



This is an electronic reprint of the original article. This reprint *may differ* from the original in pagination and typographic detail.



Korpela, K., Helle, P., Henttonen, H., Korpimäki, E., Koskela, E., Ovaskainen, O., Pietiäinen, H., Sundell, J., Valkama, J., & Huitu, O. (2014). Predator–vole interactions in northern Europe: the role of small mustelids revised. Proceedings of the Royal Society B: Biological sciences, 281(1797), Article 20142119. https://doi.org/10.1098/rspb.2014.2119

All material supplied via JYX is protected by copyright and other intellectual property rights, and duplication or sale of all or part of any of the repository collections is not permitted, except that material may be duplicated by you for your research use or educational purposes in electronic or print form. You must obtain permission for any other use. Electronic or print copies may not be offered, whether for sale or otherwise to anyone who is not an authorised user.

1	Predator-vole interactions in northern Europe: the role of small mustelids revised
2	
3	Katri Korpela ^a , Pekka Helle ^b , Heikki Henttonen ^c , Erkki Korpimäki ^d , Esa Koskela ^a , Otso
4	Ovaskainen ^e , Hannu Pietiäinen ^e , Janne Sundell ^f , Jari Valkama ^g , Otso Huitu ^h
5	
6	^a Department of Biological and Environmental Science, FI-40014 University of Jyväskylä,
7	Finland
8	^b Finnish Game and Fisheries Research Institute, FI-90014 University of Oulu, Finland
9	^c Vantaa Research Unit, Finnish Forest Research Institute, FI-01301 Vantaa, Finland
10	^d Department of Biology, FI-20014 University of Turku, Finland
11	^e Department of Biosciences, FI-00014 University of Helsinki, Finland
12	^f Lammi Biological Station, University of Helsinki, FI-16900 Lammi, Finland
13	^g Finnish Museum of Natural History, FI-00014 University of Helsinki, Finland
14	^h Suonenjoki Research Unit, Finnish Forest Research Institute, FI-77600 Suonenjoki,
15	Finland
16	
17	Corresponding author:
18	Otso Huitu, otso.huitu@metla.fi, +358 50 391 4917
19	
20	Keywords: population cycles; population dynamics; population growth rate; density
21	dependence
22	

23 Summary

24 The cyclic population dynamics of vole and predator communities is a key phenomenon 25 in northern ecosystems, and it appears to be influenced by climate change. Reports of 26 collapsing rodent cycles have attributed the changes to warmer winters, which weaken 27 the interaction between voles and their specialist subnivean predators. Using population 28 data collected throughout Finland during 1986-2011, we analyse the spatiotemporal 29 variation in the interactions between populations of voles and specialist, generalist, and 30 avian predators, and investigate by simulations the roles of the different predators in the 31 vole cycle. We test the hypothesis that vole population cyclicity is dependent on predator-32 prey interactions during winter. Our results support the importance of the small mustelids 33 for the vole cycle. However, weakening specialist predation during winters, or an 34 increase in generalist predation, was not associated with the loss of cyclicity. 35 Strengthening of delayed density dependence coincided with strengthening small 36 mustelid influence on the summer population growth rates of voles. In conclusion, a 37 strong impact of small mustelids during summers appears highly influential to vole 38 population dynamics, and deteriorating winter conditions are not a viable explanation for 39 collapsing small mammal population cycles.

40

41 Key index words: population cycles; population dynamics; population growth rate;
42 density dependence

43

45 **1. Introduction**

46

47 Trophic interactions have a profound impact on population dynamics (1). Population 48 cycles, in particular, are commonly thought to arise from trophic interactions, which can 49 introduce a delay in the regulation of population growth (1). Boreal voles of Eurasia are a 50 well-studied example of species in which predation can cause delayed density 51 dependence of population growth, and cyclic population dynamics (2, 3). Voles are often 52 the most abundant mammals in boreal and subarctic regions, and an indispensable food 53 source for numerous avian and mammalian predators (4, 5). The interaction between the 54 vole and the predator communities, and the cyclic population dynamics observed in both, 55 are key phenomena in northern Eurasian ecosystems.

56 During recent years there have been reports of collapsing rodent cycles with 57 potentially detrimental effects on the predator community (6, 7). The loss of cyclicity has 58 been attributed to milder and shorter winters, which are thought to increase density-59 independent winter mortality, and decrease the influence of delayed density dependence 60 (6, 7). However, we recently showed that mild winters are not associated with collapsing 61 cyclicity among boreal vole populations (8). Furthermore, it is not known how the 62 interactions between voles and predators vary temporally and geographically, so the 63 attribution of causality to altered predator-vole interactions is far from clear.

Practically all terrestrial carnivores in northern Europe consume voles at least occasionally, and the following predators show a clear preference for voles: the small mustelids (9), the red fox (10), the pine marten (11) and several owl and raptor species (12, 13). The small mustelids, the least weasel, *Mustela nivalis nivalis*, and the stoat,

Mustela erminea, are key predators in the boreal vole cycle (2). They are small and highly adapted to prey on voles even in their nests and under the snow cover, and can be the main cause of mortality in vole populations (14). They depend almost exclusively on voles (9), but have a much lower intrinsic growth rate than their prey, and hence a strong but delayed numerical response to vole densities, resulting in delayed density-dependent predation pressure on vole populations (9, 15). Of the two species, the stoat is considered to be more of a generalist than the least weasel (9).

Generalist predators, exploiting a variety of food sources, are thought to have a stabilizing effect on the prey populations, preying on voles during the peak phase of the cycle, and switching to alternative prey when vole densities are low (16, 17). Because of this, the generalists have the ability to transmit the cyclic population dynamics of voles to their alternative prey populations (18, 19). According to diet analyses, the red fox (*Vulpes vulpes*) and the pine marten (*Martes martes*) are generalist predators in Fennoscandia (10, 11). They are thus expected to have a cycle-dampening effect (17).

82 Birds of prey may dampen or enhance cyclicity in their prey. Nomadic species are 83 able to travel long distances and nest where vole densities are high, i.e. have a direct 84 numerical response and dampen the vole cycle (13, 20); on the other hand, migratory 85 birds are not able to survey vole densities during the winter, and may rely on last season's 86 information to decide where to nest (21). The reproductive effort and success of the 87 resident raptors is dependent on current vole densities (22, 23). Therefore, avian 88 predators might respond to vole densities of the previous autumn (decision on where to 89 nest, recruitment of last year's young), spring (reproductive effort) or the current summer 90 (survival of fledglings).

91 The interactions between the vole and the predator communities of northern Europe 92 have been studied with mechanistic models and phenomenological time-series analyses 93 (e.g. 2, 17, 24) and large-scale, yet local, manipulative experiments (reviewed by 25, 26), 94 but they are not well described on a large temporal and geographic scale, let alone using 95 observational data. Predator-vole interactions are likely to depend on environmental 96 conditions and may thus be subject to spatial and temporal variation: e.g. snow cover may 97 influence the availability of voles to avian and larger mammalian predators (23), 98 temperatures may affect the energy requirements of predators (23, 27); and food 99 availability to voles will influence the relative contribution of predation on vole 100 population growth rates (28).

101 In the present study we aim to characterize the interactions between voles and the 102 specialist mammalian, the generalist mammalian, and the avian predators using animal 103 population monitoring data collected throughout Finland during 23 years. We will 104 estimate the time lags in the predator responses to vole densities as well as the predator 105 effects on vole population growth rates. Specifically, we test the hypothesis that 106 weakening vole-specialist predator interactions during winters are associated with the 107 collapse of the vole cycle. Finally, we use the data-derived parameter estimates to 108 simulate vole population dynamics under a number of scenarios to gauge the roles of 109 different predators in the boreal vole cycle.

- 110
- 111
- 112
- 113

114 Methods

115

116 <u>Vole population data</u>

117 Vole populations were censused using biannual snap trapping [in spring before the 118 reproductive season of voles in mid-March to mid-June, and in autumn after the 119 reproductive season in mid-August to mid-October (both times dependent upon 120 geographic location and seasonal phenology)] in forest and old-field habitats in 32 121 locations during 1986-2011 (Fig. 1, Fig. S1). Voles of the genera Microtus and Myodes 122 were included in the analyses. On average each trapping session included 289 trap nights 123 (range 30-1800). Trapping was conducted with standard metal mouse snap traps. At each 124 location, a mean of 50–100 traps were set either a) in a line, in clusters of three traps with 125 an inter-trap distance of 1–2m and an inter-cluster distance of 10–20m, or b) according to 126 the small quadrat method (29). Traps were set for 1-4 nights and checked and re-set if 127 necessary once a day. Regardless of the number of traps used per session, or the number 128 of consecutive trap nights, each trap effectively traps a standard-size area. Since the 129 density of traps (traps per unit area) does not change between sites or over time, our 130 trapping indices from different areas and times are comparable.

The vole data comprise the following species: *Microtus agrestis* (28%), *M. levis* (5%) and *M. oeconomus* (6%), and *Myodes glareolus* (57%), *M. rutilus* (3%), and *M. rufocanus* (1%). Density indices were calculated as $N = \log$ [(total number of voles trapped + 1) / trap nights * 100]. Seasonal vole population growth rates were calculated as $S_t - A_{t-1}$ (winter) and $A_t - S_t$ (summer), where *S* denotes spring vole density, *A* autumn vole density and t denotes year. Each vole time series was standardized to mean = 0 to 137 correct for potential trapping-site quality bias. We decided the pool all vole species 138 despite the ecological differences between *Myodes* and *Microtus* voles. We have analysed 139 the variation in the spatiotemporal dynamics separately for *Microtus* voles in their 140 principal habitat (old fields) and for *Myodes* voles in forests. The spatiotemporal patterns 141 in the population dynamics of the different genera parallel each other, and those obtained 142 with the pooled vole densities [see Table 1 in (8)]. Furthermore, the different species are 143 known to fluctuate in synchrony (8, 30) and be subject to predation by the same predators 144 (e.g. 31, 32). Therefore, the pooled data allow us to answer the study questions more 145 clearly than the genus-specific results would.

146

147 <u>Mammalian predator data</u>

148 We obtained density indices for the mammalian predators from the Finnish Game and 149 Fisheries Research Institute (33). Mammalian predator densities were monitored by 150 counting snow tracks on previously marked transects in winter (mid-January to mid-151 March) during 1989-2011. Triangles consisting of three 4-km transects were surveyed 152 and all mammal tracks crossing the transect were counted and identified to species one or 153 two days after a pre-check or snowfall. Annually ca. 800 triangles are monitored (Fig. 1 154 and S1). As weather conditions could influence the visibility of the snow tracks, the 155 protocol set by the Finnish Game and Fisheries Research Institute rigorously defines the 156 environmental circumstances under which the snow track counts may be conducted. 157 Firstly, the transect must be walked or skied twice - first to mark all existing tracks, then 158 at least 24 hours later to count all new tracks. This time of track accumulation cannot 159 include extreme cold temperatures, heavy winds or snowfall. Alternatively, tracks may be 160 counted without a preliminary marking round, 24-48 hours after a snowfall. In both cases, 161 the snow cover must be fine and soft enough to enable the smallest recordable animals, 162 least weasels, to leave identifiable tracks. These strict guidelines ensure that the weather 163 conditions during the snow track count are geographically and temporally consistent. The 164 degree of detectability of tracks is thus unlikely to differ between geographic areas.

The density index for a given species is calculated as $\log[(n_{i,t} + n_{min})/d]$, where 165 the $n_{i,t}\xspace$ is the number of tracks observed per 10 km of survey route at location i and year 166 167 t, n_{min} is the minimum observed non-zero n, and d is the number of days during which 168 the tracks accumulated. We included the densities of four mammalian predators and 169 aggregated the predator species into two groups based on their behaviour and 170 morphology: the small mustelids (the least weasel and the stoat) formed the specialist 171 predator group, and the larger mammalian predators (the red fox and the pine marten) the 172 generalist predator group (17). Density indices of both groups were calculated for each 173 vole trapping location by distance-weighted averaging (using all data points, with weight decreasing by distance²). The mammalian predator data were globally standardized to 174 175 mean = 0 to render the values of the different predator groups comparable.

176

177 <u>Avian predator data</u>

The data for avian predators were obtained from the Finnish Museum of Natural History (34). The monitoring scheme is organized in 25 areas (Fig. 1, Fig. S1), which together cover all of Finland. In each area, all known raptor territories are visited each spring and summer, and checked for nests from which eggs and later the chicks are counted. Raptor monitoring data were available from 1986 to 2011. We included data on the following 183 species, which prey on voles and which are relatively abundant in our study area: the 184 nomadic or migratory species Asio flammeus, Asio otus, Aegolius funereus, Glaucidium 185 passerinum, Falco tinnunculus, Circus cyaneus, and Buteo lagopus; and the resident 186 species Strix uralensis, Strix aluco, Bubo bubo, and Buteo buteo. Although it is known 187 that these species react slightly differently to vole abundances and differ in their 188 specialization in voles, their densities showed strong correlations (r > 0.8), which justified the calculation of a total avian predator density index as $\log[\frac{n_{i,t}c_{i,t}+2n_{i,t}}{s_{i,t}}]$, where 189 190 $n_{i,t}$ refers to the number of nesting pairs in area i and year t, $c_{i,t}$ to the average number of 191 chicks per nest in area i and year t, and $s_{i,t}$ to the number of territories surveyed in area i 192 and year t. The avian predator density index was calculated for each vole-trapping site by 193 averaging over all raptor-monitoring areas within a 50 km distance. Prior to combining 194 the avian time series, they were de-trended, as some showed potentially artificial 195 increasing trends due to increased nest-box availability. The avian predator density was 196 calculated for each vole-trapping site by averaging over all raptor-monitoring areas 197 within a 50 km distance.

198

199 Influence of predators on vole population growth rates

To estimate the spatial and temporal variation in the impact of the different predator groups on vole populations, we modelled vole population growth rates during winter (Model 1) and summer (Model 2) as a function of vole and predator indices. Mammalian predator indices were measured in winter, and avian predator indices in summer. We assumed the linear models

206
$$Y_{1,t} = S_t - A_{t-1} = a_1 + b_1 A_{t-1} + c_1 A_{t-2} + d_1 P_{1,t} + e_1 P_{2,t} + f_1 P_{3,t-1} + \varepsilon_{1,t}$$
 (Model 1)
207 $Y_{2,t} = A_t - S_t = a_2 + b_2 S_t + c_2 S_{t-1} + d_2 P_{1,t} + e_2 P_{2,t} + f_2 P_{3,t} + \varepsilon_{2,t}$ (Model 2)
208

where P_1 refers to the density index of the small mustelids, P_2 to the generalist mammalian predators, and P_3 to the avian predators.

Because we had no *a priori* knowledge of the geographic and temporal variation in predator-vole interactions, we began with a very flexible model, and then simplified the model based on the data. Initially, we allowed the parameters a - f to vary with time and space by including a latitude*longitude*(year + year²) interaction. After fitting these models, we simplified the models using AIC (Akaike Information Criterion, 35): all terms whose elimination would have resulted in an increase in AIC were retained in the final model.

We validated the models by dividing the data set randomly into a training set (50% of the data points) and a test set (50%), refitting the models to the training data, and using these models to predict the test data; this was repeated 50 times (Fig. S2). In addition, we assessed the performance of the models by simulating vole and predator dynamics using parameter estimates from the models; adequate models should be able to create realistic dynamics.

Based on the models, we calculated the relative contributions of the different predator groups and of the non-predation-attributable density dependence to the variation in vole population growth rates for each trapping site and year as a fraction of the total variation. To do so, we decomposed the total variance (example for Model 1) as

$$Var(Y_{1,t}) = b^{2}Var(A_{t-1}) + c^{2}Var(A_{t-2}) + d^{2}Var(P_{1}) + e^{2}Var(P_{2}) + f^{2}Var(P_{3})$$

+ $2bcCov(A_{t-1}, A_{t-2}) + 2bdCov(A_{t-1}, P_{1}) + 2beCov(A_{t-1}, P_{2})$
+ $2bfCov(A_{t-1}, P_{3}) + 2cdCov(A_{t-2}, P_{1}) + 2ceCov(A_{t-2}, P_{2})$
+ $2cfCov(A_{t-2}, P_{3}) + 2deCov(P_{1}, P_{2}) + 2dfCov(P_{1}, P_{3})$
+ $2efCov(P_{2}, P_{3}) + \sigma^{2}$,

229

where the variances and co-variances are calculated from the whole data set, σ^2 is the variance of the residual term ε , and the model parameter values a - f depend on sampling location and year.

To simplify the interpretation of the results, rather than considering the relative contributions of co-variances separately, we decided to treat the co-variances by assigning half of the co-variances to each of the terms involved. As an example, the variance explained by the small mustelids was calculated as

237

$$Var_{P1} = (d^{2}Var(P_{1}) + bdCov(A_{t-1}, P_{1}) + cdCov(A_{t-2}, P_{1}) + deCov(P_{1}, P_{2}) + dfCov(P_{1}, P_{3})) / Var(Y_{1,t})$$

238

These values were summarized to represent three regions by averaging over the trapping locations in each: northern Finland (above the 66^{th} latitude), southwestern (< 64^{th} latitude and < 25^{th} longitude) and eastern (> 27^{th} longitude) Finland (Fig. 1).

242

243

245 Influence of vole population densities on predator abundance indices

Using the same initial spatiotemporal structure as in Models 1 and 2, we modelled the predator indices as a function of current and past vole densities to determine the magnitude of and the time lags in the predators' responses:

249

250
$$Y_{3,t} = a_3 + b_3 A_{t-1} + c_3 S_{t-1} + d_3 A_{t-2} + \varepsilon_{3,t}$$
, (Model 3a: Mammalian predators)

251
$$Y_{3,t} = a_3 + b_3 S_t + c_3 A_{t-1} + d_3 S_{t-1} + \varepsilon_{3,t}$$
 (Model 3b: Avian predators)

252

We did not include previous predator densities in the predator models because after accounting for the vole-cycle-attributable autocorrelation, no temporal autocorrelation was left in the predator time series. AIC-determined model reduction was performed as explained above. The relative contributions of vole densities at different time lags to the predator densities were calculated as

258

$$Var_{A_{t-1}} = (b^{2}Var(A_{t-1}) + bcCov(A_{t-1}, S_{t-1}) + bdCov(A_{t-1}, A_{t-2}))/(b^{2}Var(A_{t-1}))$$
$$+ c^{2}Var(S_{t-1}) + d^{2}Var(A_{t-2}) + 2bcCov(A_{t-1}, S_{t-1}))$$
$$+ 2bdCov(A_{t-1}, A_{t-2}) + 2cdCov(S_{t-1}, A_{t-2}) + \sigma^{2})$$

259

260 The values were summarized to regions (Fig. 3) as explained above.

261

262 <u>Roles of the different predators in the boreal vole cycle: simulation</u>

We used the parameter estimates from models 1-3 to simulate vole and predator population dynamics. The simulations were used both for model validation, i.e. to 265 confirm that the models were capable of reproducing the population dynamics observed 266 in different locations and time points, and for scenario simulations, i.e. to investigate the 267 roles of the different predators in vole population dynamics. We focused on three 268 geographic regions, which we had previously discovered to exhibit distinctly different 269 vole population dynamics: the north, the southwest, and the east (8). Using the parameter 270 estimates for the geographic locations and the year 2011 (the last available year with full 271 data records), we simulated 1000 years of vole and predator time series under eight 272 different scenarios in which one, two or all predator groups were removed by setting their 273 density to the minimum observed value in the data set.

274 We estimated the direct and delayed density dependence of vole population growth 275 rates in the simulated time series by regressing the seasonal vole population growth rates 276 against the current and the 1-year-lagged vole densities (8). To assess the variability in 277 the model predictions, we divided the 1000-year time series into 25-year sections, and 278 fitted autoregressive models to each section. Consensus density dependence values were 279 obtained by averaging over the results from the 40 sections, and annual density 280 dependence was calculated from the seasonal density dependence values as in (8). From 281 each 25-year section, we calculated the standard deviation of the population densities (s-282 index) as an index of amplitude, and seasonality as the difference between the average 283 summer and average winter population growth rates, and averaged these over all sections. 284 The type of population dynamics was inferred from the density dependence values, 285 autocorrelation values, and from visual inspection of the time series. All statistical 286 analyses were conducted with R (36).

288 **Results**

289 Model validation

290

291 Our models performed well in model validation: they produced realistic predator-vole 292 dynamics capturing the spatial and temporal variation in vole population dynamics 293 (compare Fig. 4 to ref. 8). When refitted with 50% of the data points, they predicted the 294 remaining 50% fairly well (Fig. S2). Only the small mustelid model's performance was 295 somewhat unsatisfactory, as the correlation between the observed and the predicted small 296 mustelid indices was only 0.42. The final best models based on the model selection are 297 presented in Tables S1-S4. 298 299 Spatiotemporal variation in predator-vole interactions 300

301 The relative influences of the different predator groups on vole population growth rates 302 showed substantial variation over the years and regions (Fig. 2). In the north, the 303 influence of the small mustelids on vole populations showed an increasing temporal trend 304 during both seasons, and they are currently estimated to be the strongest force affecting 305 the winter population growth rates of voles (Fig. 2a, b). According to our models, the 306 generalist predators influenced vole populations only during summers in the north, and 307 the relative impact of the avian predators was declining, particularly during winters (Fig. 308 2a, b).

309 Predators were estimated to have a modest impact on the winter population growth310 rates of voles in the southwest (Fig. 2c). However, the relative contribution of the small

311 mustelids on the summer population growth rates of voles appeared to have increased 312 considerably (Fig. 2d). The generalist predators were estimated to have very little impact 313 on vole populations in the southwest, and the avian predators to have a modest, and 314 possibly declining, impact during both seasons (Fig. 2c, d).

The factors affecting the winter population growth rates of voles in the east were similar to those in the north: a strong avian predator influence substituted in the recent years by a rapidly increasing small mustelid influence (Fig. 2e). However, during summers the generalist and avian predators were estimated to be a stronger force than the small mustelids (Fig. 2f).

320 The dependence of the predator indices on vole population densities tended to be 321 strongest, and the delays longest, in the north (Fig. 3). Particularly in the north and 322 southwest, there appeared to be a temporal trend of shortening delays in the numerical 323 responses of the predators. The small mustelids responded to all vole densities measured 324 during the previous 18 months, the longest delay being the weakest. The larger 325 mammalian predators responded to vole densities with a 10-month delay in the north, and 326 with a 5-month delay in the south. The avian predators responded to vole densities with a 327 time lag of 2-10 months.

328

329 Is predation necessary for cyclic vole population dynamics?

330

Our model correctly predicted a regular, high-amplitude 5-year cycle in the North for the
year 2011 (Fig. 4a,b black symbol; Fig. S3). Removing either the small mustelids or the
avian predators weakened the delayed density dependence (Fig. 4a, pink and lightblue

334 symbols) and amplitude (Fig. 4b), and weakened the cycle (Fig. S3). The seasonality 335 disappeared in the absence of the small mustelids, regardless of which predators 336 remained (Fig. 4c, pink, orange, darkblue and gray symbols), suggesting that the major 337 cause of winter mortality in the north is predation by the small mustelids (Fig. 2a). 338 Removing both the avian predators and the small mustelids, with or without the larger 339 mammalian predators, weakened the delayed density dependence to the extent that the 340 vole cycle collapsed (Fig. 4a, orange and gray symbols; Fig. S3), and the amplitude was 341 clearly reduced (Fig. 4b). The generalist mammalian predators did not influence vole 342 population dynamics to a great extent in the north (Fig. 4a, b, c, yellow symbols).

343 The model predicted a 3-to-4-year cycle in southwestern Finland (Fig. 4d, black 344 symbol; Fig. S4), with a lower amplitude than in the north (Fig. 4e). The removal of the 345 small mustelids had a strong impact on vole population dynamics, regardless of whether 346 the predators remained present: both direct and delayed density dependence were 347 weakened to the extent that the vole cycle collapsed (Fig. 4d, pink, orange, darkblue, and 348 gray symbols; Fig. S4) into completely seasonal (Fig. 4f), high-amplitude dynamics (Fig. 349 4e). The small mustelids were capable of maintaining cyclic vole population dynamics in 350 the absence of the other predators: removing the generalist and the avian predators 351 increased the cycle period (Fig. 4d, red symbols; Fig. S4) and weakened the seasonality 352 (Fig. 4f).

The model predicted irregular dynamics in eastern Finland (Fig. 4g; Fig. S5). Predator removal had no effect on the density dependence (Fig. 4g). Removing the small mustelids reduced, and removing the generalist mammals increased the seasonality and

356	the amplitude (Fig. 4h, i, pink and yellow symbols); removing the avian predators had no
357	influence on vole population dynamics (Fig. 4h, i, lightblue symbols).

- 358
- 359 Changes within the predator community
- 360

361 A high relative abundance of the stricter vole specialist, the least weasel, in relation to the 362 semi-generalist stoat, coincided with cyclic vole dynamics (Fig. S6). In western Finland, 363 with continuously cyclic vole dynamics, the least weasel has been more abundant than 364 the stoat; in northern Finland the relative abundance of the least weasel was very low 365 during the non-cyclic period, and is currently increasing together with the strengthening 366 cycle. Most impressively, the relative abundance of the least weasel peaked in synchrony 367 with the vole density peaks in the north: the stoat dominated during cyclic lows, and the 368 least weasel when voles were abundant. A similar pattern was observed in the east, 369 althought there the increasing relative abudance of the least weasel was evidently not 370 sufficient to strengthen the vole cycle. One possible explanation is the relative abundance 371 of the generalist mammalian predators, which in eastern Finland was in favor of the pine 372 marten, while the red fox was relatively more abundant in western Finland.

373

374 Discussion

We analysed predator-vole interactions comprehensively over a large geographic area (ca. 300 000 km²) and a long time period (26 years), capturing the return of the highamplitude vole cycle in the north as well as the collapse of the cycle in the east. Our

378 results show that the predator-vole interactions vary temporally and geographically, and379 that this variation explains many of the observed changes in vole population dynamics.

Not surprisingly, our model identified the small mustelids as key players in the boreal vole cycle: their numerical response was estimated to be delayed and sufficiently strong to cause negative delayed density dependence in vole populations, supporting earlier results (e.g. 9, 15, 24). Earlier mechanistic modelling studies on vole-predator interactions have suffered from the lack of predator time series to confirm the results. The fact that very different approaches, based on different types of data and models, all lead to the same conclusion offers strong support for the specialist predator hypothesis.

387 In the north, the small mustelids were estimated to be currently the strongest force 388 affecting the winter population growth rates of voles. However, their influence on vole 389 populations appears not to be restricted to the winter season, but occurs, increasingly, 390 during summers, as well. The increase in summer impact coincides with increasing 391 summer precipitation in the north (8). In the coastal southwest, where winters are milder 392 and shorter than in the more continental east and in the north, the small mustelids appear 393 to exert their influence on vole populations mainly during summers. Hence, mild winters 394 appear not to weaken the overall impact of the specialist predators on vole populations. 395 Furthermore, as the vole cycle has collapsed in the east despite a strong relative influence 396 of the small mustelids during winters, it appears that predation by the small mustelids in 397 winter is alone not sufficient to create cyclic vole dynamics. Rather, a sufficient impact of 398 the small mustelids during summers may be an elemental part of the vole cycle, 399 contributing to the summer declines which characterize cyclic, but not non-cyclic, vole 400 populations (3, 37, 38). In addition to the small mustelids, the avian predators were found

401 to influence vole population dynamics, and to be an important source of delayed density402 dependence in vole populations (see also 21).

403 Generalist predators are usually thought to dampen or inhibit cyclic dynamics in 404 their prey populations (17). However, the red fox is also considered strongly dependent 405 on voles, to the extent that the red fox game bag index has been used as a surrogate for 406 vole density (e.g., 39). Yet another view is that vole populations are not influenced by the 407 generalist predators, as previously shown for the red fox (18). According to our data, the 408 generalists did not depend strongly on voles, nor did they markedly influence vole 409 populations, especially in southern Finland. In the north, however, where alternative food 410 is scarce and where the climate is unfavourable for the red fox (27), the generalist 411 predator index responded occasionally quite strongly to the spring densities of voles and 412 influenced their summer population growth rates. This suggests that in unfavourable 413 environments, voles form a significant food source to fox cubs in their early life. 414 However, the overall impact of the generalists on vole population dynamics was weak.

415 All predators appear to be responding to vole densities with shortening time lags, 416 which may contribute to increasing direct, and weakening delayed density dependence in 417 vole populations. However, this may not unequivocally be the case. The predator 418 populations are monitored only once a year, which makes it difficult to estimate the time 419 lags in their responses and the timing of their impact on the vole populations. It is 420 possible for e.g. the small mustelids to be dependent on the spring densities of voles, 421 while influencing the vole populations during the following winter, or to be dependent on 422 the autumn densities of voles and to influence vole populations during the following 423 summer. In both cases, the impact on the density dependence of vole population growth

rates would be the same. The changes in the time lags of the predators' numerical responses may also be due to temporal variations in the relative abundances of the different species. Different raptor species respond to vole densities with different time lags (40), and the stoat responds to vole densities with a shorter time lag than the least weasel (15). Furthermore, the ability of the predators to track vole abundances and to adjust their reproductive effort accordingly may depend on weather conditions, which could lead to the observed temporal variation in the responses.

431 The reliability of the snow track indices is a matter of debate, especially with 432 respect to the small mustelids (discussed recently in 15, 42), Our results indicate a 433 marked amount of measurement error in the small mustelid index, as only ca. 50% of 434 variation in the index was attributable to the vole abundances, although these predators 435 are known to rely heavily on voles (9). Furthermore, a large fraction of the variation in 436 vole population growth rates was unexplained by the predator indices, although predation 437 has been shown to be a major cause of mortality in vole populations (14). The generalist 438 and avian predator indices are likely to be more accurate than the small mustelid index: 439 both indices behaved in our analyses as expected based on earlier studies, the generalists 440 cannot move under the snow cover, and the avian predator index is derived from counts 441 of the animals themselves. Measurement error in the predator indices is likely to weaken, 442 but not strenghten, the estimated interactions between voles and the predators; our 443 estimates are therefore conservative and the interactions may be stronger in reality. 444 Because of the unknown amount of measurement error in the predator indices, some of 445 the unexplained density dependence in vole population growth rates is most likely

attributable to predation, although undoubtedly other factors, such as food supply (28),also influence vole populations.

448 According to our results, predation, by the small mustelids in the southwest and by 449 the whole predator guild in the north, is a necessary contributor to the regular, high-450 amplitude vole cycle in northern Europe. The small mustelid-vole interaction is not 451 restricted to winters, confirming our previous finding that mild winters do not necessarily 452 lead to a collapse of the vole cycle (8). The observed strengthening of delayed density 453 dependence in vole populations coincided with strengthening small mustelid influence on 454 the summer population growth rates of voles. A strong impact of the small mustelids 455 during summers appears important to cyclic vole dynamics.

456

457 Acknowledgements

458 We thank all field assistants who contributed to collecting the data and Mari Lyly for the

459 illustrations in Figure 1. The study was financially supported by the Academy of Finland

460 (grant no. 133495 to OH, 250709 to EKor, 218107 and 257340 to EKos, and 250243 and

461 250444 to OO); EU grant FP7-261504 EDENext (HH); European Research Council,

462 ERC Starting Grant 205905 (OO).

463

464 Data accessibility

465 Data are archived in Dryad (doi:10.5061/dryad.h3bt7).

466

467

468

470	Re	ferences
471		
472		
473	1.	Berryman A, ed (2002) Population cycles: The case for trophic interactions (Oxford
474		University Press, New York).
475		
476	2.	Hanski I, et al. (2001) Small-rodent dynamics and predation. <i>Ecology</i> 82:1505-1520.
477	2	
478	3.	Korpimaki E, et al. (2005) Vole cycles and predation in temperate and boreal zones
4/9		of Europe. J Anim Ecol /4:1150-1159.
480	4	
481	4.	Sundell J, et al. (2004) Large-scale spatial dynamics of vole populations in Finland
482		revealed by the breeding success of vole-eating avian predators. J Anim Ecol /3:16/-
483		1/8.
404 405	5	Handen I. Dondoon D. Voccoor NC. Imp DA (2008) Imports of differential prov
405	5.	dynamics on the notantial recovery of andengared arctic for nonulations. <i>LAnnl Eacl</i>
400		45.1086 1002
407		45.1080-1075.
489	6	Ims RA Henden I Killengreen ST (2008) Collapsing population cycles Trands Ecol
490	0.	<i>Evol</i> 23:79-86
491		
492	7	Cornulier T et al. (2013) Europe-wide dampening of population cycles in keystone
493	<i>,</i> .	herbivores. Science 340:63-66.
494		
495	8.	Korpela K, et al. (2013). Nonlinear effects of climate on boreal rodent dynamics:
496		mild winters do not negate high-amplitude cycles. <i>Glob Change Biol</i> 19:697-710.
497		
498	9.	Korpimäki E, Norrdahl K, Rinta-Jaskari T (1991) Responses of stoats and least
499		weasels to fluctuating food abundances - is the low phase of the vole cycle due to
500		mustelid predation. Oecologia 88:552-561.
501		
502	10	. Dell'Arte GL, Laaksonen T, Norrdahl K, Korpimäki E (2007) Variation in the diet
503		composition of a generalist predator, the red fox, in relation to season and density of
504		main prey. Acta Oecol 31:276-281.
505		
506	11	. Helldin J (2000) Seasonal diet of pine marten Martes martes in southern boreal
507		Sweden. Acta Theriol 45:409-420.
508		
509	12	. Korpimäki E, Sulkava S (1987) Diet and breeding performance of Ural Owls Strix
510		uralensis. Ornis Fennica 64:57-66.
511		
512	13	. Korpimäki E, Norrdahl K (1991) Numerical and functional responses of kestrels,
513		short-eared owls, and long-eared owls to vole densities. <i>Ecology</i> 72:814-826.
514		

515 516	14. Norrdahl K, Korpimäki E (1995) Mortality factors in a cyclic vole population. <i>Proc R Soc Lond B</i> 261:49-53.
517 518 510	15. Sundell J, et al. (2013) Numerical response of small mustelids to vole abundance:
519 520	delayed of hot? $Oikos$ 122:1112-1120.
521 522 523	16. Erlinge S, Agrell J, Nelson J, Sandell M (1991) Why are some microtine populations cyclic while others are not. <i>Acta Theriol</i> 36:63-71.
524 525 526	 Hanski I, Hansson L, Henttonen H (1991) Specialist predators, generalist predators, and the microtine rodent cycle. J Anim Ecol 60:353-367.
527 528 529	18. Lindström ER, et al. (1994) Disease reveals the predator: sarcoptic mange, red fox predation, and prey populations. <i>Ecology</i> 75:1042-1049.
530 531 532	19. Kjellander P, Nordström J (2003) Cyclic voles, prey switching in red fox, and roe deer dynamics–a test of the alternative prey hypothesis. <i>Oikos</i> 101:338-344.
533 534 535	20. Korpimäki E, Norrdahl K (1991) Do breeding nomadic avian predators dampen population fluctuations of small mammals. <i>Oikos</i> 62:195-208.
536 537 538	 Norrdahl K, Korpimäki E (2002) Seasonal changes in the numerical responses of predators to cyclic vole populations. <i>Ecography</i> 25:428-438.
539 540 541 542	22. Karell P, et al. (2009) Population dynamics in a cyclic environment: consequences of cyclic food abundance on tawny owl reproduction and survival. <i>J Anim Ecol</i> 78:1050-1062.
543 544 545 546	 23. Lehikoinen A, et al. (2011) The impact of climate and cyclic food abundance on the timing of breeding and brood size in four boreal owl species. <i>Oecologia</i> 165:349-355.
547 548 549	24. Hanski I, Korpimäki E (1995) Microtine rodent dynamics in northern Europe - parameterized models for the predator-prey interaction. <i>Ecology</i> 76:840-850.
550 551 552	25. Korpimäki E, Brown PR, Jacob J, Pech RP (2004). The puzzles of population cycles and outbreaks of small mammals solved? <i>BioScience</i> 54:1071-1079.
553 554 555	26. Sundell J (2006) Experimental tests of the role of predation in the population dynamics of voles and lemmings. <i>Mamm Rev</i> 36:107-141.
556 557 558	27. Barton KA, Zalewski A (2007) Winter severity limits red fox populations in Eurasia. <i>Global Ecol Biogeogr</i> 16:281-289.
559 560	28. Huitu O, et al. (2003) Winter food supply limits growth of northern vole populations in the absence of predation. <i>Ecology</i> 84:2108-2118.

561	
562 29 563	9. Myllymäki A, Paasikallio A, Pankakoski E, Kanervo V (1971) Removal experiments on small quadrats as a means of rapid assessment of the abundance of small
564 565	mammals. Ann Zool Fenn 8:177-185.
565 566 30 567	9. Huitu O, Norrdahl K, Korpimäki E (2004) Competition, predation and interspecific synchrony in cyclic small mammal communities. <i>Ecography</i> 27:197-206.
569 31 570 571	. Korpimäki E (1992) Diet composition, prey choice and breeding success of long- eared owls: effects of multiannual fluctuations in food abundance. <i>Can J Zool</i> 70:2373-2381.
573 32 574 575	2. Sundell J, Eccard J, Tiilikainen R, Ylönen H (2003) Predation rate, prey preference and predator switching: experiments on voles and weasels. <i>Oikos</i> 101:615-623.
576 33 577 578	E. Lindén H, Helle E, Helle P, Wikman M (1996) Wildlife triangle scheme in Finland: methods and aims for monitoring wildlife populations. <i>Finnish Game Res</i> 49:4-11.
579 34 580 581	. Saurola P (2008) Monitoring birds of prey in Finland: A summary of methods, trends, and statistical power. <i>Ambio</i> 37:413-419.
582 35 583 584	5. Burnham KP, Anderson DR (2004) Multimodel inference: understanding AIC and BIC in model selection. <i>Sociol Method Res</i> 33:261-304.
585 36 586 587	5. R Development Core Team (2011) <i>R: A language and environment for statistical computing</i> . (R Foundation for Statistical Computing, Vienna, Austria).
588 37 589 590	⁷ . Hansson L, Henttonen H (1985). Gradients in density variations of small rodents - the importance of latitude and snow cover. <i>Oecologia</i> 67:394-402.
591 38 592 593	B. Hansson L, Henttonen H (1988) Rodent dynamics as community processes. <i>Trends Ecol Evol</i> 3:195-200.
594 39 595 596 597	 Henden J, Ims RA, Yoccoz NG (2009) Nonstationary spatio-temporal small rodent dynamics: evidence from long-term Norwegian fox bounty data. <i>J Anim Ecol</i> 78:636-645.
598 40 599 600	 Korpimäki E (1994) Rapid or delayed tracking of multiannual vole cycles by avian predators. J Anim Ecol 63:619-628.
601 41 602 603 604 605	. Hellstedt P, Sundell J, Helle P, Henttonen H (2006) Large-scale spatial and temporal patterns in population dynamics of the stoat, <i>Mustela erminea</i> , and the least weasel, <i>M. nivalis</i> , in Finland. <i>Oikos</i> 115:286-298.

606 **Figure captions**

607

608 Figure 1. Data collection locations: vole trapping locations (map a), mammalian predator 609 snow-track-monitoring locations (map b), and avian predator monitoring areas (map c). 610 Letters in map a denote the three regions from which results were summarized (N=north, 611 SW=southwest, E=east). 612 613 Figure 2. Relative contributions of predators and non-predation-attributable density 614 dependence ("Delayed DD" and "Direct DD") to the summer and winter population 615 growth rates of voles, estimated with Models 1 and 2 and averaged to northern, south-616 western and eastern Finland, as in Figure 1.

617

618 Figure 3. Relative contributions of vole densities at different time lags to predator 619 densities, estimated with Models 3a (mammalian predators) and 3b (avian predators) and 620 averaged to northern, south-western and eastern Finland, as in Figure 1. Mammalian 621 predator densities were monitored in winter, and therefore the time lags presented are ca. 622 5 months (vole density in autumn_{t-1}), ca. 10 months (vole density in spring_{t-1}), and ca. 17 623 months (vole density in autumn_{t-2}). Avian predator densities were monitored in summer, 624 and the time lags are ca. 2 months (vole density in spring_t), ca. 9 months (vole density in 625 autumn_{t-1}), and ca. 14 months (vole density in spring_{t-1}).

626

Figure 4. Results of simulations. Parameter estimates from Models 1-3 were used to
simulate vole (shown in figure) and predator (not shown) population dynamics under
different predation scenarios. The Full model scenario refers to a simulation with all

630 parameters included in the model, as thus represents the model prediction for current 631 population dynamics. In the different predation scenarios, the densities of the different 632 predator groups were set to the minimum observed value. Panels a-c show the simulated 633 vole time series in density dependence space. Multiannual cycles exist under the parabola 634 with cycle length increasing from left to right, and irregular dynamics above the parabola. 635 Panels d-f show the s-indices (averages \pm sd) and panels g-i show the seasonality in vole 636 population growth rates, calculated as the difference between average summer and 637 average winter population growth rates.









Appendices

Supplementary Figure Legends

Supplementary Figure S1. Average densities of vole (spring and autumn) and predator (one annual density) populations in northern (above the 66^{th} latitude), south-western (< 64^{th} latitude and < 25^{th} longitude), and eastern Finland (> 27^{th} longitude).

Supplementary Figure S2. Model-predicted vs. observed values. The data were randomly divided (50 times) into a training set (50%), to which the models were fitted and which was used to predict the values in the remaining 50%. (a) Winter population growth rates of voles. (b) Summer population growth rates of voles. (c) Small mustelid index. (d) Generalist predator index. (e) Avian predator index.

Supplementary Figure S3. Sections of simulated time series and the autocorrelation plots calculated based on the simulated time series. The simulations were based on parameter values from Models 1-3 for northern Finland.

Supplementary Figure S4. Sections of simulated time series and the autocorrelation plots calculated based on the simulated time series. The simulations were based on parameter values from Models 1-3 for southwestern Finland.

Supplementary Figure S5. Sections of simulated time series and the autocorrelation plots calculated based on the simulated time series. The simulations were based on parameter values from Models 1-3 for eastern Finland.

Supplementary Figure S6. Relative abundances of species within the small mustelid (top row) and the generalist predator (bottom row) groups in the different regions (black lines), and autumn vole densities (red lines).

Supplementary Tables

Supplementary Table 1. Best model (in AIC-based model selection) for the winter population growth rate of voles (year t). Latitude, longitude, and year were scaled to vary between -1 and 1. A = autumn vole density; P_1 = small mustelid density (winter); P_2 = generalist mammalian predator density (winter); P_3 = avian predator density (summer).

Parameter	Estimate	Std. Error	t-value	p-value
Intercept	-0.51	0.12	-4.30	<0.0001
A _{t-1}	-0.78	0.09	-8.28	<0.0001
A _{t-2}	-0.33	0.05	-6.10	<0.0001
P _{1.t}	-0.09	0.07	-1.15	0.25
$P_{2,t}$	0.08	0.08	1.10	0.27
P _{3. t-1}	-0.86	0.24	-3.62	<0.001
Year	-0.36	0.20	-1.84	0.07
Year ²	-0.15	0.27	-0.57	0.57
Latitude	-0.46	0.20	-2.33	0.02
Longitude	0.28	0.26	1.05	0.29
Year: At-1	0.42	0.13	3.25	<0.01
$Year^2: A_{t-1}$	0.44	0.28	1.59	0.11
Year: At-2	0.18	0.10	1.87	0.06
Year: P ₁	-0.31	0.12	-2.61	0.01
$Year^2: P_1$	0.01	0.21	0.04	0.97
Year: P ₃ t	0.85	0.48	1.78	0.08
Latitude: At-1	-0.02	0.14	-0.14	0.89
Latitude: P1 +	0.21	0.13	1.63	0.10
Latitude: P_{2+1}	0.44	0.31	1.43	0.15
Year:Latitude	0.30	0.31	0.95	0.34
Year ² ·Latitude	-0.66	0.45	-1 47	0.14
	-0.47	0.25	-1.88	0.06
Longitude: At a	0.00	0.09	-0.05	0.96
Longitude: P ₁	0.00	0.00	1 65	0.00
Longitude: $P_{2,t}$	0.19	0.10	1.63	0.10
Longitude: $P_{2,1}$	-0.13	0.45	-0.30	0.77
Year: Longitude	-0.72	0.40	-1 81	0.07
Year ² ·Longitude	-0.94	0.68	-1.39	0.16
Latitude: Longitude	0.72	0.00	1 48	0.10
A ·· Year: Latitude	0.12	0.40	0.62	0.14
A. Year ² latitude	0.12	0.13	2 29	0.04
	-0.28	0.42	-1 50	0.02
<i>P</i> . :Year ² :Latitude	-0.77	0.15	-2 14	0.10
$P_{0,1}$: Year: Latitude	-0.35	0.58	-0.61	0.00
	0.55	0.34	1 96	0.04
	1 11	0.75	1.00	0.00
A o'Year'l ongitude	0.30	0.73	1.45	0.14
	-0.42	0.17	-1 60	0.00
$P_{1,t}$. Year ² : I ongitude	-0. 4 2 _1 1/	0.20	-3.42	~0.001
$P_{1,t}$. Yoar: Longitude	-0.67	0.00	-0.74	0.001
A : l opgitudo: l otitudo	-0.07	0.90	1 25	0.40
A_{t-1} . Longitude: Latitude	-0.02	0.40	-1.55	0.10
$P_{1,t}$. Latitude. Longitude	-0.10	0.23	-0.77	0.44
P _{3,t-1} .Latitude.Longitude	0.65	0.00	1.29	0.20
Year ² d atituded anaitude	-0.76	0.07	-1.14	0.25
	-1.07	1.20	-1.31 1.24	0.19
A_{t-1} . Teal. Lallude. Longitude		0.03	1.34	0.10
At-1. Teal .Lallude:Longitude	2.Uð	1.30		0.13
	-0.66	0.44	-1.49	0.14
$\mathcal{P}_{3,t-1}$: Year: Latitude: Longitude	-2.40	1.28	-1.87	0.06

Supplementary Table 2. Best model (in AIC-based model selection) for the summer population growth rate of voles (year t). Latitude, longitude, and year were scaled to vary between -1 and 1. S =spring vole density; $P_1 =$ small mustelid density (winter); $P_2 =$ generalist mammalian predator density (winter); $P_3 =$ avian predator density (summer).

Parameter	Estimate	Std. error	t-value	p-value
Intercept	0.58	0.11	5.36	<0.0001
St	-0.47	0.08	-5.92	<0.0001
S _{t-1}	-0.26	0.04	-6.59	<0.0001
P _{1. t}	-0.08	0.05	-1.82	0.07
$P_{2,t}$	-0.23	0.10	-2.18	0.03
$P_{3,t}^{-,\tau}$	0.01	0.30	0.02	0.99
Year	-0.10	0.19	-0.54	0.59
Year ²	0.02	0.31	0.06	0.95
Latitude	0.33	0.21	1.63	0.10
Longitude	0.20	0.22	0.93	0.35
Year:St	-0.02	0.08	-0.24	0.81
Year ² :St	-0.02	0.22	-0.09	0.93
Year P ₁	-0.13	0.08	-1 74	0.08
Year: $P_{2,t}$	-0.20	0.00	-1 67	0.00
$Y_{ear}^2 \cdot P_{ar}$	0.20	0.12	1.07	0.10
Year: Pol	0.00	0.51	0.36	0.14
$V_{ear}^2 \cdot P_{ear}$	0.10	0.01	0.00	0.72
Latituda: S	0.10	0.50	3.50	~0.00
Latitudo: D	0.40	0.14	3.00	<0.001
Latitudo: P_{-}	-0.24	0.00	-2.80	<0.003
Latitude: $P_{2,t}$	-0.30	0.13	-2.00	0.01
Voord otitudo	-0.40	0.40	-1.10	0.25
Year ² :Latitude	0.04	0.52	0.11	0.91
	-0.40	0.54	-0.90	0.37
Longitude.St	0.53	0.20	2.59	0.01
Longitude: St-1	0.13	0.07	1.90	0.06
Longitude. $P_{1,t}$	0.30	0.10	2.95	<0.01
Longitude: $P_{2,t}$	-0.61	0.17	-3.54	<0.001
Longitude: $P_{3,t}$	0.90	0.59	1.53	0.13
	-0.46	0.31	-1.46	0.15
Year-:Longitude	0.38	0.56	0.67	0.50
Latitude:Longitude	0.63	0.42	1.50	0.14
St: Year ² :Latitude	-0.86	0.37	-2.35	0.02
P _{3,t} :Year:Latitude	-0.55	0.62	-0.89	0.37
P _{3,t} :Year ² :Latitude	2.99	1.15	2.60	0.01
St-1: Year:Longitude	-0.28	0.14	-1.95	0.05
St-1: Year ² :Longitude	-1.12	0.51	-2.21	0.03
P _{1,t} : Year:Longitude	0.57	0.12	4.61	<0.0001
P _{3,t} :Year:Longitude	-0.66	0.86	-0.77	0.44
P _{3,t} :Year ² :Longitude	1.47	1.61	0.91	0.36
St:Latitude:Longitude	1.28	0.39	3.27	<0.01
P _{1,t} : Latitude:Longitude	0.34	0.19	1.83	0.07
P _{2,t} : Latitude:Longitude	-1.18	0.30	-3.98	<0.0001
P _{3,t} : Latitude:Longitude	0.47	0.87	0.54	0.59
Year:Latitude:Longitude	-0.62	0.55	-1.14	0.26
Year ² :Latitude:Longitude	-0.19	1.03	-0.19	0.85
St:Year ² :Latitude:Longitude	-2.76	0.90	-3.06	<0.01
P _{3,t} : Year:Latitude:Longitude	-1.62	1.17	-1.38	0.17
P_{3t} :Year ² :Latitude:Longitude	3.90	2.48	1.58	0.12

Supplementary Table 3. Best model (in AIC-based model selection) for the winter density index of the small mustelids (year t). Latitude, longitude, and year were scaled to vary between -1 and 1. A = autumn vole density; S = spring vole density.

Parameter	Estimate	Std. error	t-value	p-value
Intercept	0.01	0.11	0.08	0.94
A_{t-1}	0.19	0.10	1.88	0.06
S _{t-1}	0.10	0.10	1.07	0.28
A _{t-2}	0.22	0.08	2.82	<0.01
Year	-0.59	0.10	-5.76	<0.0001
Year ²	0.50	0.28	1.76	0.08
Latitude	0.50	0.12	4.34	<0.0001
Longitude	-0.59	0.20	-2.90	<0.01
Year ² :Longitude	1.61	0.45	3.56	<0.001
Latitude:Longitude	0.24	0.24	1.02	0.31
A _{t-1} :Year	0.35	0.10	3.38	<0.001
A _{t-1} :Year ²	-0.43	0.24	-1.74	0.08
A _{t-1} :Latitude	-0.13	0.10	-1.23	0.22
A _{t-1} :Longitude	0.31	0.19	1.63	0.10
S _{t-1} :Year	-0.17	0.10	-1.72	0.09
S _{t-1} :Year ²	0.58	0.24	2.39	0.02
S _{t-1} :Latitude	0.22	0.10	2.22	0.03
S _{t-1} :Longitude	-0.32	0.15	-2.19	0.03
A _{t-2} :Year ²	-0.31	0.20	-1.54	0.12
A _{t-2} :Longitude	0.30	0.13	2.24	0.03
A _{t-1} :Year ² :Longitude	-0.97	0.35	-2.74	0.01
A _{t-1} : Latitude:Longitude	-0.42	0.25	-1.67	0.10
S _{t-1} :Year ² :Longitude	0.95	0.34	2.78	0.01
At-2:Year ² :Longitude	-0.66	0.35	-1.89	0.06

Supplementary Table 4. Best model (in AIC-based model selection) for the winter density index of the generalist mammalian predators (year t). Latitude, longitude, and year were scaled to vary between -1 and 1. A = autumn vole density; S = spring vole density.

Parameter	Estimate	Std. error	t-value	p-value
Intercept	0.06	0.09	0.64	0.52
A _{t-1}	-0.05	0.05	-0.90	0.37
S _{t-1}	0.09	0.04	2.09	0.04
Year	-0.31	0.12	-2.50	0.01
Year ²	-0.30	0.24	-1.25	0.21
Latitude	-0.22	0.14	-1.59	0.11
Longitude	0.26	0.18	1.41	0.16
Year ² :Latitude	0.28	0.33	0.87	0.38
Year ² :Longitude	-1.28	0.47	-2.74	0.01
Latitude:Longitude	1.00	0.29	3.48	<0.001
A _{t-1} :Year	0.17	0.06	2.78	0.01
A _{t-1} :Latitude	-0.14	0.07	-1.90	0.06
A _{t-1} :Longitude	0.12	0.05	2.29	0.02
S _{t-1} :Year	-0.12	0.05	-2.24	0.03
S _{t-1} :Latitude	0.16	0.07	2.23	0.03
S _{t-1} :Longitude	0.03	0.08	0.36	0.72
Year ² :Latitude:Longitude	-1.41	0.76	-1.86	0.06
St-1:Latitude:Longitude	-0.03	0.15	-0.22	0.82

Supplementary Table 5. Best model (in AIC-based model selection) for the summer density index of the avian predators (year t). Latitude, longitude, and year were scaled to vary between -1 and 1. A = autumn vole density; S = spring vole density.

Parameter	Estimate	Std. error	t-value	p-value
Intercept	-0.18	0.03	-6.36	<0.0001
S _t	0.05	0.02	2.54	0.01
A _{t-1}	0.06	0.03	2.31	0.02
S _{t-1}	-0.02	0.02	-0.90	0.37
Year	0.00	0.02	0.21	0.84
Year ²	-0.02	0.07	-0.28	0.78
Latitude	-0.49	0.05	-10.73	0.00
Longitude	0.01	0.07	0.07	0.94
Year ² :Latitude	0.24	0.11	2.11	0.04
Year ² :Longitude	0.13	0.16	0.83	0.41
Latitude:Longitude	0.38	0.13	2.95	<0.0001
S _t :Year	0.04	0.02	2.31	0.02
S _t :Year ²	-0.01	0.05	-0.29	0.77
S _t :Latitude	-0.03	0.03	-0.86	0.39
S _t :Longitude	-0.02	0.05	-0.38	0.71
A _{t-1} :Year ²	0.11	0.07	1.66	0.10
A _{t-1} :Latitude	0.01	0.04	0.20	0.84
A _{t-1} :Longitude	-0.01	0.07	-0.18	0.85
S _{t-1} :Year ²	-0.08	0.05	-1.53	0.13
S _{t-1} :Latitude	-0.04	0.04	-0.88	0.38
S _{t-1} :Longitude	-0.02	0.06	-0.27	0.79
Year ² :Latitude:Longitude	0.18	0.29	0.61	0.54
St:Year ² :Latitude	0.07	0.08	0.84	0.40
St:Year ² :Longitude	0.04	0.12	0.31	0.75
St:Latitude:Longitude	-0.01	0.10	-0.11	0.91
A _{t-1} :Year ² :Latitude	-0.02	0.11	-0.20	0.84
A _{t-1} :Year ² :Longitude	-0.14	0.15	-0.93	0.35
At-1:Latitude:Longitude	0.05	0.12	0.45	0.65
St-1:Year ² :Latitude	0.02	0.10	0.18	0.86
St-1:Year ² :Longitude	0.12	0.12	1.01	0.31
St-1:Latitude:Longitude	-0.13	0.11	-1.16	0.25
St:Year ² :Latitude:Longitude	0.23	0.22	1.03	0.30
A _{t-1} :Year ² :Latitude:Longitude	-0.27	0.26	-1.05	0.30
St-1:Year ⁻ :Latitude:Longitude	0.27	0.22	1.20	0.23







Predicted winter population growth rate



Predicted summer population growth rate



Predicted small mustelid index

Predicted generalist index

Predicted raptor index

1.0









year