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Research article

Norwegian lemmings, *Lemmus lemmus*: a case for a strong herbivore–plant interaction

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In his classical contributions, Olavi Kalela proposed that, due to the low primary productivity of the tundra, Norwegian lemmings are locked in a strong interaction with their winter forage plants. Proposedly, Norwegian lemmings respond to the threat of critical resource depletion by conducting long-range migrations at their population peaks. A tacit premise of this conjecture is that predation pressure on the Fennoscandian tundra is too weak to prevent runaway increases of lemming populations, creating violent boom–crash dynamics. Our results on the dynamics of Norwegian lemmings on the Finnmarksvidda tundra during 1977–2017 are in line with the predictions of Kalela's hypothesis. In contrast to the Siberian and North American tundra, densities of avian predators in our study area have been low even during lemming years, and efficient ones have been lacking from lemming habitats. Lemmings have thus increased unhinged in peak summers and crashed to densities below the trappability threshold during post-peak winters. Each lemming crash has been accompanied by massive habitat destruction. Indications of predator activity have been concentrated to productive shrublands, where lemmings have never reached high densities. Young lemmings have responded to high densities by becoming extremely mobile: they have been trapped in large numbers on islands, including a small island in the middle of Iešjávri, a 10 × 8 km tundra lake. Many lemmings have been seen swimming across the lake, and many drowned lemmings have been observed. The dynamics and behavior of Norwegian lemmings recorded by us differ radically from those of other *Lemmus* spp., indicating that cycles generated by lemming–vegetation interactions have two alternative states – one with and the other without intense summer predation. We propose that the cycles of Norwegian lemmings shifted to the latter state during their unique evolutionary history, when they survived the Last Glacial Maximum in a tiny refugium archipelago.

Keywords: Fennoscandian tundra, food limitation, herbivore–plant cycles, migration, Norwegian lemming, strong interactions

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Introduction

Mass occurrences of Norwegian lemmings *Lemmus lemmus* in the Fennoscandian tundra and their sudden appearances in areas far below the tree line have fascinated professional and lay people for centuries (Collett 1878, 1895, Ekman 1907, Kalela 1941, 1949, 1961, 1971, Henttonen and Kaikusalo 1993, Stenseth and Ims 1993, Supporting information, Appendix 1). We hope that our long-term study, to be summarized below, contributes to clarify the reasons for the exceptionally violent numerical oscillations of Norwegian lemmings and for their migrations.

A plausible reason for sudden mass occurrences of animals is limit cycle dynamics, generated by exploitive consumer–resource systems with a locally unstable equilibrium point (Gilpin and Rosenzweig 1972, Turchin 2003, Murdoch et al. 2003). Such systems are especially likely to emerge at high latitudes, where year-round active endotherms are usually dependent on a single functional group of resources during the long winters. Strong dependence on a single resource creates destabilizing type II functional responses (Hanski et al. 1991, 2001), removes stabilizing trade-offs (Vuorinen et al. 2021), and generates destabilizing evolutionary drive towards maximal efficiency to exploit these limiting resources (Oksanen et al. 2023).

The arguments summarized above apply to both predator–herbivore and herbivore–plant interactions. According to the exploitation ecosystems hypothesis (EEH, Oksanen et al. 1981, 2020), the strong interaction shifts from the predator-herbivore interface to the herbivore–plant interface along gradients of decreasing primary productivity. Productive boreal and low arctic ecosystems are thus predicted to be characterized by predation-driven vole cycles (Hanski et al. 2001, Korpimäki et al. 2004). Conversely, the lemming cycles of tundra ecosystems with low primary productivity are predicted to be driven by lemming-plant interactions (Turchin et al. 2000).

Based on field experience, Kalela (1949) proposed an idea foreshadowing EEH and providing inspiration for its development: that the dominating herbivores of unproductive tundra ecosystems – reindeer and lemmings – are limited by their winter resources. Moreover, as lemming populations can increase rapidly in summer, they were proposed to periodically overshoot carrying capacity, resulting in depletion of winter forage and, consequently, in precipitous crashes (Oksanen 1990, Turchin and Batzli 2001). Inferred from field observations and questionnaire returns, Kalela (1941, 1949, Supporting information, Appendix1, Fig. S1–S2) concluded that lemmings respond to this threat by conducting long-range migrations. Proposedly, this provides a dual advantage for lucky migrants: to avoid mass starvation and to have a chance to recolonize a piece of tundra where lemmings had gone extinct. Kalela (1949) thus implied that, in addition to providing individual fitness rewards, long-range migrations help Norwegian lemmings to persist as a metapopulation (Levins 1969, Hanski and Gilpin 1997).

Kalela (1961, 1971) realized that the advantages of the migratory strategy depend on the decisions of other lemmings. He solved this game theoretical problem by proposing that subadult males and females and old males migrate, whereas others stay. In modern terms (Maynard Smith 1979), Kalela (1961, 1971) thus implied that Norwegian lemmings meet their challenges by having an age and sex-dependent, mixed ESS.

Alternative states of tundra food webs

A shared premise of Kalela's (1949) reasoning and EEH is that the food webs of the tundra are not significantly impacted by external energy fluxes, as such energy subsidies could result in predation-driven dynamics even in areas with low primary productivity (Oksanen et al. 1992a). Evidence for large energy imports from marine ecosystems and from the temperate zone (migrating geese) have been obtained from the Canadian high Arctic (Gauthier et al. 2011, Legagneux et al. 2012, Bilodeau et al. 2014, Fauteux et al. 2016), where tundra with continuous vegetation is often restricted to small coastal pockets (Walker et al. 2005). Such geography amplifies the impacts of external energy fluxes.

In the vast Siberian–Alaskan tundra, the oscillation patterns of lemmings and the observed, strong impacts of lemmings on the vegetation indicate that the strong interaction is between lemmings and plants (Tihomirov 1959, Batzli 1975, Kirjuŝenko 1979, Batzli et al. 1980, Virtanen et al. 2006, Oksanen et al. 2008, Johnson et al. 2011, Lara et al. 2017, Zhang et al. 2023), but lemming peaks are nevertheless exploited by dense breeding populations of efficient avian predators. This predator guild is usually dominated by Pomarine jaegers *Stercorarius pomarinus* and snowy owls *Bubo scandiacus* (Batzli et al. 1980, Černjavskij and Tkačev 1982, Wiklund et al. 1999, Černjavskij 2002, Pitelka and Batzli 2007).

Pomarine jaegers coevolved with *Lemmus* spp. (Ruffino and Oksanen 2014) and are long-lived. Outside the breeding season, they live as pelagic cleptoparasites, which allows them to persist in large numbers. Snowy owls are extremely mobile and can therefore exploit regional asynchronies in lemming dynamics (Potapov and Sale 2013). Both species exploit Siberian and brown lemmings as breeding resources within their entire ranges, from Pomor tundra, NW Russia, to Baffin Island, Canada. In Fennoscandia, however, Pomarine jaegers have only few breeding records (Øien 2011, Helberg 2022), and only 52 breeding pairs of snowy owls were recorded in Norway, Sweden and Finland during the 2011 lemming peak (Jacobsen 2011).

To resolve the enigma outlined above, Oksanen et al. (2013) simulated lemming–plant cycles by adding different levels of summer predation to the Barrow model of Turchin and Batzli (2001) and by varying the abundances of graminoids. If breeding avian predators were assumed to be present in sufficient numbers, lemmings had regular cycles, with peaks occurring in spring, which is critical for avian predators.

If, however, predation pressure in summer was too low, the system collapsed to a lemming–plant chaos, characterized by sharp autumnal lemming peaks and long periods of low lemming densities. The oscillations were especially irregular, and the low periods were especially deep and long if the abundance of graminoids was assumed to be low, as typical for the Fennoscandian tundra (Oksanen and Virtanen 1995).

The results of Oksanen et al. (2013) thus imply that arctic small mammal-based food webs, where lemming cycles are driven by exploitive lemming–plant interactions, have two alternative states (Scheffer 2010): one with regular 4–5 years cycles, where lemming peaks are heavily exploited by avian predators – to be referred to as Barrow dynamics – and another, with extremely violent lemming-vegetation oscillations – to be referred to as Kilpisjärvi dynamics. If the system shifts to this state, predators will be permanently excluded (Abrams and Roth 1994). (The names were chosen to honor the classical studies performed in these areas.)

Recent discoveries by molecular biologists and geologists indicate that the Fennoscandian tundra shifted from Barrow to Kilpisjärvi dynamics during the Last Glacial Maximum (LGM). As ancestral Norwegian lemmings had already diverged from other *Lemmus* spp. during the Ålesund–Norrbotten Interstadial, they must have survived LGM within or near Fennoscandia (Lagerholm et al. 2014; see also Ekman 1920, Fedorov and Stenseth 2001). According to Spitsyn et al. (2021), the recently discovered Norwegian lemmings of Novaja Zemlja (*L. l. chernovi*) survived LGM within the continuous circumpolar tundra east of Fennoscandia and retained the dull pelage and the docile behavior, typical for *Lemmus* spp. The nominate subspecies, in turn, survived LGM in a western refugium, where it obtained its bright coloration and its characteristic, aggressive antipredator behavior (Spitsyn et al. 2021).

During LGM, the western refugium only consisted of the tip of Andøya (Vesterålen, Norway) and of nunataks on adjacent mountains (Nesje et al. 2007, Alsos et al. 2020). The abundance of *Papaver* pollen (Alsos et al. 2020) provides evidence of harsh polar desert conditions in this refugium. It could therefore only have supported small numbers of lemmings – too few and too far away to attract either Pomarine jaegers or snowy owls. Their absence triggered a shift from Barrow to Kilpisjärvi dynamics.

The refugium harbored bird cliffs (Alsos et al. 2020) and, therefore, also opportunistic predators of lemmings. In the absence of efficient predators, natural selection favored an aggressive antipredator strategy against these opportunists, and triggered the evolution of conspicuous pelage patterns, announcing the will and the ability of Norwegian lemmings to fight back (Andersson 1976a, b, 2015, Supporting information, Appendix 2, Fig. S29, S31,S32). Moreover, the ice-free areas were small and the little forage they provided could be easily depleted by lemmings. As the distances between ice-free areas were only moderate and they formed readily visible dark spots in the white landscape, natural selection favored a tendency to leave crowded habitat islands, triggering the evolution of migratory behavior.

The study system

Our studies on lemming and vole dynamics on the tundra were conducted during 1977–2017 around Iešjávri, a 10 × 8 km tundra lake on Finnmarksvidda, northernmost Norway (69°40'N, 24°10'E, at altitudes from 380 to 672 m a.s.l. (Fig. 1, Supporting information). Except for outposts of mountain birch forest on south-facing slopes, the landscape is treeless tundra. The climate of Finnmarksvidda is arctic continental. Annual precipitation is only 345 mm. Temperatures drop below −40°C in clear and calm winter periods (Tenow and Nilssen 1990, Virtanen et al. 2016). During 2010–2013, we also included a coastal reference area with a milder and more moist climate.

The landscape around Iešjávri consists of three habitat complexes with pronounced differences in primary productivity (Aunapuu et al. 2008). About ten kilometers around the lake, there is an arch of flat highlands underlain by

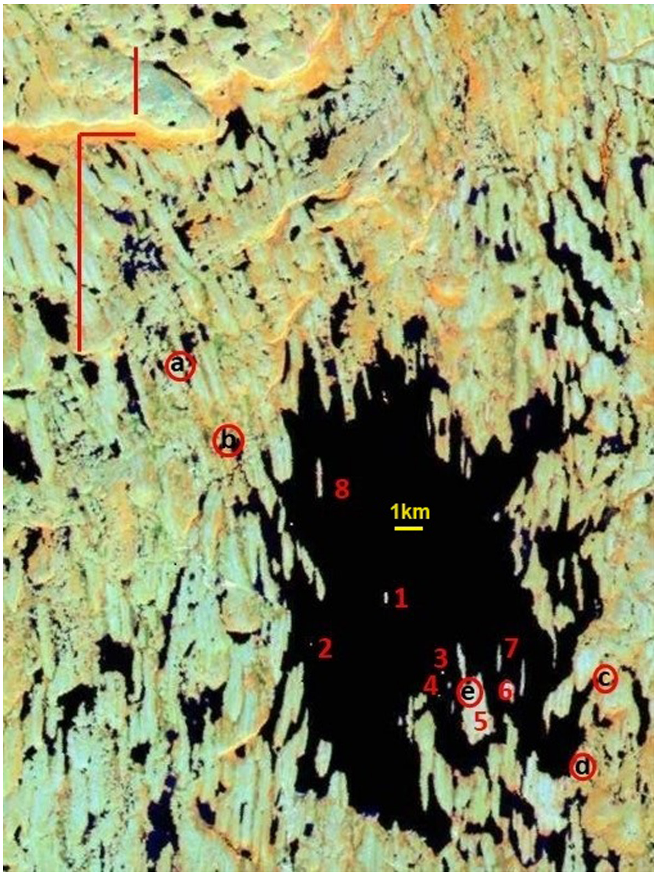

Figure 1. NDVI-based satellite image of the Iešjávri basin. Blue-turquoise: windbarrens, heaths and heath snowbeds. Pale yellow: bogs and meadow snowbeds. Orange: productive shrublands and birch forest outpost. 1 = Guovdosuolu, 2 = Doktacoagan, 3 = Doktasuolu, 4 = Luobmansuolu, 5 = Galbasuolu, 6–8 additional big islands, where trapping was conducted in 2007. Locations of the reference grids are denoted by lower case letters 'a' to 'e', surrounded by red circles. The red lines refer to the lines along which the snap trapping grids were sampled. Copyright Bernt Johansen, NINA, Tromsø.

nutrient-poor rocks, occupied by habitats with low primary productivity (Fig. 1, Supporting information, Appendix 2 Fig. S1–S4. On the slopes of these highlands, nutrient-rich shales are exposed, and microclimate is warm. Hence, these slopes are occupied by productive shrublands (Fig. 1, Supporting information, Appendix 2, Fig. S11–S17). The lowlands around Iešjávri are underlain by nutrient-poor bedrock and dominated by dry, unproductive lichen-dwarf birch heaths and bogs. (Fig. 1, Aunapuu et al. 2008, Supporting information, Appendix 2, Fig. S18–S21). In this landscape, we can thus distinguish the impacts of primary productivity from the impacts of altitude per se.

The Iešjávri basin is characterized by eskers that jut into Iešjávri as peninsulas and rise here and there as islands (Fig. 1, Supporting information, Appendix 2, Table S1, Fig. S17, S20, S22–S27). The big inner islands (5–8 in Fig 1) rise well above the lake surface and are isolated by straits no wider than the lakes that lemmings routinely cross (Supporting information, Appendix 2, Fig. S25). The outer islands are small and low (Supporting information, Appendix 2, Table S1, Fig. S19, S22–S24, S26–S27) and can only be detected at close range. Presence of lemmings on these islands indicates that the lemmings have been crossing the main body of Iešjávri, where landmarks on the other side are barely visible from the vantage point of a lemming.

The nearest marine island that a migrating lemming might reach (Sievju/Seiland, size 584 km^2) is 70 kilometers away and only 2.5 kilometers off the coast.

Material and methods

During 1977–2017, we monitored densities of small rodents in each of the three habitat complexes defined above, semi-annually, using the small quadrat method (SQM, Myllymäki et al. 1971). Spring trapping was conducted right after the snowmelt in June; fall trapping in mid-September, except for 1977, when trapping was only conducted in late July. During each trapping session, each habitat type was represented by at least five SQs (Oksanen and Oksanen 1981, Ekerholm et al. 2001, Supporting information, Appendix 3.1, Fig. S33–S34).

Activities of stoats *Mustela erminea* and weasels *M. nivalis* were studied by snow-tracking in November–December in the core study area of 16.8 km^2 (Oksanen et al. 1992b, Hoset et al. 2014, 2017, Supporting information, Appendix 3.2, Fig. S35), and by counting intact and predated winter nests in spring (Supporting information, Appendix 3.2, Fig. S36). Avian predators were studied by locating breeding pairs within the extended study area – 8 km^2 in 1978, 70 km^2 in 1988, 106 km^2 since 1993 (Oksanen and Oksanen 1981, Oksanen et al. 1997, Hoset et al. 2014, 2017, Ruffino et al. 2016, Supporting information, Appendix 3.3, Fig. S38) and by studying their breeding success.

Rodent impacts on the vegetation were quantified by assessing foraging damages in springs following rodent peaks and by exclosure experiments (Oksanen and Oksanen 1981, Moen et al. 1993, Moen and Oksanen 1998, Olofsson et al. 2014, Hoset et al. 2014, 2017, Ruffino et al. 2016, Supporting information, Appendix 3.4, Fig. S39–S42).

Evidence for lemming migrations was obtained from a long-term (1991–2011) island experiment on vole–vegetation interactions. We live-trapped rodents on four small, isolated islands (Guovdosuolu, Doktasuolu, Luobmansuolu and Doktacoagan; Fig. 1, Supporting information), which were entirely covered by trapping grids, and on five reference grids of 100 × 50 meters on the mainland and on the large, near-shore island Galbasuolu (Fig. 1). Trapping was conducted right after the spring break-up in early July, and in August–September (Hambäck et al. 2004, Dahlgren et al. 2007, 2009, Tuomi et al. 2019). During the 2007 lemming peak, we had additional refence grids on three other large islands. Except for the heath-dominated Guovdosuolu (Supporting information, Appendix 2, Table S1,Fig. S23–S27), all grids were in hummock bogs (Supporting information, Appendix 2, Fig. S1) i.e. in the best vole and lemming habitat of the lowland. Lemming densities were estimated as minimum number known alive (MNKA), converted to numbers per ha. We excluded windbarrens from the area of Guovdosuolu, as neither voles nor lemmings were trapped there.

We defined lemmings weighing less than 30 g as juveniles, lemmings weighing between 30 and 45 g as subadults, and lemmings weighing above 45 g as old adults. 'Subadults' corresponded to post-juvenal and early pre-adult stages of Koponen (1970), i.e. to the age group that is, proposedly, prone to migrate (Kalela 1971).

Kalela's (1949) idea of empty islands that could be colonized by lemmings was tested by ski-hiking on Sievju/Seiland, a marine island, during the snowmelt period in 2011.

All statistical analyses were done with SPSS.

Results

Overview of lemming dynamics

During our study period, lemmings had four peaks in the highlands: in the years 1978, 1988, 2007 and 2011 (Fig. 2a). They all repeated the same pattern. During peak year springs, lemming densities were low (1978, 2007) or moderate (1988, 2011). During peak summers lemming populations increased rapidly. The autumnal peaks thus generated were followed by winter crashes to densities below the trappability threshold (Fig. 2a, Supporting information, Appendix 4, Fig. S44). In three post-peak years, (1979, 2008, and 2012), no lemmings were trapped in fall, either, although one lemming was sighted in summer 2008 (Supporting information, Appendix 2, Fig. S29). The 2011 peak was followed by three lemming-free years. During 1990–2006, lemmings oscillated irregularly at low levels (Supporting information, Appendix 4, Fig S44). In this phase, lemmings preferred wetlands and meadow snowbeds on highlands throughout the year (Supporting information, Appendix 4, Table S8).

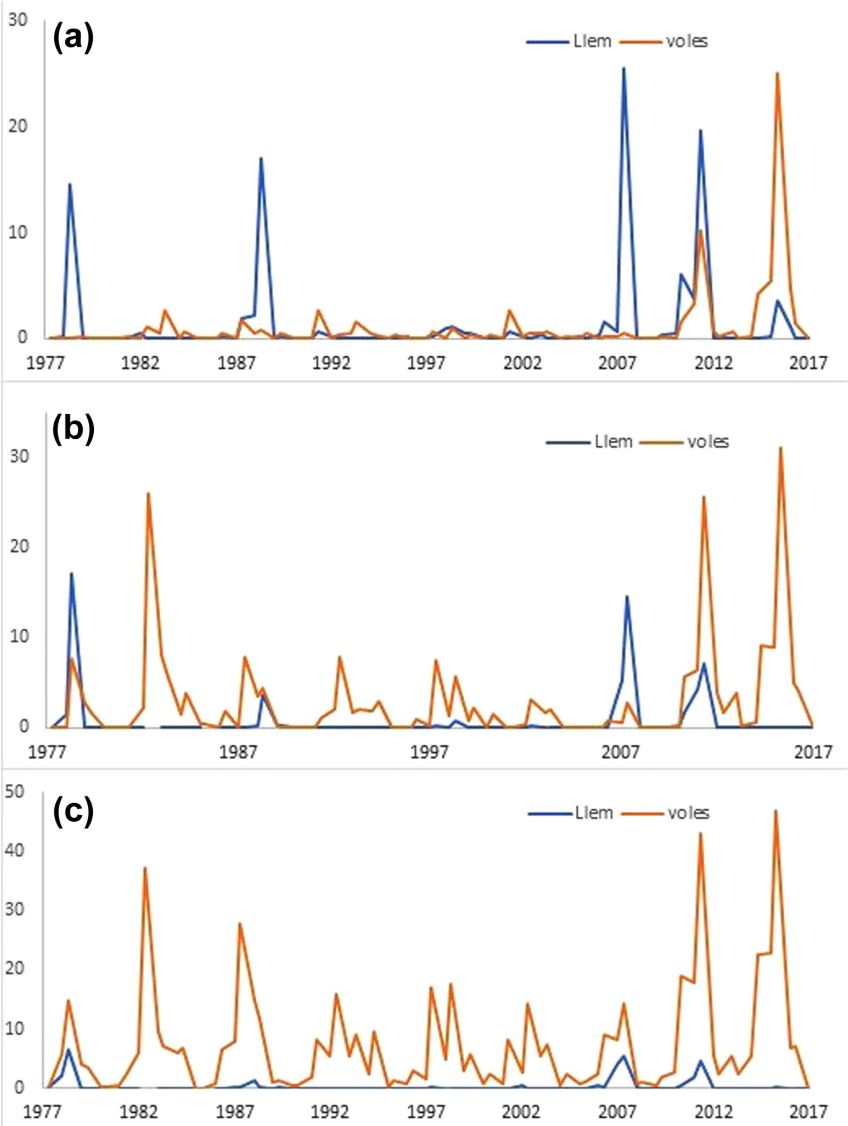

Figure 2. Density indices of Norwegian lemmings (*Lemmus lemmus*) and voles (mainly gray-sided voles, *Myodes rufocanus*) in the three different habitat complexes of the study area during 1977–2017. (a) highlands above the willow shrubland limit; (b) heaths and bogs of the lowland tundra; (c) productive shrublands. The values are weighted averages of habitat-specific indices (captures per 100 trap nights), with abundances of habitat types as weighting factors. To make the contrasting patterns easy to see, the figure has been adjusted so that peaks look equally high in all three habitat complexes.

In the unproductive Iešjávri lowlands, lemming dynamics followed the highland pattern except that the 1988 peak was low (Fig. 2b).

The productive shrublands were characterized by regular 5-year vole cycles, where peaks included an extended high-density phase and where declines were gradual, lasting usually for two subsequent years (Fig. 2c). Lemmings never obtained high densities in these habitats.

Lemming and vole dynamics were not always synchronous. In winter 1978–1979, lemmings crashed, whereas voles, by contrast, obtained their highest spring densities in 1979. In summer 1988, voles declined in productive shrublands, whereas lemming densities rose rapidly in highlands (Fig. 2).

During 1977–2010, the highland rodent community consisted almost exclusively of lemmings. During the 2011 peak, gray-sided voles were also numerous (Fig. 2a). During 2014–2017, highlands had a typical vole cycle. Lemmings there were then present in low numbers only.

During 2011–2013, lemming dynamics were similar in the inland and at the coast (Supporting information, Appendix 4, Fig. S45). On Sievju, neither lemmings nor their tracks were seen during the 2011 snowmelt.

In highlands and lowlands, long-tailed jaegers were the only even moderately common avian predators. In lemming years, densities of their successfully breeding pairs ranged from zero (in 2007) to 0.54 per km^2 (in 2011) in highlands and from

0.33 to 0.72 per km^2 in lowlands (Supporting information, Appendix 4, Table S2). In the coastal study area, jaegers were subsidized by marine-based resources, (Supporting information, Appendix 4, Fig. S46) but their densities were nevertheless on the same level as in the inland tundra (Supporting information, Appendix 4. Table S2). Rough-legged buzzards *Buteo lagopus* were only abundant on the productive slope, and declined even there during the 1990–2005 period of low vole peaks (Supporting information, Appendix 4, Table S2, Appendix 3, Fig. S38, see also Terraube et al. 2015).

During the lemming crash of 1978–1979, we did not find tracks of weasels or stoats in our study area during the first snow. None of the hundred winter nests inspected in spring 1979 had signs of predation, and the tundra was littered with dead, intact lemmings (Fig. 3b, Supporting information, Appendix 4, Table S3). During the lemming crash winters of 1988–1989, 2007–2008 and 2011–2012, activity of weasels and stoats was concentrated on productive shrublands (Fig. 3c, d, Supporting information, Appendix 4, Fig. S43). There was an order-of-magnitude difference in the percentage of predator-visited winter nests and in the percentages of predator impacted lemming bodies discovered at the snowmelt between the highland and the productive slope (Fig. 3b, Supporting information, Appendix 4, Table S3, S4).

In fall 2016, weasel tracks were observed in highlands, too, and two weasels were trapped there.

Except for productive shrublands, each lemming crash was accompanied by profound impacts on the vegetation (Fig. 4–6, Supporting information, App endix 4, Table S5,Fig. S47–S51), especially on preferred forage plants of lemmings or gray-sided voles: graminoids, bilberry twigs and small mosses (Fig. 6, Supporting information, Appendix 4, Table S5,Fig. S47–S51). Evergreen dwarf shrubs were strongly impacted, too, though they are inedible for lemmings (Kalela 1961, 1971, Soininen et al. 2017) and shunned by gray-sided voles (Kalela 1957). Conversely, hepatics and pioneer lichens were immediately favored by the action of lemmings and voles (Fig. 6).

The contrast between the short-term exclosures harvested in 2012 and the 10 years exclosures harvested in 2008 (Fig. 6)

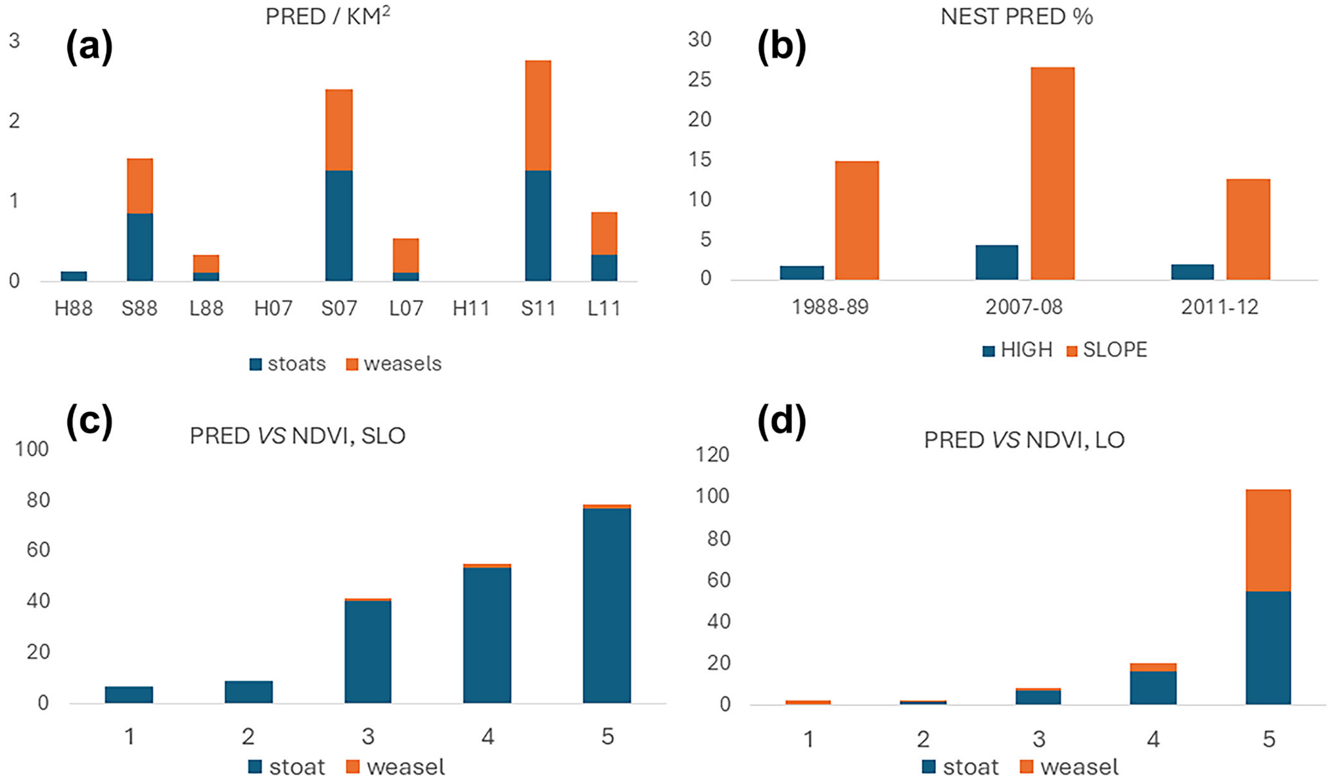

Figure 3. Indices of predator activity for the winters of 1988–1989, 2007–2008 and 2011–2012, related to subarea and NDVI, reflecting primary productivity. (a) Numbers of stoats and weasels per km^2 during the December tracking periods in 1988, 2007 and 2011 in highland (H), productive slope (S) and lowland (L). (b) Percentages of lemming winter nests with signs of predation in highland and on the slope. Lowland was excluded as most winter nests were there dug in peat hummocks. For statistics see the Supporting information and Table 5. Percentages of 10 × 10 m pixels that were visited by stoats or weasels on the slope (c) and in the lowland (d) during the tracking period of December 2011 for each of the five NDVI classes, representing different levels of primary productivity. Their abundances were as follows: Slope 1: 1.1%, 2: 2.5%, 3: 18.5%, 4: 25.5%, 5: 52.4%; Lowland: 1: 21.8%, 2: 34.7%, 3: 38.2%, 4: 4.9%, 5: 0.4%. The NDVI classes correspond to following habitat types: 1 = windbarrens; 2 = heaths and open bogs (mainly); 3 = bilberry dwarf birch shrub, parts of heaths and open bogs; 4 = forb-rich dwarf birch shrubland, willow mire, hummock bog; 5 = forb-rich willow shrublands and alluvial habitats (for statstics, see Supporting information, Appendix 4, Table S3 and S4)). Notice that on the slope, where productive habitats abound, predation 'spills over' to less productive habitats, too (Oksanen et al. 1992a, b).

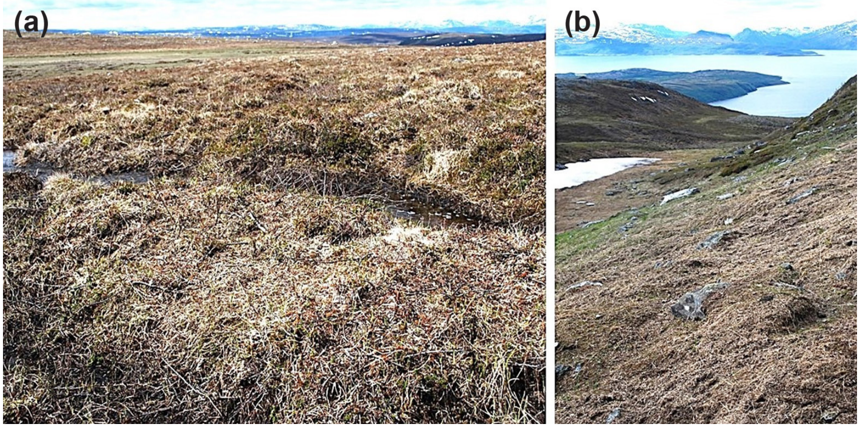

Figure 4. The tundra in June after a lemming year. (a) inland (hummock bog on highland) (b) coast (meadow snowbed). For close-ups taken in the same season see the Supporting information, Appendix 3, Fig. S39.

reveals that while the immediate impact of lemmings on small mosses is negative, their long-term impact can be positive.

Lemming movements at Iešjávri

In late August– early September 1978, we observed lemmings on all islands of Iešjávri that we then visited (islands 1, 3, 5, 6, and 7 in Fig. 1). During 1991–2006, lemmings were neither seen nor trapped on any island or in mainland reference grids.

In May 2007, moving lemmings were again seen all around the mainland tundra. In early July 2007, lemmings were trapped on all mainland grids and on all big islands. Six lemmings were trapped on the small outer islands. One of them, a mature but unmated female, was trapped on the maximally isolated Guovdosuolu (Supporting information, Appendix 4, Table S6). After the snowmelt, lemming movements rapidly subsided, as reported by Kalela (1961, 1971, Aho and Kalela 1966).

Moving lemmings were seen again in early August, many in tips of peninsulas or swimming or drowned (Supporting information, Appendix 2, Fig. S30–S31, Appendix 4, Box 1). In fall 2007, we trapped 26 lemmings on mainland reference grids and 88 on big islands (Supporting information, Appendix 4, Table S6). The mean lemming density on big islands was three times as high as in mainland reference grids. The difference was statistically significant ($t=3.948$, $p=0.008$, $df=6$). Lemming densities were still higher in the small islands, where we trapped 73 lemmings – mainly subadults (Supporting information, Appendix 4, Table S6,Fig. S52–S53); they were all unmarked. 63 lemmings were trapped on the barren and maximally isolated Guovdosuolu (Supporting information, Appendix 2, Table S1,S6, Fig. S19, S20,S52) and 7 on the tiny, isolated Doktacoagan (Supporting information, Table S1, S6, S52, Appendix 2, Fig. S24, S27). For locations of these islands see Fig. 1 and the Supporting information, Appendix 2, Fig. S22.

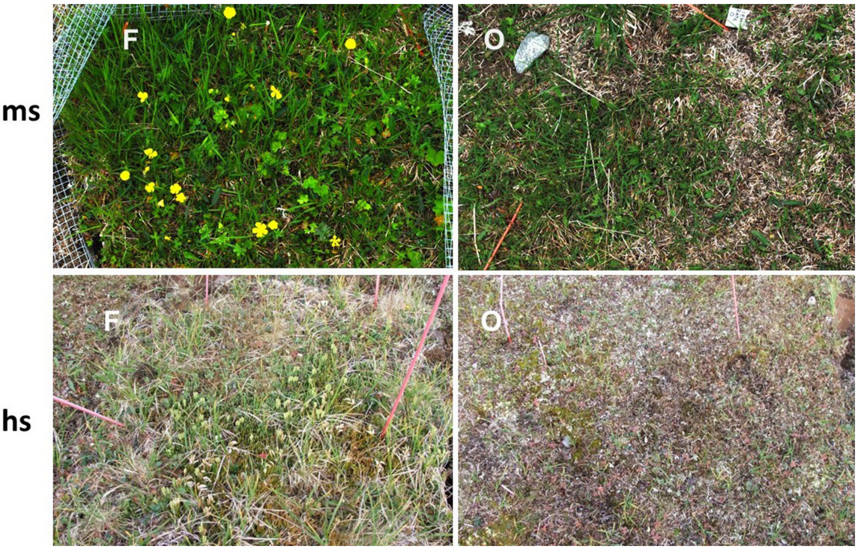

Figure 5. Pairs of fenced (F) and open (O) snowbed plots in July after a lemming year. ms = meadow snowbed (coast, 2012); hs = heath snowbed (inland, 2008).

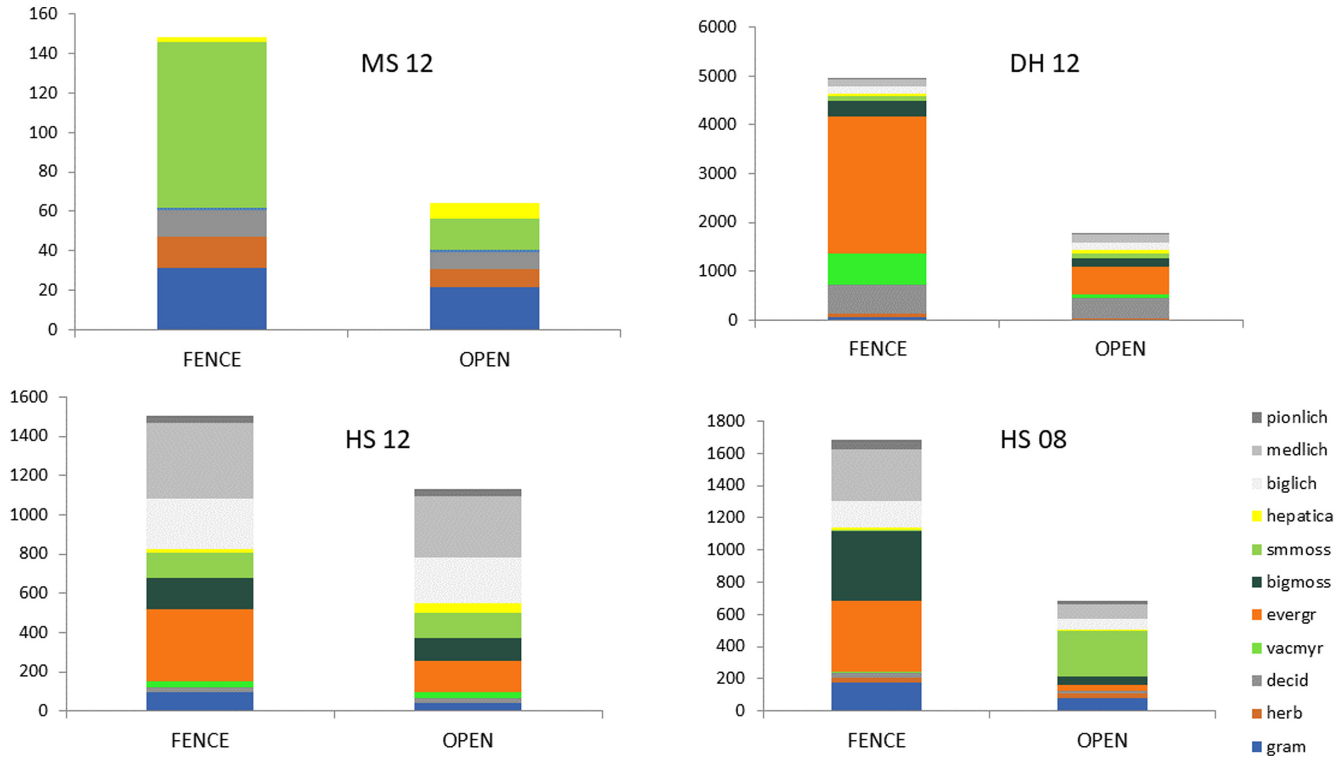

Figure 6. Biomasses of different functional plant groups in open plots and exclosures in August after a lemming year. HS = heath snowbed, MS = meadow snowbed, DH = lichen-dwarf birch heath. The numbers refer to the year of harvesting. The 2012 plots were short-term experiments; 2008 plots had stood for a decade. gram = graminoids, herb = herbs, decid = deciduous dwarf shrubs, vaccmyr = bilberry, bigmoss = big, layering mosses and *Polytrichum* spp., smmoss =other mosses, mainly *Dicranum* spp. and *Kiaeria* spp., hepatica = hepatics, biglich = *Cladina* spp., medlich = other fruticose lichens and big foliose lichens, pionlich = crustose lichens and *Solorina crocea.* The difference between fenced and open plots was statistically significant for community level biomass, graminoids, bilberry (2012 only), deciduous dwarf shrubs (2008 only), evergreens, small mosses (notice that the short- and long-term impacts were to opposite directions), and small and medium lichens (2008 only). Tentatively significant (0.1 > p > 0.05) differences were obtained for hepatics and pioneer lichens. For statistics, see the Supporting information, Appendix 4, Table S5 Table 3 in Olofsson et al. (2014).

During 2008 and 2009, no lemmings were caught on the islands of Iešjávri or in mainland reference grids. In fall 2010, 23 lemmings were trapped on mainland grids but none on islands. In 2011, the pattern of 2007 was repeated. During the snowmelt, numerous lemmings were observed moving on the mainland. By early July 2011, Galbasuolu, Guovdosuolu, Doktasuolu and Luobmansuolu had been colonized by lemmings (Supporting information, Appendix 4, Table S7). In early August, lemmings started to move again and, again, many were seen swimming across the lake. Again, large numbers of drowned lemmings were observed (Supporting information, Appendix 4, Box 1). In August–September, lemming density on Galbasuolu was again three times as high as on mainland reference grids. 38 lemmings were captured on small islands. Again, most of them were subadults and most of them were trapped on Guovdosuolu (Supporting information, Appendix 4, Table S7).

Pooling autumnal data from 2007 and 2011, we get the following age distributions – mainland: 16 juveniles, 14 subadults, and 6 old adults; big islands: 17 juveniles, 70 subadults, and 35 old adults; small islands: 16 juveniles, 76 subadults, and 19 old adults. The difference in age distributions is statistically significant ($\chi^2 = 23.620$, $p < 0.001$). The difference between small and big islands is not ($\chi^2 = 4.334$, $p = 0.114$, for details see the Supporting information, Appendix 4. Fig. S53).

Discussion

Our results are consistent with Kalela's (1949) hypothesis that, in Fennoscandian tundra habitats with low primary productivity, the numerical oscillations of Norwegian lemmings are driven the lemming–plant interaction. In concordance with simulated Kilpisjärvi dynamics, lemming peaks have only been exploited by sparse populations of long-tailed jaegers (Supporting information, Appendix 4, Table S2; also see Andersson 1976a, b, 2015, Vader 1994). The pattern of rapid population growth of Norwegian lemmings in peak summers appears to be typical for the entire Fennoscandian tundra (Turchin et al. 2000, Kausrud et al. 2008, Ims et al. 2011, Olofsson et al. 2012, Ruffino et al. 2016). The autumnal lemming peaks thus generated are followed by steep and deep winter crashes (Fig. 2a, Turchin et al. 2000, Kausrud et al. 2008, Ims et al. 2011, Olofsson et al. 2012, Ruffino et al. 2016, Soininen et al. 2025), accompanied by profound devastation of perennially available plants (Fig. 4–6, Supporting information, Appendix 3.4, Fig. S39, Appendix 4 Fig. S47–S51; Kalela 1971, Kalela and Koponen 1971, Virtanen 2000, Virtanen et al. 2002, Ravolainen et al. 2011, 2014, Olofsson et al. 2012), indicating that these crashes of Norwegian lemmings in tundra landscapes with low primary productivity were caused by acute depletion of winter forage (Supporting information, Appendix 3.2, Fig. S37).

The consequences of strong lemming–plant interactions on the vegetation do not only depend on forage preferences. Evergreen dwarf shrubs were profoundly impacted though they are not preferred by either lemmings or gray-sided voles (Kalela 1957, 1961). However, small mammals seem to broaden their diets under the harsh winter conditions of the tundra (Dahlgren et al. 2009, Soininen et al. 2017). Moreover, winter grazing lemmings bulldoze the vegetation and mow everything on their way (Fig. 4, 5, Supporting information, Appendix 3.4, Fig. S39, Appendix 4, Fig. S51). Gray-sided voles, too, inflict mechanical damage on woody plants in winter (Dahlgren et al 2009). As evergreens have most of their resources in above-ground shoots, they suffer most from such indiscriminate actions.

The net impacts of lemmings and voles on plants depended on time scale. Only hepatics and pioneer lichens gained immediately from grazing (Fig. 6). The immediate impact of lemmings on small mosses was negative, but in a long perspective, small mosses succumbed in the absence of lemmings, due to competition with taller plants (Fig. 6). In the exclosures of Saccone et al. (2014), graminoids first gained from the exclusion of lemmings, but after twenty years, graminoids were decimated as robust mosses or dwarf shrubs increased. The exclusion of these keystone animals thus imposes radical changes in vegetation processes: the intensity of plant–plant competition increases (Olofsson et al. 2002), and chances of seedling establishment decline, which gradually but profoundly changes the vegetation. Due to their keystone role, the survival of Norwegian lemmings is crucial for the floristic diversity of the snowbeds of the Fennoscandian tundra, as they are dominated by small, sexually reproducing vascular plants and by small, competition-shy bryophytes (Söyrinki 1938, 1939, Gjærevoll 1956, Oksanen and Virtanen 1997).

The dynamics of Norwegian lemmings in unproductive tundra areas thus differ clearly from the dynamics of voles in boreal landscapes and in productive low arctic shrublands, where cycles are characterized by extended peak phases, long enough to allow predator populations to build up, and each peak is followed by a gradual decline (Fig. 2c; Krebs and Myers 1974, Hanski et al. 1991, 2001, Krebs 1996, 2013). Moreover, the dynamics Norwegian lemmings also differ from the dynamics of other *Lemmus* species, as their populations usually increase in winter and decline in summer, due to intense avian predation (Batzli et al. 1980, Černjavskij 2002, Pitelka and Batzli 2007, Gauthier et al. 2024). The observed differences between the dynamics of Norwegian lemmings and other *Lemmus* species match the predicted differences between Barrow and Kilpisjärvi dynamics (Oksanen et al. 2013).

While predators appear to drive vole cycles in productive shrublands (Ekerholm et al. 2004, Hambäck et al. 2004), they could not have caused the 1978–1979 lemming crash, as no predator activity was then observed, and vole densities remained high (Fig. 2; see Fig. 2 in Oksanen and Oksanen 1981). During the lemming crashes of 1988–1989, 2007–2008 and 2011–2012, the activity of stoats and weasels was strongly concentrated on productive shrublands, where also many winter nests were visited by predators (Fig. 3, Supporting information, Appendix 4, Table S3–S4 see also Vigués et al. 2022).

The similarities between lemming dynamics in highlands and lowlands (Fig. 2a, b) implies that, in a large spatial scale, what counts most for Norwegian lemmings is low primary productivity and the consequently low predator activity (Fig. 3, Supporting information, Appendix 4, Fig. S43; Le Vaillant et al. 2018). In productive habitats, Norwegian lemmings succumb in apparent competition with more agile voles (Fig. 2c; Holt 1977, Oksanen 1993). As the warming climate will increase primary productivity and favor ericaceous dwarf shrubs (Vowles et al. 2017, Vuorinen et al. 2017) – the winter forage of gray-sided voles (Kalela 1957) – Norwegian lemmings are likely to be replaced by voles in large parts of their current range, as indicated by our data for 2014–2017.

Comparisons between highland and lowland data for 2007 and 2011 (Fig 2a, b) indicates net movements of lemmings from highlands to lowlands in spring and back to highlands in autumn, as proposed by Kalela (1961, 1971). However, lemmings wintering in meadow snowbeds appeared to stay there for the summer, too, as these habitats are well drained and provide resources for both seasons (Oksanen and Oksanen 1981). The seasonal habitat changes of Norwegian lemmings thus seem to depend on local conditions.

A puzzling feature in our record is the long periods when lemmings oscillated irregularly at low numbers and were mainly found in meadow snowbeds and highland mires (Supporting information, Appendix 4, Table S8, Fig. S44). The absence of a clear pattern indicates that density-independent factors accounted for these low-density periods.

In autumns of lemming years, Norwegian lemmings have been observed far from their normal habitats, even in cities. This has traditionally been regarded as evidence for long-range migrations (Collett 1895, Kalela 1941, 1949, Henttonen and Kaikusalo 1993). Conversely, Krebs (2024) claims that 'movements of individual lemmings are measured in a few kilometers' and proposes that local movements of previously undetected resident lemmings account for the observations of lemmings in lowlands (Krebs 1964, 1993). It seems, however, unlikely that such hypothetical local lemmings could have escaped being detected in spring, when lemmings are easy to see (Aho and Kalela 1966, Kalela 1961, 1971, Oksanen and Oksanen 1981). The conjecture of local movements is also contradicted by the gradual spreading of lemming observations from mountains to lowlands in peak summers (Kalela

1941, 1949, Henttonen and Kaikusalo 1993). Moreover, the genetic homogeneity of Norwegian lemmings (Lagerholm et al. 2017) indicates that individual lemmings frequently cover distances of about hundred kilometers.

Our data provides further evidence for the migratory behavior of Norwegian lemmings in peak years. Had it been just a question of seasonal habitat change (Krebs 1964, 1993), lemmings had not needed to venture to the icefields of Iešjávri, where landmarks on the other side are barely visible for them. Nor had they needed to risk their lives by starting to swim across this mighty lake in late summer. Notice also that most lemmings found on islands were subadults, which are proposedly especially prone to migration (Kalela 1961, 1971). The high densities of lemmings on the large near-shore islands and the still higher lemming densities on the small, isolated islands indicate that these lemmings knew what they were doing. When facing the main body of Iešjávri, they waited for calm weather (compare with Myllymäki et al. 1962 and de Kock and Robinson 1966) and were therefore 'dammed up' on the large near-shore islands. Moreover, if a lemming crossing Iešjávri stumbled on a small island, it improved its survival chances by resting and feeding before moving on. The behavior of lemmings in peak summers thus represented a trade-off between wanderlust – a desire to leave a crowded area – and risk minimization.

The presence of a big, lemming-free marine island only 70 km from our study area in 2011 supports Kalela's (1949) argument that migrations can provide huge fitness rewards, as a successful migrant can colonize and empty area and found a new population. The migratory behavior of Norwegian lemmings also increases their chances to survive as a metapopulation in the warming climate, where their habitats will shrink and become more isolated from each other.

Conclusions

Our results support Kalela's (1949) conjecture that the cycles of Norwegian lemmings are driven by a strong lemming–plant interaction. As predicted by EEH (Oksanen et al. 1981, 2020), the scanty winter resources produced by barren tundra habitats cannot sustain high lemming densities. Therefore, increases of lemmings are promptly followed by depletion of winter forage, followed by a precipitous crash. The impacts of predators amount to too little and too late to prevent critical resource depletion. In response to their violent dynamics, Norwegian lemmings have developed a strong tendency to migrate from crowded tundra areas, as proposed by Kalela (1949). In addition to providing individual fitness benefits, migrations help Norwegian lemmings to persist as a metapopulation in the archipelago-like Fennoscandian tundra.

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Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.XXXX (Oksanen et al. 2024).

Supporting information

The Supporting information associated with this article is available with the online version.

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