

ARTICLE

Seasonal role of a specialist predator in rodent cycles: Ermine–lemming interactions in the High Arctic

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Abstract

The exact mechanisms behind population cycles remain elusive. An ongoing debate centers on whether predation by small mustelids is necessary and sufficient to generate rodent cycles, as stipulated by the specialist predator hypothesis (SPH). Specifically, the SPH predicts that the predator should respond numerically to the abundance of its prey with a delay of approximately one year, leading to delayed density-dependence in the dynamics of the prey population. Here, we analyze the numerical response of a small mustelid, the seasonality of its interaction with rodents, and its impact on population cycles using long-term seasonal data on ermines and cyclic lemmings in the High Arctic. Our results show that the numerical response of ermines to lemming fluctuations was delayed by one year and could mediate delayed density-dependence in lemming growth rate. The impact of ermines on the growth rate of lemmings was small but mostly circumscribed to winter, a critical period when shifts in cycle phases occur and direct density-dependence seems relaxed. Our simulations of lemming population with and without ermines suggest that these small mustelids are neither necessary, nor sufficient to generate cycles *per se*. However, the presence of small mustelids may be necessary to prolong the low-abundance phase and delay the recovery of lemming populations, promoting the presence of a multiannual low phase typical of lemming cycles. Our study corroborates the idea that population declines of cyclic populations are best explained by direct density-dependence; however, the delayed response of specialized predators induces the multiannual low phase and leads to longer periodicities, which are typically of 3–5 years in rodents.

KEYWORDS

Arctic, lemmings, population cycles, predation hypothesis, rodents, small mustelids, specialist predator

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INTRODUCTION

The causes of population cycles have been debated since their first description to the scientific community (Elton, 1924). Early models and empirical studies concluded that, for populations to cycle, their growth had to be regulated by factors dependent on past population densities (May, 1976; Stenseth, 1999). Resident predators that specialize on a single prey species, and who need to convert prey into offspring, were quickly recognized as potential drivers of population cycles (Rosenzweig & MacArthur, 1963). Their potential role in prey population dynamics was formulated as the specialist predator hypothesis (SPH). It states that to destabilize a prey population and induce cycles, resident specialist predators must respond numerically to the prey abundance with a delay and exert a sufficient predation pressure to regulate the prey population (Andersson & Erlinge, 1977; Hanski et al., 2001; Korpimäki & Krebs, 1996).

In the context of rodent cycles, small mustelids like weasels and ermines (*Mustela* spp.) are often considered specialist predators. In northern environments such as the High Arctic, these resident predators show an almost exclusive reliance on rodent prey (Gilg et al., 2006; Korpimäki et al., 1991), and even chase them under the snowpack (King & Powell, 2006; Sittler, 1995). The year-round activity of small mustelids and their capacity to enter most rodent burrows leaves their prey little spatial and seasonal refuges (Jędrzejewski et al., 1992; MacLean et al., 1974; Mougeot et al., 2020). Moreover, their prey-caching behavior, which results in the killing of more individual prey than necessary for their daily survival (i.e., surplus killing), could enable them to rapidly deplete prey populations (Jędrzejewska & Jędrzejewski, 1989; Oksanen et al., 1985). At the other end of the spectrum, the term “generalist predators” (sensu Andersson & Erlinge, 1977, Korpimäki & Krebs, 1996) englobes predators that respond without delay to changes in a prey population, either functionally through prey switching or numerically through aggregation. Such direct responses are thought to stabilize the prey dynamics (Andersson & Erlinge, 1977; Hanski et al., 2001; Korpimäki, 1993). In the High Arctic, predators such as arctic foxes (*Vulpes lagopus*), long-tailed jaegers (*Stercorarius longicaudus*), and snowy owls (*Bubo scandiacus*) also specialize in lemmings during summer but either drastically change their diet or simply vanish when lemmings are scarce (Gilg et al., 2006; Therrien et al., 2014). Despite their short-term specialization, their yearly shifts in diet or abundance lend them characteristics typically attributed to generalist predators.

The critical prediction of the SPH that mustelid numbers show a delayed response to their prey (typically 9–12 months) has found support in observational studies

conducted on voles in Fennoscandia (Hanski et al., 1991; Korpela et al., 2014; Korpimäki et al., 1991; Sundell et al., 2013) and in Greenland on collared lemmings (*Dicrostonyx groenlandicus*, Gilg et al., 2006). However, similar studies in temperate Europe were not able to find any delayed response of small mustelids (Graham, 2001; Jędrzejewski et al., 1995; Mougeot et al., 2019). Even though Fennoscandian experiments (Korpimäki & Norrdahl, 1998) and observational studies in temperate Europe (Jędrzejewski et al., 1995) have shown that mustelids alone are not sufficient to drive rodent cycles, there still remains a boreal-temperate discrepancy in their alleged role. This could be explained by differences in seasonality as snow, a physical barrier that isolates rodents and mustelids from other predators, has been shown to promote cycles in northern environments (Hanski et al., 2001; Norrdahl & Korpimäki, 2002; Stenseth et al., 2002). Nonetheless, the presence of small mustelids could still be a necessary condition to maintain small mammals at low abundances for an extended period (Boonstra et al., 1998; Korpimäki et al., 1991), and thus generate 4- to 5-year cycles. Indeed, in northern islands free of mustelids, rodent populations either exhibit cycles of unusually long periodicities (>5 years) or no periodicity at all (Fauteux et al., 2021; Fay & Rausch, 1992; Menyushina et al., 2012). As far as observational studies go, the role of small mustelids in rodent cycles should ideally be investigated with seasonal, long-term, and synchronous empirical data on both predator and prey. However, acquiring empirical data of population abundance throughout the year on both predators and prey synchronously is challenging, as rodents are hardly trappable in winter and mustelids leave no tracks in summer. Hence, due to logistical constraints, such studies are extremely rare in environments characterized by long winters (Kleiven, 2022) during which the snowpack can isolate the rodent–mustelid system from the stabilizing influence of generalist predators (Korpimäki & Norrdahl, 1989; Oksanen et al., 2001). Here, we used a long-term monitoring program conducted in the High Arctic (Bylot Island, Nunavut, Canada) to evaluate the predictions of the SPH and investigate the potential role of small mustelids (ermine, *Mustela richardsonii*) in the population dynamics of cyclic brown (*Lemmus trimucronatus*) and collared lemmings. First, we addressed a key prediction of the SPH, that small mustelids respond numerically with a delay of one year to fluctuations of abundance of their prey. At an annual scale, when lemming populations grow, we expect a direct response from ermines even though it may be limited by their restrictive reproductive physiology (Sandell, 1984). When lemmings decline, a delayed response could be mediated by surplus killing and food

caching (Jedrzejewska & Jedrzejewski, 1989), which should enable ermines to survive at moderate to low prey abundance. Hence, both current and past prey densities are likely to impact ermine abundance through different mechanisms.

Secondly, we aim to assess the impact of ermine abundance on seasonal population growth rates of lemmings. On Bylot Island, lemming declines are mostly observed during fall, whereas growth leading to peak abundances occurs over winter through subnivean reproduction (Duchesne et al., 2011; Fauteux et al., 2015). If ermines are to drive lemming cycles, their impact should be strongest during fall and winter, either by decimating the lemming population or limiting its subnivean growth. Their impact during summer is thought to be limited because pups are not yet weaned (King & Powell, 2006), intraguild predators may constrain the activity of small mustelids (Zub et al., 2008), and lemming reproductive rate is high (Bilodeau, 2013; Pitelka & Batzli, 2018).

Finally, we used the estimates of ermine and lemming abundance variations to generate empirical predator and prey zero growth isoclines and assess the potential role of ermines in generating lemming cycles. The ability of small mustelids to initiate prey population declines, hence their sufficiency, should be reflected by the range of prey densities encompassed by the prey isocline. Moreover, if ermines are a necessary component for the observed cycles, then lemming populations simulated without ermines should display cycles whose characteristics differ from those observed on Bylot. Their periodicity or the frequency of multiannual low phases should tend toward what is observed in rodent populations where small mustelids are absent or have no role (Menyushina et al., 2012; Mougeot et al., 2019).

MATERIALS AND METHODS

Study area

Our study area (73°08' N, 80°00' W) is located in the Qarlikturvik Valley on Bylot Island, Nunavut, Canada. The valley bottom is a mosaic of wetlands, characterized by ice-wedge polygons mostly covered by graminoids and mosses, and of mesic tundra covered by herbs, graminoids, and prostrate shrubs (Gauthier et al., 2011). The wet and mesic tundra comprise approximately 14% and 76% of our study area, respectively. The remaining 10% is covered by the riparian habitat made of linear depressions carved by streams running through mesic tundra. The riparian habitat is particularly

important for small mammals in winter because they are conducive to heavy snow accumulation and provide the most insulated habitat against extreme cold temperatures (Poirier et al., 2023). Brown and collared lemmings are the only rodents present and both species fluctuate in abundance according to 3- to 5-year cycles (Bolduc et al., 2023; Gruyer et al., 2008). Brown lemmings have high amplitude cycles with more than 100-fold between peaks and lows, whereas collared lemmings are much less abundant and have low amplitude fluctuations. The ermine is the only mustelid on the island and its abundance is correlated with that of lemmings (Bolduc et al., 2023). The other resident predators are arctic foxes and, when lemming density is high, snowy owls, rough-legged hawks (*Buteo lagopus*), and long-tailed jaegers are abundant (Therrien et al., 2014).

Lemming, ermines, and winter nest abundances

The summer abundance of each lemming species was estimated in the two main habitats (wetland and mesic) by trapping them from 1993 to 2022. Snap trapping (720 trap-nights/habitat) was conducted in late July or early August from 1993 to 2016, and live trapping on two 11-ha grids (one per habitat, 864 trapping occasions/grid/session) was conducted in mid-June ($D_{\text{June},t}$), mid-July ($D_{\text{July},t}$), and mid-August ($D_{\text{August},t}$) from 2004 to 2022, except in 2020 and the two first sessions of 2021 due to COVID-19. Snap-trapping estimates were converted into annual population densities ($D_{\text{Annual},t}$), based on the equations of Fauteux et al. (2018). For years when live trapping was conducted, $D_{\text{Annual},t}$ was equal to $D_{\text{July},t}$. As we were interested in the lemming density over the study area, the densities of both lemming species were summed and weighed based on the proportion of wetland (14%) and mesic habitats (86%, as it comprised the unmonitored riparian habitat) present in the study area to create a single estimate per year (Figure 1).

We estimated ermine relative abundances from the testimonials of opportunistic observations made by fieldworkers on Bylot Island from 1993 to 2019 and in 2022 (216 fieldworker-year). Their accounts, collected from memories, notebooks, or photographs, were translated on an ordinal scale (0 = no ermine sightings, 1 = one ermine sighting, 2 = multiple sightings of lone ermines, and 3 = sighting of an ermine family). The average of these yearly scores provided an ermine relative abundance index (hereafter Ermine_t for year t , Figure 1). This index was shown to be a good proxy of ermine abundance as it was well correlated with another measure of abundance derived from systematic surveys of incidental

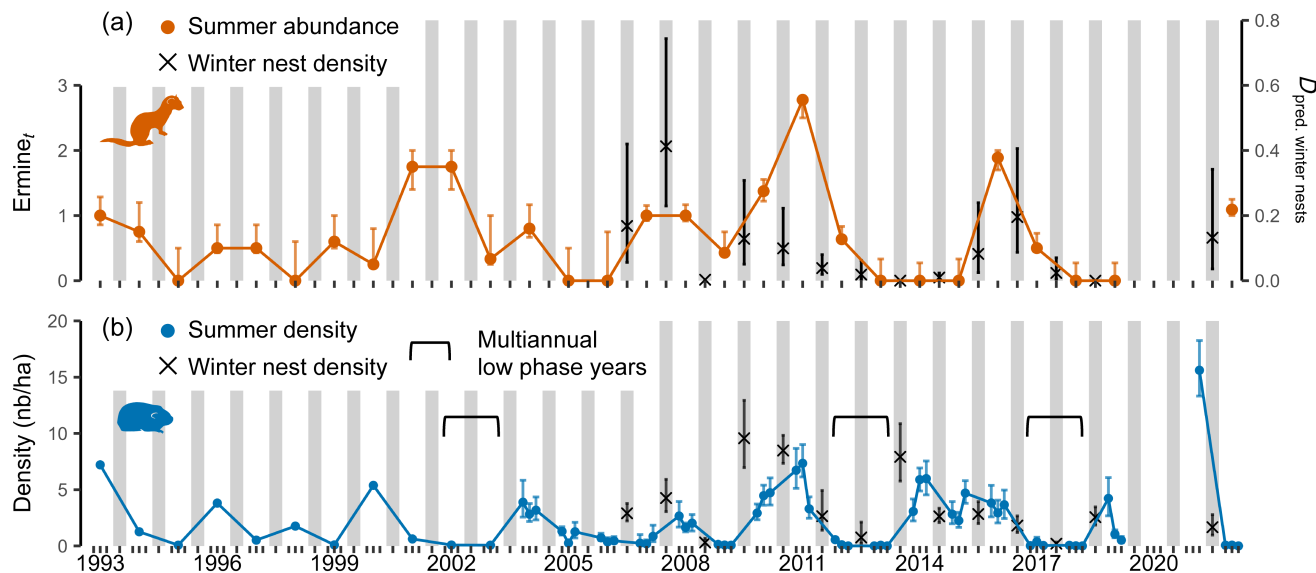


FIGURE 1 Seasonal time series of ermine and lemming abundance on Bylot Island (Nunavut, Canada). Shaded area represents winter. (a) Ermine relative abundance index (solid line, orange dots) in summer and density of lemming winter nests with signs of ermine predation (black crosses) and their 95% CI. (b) Habitat-weighted summer lemming density (solid line, blue dots) and density of all winter nests (gray crosses) with their 95% CI when available. On the x-axis, ticks within summers align with the 15th of June, July, and August. Multiannual low-phase years are grouped under braces and are defined as (1) years of <0.5 ind/ha preceded by a decline and followed by lower or equal density or (2) a year of low density following a year compliant with (1). Lemming and ermine icon credits: David Bolduc.

observations conducted over a shorter time period ($\rho = 0.86$, see Bolduc et al., 2023).

From 2007 to 2022, lemming winter nests were sampled at snowmelt by walking 30 to 74–500 m permanent transects in mesic, wetland, and riparian habitats. Detected nests were dissected and destroyed to avoid counting the following year. For each nest, signs of predation (e.g., lemming body parts such as paws, skulls, skin, stomachs, abundant hairs, etc.) were noted. Nest densities were estimated by distance sampling (Buckland et al., 2015) separately for each habitat. The rare nests at more than 30 m from the transect were removed from the analyses (i.e., data truncation). Detection probabilities were modeled across years by selecting the best model in each habitat (half-normal function in mesic habitat, hazard rate in other habitats) even in low-abundance years, which are data deficient. A yearly density estimate of all nest ($D_{\text{winter nests}, t+1}$) or only those with predation ($D_{\text{pred. winter nests}, t+1}$) was obtained by summing the densities from mesic, wetlands, and riparian habitats, weighed by their respective cover in our study area (76%, 14%, and 10%).

Lemming population growth rates

To assess the seasonality of the impact of ermines on lemmings, we calculated interannual ($R_{\text{interan.}}$) and seasonal growth rates ($R_{\text{summer}}, R_{\text{fall-spring}}$) of the lemming

population using annual, spring, and fall densities (see equations in Appendix S1: Section S1). To do so, a constant equivalent to half of the lowest lemming density measured during our study (0.0235 ind/ha) was added to all lemming densities to allow log transformation. Because growth rates are calculated on periods of different lengths, R values were transformed into instantaneous growth rates using $R_{\text{daily}} = R^{\text{Span}^{-1}}$, where Span is the number of days separating live-trapping sessions. Span was of 365 days for $R_{\text{interan.}}$, 56 ± 5 days for R_{summer} , and of 307 ± 3 for $R_{\text{fall-spring}}$.

We made two assumptions regarding lemming populations over the nine months covered by $R_{\text{fall-spring}}$. First, we assumed that the density of winter nests at snowmelt reflected the maximal density reached by lemmings over the winter. Even if lemmings may die or disperse during the winter, their nests will remain. Second, we assumed that the lemming population trajectory (growth or decline) did not change over the winter, which is true at least in Norwegian lemming (*Lemmus lemmus*), Kl. Consequently, we assumed that if the lemming population was declining between fall t and spring $t+1$, the nest density at snowmelt should be representative of lemming density in early winter of year t when nests are formed. Alternately, if the population was growing, it should be representative of lemming density in late winter of year $t+1$, when nests are abandoned. The first year of the survey was excluded from these calculations

(see justification in Appendix S1: Section S3). These assumptions enabled us to estimate four different proxies of seasonal population growths (R') at key points in time: R'_{fall} and $R'_{\text{early winter} - \text{spring}}$ in years of winter decline and $R'_{\text{fall} - \text{late winter}}$ and R'_{spring} in years of winter growth. All equations regarding growth rates and their proxies, as well as a recapitulative figure of the methodology, are given in Appendix S1: Section S1.

STATISTICAL ANALYSIS

Numerical response of ermines to lemming densities

We examined how ermines responded to current (t) and past ($t - 1$) lemming densities as well as their own past abundances using quasi-binomials generalized linear models, which are suited to handle bounded data like the ermine abundance index (Gómez-Déniz et al., 2020). Ermine_t was divided by three to rescale it between 0 and 1, and models were weighted by the number of testimonials used to derive each relative abundance estimate. After confirming the absence of collinearity between covariates (covariance inflation factor < 3) and scaling them, we considered five hypotheses with various combinations of lemming and ermine densities (see Appendix S1: Section S2 for model details). These models were evaluated against a null model using model selection based on the second-order quasi-Akaike information criterion (QAIC_c). The coefficients of parameters present in models with $\Delta\text{QAIC}_c \leq 2$ were model-averaged.

Impact of ermines on lemming growth rate

To assess the impact of ermines on lemming growth rates, we used two indices of abundance (Ermine_t , $D_{\text{pred. winter nests}, t+1}$) and one index of activity representing the predation pressure of ermines on lemmings during winter, the predation ratio ($\text{PR} = D_{\text{pred. winter nests}, t+1} / D_{\text{winter nests}, t+1}$). Like any ratio, PR could be problematic, and we ensured that this was not the case (Appendix S1: Section S4). We modeled the instantaneous growth rates (R) as a function of their respective initial lemming density ($D_{i,t}$, see Appendix S1: Section S1) to test for density-dependence and Ermine_t . $R_{\text{fall} - \text{spring}}$ was also modeled as a function of $D_{\text{pred. winter nests}, t+1}$, and PR as these indices could reflect ermine abundance during this period. These models were weighted by the number of winter nest transects sampled. Model details are given in Appendix S2: Table S2. For R' values, ermine-related

covariates were considered if they reflected ermine abundance or activity during or before the considered growth rate proxy. Moreover, depending on R' , initial lemming density was either $D_{\text{August}, t}$ or the density of lemming winter nest found in the following spring ($D_{\text{winter nests}, t+1}$). Even though sample size was restrictive ($n = 5$ or 8), we evaluated the impact of density-dependence and ermine simultaneously. Model details and the original data are presented in Appendix S2: Table S3 and Figure S1.

Delayed density-dependence in lemmings

We examined whether past densities of lemmings ($D_{\text{Annual}, t-1}$) could influence their annual growth rate ($R_{\text{interan.}}$) directly when ermine abundance (Ermine_t) was considered. We tested this hypothesis with a path analysis (Shipley, 2009) from models predicting Ermine_t (Appendix S2: Table S1, M1) and $R_{\text{interan.}}$ (Appendix S2: Table S2, M1), which used data from 1993 to 2019. Independence between $R_{\text{interan.}}$ and $D_{\text{Annual}, t-1}$, which tests for delayed density-dependence generated by another factor than ermine abundance, was assessed at $\alpha < 0.05$ using Shipley's d-sep test (Shipley, 2009). A schematic representation of this analysis is presented in the results.

Potential limitation of lemmings by ermines

The limitation of lemmings by ermines was assessed in two different ways. First, we determined ermine and lemming zero growth isoclines based on our empirical time series. We did so by solving both the ermine and lemming interannual growth models to find combinations of ermine and lemming abundances that yielded zero growth (Appendix S1: Section S5, Equations S14 and S15). These combinations of abundances were plotted to draw the ermine and lemming isoclines. Second, we simulated lemming abundance time series under different scenarios: (1) without stochasticity; (2) with stochasticity; and (3) with stochasticity and without ermines. From the simulated and observed lemming time series, we extracted the periodicity of cycles using wavelet analysis, the proportion of years in multiannual low phase, and the frequency distribution of annual lemming densities. A year was considered to be part of a multiannual low phase if (1) $D_{\text{July}, t} < 0.50$ ind/ha and $R_{\text{interan.}}$ and $R_{\text{interan.}, t-1} \leq 0$ (e.g., a low-density value both preceded and followed by a declining or stable growth rate) or (2) a year of low density (< 0.50 ind/ha) following a year identified as a low phase. The threshold of

0.50 ind/ha is very conservative, as at our study site, densities observed during multiannual low phases were all <0.1 ind/ha (Figure 1). Simulated time series were considered different from the observed one if the observed value was not contained in the 95% CI of densities, periodicities, and proportion of years in the multiannual low phase. See Appendix S1: Section S5 for details of this analysis.

RESULTS

Numerical response of ermines to lemming densities

The best model explaining ermine abundance included lemming density at time t and $t - 1$ ($D_{\text{Annual},t}$ and $D_{\text{Annual},t-1}$) as predictors but a competing model also included Ermine_{t-1} (Appendix S2: Table S1). Both current and past lemming densities had a positive influence of similar size on ermine abundance (Figure 2), suggesting equally strong direct and delayed density-dependent numerical responses of ermines (model-averaged scaled $\beta = 0.66$ [0.04; 1.27] for $\ln(D_{\text{Annual},t})$ and 0.56 [0.02; 1.10] for $\ln(D_{\text{Annual},t-1})$). Ermine_t seemed to be positively influenced by its past abundance (Ermine_{t-1}), but the effect was imprecise (model-averaged scaled $\beta = 0.41$ [-0.15; 0.98]). Hence, further path analysis and simulations will only use the model, including lemming density at time t and $t - 1$ (Appendix S2: Table S1, M1).

Seasonal impact of ermines on lemming growth rate

Density-dependence and ermine abundance both had a negative influence on interannual lemming growth rate, but the direction and magnitude of their effect varied seasonally (Figure 3). Indeed, none of the covariates influenced lemming summer growth rate. Similar to what was detected on an annual basis, fall-to-spring growth rate was negatively related to current lemming density and some ermine covariates (but not density of winter nests predated by ermines, Appendix S2: Table S2). As for the seasonal growth proxies dividing the fall-to-spring period (R'), the impact of density-dependence was strongly negative during fall and to a lesser extent also in spring, but it was null or even positive in winter (Figure 3, Appendix S2: Table S3). In contrast, lemming growth rate proxies were negatively related to ermine covariates during winter, but not during fall nor spring (Figure 3, Appendix S2: Table S3).

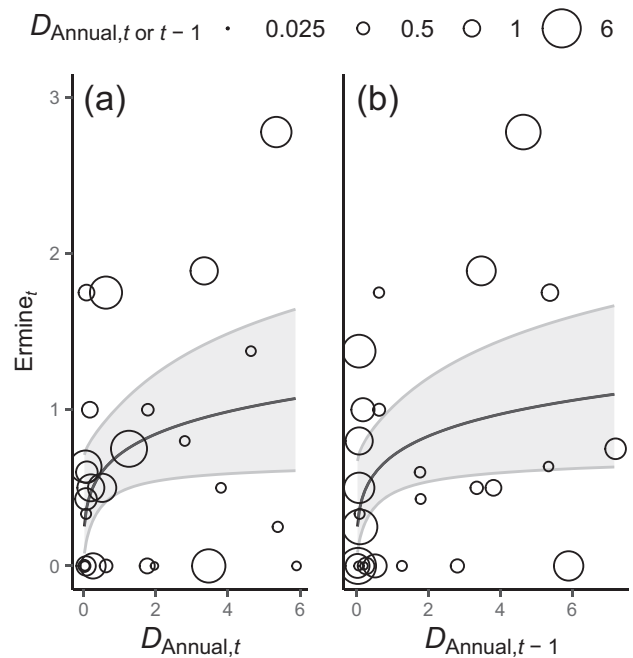


FIGURE 2 Relationship between the ermine abundance index and (a) current (t) and (b) previous ($t - 1$) lemming densities (D_{Annual}) on Bylot Island (Nunavut, Canada). Dot size is proportional to (a) $D_{\text{Annual},t-1}$ and (b) $D_{\text{Annual},t}$. Gray-shaded areas represent 95% CI. Predictions were obtained from top-ranked model in Appendix S2: Table S1. McFadden pseudo- R^2 is 0.24 and Nagelkerke's is 0.47.

Delayed density-dependence in lemmings

The path analysis revealed that the delayed density-dependence in the lemming population growth rate could be mediated by Ermine_t (Figure 4). However, other factors could also contribute to delayed density-dependence as the independence test (d-sep test) between $D_{\text{Annual},t-1}$ and R_{interan} returned a p value of 0.10 and the overall model, a Fisher's C of 4.64. This rather poor fit indicates that covariates are missing or are too imprecise.

Impact of ermines on lemming cycles

The ermine zero growth isocline rapidly reached a plateau over observed lemming densities, whereas the one for lemmings declined steeply over densities of 0.06–1.05 ind/ha (Figure 5). Isoclines crossed when Ermine_t was at 0.62 and $D_{\text{Annual},t}$ was at 0.57 ind/ha. We also note that population trajectories tend to make a counterclockwise circular pattern on the isocline graph, which is typical of a delayed response by the predator (Gotelli, 2008), despite large variations. The deterministic simulation quickly

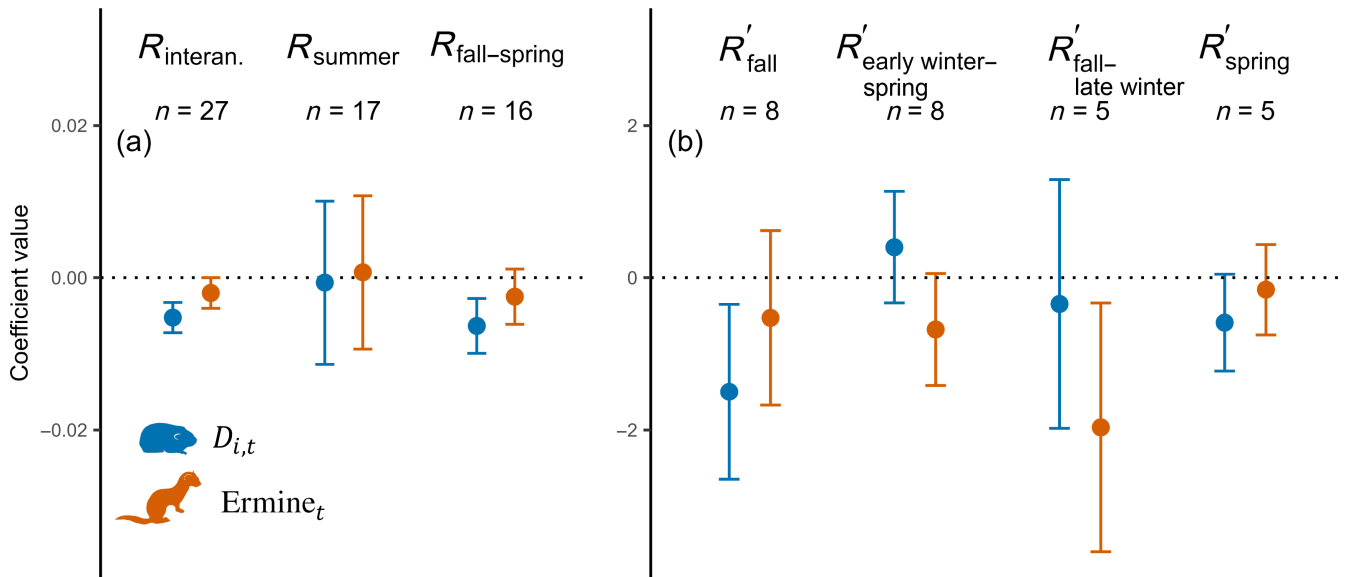


FIGURE 3 Seasonal influence of ermines and density-dependence on lemming population growth rates (a, R) or its proxies (b, R') between current time t and $t + i$ on Bylot Island, Nunavut, Canada. Covariates are current lemming density ($D_{i,t}$) and ermine abundance ($Ermine_t$). Dots are coefficient values (β) of the relationships, error bars represent 95% CI, and the number of observations in each model (n) is given. See model details in Appendix S2: Tables S2 and S3. (a) Coefficient values are scaled and comparable between seasons as R s are instantaneous growth rates. (b) Because of the unmeasured duration of periods associated with seasonal proxies (R'), coefficients are not comparable between seasons but are scaled and comparable within seasons. Lemming and ermine icon credits: David Bolduc.

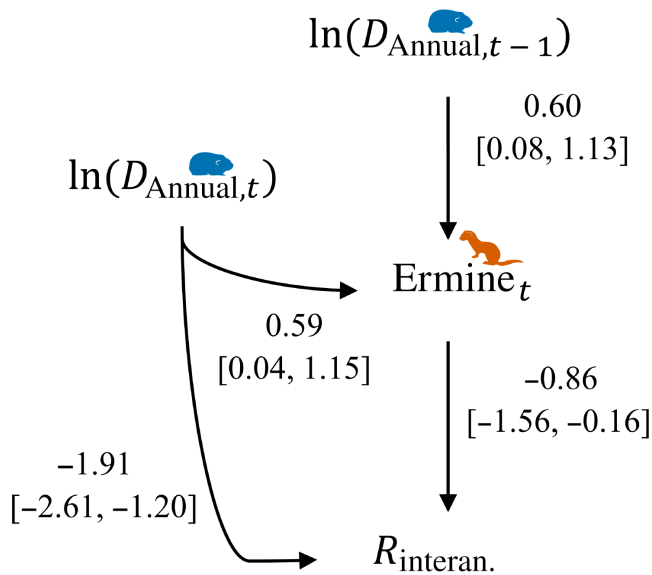


FIGURE 4 Standardized path coefficients illustrating direct ($\ln(D_{Annual,t})$) and delayed ($\ln(D_{Annual,t-1})$) density-dependence effect on annual lemming growth rate ($R_{interan.}$) in the presence of ermines ($Ermine_t$) on Bylot Island, Nunavut, Canada, for the period 1993–2019. Numbers are standardized beta coefficients, with 95% CI in brackets. Black arrows are causal pathways. Fisher's $C = 4.64$. Lemming and ermine icon credits: David Bolduc.

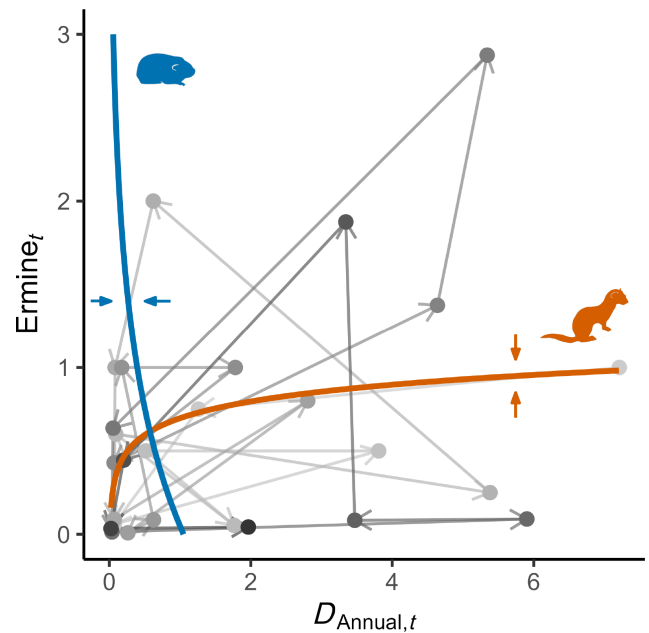


FIGURE 5 Zero growth isoclines of ermines (orange line) and lemmings (blue line) on Bylot Island, Nunavut, Canada, derived from empirical data. Colored arrows are the predicted direction of change in abundance relative to the isoclines. Dots represent original data, with gray arrows representing the direction and magnitude of change between t and $t + 1$. Line and dots become progressively darker over time. Lemming and ermine icon credits: David Bolduc.

reached an equilibrium exactly where the isoclines crossed (Figure 5), and thus comparing the characteristics of this simulation to the original data is of little

interest. Both stochastic simulations gave rise to cycles (1–4.5 years with ermines, 2.4–3.3 years without ermines, 3.6–4.4 years in the observed time series, Figure 6). Similarly, multiannual low phases were present in both stochastic simulations. The proportion of years in these low phases was 0.22 in the observed data, a proportion included in the 95% CI of the simulation with ermines (0.00, 0.41) but not in the simulation without ermines (0, 0.19) (Figure 6). Lemming densities in the observed time series were included in the 95% CI of both simulations, even though we note that densities were generally higher without ermines.

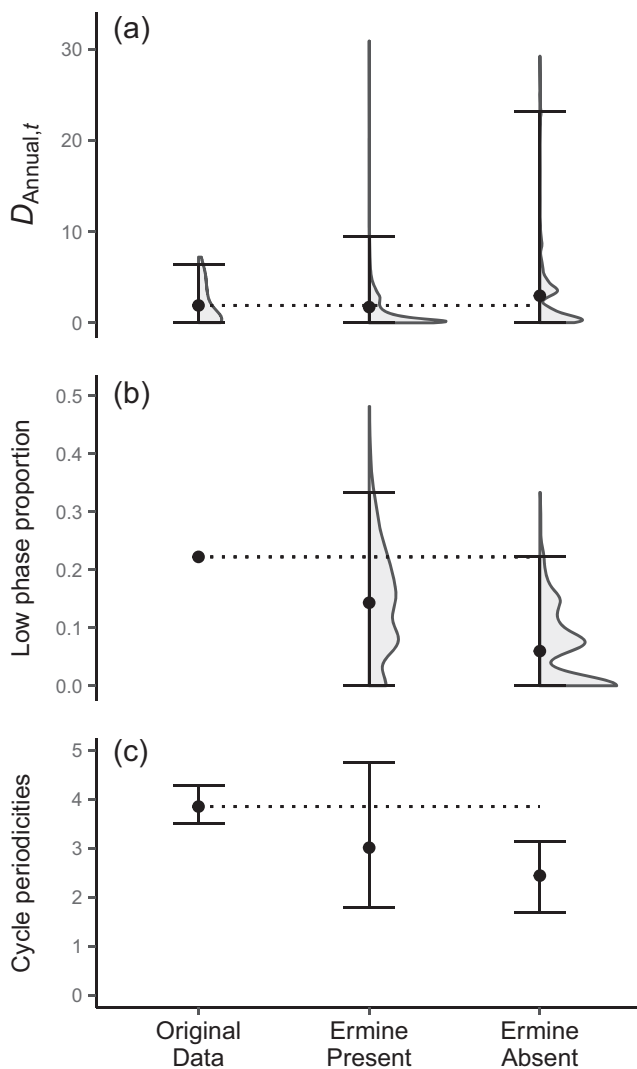


FIGURE 6 Comparison of the observed time series and stochastic simulations of lemming populations with or without ermines. (a) Frequency distribution, mean, and 95% CI of lemming densities observed in July ($D_{\text{Annual},t}$). (b) Frequency distribution, mean, and 95% CI of the proportion of years when lemmings were considered in their multiannual low phase. (c) Dominant periodicities with 95% CI detected using wavelet analyses. Dotted line is the mean in the original data.

DISCUSSION

Our empirical analysis suggests that ermine predation alone is insufficient to generate the observed lemming cycles. Nonetheless, these small mustelids could still play a critical role in lemming population dynamics as we found evidence for an ~1-year delayed numerical response by ermines, a key prediction of the SPH. Our path analysis further suggested that this delayed numerical response could partly mediate the delayed density-dependence observed in the lemming population growth rate, even though other factors are probably also at work. Additionally, the limited negative impact of ermines seemed restricted to winter, a crucial season for periodic population outbreaks of lemmings in the High Arctic (Fauteux et al., 2015). Finally, our empirical isoclines and simulations highlighted the potential role of ermines in limiting lemming maximal prey population densities and in maintaining their abundance to low levels for more than a year.

Direct and delayed numerical response of ermines

Our observation that ermines could respond directly to their prey abundance fluctuation at an annual scale is not surprising. This was reported by all studies conducting seasonally synchronous monitoring of small mustelids and their rodent prey (Gilg et al., 2006; Graham, 2001; Jedrzejewski et al., 1995; Mougeot et al., 2019). However, a 1-year delayed response similar to the one that we found was only reported at northern locations like Fennoscandia (Korpimäki et al., 1991; Sundell et al., 2013) and Greenland (Gilg et al., 2006). In contrast, no or relatively short (<8 months) delays were detected in temperate Europe (Poland; Jedrzejewski et al., 1995, England; Graham, 2001, Spain; Mougeot et al., 2019). This north–south dichotomy in the observed numerical response of small mustelids substantiates a strong latitudinal effect on mustelid–rodent interaction (Hansson & Henttonen, 1985). A higher density of alternative prey in the south than in the north, especially in winter, could improve mustelid survival and promote a more immediate response during the rodent increase phase. In addition, a greater abundance of generalist predators (Hanski et al., 2001; Lambin et al., 2000) and lack of or inefficient protection from the snowpack could increase the vulnerability of mustelids, especially when rodent populations crash, and speed up the decline (Korpimäki & Norrdahl, 1989; Powell, 1973). Other mechanisms could also favor delayed responses by small mustelids in northern locations. Colder temperatures

may improve and prolong the conservation of cached carcasses and extend the period of continued presence of small mustelids after peak prey abundance (Jedrzejewska & Jedrzejewski, 1989; Oksanen et al., 1985). These cold temperatures were also observed to benefit the food-caching Eurasian Pygmy Owl (*Glaucidium passerinum*, Masoero et al., 2020). Direct observations of the foraging activity of radio-collared ermines during a summer of very low lemming density on Bylot Island (0.07 ind/ha) support this hypothesis: 68% of carried food items ($n = 19$, including small passerines and lemmings) and 86% of carried lemmings ($n = 15$) were retrieved from old caches as suggested by their either frozen or partially decayed state (Bolduc et al. unpublished).

Seasonally varying impact of ermine predation and density-dependence

The impact of density-dependence and ermines on lemming populations varied greatly between seasons, being absent during summer and most significant from fall to spring. This suggests that summer reproduction can more or less compensate for the toll taken by ermines and the density-dependent predation of other predators (Gilg et al., 2006; Therrien et al., 2014), possibly due to good foraging conditions. The fact that ermines do not cause summer declines is not surprising as their predation rate had been estimated to be half the daily growth of lemmings (1.2% vs. 2.2% per day, Bilodeau, 2013; Therrien et al., 2014). Their comparatively slow reproduction likely prevents them from catching up with their prey, unlike the faster reproducing least weasel, which was found to reduce the summer growth rates of voles in Fennoscandia (Korpela et al., 2014). Moreover, the shape of the predator isocline suggests that ermines quickly become limited by factors other than prey abundance. During summer, territoriality could limit their numbers, whereas the large number of other predators could reduce ermine activity and survival, thereby limiting their impact on lemmings (Gotelli, 2008; King & Powell, 2006; Korpimäki & Norrdahl, 1989).

As observed in many small rodent populations, we found that variations in lemming numbers were most pronounced between the end of summer and the following spring (Fauteux et al., 2015; Krebs et al., 2023; Pinot et al., 2016). These fluctuations were largely the result of direct density-dependence, especially in fall (Figure 3), suggesting that delayed density-dependence mediated by ermine predation is unlikely to cause the fall declines (Fauteux et al., 2015). A reduction in reproductive activity at the onset of fall caused by falling temperatures

(Pitelka & Batzli, 2018) combined with the direct functional and numerical response of both generalist and specialist predators feeding on lemmings might be a better explanation to these drastic declines (Fauteux et al., 2016; Gilg et al., 2006; Korpela et al., 2014; Korpimäki, 1993; Therrien et al., 2014). The idea that these declines are mostly directly density-dependent is in line with recent modeling work (Barraquand et al., 2014, 2022; Bergeron, 2022) and could explain the presence of short cycles in temperate Europe (Barraquand et al., 2014; Mougeot et al., 2019; Zub et al., 2012). Other hypotheses regarding the causes of fall declines, such as lack of food due to overgrazing (Bilodeau et al., 2014; Legagneux et al., 2012) or negative density-dependent reproduction (Fauteux et al., 2015; Fauteux & Gauthier, 2022), have found no support on Bylot Island.

Interestingly, the detailed analysis of the fall-to-spring period suggests that negative density-dependence on lemmings is relaxed when snow cover is present but is replaced by a negative impact of ermines. The arrival of snow partially protects lemmings from arctic foxes (Bilodeau et al., 2013) and coincides with the departure of avian predators, two sources of direct density-dependence (Gilg et al., 2006; Korpela et al., 2014; Therrien et al., 2014). Recent analyses even suggest a positive effect of lemming density on their own winter reproduction (Poirier et al., unpublished). In contrast, the impact of small mustelids could be enhanced during winter for two reasons. First, ermines are largely relaxed from intraguild predation as they can safely move and hunt under the snowpack (Zub et al., 2008). Second, intense winter reproduction is required for lemmings to reach high abundance (Fauteux et al., 2015; Reid & Krebs, 1996) but ermines may interfere with recruitment. Some evidence suggests that female lemmings suffer heavier predation from small mustelids than males during winter (MacLean et al., 1974; Schmidt et al., 2021; Sittler, 1995), which could further reduce recruitment and explain why males are more abundant at low density (Fauteux & Gauthier, 2022).

Low-abundance phase

The low-abundance phase of small mammal cycles is thought to emerge mostly from delayed density-dependence (Boonstra et al., 1998), which here could be mediated by the ermine delayed numerical response. As suggested by the isoclines, ermine abundance may be decisive in maintaining lemmings at low densities once they have reached such levels (i.e., between 0.06 and 1.05 ind/ha). These isoclines also suggest the presence of a refugial density for lemmings: when they drop

below 0.06 lemmings/ha, most ermines probably starve or leave the system in an attempt to find prey elsewhere and thus stop searching for lemmings (Brown et al., 2001), hence allowing lemmings to enter the growth phase. Such a low refugial density highlights the potential role of metapopulation dynamics in the High Arctic as lemmings may become locally extinct. Although the observed population trajectories do not fully fit with predictions of the isoclines (Figure 5), possibly due to the role of other factors like snow conditions (Domine et al., 2018) or unaccounted activity of other predators, it is striking to see that a simple model built with population data from a single season performs so well and shares features with isoclines generated mechanistically (Brown et al., 2001; Gilg et al., 2006).

Adding a layer to our understanding of the system, the stochastic simulations suggest that ermines play a role in maintaining lemmings at low abundance for more than a year. Their presence allowed the presence of cycles of longer periodicities (4–5 years), like those frequently observed on Bylot Island, which was not the case when ermines were absent. They were, however, not necessary to generate cyclic fluctuations per se as cycles were also found in the ermine-less simulations. This aligns with the models of Gilg et al. (2006) and Barraquand et al. (2022) on lemmings and of Korpela et al. (2014) on voles as they all stated that predation by small mustelids alone was insufficient to generate cycles. Therefore, the simulation results do not support the sufficiency prediction of the SPH considering that lemming cycles may occur without ermines. However, they indicate that cycles of >3 years, as most often seen on Bylot Island and in other northern regions (Gauthier et al., 2024), are partly shaped by small mustelids and likely necessitate their presence.

Study limitations

The ermine-related data we used are indirect and bounded, and it is worth underlining how this may have affected our results. The delayed response of ermines, derived from the testimonials, could partly be an artifact if these predators increase their activity, and thus their detectability, when prey abundance is low (Graham, 2001; Klemola et al., 1999). Whether they do so or not remains unclear (reviewed in Sundell et al., 2013), but our method may have circumvented this by promoting the detection of a direct rather than a delayed response by ermines. As reported by participants of our survey (Bolduc et al., 2023), ermine families, the highest observation category in our methodology, were often observed in years of peak lemming abundance. Hence,

the reliance on ermine reproductive signs to generate the index rather than simply the number of sightings could make our index more robust to variations in ermine activity. This index is also highly correlated with relative abundance derived from incidental observations (Bolduc et al., 2023). Contrary to our prediction, we did not find a negative relationship between lemming fall-to-spring growth and the absolute number of predated nests when taking density-dependence into account. What first seemed like a spurious effect may actually highlight the limits of density of winter nest with signs of predation as an index of ermine abundance. Indeed, this proxy may not properly represent ermine abundance during fall and spring, as indicated by the inconclusive relationships with ermine nest densities during these seasons (Appendix S2: Table S3). Therefore, results based on ermine winter nests must be considered with caution. Finally, we have pooled the abundance of the two species of lemmings present on Bylot Island. In doing so, we likely oversimplified their interactions with small mustelids. Indeed, these two species were shown to suffer differential predation from avian predators (Seyer et al., 2020; Therrien et al., 2014), and thus we cannot exclude that their sensitivity to ermines may also differ. Nonetheless, our study site is heavily dominated by brown lemmings as they are up to 10 times more abundant than collared lemmings in peak years, and of similar abundance in low years. Therefore, our analysis of the impact of ermines on lemmings may be more conclusive for brown lemmings, which made most of the pooled densities, than for collared.

CONCLUSION

Our results suggest that the impact of small mustelids on lemming populations in the High Arctic is mostly circumscribed to winter, a period critical to lemming growth where direct density-dependence, likely caused by other predators (Fauteux et al., 2016; Legagneux et al., 2012; Therrien et al., 2014), is relaxed. Seasonal variations in both direct density-dependence and the impact of ermines highlight the need to consider multiple biotic (e.g., behavior, intraguild predation) and abiotic (e.g., snow conditions) factors that change radically between summer and winter. They also reinforce the hypothesis that top-down regulation is a likely mechanism driving rodent cycles in the Arctic (Bergeron, 2022; Fauteux et al., 2016; Gilg et al., 2006; Reid & Krebs, 1996; Therrien et al., 2014; Wilson et al., 1999) and in northern Europe (Ekerholm et al., 2004; Korpimäki et al., 2002, 2005; Korpimäki & Norrdahl, 1998).

By providing empirical evidence that ermines may limit their prey only during winter, our results help explain the north–south dichotomy regarding the SPH (reviewed in Korpimäki et al., 2005, but see also Mougeot et al., 2019; Zub et al., 2008). The fact that a long-lasting snowpack is necessary for limitation by small mustelids is not a new idea (Hansson & Henttonen, 1985; Stenseth et al., 2002), but our results provide evidence in this direction. In the absence of ermines, our simulations generated only short cycles like those observed in temperate Europe (Barraquand et al., 2014), where snow cover is limited and a mustelid delayed response is not detected. In their presence, however, our simulations frequently yield longer cycles with more multiannual phases of low abundance, as typically observed in northern and boreal regions. The critical role of ermines in maintaining prey at low abundance helps explain the results of predator-exclusion experiments conducted in the Arctic. These experiments generally led to increased abundance and delayed population declines, but they unanimously failed to prevent the low-abundance phase (reviewed in Korpimäki et al., 2005, but see also Fauteux et al., 2016). Their inability to effectively exclude small mustelids, especially during winter, may be the reason.

In conclusion, our study does not support the necessity and sufficiency of small mustelids in causing rodent cycles per se, but indicates that these predators may be necessary to extend the low phase and prolong the periodicities, as typically observed in northern small rodent cycles and previously suggested by MacLean et al. (1974) and Korpimäki et al. (1991). Despite a limited and seasonally circumscribed impact on lemming populations, ermines act at a critical moment and can therefore change the overall population dynamics of their prey. Further investigations on mustelid–rodent systems will greatly benefit from the year-round monitoring of abundance provided by recent technologies (e.g., subnivean automatic cameras, Kalhor et al., 2021; Kleiven, 2022). This increase in the temporal grain of time series will improve the investigation of seasonal variations in vital parameters of both prey and predators and the impact of climatic variables, like snow cover duration, on rodent–mustelid interactions.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Bolduc et al., 2024a) are provided in Dryad at <https://doi.org/10.5061/dryad.6t1g1jx7x>. Code (Bolduc et al., 2024b) is provided in Zenodo at <https://doi.org/10.5281/zenodo.13971203>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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