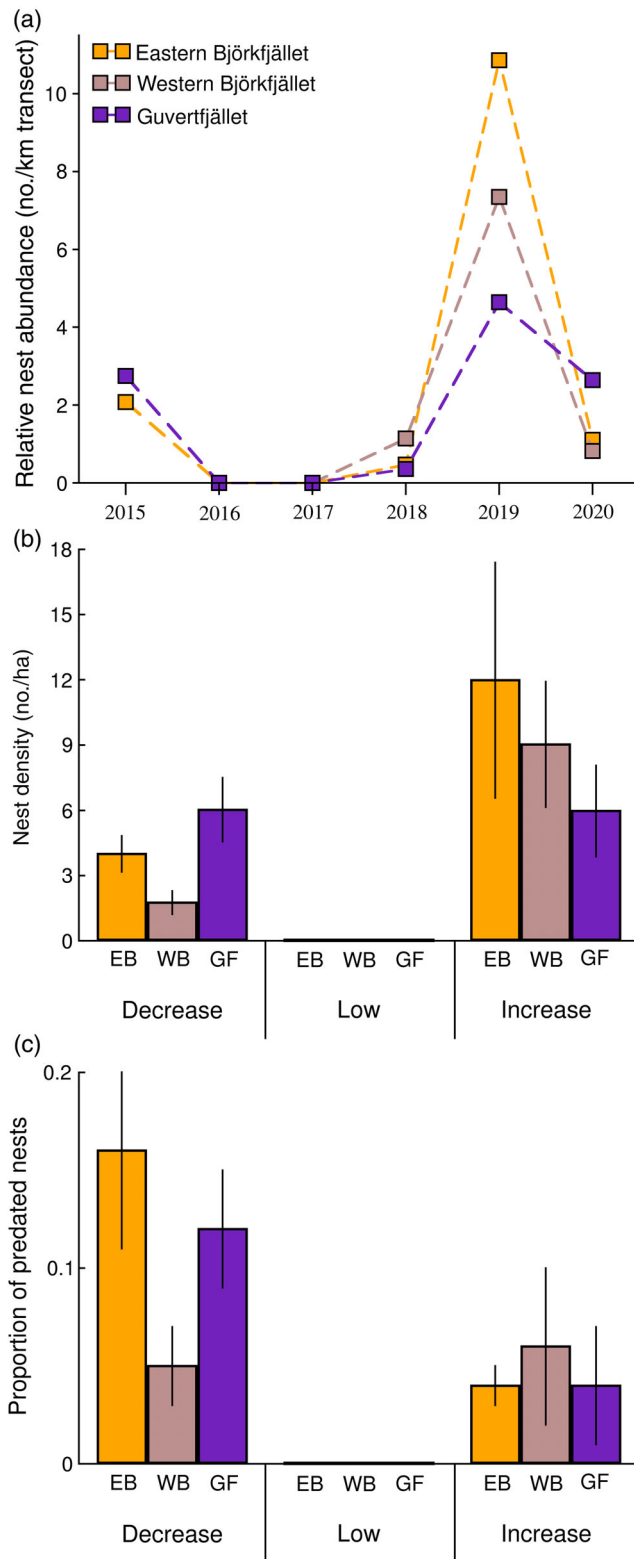


FIGURE 2 Number of observed lemming nests per kilometer of survey in three neighboring mountain areas (a), as well as lemming nest abundance (b) and proportion of nests predated by mustelids (c) in eastern (EB) and western (WB) Björkfjället as well as in Guvertfjället (GF) during winters classed as decrease, low, or increase phases of the local lemming population. Demographic phases were based on time series of spring trapping data. Figure presents mean estimated density and mean proportion of predated nests \pm SE.

variables included NDVI ($\chi^2 = 12.97$, $df = 4$, $p = 0.011$) and distance to tree line ($\chi^2 = 10.87$, $df = 4$, $p = 0.028$) (Appendix S1: Table S2). The association between lemming nest locations and NDVI differed between increase and decrease phases in eastern ($\beta = 0.71$, $SE_{\beta} = 0.24$, $p = 0.003$) and western Björkfjället ($\beta = 1.06$, $SE_{\beta} = 0.39$, $p = 0.006$), but not in Guvertfjället ($\beta = 0.21$, $SE_{\beta} = 0.17$, $p = 0.218$). By contrast, the association between lemming nest locations and distance to the tree line differed between increase and decrease phases in Guvertfjället ($\beta = -0.41$, $SE_{\beta} = 0.19$, $p = 0.035$), but not in either eastern ($\beta = 0.08$, $SE_{\beta} = 0.15$, $p = 0.619$) or western Björkfjället ($\beta = 0.26$, $SE_{\beta} = 0.29$, $p = 0.370$). Averaged across all areas, there were differences between the demographic phases in the association between lemming nest locations and both slope ($\beta = -0.31$, $SE_{\beta} = 0.14$, $p = 0.030$) and elevation ($\beta = 1.23$, $SE_{\beta} = 0.19$, $p = 0.030$) (Table 2).

Lemming nest locations were negatively associated with fresh heath ($\beta = -1.09$, $SE_{\beta} = 0.46$, $p < 0.001$) but positively associated with meadows ($\beta = 0.57$, $SE_{\beta} = 0.45$, $p = 0.006$). Nests were also positively associated with NDVI in Guvertfjället ($\beta = 0.41$, $SE_{\beta} = 0.08$, $p < 0.001$) and during the increase phase in both eastern ($\beta = 0.28$, $SE_{\beta} = 0.15$, $p < 0.001$) and western Björkfjället ($\beta = 0.81$, $SE_{\beta} = 0.16$, $p < 0.001$), but negatively associated with NDVI in eastern Björkfjället during the decrease phase ($\beta = -0.15$, $SE_{\beta} = 0.15$, $p = 0.020$). There were positive associations between lemming nests and distance to tree line in Guvertfjället (increase phase $\beta = 0.28$, $SE_{\beta} = 0.15$, $p < 0.001$; decrease phase $\beta = 0.69$, $SE_{\beta} = 0.13$, $p < 0.001$) and eastern Björkfjället ($\beta = 0.27$, $SE_{\beta} = 0.08$, $p < 0.001$), but there was a negative association in western Björkfjället ($\beta = -0.13$, $SE_{\beta} = 0.14$, $p = 0.030$). Nest locations were further positively associated with slope during the increase phase ($\beta = 0.12$, $SE_{\beta} = 0.07$, $p < 0.001$) and negatively associated with slope during the decrease phase ($\beta = -0.15$, $SE_{\beta} = 0.09$, $p < 0.001$), tangential curvature ($\beta = -0.39$, $SE_{\beta} = 0.10$, $p < 0.001$), and elevation ($\beta = -0.40$, $SE_{\beta} = 0.14$, $p = 0.006$). There were no significant associations between nests and fen, dry heath, grass heath, profile curvature, or aspect (Table 3).

Habitat associations of nest predation

There were no significant three-way interactions between demographic phase, area, and any of the environmental variables (Appendix S1: Table S2), suggesting that the three areas did not vary in the observed differences in habitat associations of nest predation between increase and decrease phases. Except for dry heath ($\beta = -1.16$, $SE_{\beta} = 0.34$, $p < 0.001$) and western aspect

TABLE 2 Differences between decline and increase phases of the lemming population in habitat associations of lemming nest locations and the locations of predated lemming nests.

Environmental variable	β	SE	<i>p</i>
Nest locations			
Fen	0.86	0.95	0.365
Dry heath	0.28	0.88	0.755
Fresh heath	-1.12	0.92	0.225
Grass heath	-0.22	0.96	0.818
Meadow	0.50	0.91	0.581
NDVI, eastern Björkfället	0.71	0.24	0.003
NDVI, western Björkfället	1.06	0.39	0.006
NDVI, Guvertfället	0.21	0.17	0.218
Dist. tree line, eastern Björkfället	0.08	0.15	0.619
Dist. tree line, western Björkfället	0.26	0.29	0.370
Dist. tree line, Guvertfället	-0.41	0.19	0.035
Slope	-0.31	0.14	0.030
Profile curvature	0.09	0.15	0.568
Tangential curvature	0.08	0.16	0.606
South aspect	0.18	0.14	0.201
West aspect	0.28	0.14	0.051
Elevation	1.23	0.19	<0.001
Nest predation			
Fen	-1.44	0.75	0.056
Dry heath	-1.16	0.34	<0.001
Fresh heath	-2.08	1.14	0.069
Grass heath	-15.92	228.97	0.945
Meadow	-0.22	0.56	0.691
NDVI	0.11	0.27	0.687
Dist. tree line	-0.02	0.27	0.948
Slope	0.09	0.23	0.701
Profile curvature	0.04	0.24	0.859
Tangential curvature	-0.26	0.23	0.261
South aspect	0.16	0.23	0.486
West aspect	-0.52	0.24	0.031
Elevation	-0.48	0.31	0.115

Note: Parameter values describe two-way interactions between phase and each of the environmental predictors and are extracted from generalized linear mixed models. Significant differences in habitat associations between lemming demographic phases, at an α level of 0.05, are indicated in bold face.

Abbreviation: NDVI, normalized difference vegetation index.

($\beta = -0.52$, $SE_{\beta} = 0.24$, $p = 0.031$), there were no significant two-way interactions between demographic phase and environmental variables (Table 2), suggesting that any other habitat associations did not differ between increase and decrease phases averaged across the three areas.

Nest predation was negatively associated with fen ($\beta = -2.35$, $SE_{\beta} = 0.17$, $p < 0.001$), dry heath (increase

phase $\beta = -3.20$, $SE_{\beta} = 0.25$, $p < 0.001$; decrease phase $\beta = -2.02$, $SE_{\beta} = 0.24$, $p < 0.001$), fresh heath ($\beta = -3.25$, $SE_{\beta} = 0.57$, $p < 0.001$), meadow ($\beta = -3.01$, $SE_{\beta} = 0.28$, $p < 0.001$), and distance to the tree line ($\beta = -0.43$, $SE_{\beta} = 0.19$, $p = 0.026$), but there were no significant associations between nest predation and grass heath, NDVI, slope, curvature, aspect, or elevation (Table 3).

TABLE 3 Average log odds ratios (β) for habitat associations of lemming nest locations and locations of predated lemming nests, extracted from generalized linear mixed models.

Environmental variable	β	SE	<i>p</i>
Lemming nest locations			
Dry heath	-0.09	0.44	0.341
Fen	-0.1	0.48	0.338
Fresh heath	-1.09	0.46	0.000
Grass heath	-0.06	0.48	0.400
Meadow	0.57	0.45	0.006
NDVI, eastern Björkfjället Decline phase	-0.15	0.15	0.020
NDVI, eastern Björkfjället Increase phase	0.56	0.19	0.000
NDVI, western Björkfjället Decline phase	-0.254	0.35	0.074
NDVI, western Björkfjället Increase phase	0.81	0.16	0.000
NDVI, Guvertfjället	0.41	0.08	0.000
Dist. tree line, eastern Björkfjället	0.27	0.08	0.000
Dist. tree line, western Björkfjället	-0.13	0.14	0.030
Dist. tree line, Guvertfjället decline phase	0.69	0.13	0.000
Dist. tree line, Guvertfjället increase phase	0.28	0.15	0.000
Slope, decrease phase	-0.15	0.09	0.000
Slope, increase phase	0.12	0.07	0.000
Profile curvature	-0.14	0.09	0.135
Tangential curvature	-0.39	0.10	0.000
South aspect	0.00	0.10	0.974
West aspect	0.07	0.10	0.467
Elevation	-0.40	0.14	0.006
Predated lemming nests			
Dry heath decline phase	-3.20	0.25	<0.001
Dry heath increase phase	-2.02	0.24	<0.001
Fen	-2.35	0.17	<0.001
Fresh heath	-3.25	0.57	<0.001
Grass heath	-10.62	114.48	0.427
Meadow	-3.01	0.28	<0.001
NDVI	-0.05	0.16	0.788
Dist. tree line	-0.43	0.19	0.026
Slope	0.05	0.16	0.733
Profile curvature	0.09	0.15	0.538
Tangential curvature	-0.20	0.13	0.123
South aspect	0.05	0.16	0.780
West aspect decline phase	-0.23	0.18	0.206
West aspect increase phase	0.24	0.18	0.170
Elevation	0.25	0.21	0.226

Note: β values significantly different from 0, at an α level of 0.05, are indicated in bold face. Abbreviation: NDVI, normalized difference vegetation index.

DISCUSSION

While we observed perfect synchrony in the direction of temporal change of lemming nest abundance among the three neighboring mountain areas, we did observe that differences in lemming winter abundance among areas varied between demographic phases of the lemming population. Such spatial variation in abundance has been found in other Arctic vertebrates, for instance, Arctic hares (Dalerum et al., 2017), and has been attributed to a range of different biotic and abiotic factors (Bjørnstad et al., 1999; Kendall et al., 2000). In addition, we detected habitat associations of both lemming nest locations and of the locations of predated nests. Many of the habitat associations of nest locations differed between demographic phases of the lemming population, whereas the habitat associations of predated nests varied less over demographic phases.

The observed spatial variation in lemming nest abundance seems to have been caused by spatial differences in the amplitude of temporal fluctuations. We observed several environmental characteristics that were important for lemming nest locations, which imply that environmental variability between our three areas may have influenced the amplitude of temporal fluctuations. Due to its overall higher elevation, Björkfjället has a lower abundance of shrub habitats and higher abundance of meadows, which appears to be a favored habitat for other lemming species (Batzli et al., 1983; Duchesne et al., 2011a; Fuller et al., 1975), than Guvertfjället. Hence, the environment on Björkfjället may have been able to support higher lemming populations during peak years, and, subsequently, more dramatic demographic declines. By contrast, the environment on Guvertfjället may not have allowed for lemming populations to reach required densities for a population collapse to occur. Such arguments agree with suggestions of strong bottom-up regulation of lemming populations (Turchin et al., 2000), providing that population growth during the increase phase is not hampered by other processes such as predation or competition.

However, we also suggest that the amplitude of temporal fluctuations on Guvertfjället may have been dampened by predation in years with high winter abundances similarly to the predator pit suggested to have stabilized lemming population in northern Canada (Reid et al., 1997). Such a suggestion would highlight that bottom-up and top-down regulation may act in concert (Hunter & Price, 1992), and show that the relative strength of these forces can vary even among neighboring mountain areas. We observed a positive association between lemming nest abundance and distance to nearest tree line for Guvertfjället and eastern Björkfjället,

which are closer to the forest than western Björkfjället, and, overall, a negative association between distance to tree line and predation. These findings suggest that lemmings may have tried to avoid predation by stoats and weasels, which are more abundant closer to the tree line (Oksanen et al., 1992). However, we recognize that an avoidance of areas in close proximity to the forest could also have been caused by direct competition with voles (A. H. Henttonen et al., 1977; Oksanen, 1993; Oksanen et al., 2008).

Lemming nests were predominantly observed in meadows, whereas habitats prone to flooding were underrepresented. These results are in accordance with previous observations of both this (Soininen et al., 2017) and other lemming species (Batzli et al., 1983; Duchesne et al., 2011a; Fuller et al., 1975). We suggest that meadow habitats could provide lemmings with high-quality food supply during the winter months (Soininen et al., 2017), as well as the material needed to build the winter nests. The fresh heath is a relatively wet habitat type (Le Vaillant et al., 2018), and the observed avoidance of this agrees with suggestions of habitat shifts from wet to dry habitats during winter (H. Henttonen & Kaikusalo, 1993; Koponen, 1970). Fresh heath is prone to flooding and is also susceptible to freeze–thaw dynamics, which can affect the accessibility to a good subnivean space, which is essential for lemming winter survival (Korslund & Steen, 2006). Moreover, fresh heath is mainly consisting of dwarf shrubs, mostly of low palatability, which could contribute to it not being favored for nest placement during winter (Hoset et al., 2014).

Our results contradicted multiple studies that have demonstrated the importance of snow depth and snow cover for habitat selection of lemmings during winter (Bilodeau et al., 2013; Duchesne et al., 2011a; Korslund & Steen, 2006; Penczykowski et al., 2017). North- and northeast-facing slopes are expected to have the deepest snow cover due to snow accumulation as a result of prevailing winds (Alexandersson, 2006; Dacic et al., 2010) and relative lack of sun exposure (Virtanen et al., 2002). In contrast with these relationships between topography and snow depth, we did not find any associations between slope aspect and lemming nest locations. We suggest that sufficient snow cover in south- and west-facing slopes could have caused a lack of preference for northern and northeastern aspects. Previously, the effect of snow depth on lemming nest location preference has reached an asymptote at approximately 60 cm of snow depth (Duchesne et al., 2011a). This is considerably less than the average depth of 91 cm found in our study area. Furthermore, convex topographic structures seemed to have been preferred, which further supports the interpretation that snow accumulation had not been a limiting

factor for lemming winter populations in our study area. Instead, we suggest that the avoidance of concave topographic structures can be a result of a strategy to minimize flooding occurrences and unwanted moisture.

Mustelid predation was higher in decreasing than in increasing lemming populations but did not differ among the three areas. Time lags in predation are characteristic of specialist mammal predators such as weasels (Korpimäki et al., 1991), and the associated low predation during the increase phase has been hypothesized to contribute to the onset and maintenance of rodent cycles (Andersson & Erlinge, 1977; Feige et al., 2012; Hanski et al., 2001; Korpimäki & Krebs, 1996; Maclean et al., 1974; Pitelka & Batzli, 2007; Reid et al., 1997). Although stoats may switch to alternative prey when microtine abundances are low, both stoats and weasels are heavily specialized on small microtine rodents (Elmeros, 2006; Feige et al., 2012; Korpimäki et al., 1991). Hence, a lack of a relationship between nest abundance and probability of nest predation is in agreement with a strong type II functional response (*sensu* Holling, 1959a, 1959b), if the abundances are above where the predators maintain a high preference for its main prey. A strong type II functional response would also agree with recent suggestions that most winter predation on lemming nests in the study area is carried out by the least weasel, which seems to be more dependent on rodents than the stoat (Elmeros, 2006; Korpimäki et al., 1991), during all phases of the lemming cycle (Vigués et al., 2021). We suggest that specialized mustelid predation on lemmings during the decrease phase may have accelerated lemming population decline, and hence contributed to lemming population fluctuations in this region (Ekerholm et al., 2004).

Mustelid predation was most common close to the tree line, but predation was also associated with vegetation characteristics, possibly related to mustelid movement and winter habitat use. However, predation was not associated with geomorphological characteristics related to snow depth. Fen and meadow, as well as dry and fresh heath, appeared to have been favored vegetation types for nest predation. The negative association between the locations of predated nests and distance to the tree line suggests a higher predation risk closer to forested areas. This may be caused by predator populations being supported by boreal microtines, such as bank and field voles (Oksanen et al., 1992). The apparent lack of influence of snow depth on predation could be expected, since small mustelids are adapted to navigate the network of tunnels connecting lemming nests in the subnivean space (Gilg et al., 2006; Sittler, 1995). Although not explicitly evaluated by our analyses, the lack of a spatial correlation structure in the environmental characteristics associated with predated nests does not suggest that

predation events were spatially clustered, at least not within the spatial scales evaluated in this study.

While we generally regard our results as robust, we do provide some caveats to our study. First, we used trapping data from consecutive springs to assign each year to a lemming demographic phase. This resulted in relatively large variations in abundance between years within the same phase. However, we regard our definition of demographic phases to still be relevant, as the temporal demographic changes are one of the core components of animal population dynamics (Moss et al., 1983). One potential drawback with using the trapping data to define demographic phases is that it lacks the spatial resolution over which we made our analyses of lemming winter populations. However, we prefer to use an independent dataset to define demographic phase. Furthermore, lemming population dynamics in Scandinavia are generally defined by summer trapping data (Angerbjörn et al., 2001; Selås, 2016), making our study congruent with existing literature. We therefore regard the spring trapping data as the most appropriate estimate of the demographic phase of the lemming population each year. We have assigned the location of lemming winter nests in summer as directly reflecting the location of the same nest the previous winter. While lemming nests may occasionally move during snow melt (personal observation), we do not regard such movements to be sufficient to be of any relevance considering the spatial scales used in this study. Similarly, we have assumed that the location of nests with signs of predation has been reflecting the spatial distribution of predation events. We regard this as a reasonable assumption, which is congruent with previous studies utilizing the locations of predated winter nests to study winter predation by stoats (Duchesne et al., 2011a; Schmidt et al., 2021; Sittler, 1995). However, we do recognize that there are currently poor data directly quantifying stoat predation behavior under the snow. Further, our environmental predictors had different spatial resolutions. Spatial resolution may be highly influential for environmental niche models (Connor et al., 2018), and we acknowledge that shifting resolutions may alter the results of our spatial analyses. However, we regard the spatial resolutions of our environmental data to be relevant for the questions asked but encourage further studies including multiple spatial scales of lemming habitat selection in winter. Finally, we recognize that our study was done over one single demographic cycle, and we encourage further studies expanding the temporal scope to fully be able to investigate spatial synchrony of lemming winter populations in this and similar areas.

To conclude, despite perfectly synchronized directional changes in lemming winter nest abundance

between three neighboring mountain areas, we observed differences in nest abundances that appeared to have been caused by contrasting amplitudes of winter population fluctuations, with limited fluctuations in one mountain area and larger temporal variations in two others. Lemming nests were mostly found in meadows and dryer habitats, as well as in areas relatively far from the forest. Mustelid predation was higher in decreasing than in increasing winter populations, which could accelerate population declines in winter. Our results did not suggest that predation risk during winter was related to snow depth, but rather to the proximity of forested areas. Furthermore, our study supports that the relative strength of bottom-up and top-down regulation of lemming winter populations may vary even among neighboring mountain areas. We encourage further studies designed to identify the relative importance of these two processes for generating spatial variation in animal population dynamics at different spatial scales.

ACKNOWLEDGMENTS

We thank Mikael Vinka, Silvia Menci, Camille Garcera, Martin Hubert, and Birgith Unterthurner for assistance with field data collection. This study was funded by the Oscar and Lili Lamm Memorial Foundation (FO2018-0022), the Wildlife Management Fund (802-0199-18) by the Swedish Environmental Protection Agency, WWF Sweden, Fjällräven International AB, and EU Interreg Felles Nord II (20203530). We are grateful to two anonymous reviewers for improving the manuscript's quality.

CONFLICT OF INTEREST

The authors declare no conflict of interest.


DATA AVAILABILITY STATEMENT

Data (Vigues et al., 2022) are available from Figshare: <https://doi.org/10.6084/m9.figshare.19565737.v1>.

ORCID

Jan Vigués  <https://orcid.org/0000-0002-2468-3366>

Karin Norén  <https://orcid.org/0000-0002-9707-5206>

Caitlin Wilkinson  <https://orcid.org/0000-0002-2831-8235>

Marianne Stoessel  <https://orcid.org/0000-0001-6976-8139>

Anders Angerbjörn  <https://orcid.org/0000-0001-5535-9086>

Fredrik Dalerum  <https://orcid.org/0000-0001-9737-8242>

REFERENCES

Alexandersson, H. 2006. *Vindstatistik för Sverige 1961–2004*. Norrköping: Swedish Meteorological Institute.

- Andersson, M., and S. Erlinge. 1977. "Influence of Predation on Rodent Populations." *Oikos* 29: 591–7.
- Angerbjörn, A., M. Tannerfeldt, and H. Lundberg. 2001. "Geographical and Temporal Patterns of Lemming Population Dynamics in Fennoscandia." *Ecography* 24: 298–308.
- Bates, D., M. Mächler, B. M. Bolker, and S. C. Walker. 2015. "Fitting Linear Mixed-Effects Models Using lme4." *Journal of Statistical Software* 67: 1–48.
- Batzli, G. O., F. A. Pitelka, and G. N. Cameron. 1983. "Habitat Use by Lemmings near Barrow, Alaska." *Ecography* 6: 255–62.
- Bilodeau, F., G. Gauthier, and D. Berteaux. 2013. "Effect of Snow Cover on the Vulnerability of Lemmings to Mammalian Predators in the Canadian Arctic." *Journal of Mammalogy* 94: 813–9.
- Bivand, R. S., and D. W. S. Wong. 2018. "Comparing Implementations of Global and Local Indicators of Spatial Association." *TEST* 27: 716–48.
- Bjørnstad, O. N., R. A. Ims, and X. Lambin. 1999. "Spatial Population Dynamics: Analyzing Patterns and Processes of Population Synchrony." *Trends in Ecology & Evolution* 14: 427–32.
- Brown, J. S., and B. P. Kotler. 2004. "Hazardous Duty Pay and the Foraging Cost of Predation." *Ecology Letters* 7: 999–1014.
- Brown, J. S., J. W. Laundre, and M. Gurung. 1999. "The Ecology of Fear: Optimal Foraging, Game Theory, and Trophic Interactions." *Journal of Mammalogy* 80: 385–99.
- Buckland, S., D. Anderson, K. Burnham, J. Laake, D. Borchers, and L. Thomas. 2004. *Advanced Distance Sampling*. London: Oxford University Press.
- Buonaccorsi, J. P., J. S. Elkinton, S. R. Evans, and A. M. Liebhold. 2001. "Measuring and Testing for Spatial Synchrony." *Ecology* 82: 16689–1679.
- Carlsson, B. A., P. S. Karlsson, and B. M. Svensson. 1999. "Alpine and Subalpine Vegetation." *Acta Phytogeographica Suecica* 84: 75–90.
- Chitty, D. 1960. "Population Processes in the Vole and their Relevance to General Theory." *Canadian Journal of Zoology* 38: 99–113.
- Connor, T., V. Hull, A. Viña, A. Shortridge, Y. Tang, J. Zhang, F. Wang, and J. Liu. 2018. "Effects of Grain Size and Niche Breadth on Species Distribution Modeling." *Ecography* 41: 1270–82.
- Creel, S., and D. Christianson. 2008. "Relationships between Direct Predation and Risk Effects." *Trends in Ecology & Evolution* 23: 194–201.
- Dadic, R., R. Mott, M. Lehning, and P. Burlando. 2010. "Wind Influence on Snow Depth Distribution and Accumulation over Glaciers." *Journal of Geophysical Research* 115: 1–8.
- Dalerum, F., L. Dalén, C. Fröjd, N. Lecomte, Å. Lindgren, T. Meijer, P. Pecnerova, and A. Angerbjörn. 2017. "Spatial Variation in Arctic Hare (*Lepus arcticus*) Populations around the Hall Basin." *Polar Biology* 40: 2113–8.
- Denison, R. F., R. O. Miller, D. Bryant, A. Abshahi, and W. E. Wildman. 1996. "Image Processing Extracts More Information from Color Infrared Aerial Photos." *California Agriculture* 50: 9–13.
- Duchesne, D., G. Gauthier, and D. Berteaux. 2011a. "Habitat Selection, Reproduction and Predation of Wintering Lemmings in the Arctic." *Oecologia* 167: 967–80.
- Duchesne, D., G. Gauthier, and D. Berteaux. 2011b. "Evaluation of a Method to Determine the Breeding Activity of Lemmings in their Winter Nests." *Journal of Mammalogy* 92: 511–6.

- Ecke, F., and B. Hörnfeldt. 2021. *Miljöövervakning av smågnagare*. Umeå: Swedish University of Environmental Sciences. <http://www.slu.se/mo-smagnagare>.
- Ekerholm, P., L. Oksanen, T. Oksanen, and M. F. Schneider. 2004. "The Impact of Short-Term Predator Removal on Vole Dynamics in an Arctic-Alpine Landscape." *Oikos* 106: 457–68.
- Elmeros, M. 2006. "Food Habits of Stoats *Mustela erminea* and Weasels *Mustela nivalis* in Denmark." *Acta Theriologica* 51: 179–86.
- Elton, C. S. 1924. "Periodic Fluctuations in the Numbers of Animals: Their Causes and Effects." *British Journal of Experimental Biology* 2: 119–63.
- Elton, C. S., and M. Nicholson. 1942. "The Ten-Year Cycle in Numbers of the Lynx in Canada." *Journal of Animal Ecology* 11: 215.
- Engen, S. 2007. "Stochastic Growth and Extinction in a Spatial Geometric Brownian Population Model with Migration and Correlated Noise." *Mathematical Biosciences* 209: 240–55.
- Engen, S., R. Lande, and B. Sæther. 2002. "The Spatial Scale of Population Fluctuations and Quasi-Extinction Risk." *The American Naturalist* 160: 439–51.
- Erlandsson, R., M. Stoessel, H. Skånes, M. Wennbom, and A. Angerbjörn. 2019. "An Innovative Use of Orthophotos – Possibilities to Assess Plant Productivity from Colour Infrared Aerial Orthophotos." *Remote Sensing in Ecology and Conservation* 5: 291–301.
- Feige, N., D. Ehrich, I. Y. Popov, and S. Broekhuizen. 2012. "Monitoring Least Weasels after a Winter Peak of Lemmings in Taimyr: Body Condition, Diet and Habitat Use." *Arctic* 65: 273–82.
- Fuller, W. A., A. M. Martell, R. F. C. Smith, and S. W. Speller. 1975. "High-Arctic Lemmings, *Dicrostonyx groenlandicus*. II. Demography." *Canadian Journal of Zoology* 53: 867–78.
- Gaillard, J., M. Festa-Bianchet, N. G. Yoccoz, A. Loison, and C. Toïgo. 2000. "Temporal Variation in Fitness Components and Population Dynamics of Large Herbivores." *Annual Review of Ecology and Systematics* 31: 367–93.
- Gilg, O., I. Hanski, and B. Sittler. 2003. "Cyclic Dynamics in a Simple Vertebrate Predator-Prey Community." *Science* 302: 866–8.
- Gilg, O., B. Sittler, B. Sabard, A. Hurstel, R. Sané, P. Delattre, and I. Hanski. 2006. "Functional and Numerical Responses of Four Lemming Predators in High Arctic Greenland." *Oikos* 113: 193–216.
- GRASS Development Team. 2018. *Geographic Resources Analysis Support System (GRASS GIS) Software*. Beaverton, OR: Open Source Geospatial Foundation.
- Hansen, T. F., N. C. Stenseth, and H. Henttonen. 1999. "Multi-annual Vole Cycles and Population Regulation during Long Winters: An Analysis of Seasonal Density Dependence." *The American Naturalist* 154: 129–39.
- Hansen, B. B., V. Grotan, R. Aanes, B.-E. Saether, A. Stien, E. Fuglei, R. A. Ims, N. G. Yoccoz, and A. O. Pedersen. 2013. "Climate Events Synchronize the Dynamics of a Resident Vertebrate Community in the High Arctic." *Science* 339: 313–5.
- Hanski, I., L. Hansson, and H. Henttonen. 1991. "Specialist Predators, Generalist Predators, and the Microtine Rodent Cycle." *Journal of Animal Ecology* 60: 353–67.
- Hanski, I., H. Henttonen, E. Korpimäki, L. Oksanen, and P. Turchin. 2001. "Small-Rodent Dynamics and Predation." *Ecology* 82: 1505–20.
- Hansson, L., and H. Henttonen. 1998. "Rodent Fluctuations in Relation to Seasonality in Fennoscandia and Hokkaido." *Researches on Population Ecology* 40: 127–9.
- Hartig, F. 2022. "DHARMA: Residual Diagnostics for Hierarchical (Multi-Level/Mixed) Regression Models." R Package Version 0.4.5. <https://CRAN.R-project.org/package=DHARMA>.
- Heino, M., V. Kaitala, E. Ranta, and J. Lindström. 1997. "Synchronous Dynamics and Rates of Extinction in Spatially Structured Populations." *Proceedings of the Royal Society, Series B: Biological Sciences* 264: 481–6.
- Henden, J. A., R. A. Ims, and N. G. Yoccoz. 2009. "Nonstationary Spatio-Temporal Small Rodent Dynamics: Evidence from Long-Term Norwegian Fox Bounty Data." *Journal of Animal Ecology* 78: 636–45.
- Henttonen, H., and A. Kaikusalo. 1993. "Lemming Movements." In *The Biology of Lemmings*, edited by N. C. Stenseth and R. A. Ims, 157–86. London: Academic Press.
- Henttonen, A. H., A. Kaikusalo, J. Tast, and J. Viitala. 1977. "Competition between Small Rodents in Subarctic and Boreal Ecosystems." *Oikos* 29: 581–90.
- Holling, C. S. 1959a. "The Components of Predation as Revealed by a Study of Small-Mammal Predation of the European Pine Sawfly." *The Canadian Entomologist* 91: 293–320.
- Holling, C. S. 1959b. "Some Characteristics of Simple Types of Predation and Parasitism." *The Canadian Entomologist* 91: 385–98.
- Holmes, E. E., M. A. Lewis, J. E. Banks, and R. E. Veit. 1994. "Partial Differential Equations in Ecology: Spatial Interactions and Population Dynamics." *Ecology* 75: 17–29.
- Hörnfeldt, B. 2004. "Long-Term Decline in Numbers of Cyclic Voles in Boreal Sweden: Analysis and Presentation of Hypotheses." *Oikos* 107: 376–92.
- Hoset, K. S., K. Kyrö, T. Oksanen, L. Oksanen, and J. Olofsson. 2014. "Spatial Variation in Vegetation Damage Relative to Primary Productivity, Small Rodent Abundance and Predation." *Ecography* 37: 894–901.
- Hunter, M. D., and P. W. Price. 1992. "Playing Chutes and Ladders: Heterogeneity and the Relative Roles of Bottom-Up and Top-Down Forces in Natural Communities." *The American Naturalist* 73: 724–32.
- Ims, R. A., and H. P. Andreassen. 2000. "Spatial Synchronization of Vole Population Dynamics by Predatory Birds." *Nature* 408: 194–6.
- Ims, R. A., and E. Fuglei. 2005. "Trophic Interaction Cycles in Tundra Ecosystems and the Impact of Climate Change." *Bioscience* 55: 311–22.
- Ims, R. A., and H. Steen. 1990. "Geographical Synchrony in Microtine Population Cycles: A Theoretical Evaluation of the Role of Nomadic Avian Predators." *Oikos* 57: 381–7.
- Jarillo, J., B. E. Sæther, S. Engen, and F. J. Cao-García. 2020. "Spatial Scales of Population Synchrony in Predator-Prey Systems." *The American Naturalist* 195: 216–30.
- Kendall, B. E., O. N. Bjørnstad, J. Bascompte, T. H. Keitt, and W. F. Fagan. 2000. "Dispersal, Environmental Correlation, and Spatial Synchrony in Population Dynamics." *The American Naturalist* 155: 628–36.
- Koponen, T. 1970. "Age Structure in Sedentary and Migratory Populations of the Norwegian Lemming, *Lemmus lemmus* (L.), at Kilpisjärvi in 1960." *Annales Zoologici Fennici* 7: 141–87.

- Korpimäki, E., and C. J. Krebs. 1996. "Predation and Population Cycles of Small Mammals: A Reassessment of the Predation Hypothesis." *Bioscience* 46: 754–64.
- Korpimäki, E., K. Norrdahl, and T. Rinta-Jaskari. 1991. "Responses of Stoats and Least Weasels to Fluctuating Food Abundances: Is the Low Phase of the Vole Cycle Due to Mustelid Predation?" *Oecologia* 88: 552–61.
- Korpimäki, E., P. R. Brown, J. Jacob, and R. R. Pech. 2004. "The Puzzles of Population Cycles and Outbreaks of Small Mammals Solved?" *Bioscience* 54: 1071–9.
- Korslund, L., and H. Steen. 2006. "Small Rodent Winter Survival: Snow Conditions Limit Access to Food Resources." *Journal of Animal Ecology* 75: 156–66.
- Krebs, C. J. 2002. "Beyond Population Regulation and Limitation." *Wildlife Research* 29: 1–10.
- Krebs, C. J. 2011. "Of Lemmings and Snowshoe Hares: The Ecology of Northern Canada." *Proceedings of the Royal Society, Series B: Biological Sciences* 278: 481–9.
- Krebs, C. J., A. J. Kenney, S. Gilbert, K. Danell, A. Angerbjörn, S. Erlinge, R. G. Bromley, C. Shank, and S. Carriere. 2002. "Synchrony in Lemming and Vole Populations in the Canadian Arctic." *Canadian Journal of Zoology* 80: 1323–33.
- Krebs, C. J., F. Bilodeau, D. Reid, G. Gauthier, A. J. Kenney, S. Gilbert, D. Duchesne, and D. J. Wilson. 2012. "Are Lemming Winter Nest Counts a Good Index of Population Density?" *Journal of Mammalogy* 93: 87–92.
- Le Vaillant, M., R. Erlandsson, B. Elmhagen, B. Hörnfeldt, N. E. Eide, and A. Angerbjörn. 2018. "Spatial Distribution in Norwegian Lemming *Lemmus lemmus* in Relation to the Phase of the Cycle." *Polar Biology* 41: 1391–403.
- Lenth, R. V. 2021. "emmeans: Estimated Marginal Means, Aka Least-Squares Means." R Package Version 1.6.2-1. <https://CRAN.R-project.org/package=emmeans>.
- Liebhald, A., W. D. Koenig, and O. N. Bjørnstad. 2004. "Spatial Synchrony in Population Dynamics." *Annual Review of Ecology, Evolution, and Systematics* 35: 467–90.
- Lima, S. L. 1998. "Nonlethal Effects in the Ecology of Predator-Prey Interactions." *Bioscience* 48: 25–34.
- Lindén, H. 1996. "Wildlife Triangle Scheme in Finland: Methods and Aims for Monitoring Wildlife Populations." *Finnish Game Research* 49: 4–11.
- Maclean, S. F., B. M. Fitzgerald, and F. A. Pitelka. 1974. "Population Cycles in Arctic Lemmings." *Arctic and Alpine Research* 6: 1–12.
- Miller, D. L., E. Rexstad, L. Thomas, L. Marshall, and J. L. Laake. 2019. "Distance Sampling in R." *Journal of Statistical Software* 89: 1–28.
- Molofsky, J. 1994. "Population Dynamics and Pattern Formation in Theoretical Populations." *Ecology* 75: 30–9.
- Moran, P. A. P. 1953. "The Statistical Analysis of the Canadian Lynx Cycle. II. Synchronization and Meteorology." *Australian Journal of Zoology* 1: 291–8.
- Morris, D. W. 1988. "Habitat-Dependent Population Regulation and Community Structure." *Evolutionary Ecology* 2: 253–69.
- Moss, R., A. Watson, and J. Ollason. 1983. *Animal Population Dynamics*, First ed. London: Chapman and Hall.
- Oksanen, T. 1993. "Does Predation Prevent Norwegian Lemmings from Establishing Permanent Populations in Lowland Forests?" In *The Biology of Lemmings*, edited by N. C. Stenseth and R. A. Ims, 425–37. London: Academic Press.
- Oksanen, T., L. Oksanen, and M. Norberg. 1992. "Habitat Use of Small Mustelids in North Fennoscandian Tundra: A Test of the Hypothesis of Patchy Exploitation Ecosystems." *Ecography* 15: 237–44.
- Oksanen, T., L. Oksanen, J. Dahlgren, and J. Olofsson. 2008. "Arctic Lemmings, *Lemmus* spp. and *Dicrostonyx* spp.: Integrating Ecological and Evolutionary Perspectives." *Evolutionary Ecology Research* 10: 415–34.
- Penczykowski, R. M., B. M. Connolly, and B. T. Barton. 2017. "Winter Is Changing: Trophic Interactions under Altered Snow Regimes." *Food Webs* 13: 80–91.
- Pitelka, F. A., and G. O. Batzli. 2007. "Population Cycles of Lemmings near Barrow, Alaska: A Historical Review." *Acta Theriologica* 52: 323–36.
- Prevedello, J. A., C. R. Dickman, M. V. Vieira, and E. M. Vieira. 2013. "Population Responses of Small Mammals to Food Supply and Predators: A Global Meta-Analysis." *Journal of Animal Ecology* 82: 927–36.
- R Development Core Team. 2021. *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing. <https://www.r-project.org>.
- Ranta, E., V. Kaitala, and J. Lindström. 1997. "Dynamics of Canadian Lynx Populations in Space and Time." *Ecography* 5: 454–60.
- Ranta, E., V. Kaitala, and P. Lundberg. 1998. "Population Variability in Space and Time: The Dynamics of Synchronous Population Fluctuations." *Oikos* 83: 376–82.
- Reid, D. G., C. J. Krebs, and A. J. Kenney. 1997. "Patterns of Predation on Noncyclic Lemmings." *Ecological Monographs* 67: 89–108.
- Reid, D. G., F. Bilodeau, C. J. Krebs, G. Gauthier, A. J. Kenney, B. S. Gilbert, M. C. Y. Leung, D. Duchesne, and E. Hofer. 2012. "Lemming Winter Habitat Choice: A Snow-Fencing Experiment." *Oecologia* 168: 935–46.
- Rousset, F., and J. B. Ferdy. 2014. "Testing Environmental and Genetic Effects in the Presence of Spatial Autocorrelation." *Ecography* 37: 781–90.
- Ruckstuhl, K., E. Johnson, and K. Miyanishi. 2008. "Introduction. The Boreal Forest and Global Change." *Philosophical Transactions of the Royal Society, B: Biological Sciences* 363: 2243–7.
- Schmidt, N. M., F. M. van Beest, A. Dupuch, L. H. Hansen, J. P. Desforges, and D. W. Morris. 2021. "Long-Term Patterns in Winter Habitat Selection, Breeding and Predation in a Density-Fluctuating, High Arctic Lemming Population." *Oecologia* 195: 927–35.
- Selås, V. 2016. "Timing of Population Peaks of Norway Lemming in Relation to Atmospheric Pressure: A Hypothesis to Explain the Spatial Synchrony." *Scientific Reports* 6: 1–7.
- Sheppard, L. W., J. R. Bell, R. Harrington, and D. C. Reuman. 2015. "Changes in Large-Scale Climate Alter Spatial Synchrony of Aphid Pests." *Nature Climate Change* 6: 610–3.
- Sittler, B. 1995. "Response of Stoats (*Mustela erminea*) to a Fluctuating Lemming (*Dicrostonyx groenlandicus*) Population in North East Greenland: Preliminary Results from a Long Term Study." *Annales Zoologici Fennici* 32: 79–92.
- Soininen, E. M., L. Zinger, L. Gielly, N. G. Yoccoz, J.-A. Henden, and R. A. Ims. 2017. "Not Only Mosses: Lemming Winter Diets as Described by DNA Metabarcoding." *Polar Biology* 40: 2097–103.
- Solonen, T. 2006. "Overwinter Population Change of Small Mammals in Southern Finland." *Annales Zoologici Fennici* 43: 295–302.

- Stein, M. L. 1999. *Interpolation of Spatial Data: Some Theory for Kriging*. New York: Springer.
- Stenseth, N. C., K. Chan, H. Tong, R. Boonstra, S. Boutin, C. J. Krebs, E. Post, et al. 1999. "Common Dynamic Structure of Canada Lynx Populations within Three Climatic Regions." *Science* 285: 1071–3.
- Stoessel, M., B. Elmhagen, M. Vinka, P. Hellström, and A. Angerbjörn. 2019. "The Fluctuating World of a Tundra Predator Guild: Bottom-up Constraints Overrule Top-Down Species Interactions in Winter." *Ecography* 42: 488–99.
- Tucker, C. J. 1979. "Red and Photographic Infrared Linear Combinations for Monitoring Vegetation." *Remote Sensing of Environment* 8: 127–50.
- Turchin, P. D., L. Oksanen, P. Ekerholm, T. Oksanen, and H. Henttonen. 2000. "Are Lemmings Prey or Predators?" *Nature* 405: 562–5.
- Vigués, J., S. Menci, C. Wilkinson, M. Le Vaillant, A. Angerbjörn, and K. Norén. 2021. "A Beacon of Dung: Using Lemming (*Lemmus lemmus*) Winter Nests and DNA Analysis of Faeces to Further Understand Predator–Prey Dynamics in Northern Sweden." *Polar Biology* 44: 2269–76.
- Vigués, J., K. Norén, C. Wilkinsson, M. Stoessel, A. Angerbjörn, and F. Dalerum. 2022. "Data for Vigués Et Al. Abundance, Predation and Habitat Associations of Lemming Winter Nests in Northern Sweden." Figshare. Dataset. <https://doi.org/10.6084/m9.figshare.19565737>.
- Virtanen, R., J. Parviainen, and H. Henttonen. 2002. "Winter Grazing by the Norwegian Lemming (*Lemmus lemmus*) at Kilpisjärvi (NW Finnish Lapland) during a Moderate Population Peak." *Annales Zoologici Fennici* 39: 335–41.
- Walter, J. A., L. W. Sheppard, T. L. Anderson, J. H. Kastens, O. N. Bjørnstad, A. M. Liebhold, and D. C. Reuman. 2017. "The Geography of Spatial Synchrony." *Ecology Letters* 20: 801–14.
- Wirsing, A. J., M. R. Heithaus, J. S. Brown, B. P. Kotler, and O. J. Schmitz. 2021. "The Context Dependence of Non-consumptive Predator Effects." *Ecology Letters* 24: 113–29.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: Vigués, Jan, Karin Norén, Caitlin Wilkinson, Marianne Stoessel, Anders Angerbjörn, and Fredrik Dalerum. 2022. "Abundance, Predation, and Habitat Associations of Lemming Winter Nests in Northern Sweden." *Ecosphere* 13(6): e4140. <https://doi.org/10.1002/ecs2.4140>