

1 Impacts of predator-mediated interactions along a climatic gradient
2 on the population dynamics of an alpine bird

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14

15 **Abstract**

16 According to classic theory, species' population dynamics and distributions are less influenced by
17 species interactions under harsh climatic conditions compared to under more benign climatic
18 conditions. In alpine and boreal ecosystems in Fennoscandia, the cyclic dynamics of rodents strongly
19 affect many other species, including ground-nesting birds such as ptarmigan. According to the
20 'alternative prey hypothesis' (APH), the densities of ground-nesting birds and rodents are positively
21 associated due to predator-prey dynamics and prey-switching. However, it remains unclear how the
22 strength of these predator-mediated interactions change along a climatic harshness gradient in
23 comparison with the effects of climatic variation. We built a hierarchical Bayesian model to estimate
24 the sensitivity of ptarmigan populations to interannual variation in climate and rodent occurrence
25 across Norway during 2007–2017. Ptarmigan abundance was positively linked with rodent
26 occurrence, consistent with the APH. Moreover, we found that rodent dynamics had stronger effects
27 on ptarmigan in colder regions. Our study highlights how species interactions play an important role
28 for the population dynamics of species at higher latitudes and suggests that they can become even
29 more important in the most climatically harsh regions.

30

31 **Keywords:** Boreal ecosystems; Climate change; Indirect interactions; Population cycles; Predator-
32 prey interactions

33 Introduction

34 Climatic variability and species interactions are two key drivers influencing the spatial and temporal
35 patterns in the distribution and abundance of organisms [1, 2]. An old hypothesis, originally proposed
36 by Darwin, posits that climate is the main determinant of species' range limits in harsh abiotic
37 regions whereas species interactions are a more important determinant under benign abiotic
38 conditions (hereafter the 'classic hypothesis') [3]. Range limits are determined by local population
39 growth rates; hence, this hypothesis also implies that population growth rates should be more
40 sensitive to climate variability in climatically harsh regions but more sensitive to species interactions
41 in more climatically benign regions. Previous studies have examined changes in demographic and
42 population processes along elevational and latitudinal climatic gradients [4-7], but few studies have
43 been able to tease apart the sensitivity of population growth to climate and species interactions over
44 large spatial and temporal scales.

45 In the cold environments of alpine and boreal areas, vertebrate species co-exist in relatively
46 simple food-webs but biotic interactions still exert strong impacts on species' population dynamics
47 [8]. One particular characteristic of northern alpine and boreal ecosystems in Fennoscandia is the
48 rodent population dynamics, which are characterized by large inter-annual cyclic fluctuations in
49 abundance, with peak years coming at regular intervals [9, 10]. Similar cycles are seen with other
50 species in other parts of the world e.g., the snowshoe hare (*Lepus americanus*) in the boreal
51 ecosystems of North America [11]. Although the mechanisms are still contested, predator-prey
52 interactions are generally regarded as the most parsimonious explanation underlying the cyclic
53 dynamics of rodents [12, 13], especially due to specialist predators, such as mustelids [14].

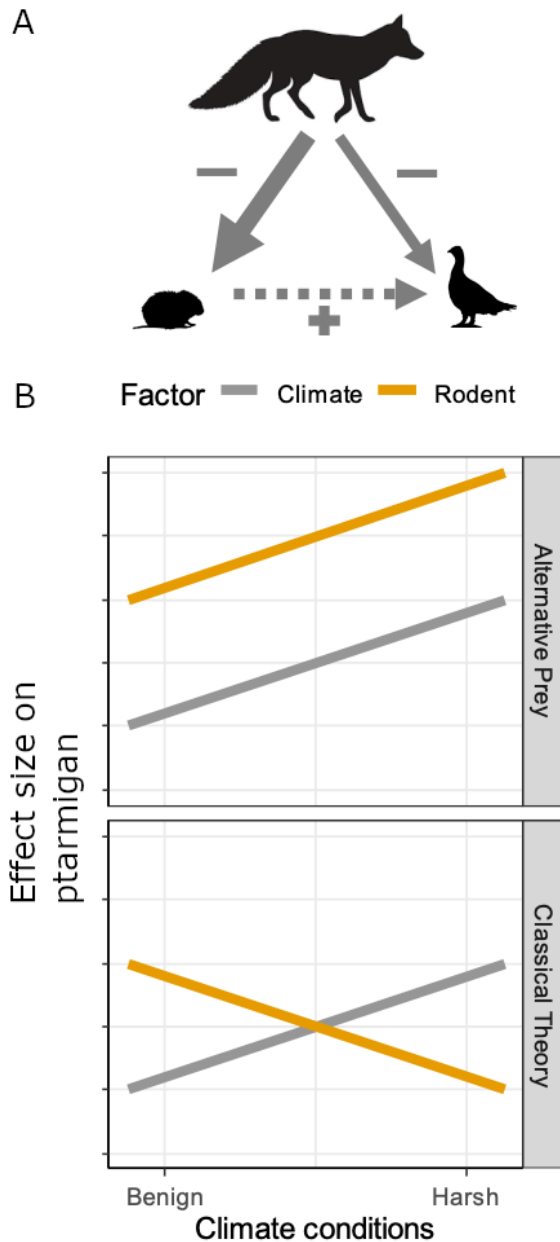
54 The population dynamics of many species of alpine and boreal communities, including the
55 avian community, often covary with the phase of the rodent cycle [15, 16]. One hypothesised reason
56 for this covariation is that ground-nesting birds (such as ptarmigan and grouse, *Tetraonidae*) and
57 rodents share a similar set of generalist predators, including the red fox (*Vulpes vulpes*) and corvids
58 [17, 18]. Hagen [19] proposed the 'alternative-prey hypothesis' (APH), stating that ground-nesting
59 birds are less vulnerable to predation in peak rodent years because generalist predators switch to
60 feeding on rodents. By contrast, ground-nesting birds suffer greater predation in rodent
61 decline/crash years because there are fewer prey options available to hunting predators. Other
62 indirect interactions based on shared predators, such as apparent competition, are typically
63 predicted to lead to negative correlations in the abundance of alternative prey species [20]. Here,
64 predator-mediated interactions between rodents and ground-nesting birds are hypothesized to lead
65 to a positive association, such that ground-nesting birds are more abundant in peak rodent years.

66 Similar indirect effects of rodent population dynamics have been examined in a range of ecosystems,
67 and across a range of alternative prey species [16, 21, 22].

68 Previous studies have found partial support for the main predictions of the APH [16, 23];
69 however, the APH also makes secondary predictions about how the relative importance of predator-
70 mediated interactions should change along ecological gradients. In particular, Angelstam [15]
71 predicted that interactions should be stronger in regions with fewer prey species because the
72 predators become functionally more specialist, causing tighter linkages between predators and prey.
73 By contrast, in regions where predators have access to a more diverse array of prey species,
74 fluctuations in rodent populations should have weaker effects on the dynamics of predator
75 populations. Indeed, the reduced amplitude of the rodent population cycle at lower latitudes is
76 probably due to a stabilising effect of more generalist predators [24-26]. Climatic conditions,
77 especially snow cover, has also been linked with characteristics of the rodent cycles, with more cyclic
78 behaviour in regions with greater snow cover [16, 27, 28]. Based on these arguments, ground-nesting
79 birds might be less affected by the rodent cycle in less climatically harsh areas, where there is a more
80 diverse set of prey resources and weaker linkage between rodents and predators.

81 Alpine birds in Fennoscandia are reported to be declining in abundance over the last decades
82 [29], but the underlying causes for the widespread declines remain poorly understood. Willow
83 ptarmigan (*Lagopus lagopus*) are a resident species of montane habitats. Previous studies of
84 population dynamics have shown that the abundance of willow ptarmigan typically fluctuate in
85 synchrony with the small rodent dynamics [16, 30]. In addition, recruitment rates are affected by
86 weather conditions during the breeding season [30]. Thus, ptarmigan are a good model species for
87 testing alternative hypotheses about the relative importance of climate forcing and species
88 interactions on population dynamics. In this study, we compared the sensitivity of the population
89 dynamics of willow ptarmigan to temporal variability in both climate and rodent populations using a
90 multi-year (2007–2017) dataset covering a large geographic gradient across Norway. We assumed no
91 direct effect of rodents on ptarmigan but rather we expected their population dynamics to be linked
92 due to prey-switching of shared predators as predicted by the APH. Therefore, we used the statistical
93 relationship between rodent abundance and ptarmigan population dynamics as a signal of predator-
94 mediated interactions (Fig. 1). Although we use the term “harsh” to describe the coldest climatic
95 conditions within our study sites, we note that they are not necessarily harsh for the ptarmigan, a
96 species well-adapted to cold conditions. We tested three key predictions that emerge based on the
97 classic hypothesis about the relative importance of climate vs species interactions, and the
98 alternative prey hypothesis (Fig. 1):

- 99 1) Under the classic hypothesis, we predicted that predator-mediated interactions, and hence
100 rodent population dynamics, would more strongly affect ptarmigan in warmer regions. By
101 contrast, under the APH, we predicted that predator-mediated interactions, and hence
102 rodent population dynamics, would more strongly affect ptarmigan in colder regions, where
103 there are fewer prey sources for predators and stronger trophic linkages between predators
104 and their prey populations.
- 105 2) Under both hypotheses, we predicted that ptarmigan population growth would be more
106 sensitive to inter-annual climatic variability in colder regions, because they are closer to the
107 edge of their physiological (climate) and ecological (food availability) niche, which may
108 render them more sensitive to climatic variability.
- 109 3) Last, we predicted that the standardized effect sizes of rodents on the population growth
110 rate of ptarmigan would be generally greater than the effect of climate because ptarmigan
111 are well-adapted for life in cold environments and predation is a major determinant of
112 reproductive success.



113

114 **Fig. 1** (A) The hypothesized direct (solid) and indirect (dashed) relationships between ptarmigan and
115 rodents as alternative prey, and their generalist predators, such as the red fox. In peak rodent years,
116 ptarmigan are mostly ignored by predators; by contrast, in crash rodent years, ptarmigan are more
117 frequently depredated. Together, these processes lead to a positive effect of rodent abundance on
118 ptarmigan abundance. (B) Predicted effects of interannual climatic variability (grey lines) and rodent
119 abundance (orange lines) on ptarmigan population dynamics according to the classic hypothesis
120 (bottom) versus the 'alternative prey hypothesis' (top).

121

122 Methods

123 Population abundance data

124 We used a dataset of line-transect surveys covering almost the full latitudinal extent of Norway for
125 an 11-year period (2007–2017). The surveys come from a structured citizen science program, based
126 on coordinated collection by local and regional initiatives. Volunteer surveyors were instructed to
127 follow common field procedures for estimation of ptarmigan densities using distance-sampling
128 methods [31]. At a national or regional scale, however, the program does not allow for a random
129 selection of study sites, because site selection is focused on the alpine habitats used by ptarmigan
130 and is contingent on landowners establishing surveys on private and public lands. During the surveys,
131 a team of two persons followed pre-defined transect lines, using trained pointing dogs to search both
132 sides of the transect line, usually during August. For each detection of a cluster of ptarmigan (a group
133 or an individual), surveyors recorded the perpendicular distances of the ptarmigan from the transect,
134 the number of birds, the GPS coordinates and the date and time of day. In addition, length (and
135 geographical position) of the transect line is recorded, as well as some other auxiliary data [32]. Since
136 2013, all data management, development of field procedures and planning of study design has been
137 coordinated by the Hønsfuglportalen project (<http://honsfugl.nina.no>). Transects are spatially
138 clustered into survey regions (median of 17 line-transects per survey region), reflecting data that are
139 reported to the same survey coordination node. We used all data collected since 2007, when the
140 monitoring was substantially expanded, until 2017. The total effort varied across the period, and not
141 all study sites were surveyed each year. We subsetted our analysis to 708 line-transects that were
142 visited in at least 6 years (a median of 10 years), each with a mean length of 3.7 km. We excluded
143 observations made at distances greater than 200 m from the transect line, as well as detections by
144 the surveyor, and not by the dog, at distances > 10 m away from the transect line because those
145 observations were likely due to the surveyor flushing birds when moving towards the pointing dog
146 which were observed only because the surveyor left the transect line.

147

148 Covariate data

149 *Rodent data:* During the line surveys, surveyors recorded whether rodents were observed along the
150 transect as a binary variable (yes/no). The surveyors were not asked to distinguish among rodent
151 species, but the five main species in the study area that show cyclic dynamics include: Norwegian
152 lemming (*Lemmus lemmus*), tundra vole (*Microtus oeconomus*), field vole (*M. agrestis*), bank vole
153 (*Myodes glareolus*) and the grey red-backed vole (*M. rufocanus*). Rodent occurrence is denoted by *R*
154 in subsequent statistical models.

155 *Climatic data:* We obtained high-resolution climatic data from the Norwegian Meteorological
156 institute (MET Norway: www.met.no). Data were based on an interpolation from local weather
157 stations, with a spatial resolution of 1x1 km and are available on a daily basis. For each line-transect,
158 we applied a buffer of 200 m and matched our transect locations with the climate data. With the
159 compiled data, we characterised the spatio-temporal variation in climatic conditions during spring
160 (prior to and at the start of the breeding period) and winter (marking the end of the breeding
161 period). Specifically, we calculated:

- 162 1) Spring onset - first year day with a rolling 7-day mean snow depth of zero. We use the term
163 'spring' loosely since snow cover did not completely disappear until summer in some regions.
- 164 2) Spring temperature - average daily mean temperature during March, April and May
- 165 3) Winter onset - first year day with a rolling 7-day mean snow depth above zero
- 166 4) Winter temperatures – average daily mean temperature during December, January and
167 February

168 For each climatic variable, we calculated (1) the average climatic conditions for each transect
169 between 2007 and 2017, which defined the spatial climatic gradient (denoted as *CS*) and (2) the
170 difference between the climatic value of each year at each transect and the spatial variable of each
171 transect, which defined the temporal variation (i.e., anomalies, denoted as *CT*). Hence, we
172 considered the effects of different characterisations of the climatic harshness gradient.

173 *Harvesting data:* We also compiled available data on harvest bags on ptarmigan but this data was
174 only available at a coarse scale of administrative units and not at the line-transect scale (see SOM A
175 for further details – no effect of harvesting on ptarmigan was found in our subsequent analysis but
176 the covariate was retained in our model regardless).

177

178 [Statistical analysis](#)

179

180 [Ptarmigan dynamics](#)

181 We modelled ptarmigan dynamics using a hierarchical Bayesian model that included two linked
182 models: a model for the observation process along each transect line (i.e. the observation model)
183 and a model that described the ecological dynamics including the effect of climate and rodents on
184 ptarmigan density as the latent variable (i.e. the state model).

185 (1) *Observation model: Estimation of effective strip width of the ptarmigan line-transects*

186 We fitted a distance-sampling detection model to estimate the effective strip width of each transect
187 [31]. The central assumption of distance-sampling theory is that the detection probability decreases
188 with increasing distance from the line-transect. We modelled the perpendicular distances of
189 observation events (one or more birds in a group) from the transect as a half-normal distribution. On
190 the transect line, we assumed perfect detection – a common assumption in distance-sampling [31].
191 We modelled sigma - the parameter of this half-normal distribution that reflects the rate of distance-
192 decay of detections - to be dependent on group size (i.e. the number of birds in each observation).
193 Mean group size was modelled with a Poisson mixed-effects model with line and survey region,
194 interacting with year (as a factor). To allow for any spatial variation in sigma, we additionally
195 included random effects for transect line (L, in equation below) and survey region (SR), allowing
196 some differences in how detectability declines with distance due to landscape or habitat features.
197 We also considered fixed effects of forest cover or precipitation during the survey but found no
198 effects (95% credible intervals overlapped zero) and thus did not include these factors in the model.
199 The final model for sigma was:

$$200 \quad \log(\sigma_{i,t}) = b_0 + b_{GS} \text{GroupSize}_{i,t} + L_i + SR_i$$

201 The effective strip width of each transect (i) in each year (t) was calculated from sigma based on the
202 following equation:

$$203 \quad ESW_{i,t} = \sqrt{\frac{(\pi * \sigma_{i,t}^2)}{2}}$$

204

205 (2) State model: Testing the effect of climate and rodent on ptarmigan populations

206 We then used the estimated effective strip width (ESW) and data on transect length (TL) to relate
207 the total number of individuals observed along each transect (N , as following a negative binomial
208 distribution with constant dispersion parameter, r) to the latent variable, ptarmigan density, D ,
209 (abundance per km²) for each year t and each transect i :

$$210 \quad \text{Ptarmigan_Obs}_{i,t} \sim \text{Negative Binomial}(N_{i,t}, r)$$

$$211 \quad N_{i,t} = D_{i,t} \times TL_{i,t} \times ESW_{i,t} \times 2$$

212 Ptarmigan density ($D_{i,t}$) was modelled in two different ways. In a first model (“random-effects
213 model”), we modelled the ptarmigan dynamics using a series of random effects that reflected the
214 spatial and temporal structure of the data. The random terms included year (as a factor), transect

215 line, survey region and survey region-year. We used this model to make predictions of the realized
216 ptarmigan dynamics, without explicitly specifying the underlying ecological covariates.

217 In a second set of models (“mixed-effects model”), we tested the additive effects of the two main
218 ecological variables of interest: rodent occurrence and climate as well as the interaction between
219 rodent occurrence and the spatial climatic variable. We tested the four climatic variables (winter
220 temperature, winter onset, spring temperature, spring onset) in separate models.

221 Density in year 1 was modelled using spatial random effects among line-transects. Density in
222 subsequent years were modelled as spatial (i) and temporal (t) variation in the population growth
223 rate as:

$$224 \quad \ln D_{i,t} = \ln D_{i,t-1} + r_{i,t}$$

225 where the growth rate, r , was decomposed into:

$$226 \quad r_{i,t} = b_0 + b_A \ln D_{i,t-1} + L_i + SR_i + Year_t + b_{CS} CS_i + b_{CT} CT_{i,t} + b_R R_{i,t} + b_{RL} R_{i,t-1} + \\ 227 \quad b_h H_{i,t-1} + b_{int_CT} CS_i CT_{i,t} + b_{int_R} CS_i R_{i,t}$$

228

229 where b_A assumes a Gompertz form of density-dependence, an assumption made by previous
230 ptarmigan studies [33, 34]. L and SR were random effects to account for the spatial grouping of data
231 into line-transects (L) and survey region (SR). A year (as a factor) random effect was included to
232 account for any additional causes of temporal variability.

233 CS and CT were covariates for the spatial gradient in climate and temporal anomalies for the climatic
234 variable, respectively. Two coefficients (b_R and b_{RL}) for rodents (R) tested the effects of rodent
235 occurrence immediately preceding the ptarmigan survey (during the same year, t) and a lagged effect
236 of rodent occurrence during the previous year (RL , $t-1$). We also accounted for the potential effect of
237 harvesting (H) on ptarmigan growth. All covariates were centered and scaled to units of 1 standard
238 deviation prior to analysis.

239 The critical tests of the classic versus the alternative prey hypotheses were based on the interaction
240 terms of our model. The interaction terms were: (1) between CS and CT to test whether the effect of
241 annual climatic anomalies changed along the climate gradient or (2) between CS and R (of the same
242 year) to test whether the effect of rodents changed along the climatic gradient.

243 In preliminary analyses, we explored additional random effects (a coarser spatial term) but they had
244 little effect on our results so we retained the simpler model.

245

246 Table 1. Table of model parameters on ptarmigan density and their meanings.

Term of model	Type	Statistical meaning
b_0	Fixed	Intercept
b_A	Fixed	Density-dependence
b_{CS}	Fixed	Spatial climatic variable
b_{CT}	Fixed	Temporal climatic anomalies
b_R	Fixed	Rodent occurrence (same year)
b_{RL}	Fixed	Lagged effect of rodent occurrence (previous year)
b_H	Fixed	Harvesting during the previous hunting season
b_{int_CT}	Fixed	Interaction term between temporal and spatial climate
b_{int_R}	Fixed	Interaction term between rodents and spatial climate
L	Random	Line-transect effect
SR	Random	Survey region effect
$Year$	Random	Year effect

247

248 Rodent dynamics

249 We included a submodel for rodent occurrence (presence/absence, modelled as a Bernoulli
 250 distribution) within our hierarchical model for ptarmigan. This submodel was based on a series of
 251 random intercept terms (for survey region [SR], year [Y], as a factor] and their interaction) to flexibly
 252 predict the interannual variability in rodent dynamics. Hence, the rodent submodel was:

$$253 \quad \text{Rodent_Occ}_{i,t} \sim \text{Bernoulli}(R_{i,t})$$

$$254 \quad \text{logit}(R_{i,t}) = b_0 + Y_t + SR_i + Y_t SR_i$$

255 Modelling rodent occurrence allowed us to impute missing data in the observed rodent dataset.
 256 Additionally, the model predicted the probability of rodent occurrence at the level of the survey
 257 region rather than at the transect-level, which mean meant smoothing over local reporting and
 258 ecological variation. This choice was based on the assumptions that many predators (especially birds
 259 of prey) forage over reasonable distances and are not likely affected by fine-scale transect-level
 260 variation. We also considered a more complicated autoregressive model of order 2 for the rodent
 261 dynamics, but similar cyclic dynamics were obtained, and similar effects on ptarmigan were found
 262 (SOM B), so we proceeded with the simpler assumption-free random-effects model.

263 In further models, we also investigated how rodent dynamics changed along the climatic gradient. In
 264 Bayesian mixed-effects models with binomial errors, we tested the effects of the spatial climatic

265 variables and temporal climatic anomalies variables on the probability of rodent occurrence. Line-
266 transect and survey regions were also included as random intercepts. Each of the four types of
267 climatic variables (winter temperature, winter onset, spring temperature, spring onset) were tested
268 in separate models.

269 Models were fitted using JAGS within R version 3.6.0. We used three MCMC chains, ran for 50,000
270 iterations, discarding the first 25,000 iterations as a burn-in period. We used uninformative or weakly
271 informative priors for all parameters, but a narrower prior for the density-dependence term (a
272 uniform prior between -2 and 0) to help convergence. We assessed model convergence using MCMC
273 chain traceplots and the Gelman-Rubin R-hat statistic (all <1.1). To assess the fit of the model, we
274 used the DHARMA package [35] that uses simulations from the fitted model to create scaled
275 residuals, which were then checked against the expected distribution using a quantile-quantile plot
276 and against the model predictions to check for any systematic deviations in fit. Covariate effects
277 were inferred when the 95% credible intervals did not overlap zero. Code for the fitted model is
278 available in the SOM C.

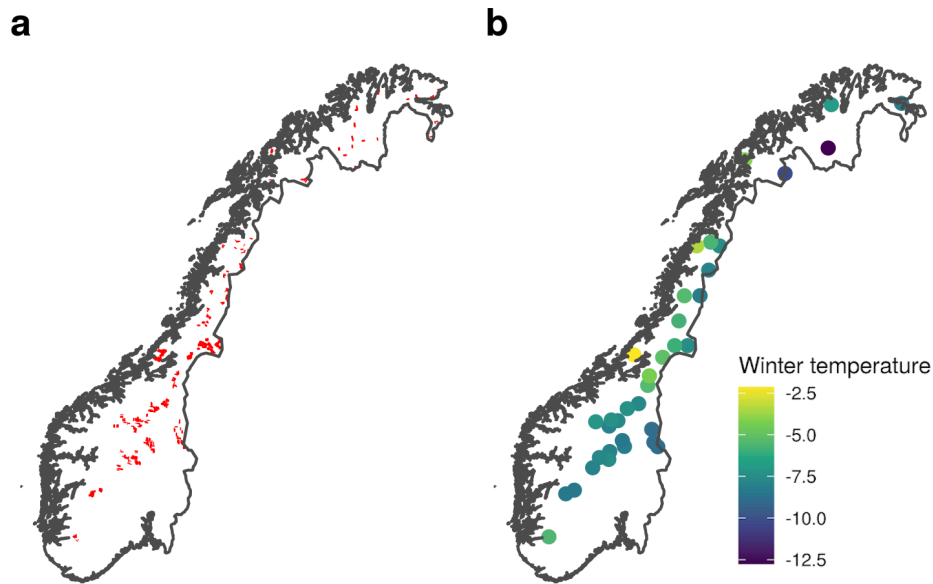
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280 Results

281 *Data description*

282 The 708 line-transects (Fig. 2a) were clustered into 36 survey regions (Fig. 2b) distributed along a
283 wide latitudinal and climatic gradient across Norway. The warmest regions were those nearest the
284 coast and the coldest regions were inland and upland (Fig. 2b). Along each transect, a median of 2
285 groups were observed (range = 0–18), with a median of 4 (1–35) individuals seen per group. As
286 expected by distance-sampling theory, the frequency of observations declined with increasing
287 distance from the line-transect (Fig. 3). The average effective strip width was 107 m (interquartile
288 range = 100–114 m). Sigma of the half-normal distribution was positively affected by group size, with
289 the estimated effective strip width being 95 m for the smallest group size and 126 m for the largest
290 group size (Fig. 3).

291

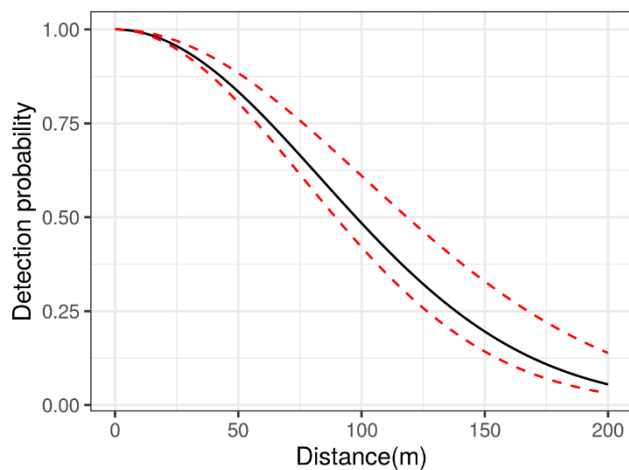


292

293 **Fig. 2** (a) Location of the 708 line-transects across Norway are shown by red lines. (b) The location of
294 each of the 36 survey regions (a survey region is a cluster of neighbouring line-transects), coloured by
295 their mean winter temperature during 2007–2017. Fig. S1 shows the same maps for the other
296 climatic variables.

297

298



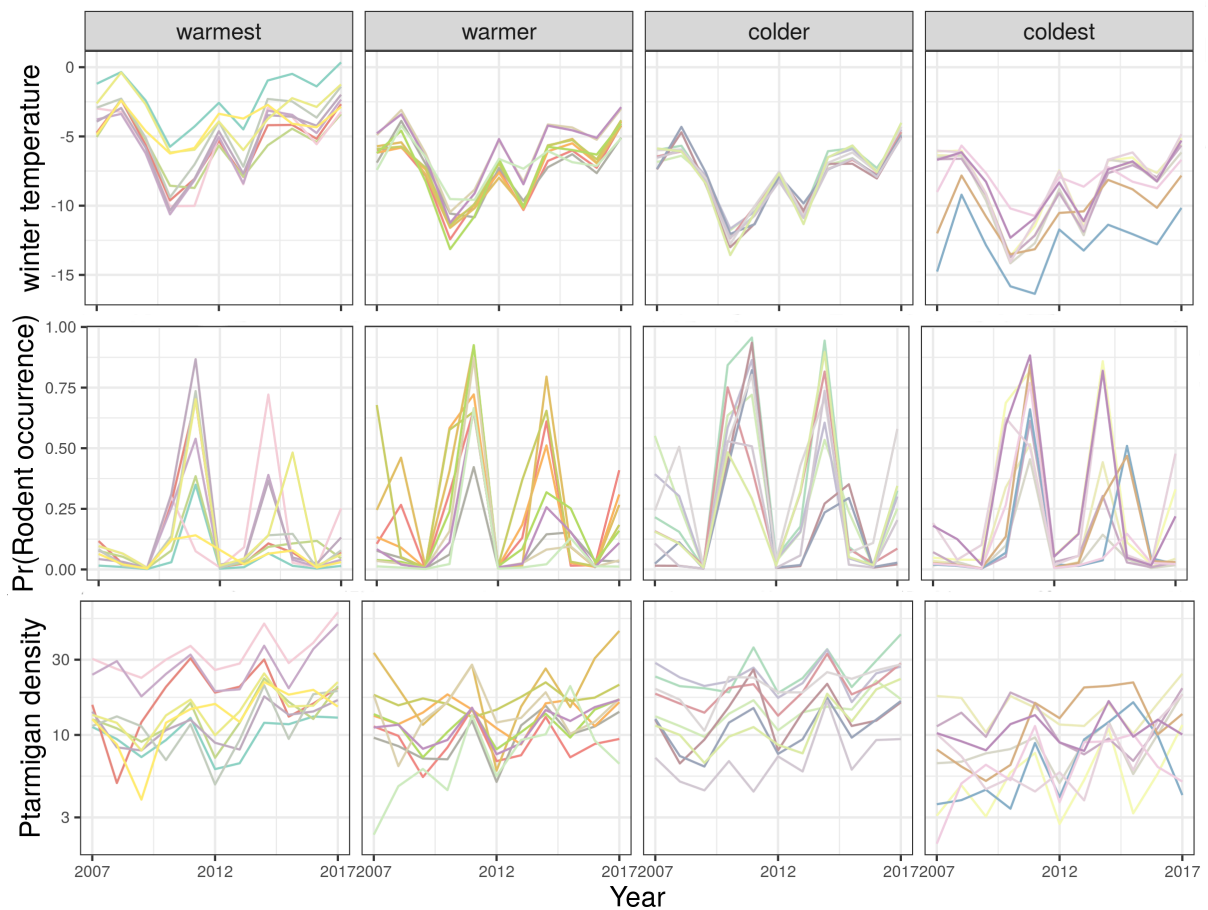
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300 **Fig. 3.** Distance-dependent decay of ptarmigan detectability along the line-transects. The black line is
301 the prediction for the median ptarmigan group size; the lower and upper dashed red lines are the
302 predictions for the minimum and maximum ptarmigan group size.

303

304 *Climatic, rodent and ptarmigan population variation*

305 Climate and rodent occurrence both showed large and generally spatially synchronized fluctuations
306 (Fig. 4, note: this figure shows the climatic gradient split into simplified quartiles, but climate was
307 treated as a continuous variable in all analyses). Our 11-year dataset spanned c. 3 rodent cycles. The
308 probability of rodent occurrence increased along the climatic harshness gradient, driven by higher
309 occurrence probability in peak years within colder regions (Table S1). For instance, in the first peak
310 rodent years, during 2010/2011, mean rodent occurrence across transects was 38% in the region of
311 the warmest quartile (based on winter temperature) but 64% in the coldest. In the second peak
312 rodent years, during 2014/2015, rodent occurrence was 18% in the warmest and 37% in the coldest.
313



314

315 **Fig. 4** Time-series of winter temperature (°C), probabilities of rodent occurrence and willow
316 ptarmigan densities in August (birds per km²) as predicted by the random-effects models. In our
317 analysis, the spatial climatic gradient was treated as a continuous variable. Here, for presentation
318 purposes we divided here the spatial climatic gradient into quartiles with equal numbers of transects
319 within each. Lines shown are means for each of the 36 survey regions (averaged over the transects

320 within each). Fig. S2 shows the time-series for the other climatic variables and Fig. S3 shows the
321 locations of each quartile.

322

323 *Mean effects of climatic and rodent fluctuations on ptarmigan populations*

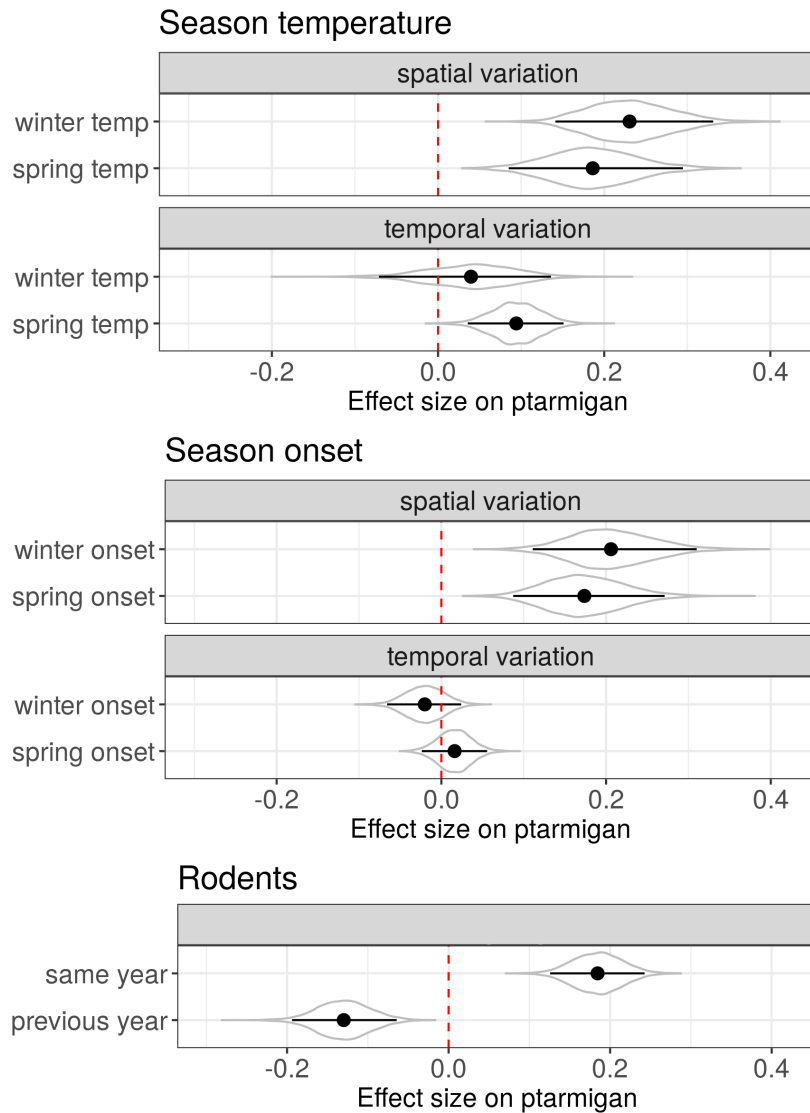
324 Ptarmigan growth was higher in more climatically benign regions (positive spatial effects of climate
325 shown in Fig. 5), described by warmer springs and winters, and later winters and earlier springs.

326 Similarly, temporally, ptarmigan growth increased in years with warmer spring temperatures but was
327 less affected by the timing of seasonal onsets and winter temperatures (temporal effects of climate

328 shown in Fig. 5). Ptarmigan density was positively associated with rodent occurrence of the same

329 year, but negatively associated with rodent occurrence in the previous year (Fig. 5). Effects sizes of

330 rodents were larger than the effect sizes of the temporal variability in climate.



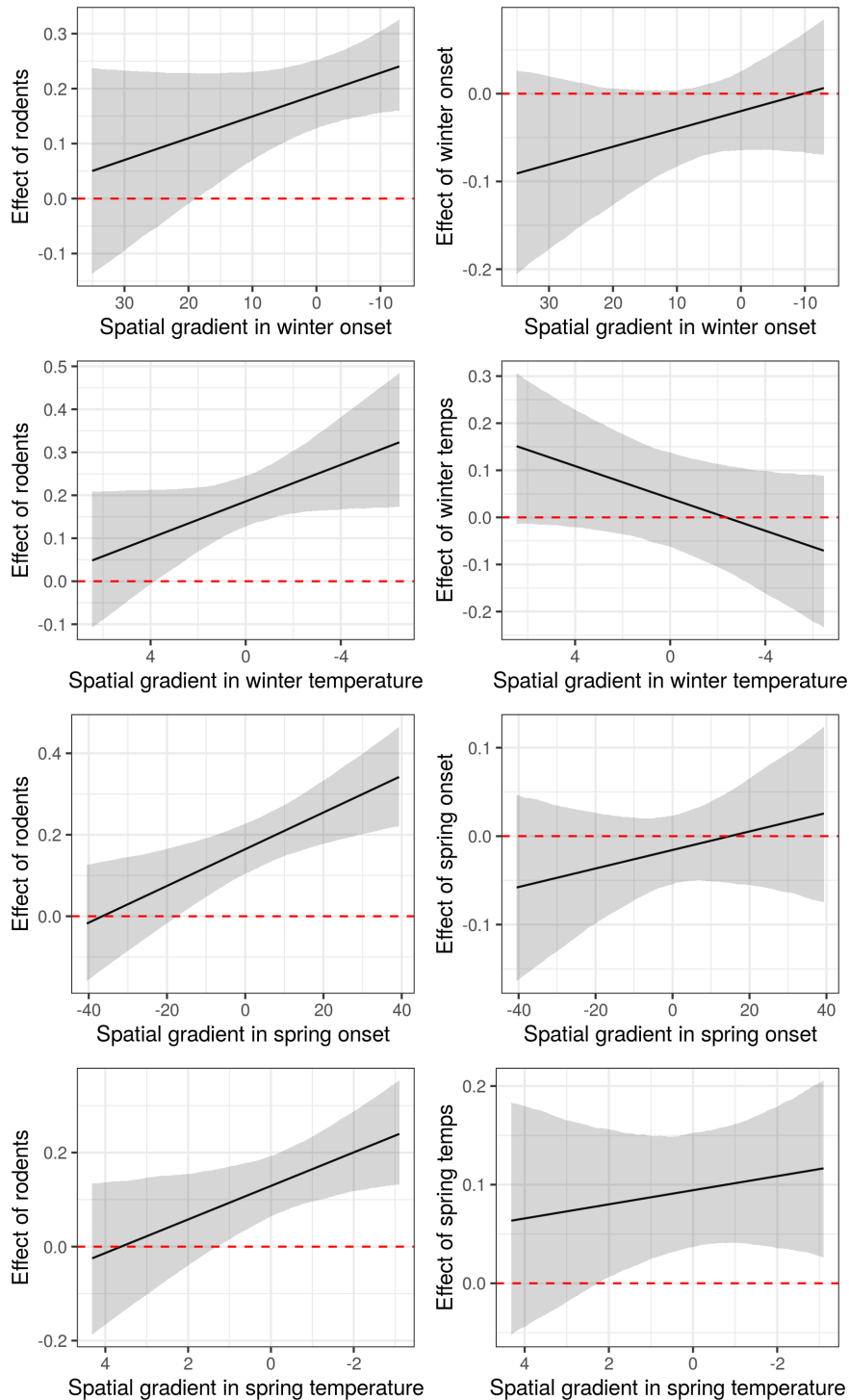
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332 **Fig. 5** Effects of seasonal temperatures, seasonal onsets, and rodent occurrence on changes in
333 ptarmigan population density. Climate variables are split into a spatial variable (mean values across
334 years) and a temporal variable (annual anomalies around the mean spatial variation). Covariates
335 were standardized to units of standard deviation to facilitate comparison of effect sizes. Violins
336 represent the full posterior distributions. Point and ranges represent mean effects and 95% credible
337 intervals of the distributions. The dashed vertical red line is the line of no effect. The sign of the
338 effects of spring onset were flipped so that larger values represent lower climatic harshness (i.e.,
339 earlier springs), consistent with the other climatic variables.

340

341 *Changes in the effects of climatic and rodent fluctuations along the climatic harshness gradient*

342 The statistical effects of rodent occurrence probability on ptarmigan densities were more positive in
343 more climatically harsh areas compared with in more climatically benign areas (Fig. 6, left). In fact,
344 the predicted effects of rodent occurrence were close to zero in regions with the warmest and
345 earliest springs but strongly positive in the coldest regions with earliest winters and latest springs.
346 The effects of temporal climatic variability also tended to become more positive along the climatic
347 harshness gradient, when described in terms of spring temperature (Fig. 6, right) but the 95%
348 credible intervals of the interaction terms overlapped zero (Fig. S4).



349

350 **Fig. 6** Changes in the effect sizes of temporal variability in climate and rodent occurrence and along
 351 each climatic spatial gradient on ptarmigan density. X-axes are transformed so that left to right is an
 352 increasing climatic harshness gradient (i.e., the values towards the right represent colder
 353 temperatures, earlier winters and later spring). Shown are the mean standardized effect size and
 354 95% credible interval. Each x-axis is centered around the median values for each variable (oC for
 355 temperatures and days for onset). 95% credible intervals for the interaction terms are shown in Fig.
 356 S4.

357

358 Discussion

359 Understanding how fluctuations in climatic conditions and species interactions affect species'
360 population dynamics is central to current research in population ecology. We outlined two different
361 hypotheses about how the strength of species interactions might vary along a climatic gradient, and
362 tested our predictions using a large-scale dataset on the willow ptarmigan. Our results suggest that
363 the impacts of predator-mediated interactions on willow ptarmigan increase along the climate
364 gradient, indicated by more strongly positive signals of rodent dynamics in colder areas. Hence, our
365 results were consistent with predictions stemming from the alternative prey hypothesis (APH) rather
366 than the classical view of how species interactions change with increasing climatic harshness.

367 Our results support our main prediction based on the APH: a stronger link between rodent
368 fluctuations and ptarmigan dynamics in colder regions. According to the APH, shared predators are
369 expected to prey-switch towards rodents and away from ptarmigan, when rodents are more
370 abundant [15, 19, 23]. Ptarmigan had higher growth rates during years with more rodents, which
371 would be consistent with lower predation pressure. Hence, our results are consistent with the APH,
372 previously tested over smaller-scales [23, 25, 36]. While the APH primarily considers the immediate
373 functional response of predators, the contrasting negative lagged effects of rodents is consistent
374 with a numerical response of predators due to greater prey density, leading to negative effects of
375 rodents on ptarmigan in the subsequent year. The weaker effect of rodents, and hence predator-
376 mediated interactions, on ptarmigan density in warmer regions could be caused by greater prey
377 diversity and more generalist predators, weakening the trophic links among the dynamics of
378 predators and prey species [8, 15].

379 Previous research has shown how the role of species interactions can increase or decrease in
380 strength along an ecological gradient due to different biotic and abiotic processes [5, 37-39].
381 Probably the most common reason for changing strengths of interactions over a geographic range is
382 changes in community assemblages and the abundance of interacting partners [3, 40, 41]. Our results
383 appear to be at odds with the classic prediction of stronger species interactions at the warmer end of
384 a species range [3], but the prediction arises from the assumption that the abundance of interacting
385 partners is greater in warmer regions. The assumption may hold in many scenarios, but in our case
386 rodents showed greater peaks in occurrence in colder regions. Indeed, other studies have shown an
387 increase in the amplitude of rodent dynamics from southern to northern Fennoscandia [8]. Hence,
388 our results are consistent with species interactions being important in areas where potential
389 interacting partners are more common, at least periodically.

390 Another factor likely to affect the changing importance of species interactions is whether the
391 predators are specialist or generalist species. When interactions involve specialists, they can be
392 important over the whole distributional range of an organism [42]. Although none of the interactions
393 between ptarmigan, rodents and predators are intrinsically specialist, they may be regarded as
394 functionally specialist in cold regions due to the relatively low number of species in the food web.
395 Since interaction networks at high latitudes tend to be often more specialised [43], other type of
396 indirect interactions may also become more important in more northerly regions.

397 We found weaker support for interannual climatic variability having a greater effect on
398 ptarmigan populations in colder regions. Climatic effects may be direct and related to species'
399 physiology, or more likely indirect and related to climate-caused changes in the availability of
400 resources or suitable habitat. Harsh conditions may expose an organism to the edge of its niche
401 space, hence climatic variation at the colder edge of a species' range should be more likely to affect
402 its population growth [44]. However, the ptarmigan is a well-adapted alpine species able to inhabit
403 regions with harsher climates than those in our study area (e.g., in Alaska and Siberia). Our study
404 does not therefore address the geographic range limits of the ptarmigan. However, other studies
405 have found clearer evidence that species' sensitivity to climate increases towards the range edge [45,
406 46]. Further work might consider the non-linearity in the relationship between climatic conditions
407 and ptarmigan density to examine in more depth the effects of climatic variation at the climatic
408 extremes.

409 High-altitude or -latitude organisms are among those most strongly exposed to climate
410 change [47]. Our findings help understand the main pathways through which climate change may
411 affect the population dynamics of ptarmigan, including the direct effects of warming versus indirect
412 effects mediated through predators [48, 49]. Ptarmigan benefit from warmer springs, hence, climate
413 change, at least in the short-term, may have some positive effects [50]. However, our results suggest
414 that changes in predation pressure mediated via rodents are likely to be more important. One
415 predicted consequence of climate change is a dampening of rodent cycles [16, 51]. Dampening cycles
416 could mean no or less frequent years of high rodent abundance, which offer temporal refuges from
417 predation that yield 'boom' years with high ptarmigan productivity. Hence, a warming climate may
418 lead to a more constant rate of predation pressure on ptarmigan, lowering mean population growth
419 rates. However, dampening of the cycles might also reduce the long-term abundance of predators,
420 lowering predation pressure on the ptarmigan [12]. In particular, more frequent years with low vole
421 abundance is expected to directly affect predator reproduction in the spring [51].

422 Our analysis has several limitations. First, the rodent data was only collected as a binary
423 presence/absence variable along each line-transect and hence may not reflect the full changes in the
424 relative abundances of rodents among years. Moreover, our rodent data was collected in the
425 autumn, but rodent abundance in spring and early summer is probably the key parameter that drives
426 predation pressure on ptarmigan and other ground-nesting birds. However, no comparable spring
427 data for rodents are available spanning the range of our study system. Usually, we could expect
428 spring and autumn rodent densities of the same year to be correlated [16] but that might vary with
429 climatic conditions [51]. Overall, the patterns in the proportion of rodents seen within our data
430 showed the expected large-scale synchronised annual cycles or rodents reported elsewhere [52].
431 Second, although we can reasonably infer the interaction between ptarmigan and rodents to be
432 caused by shared predators, data on predators would also help better understand the links between
433 predator abundance, prey preference, and alternative prey availability [23]. Last, our analysis only
434 focused on changes in the strength of one specific type of species interaction. Willow ptarmigan may
435 be involved in various other types of species interactions such as competition with other herbivorous
436 species, including ungulates, which differ in their strength along the climate harshness gradient.
437 Hence, cumulatively, species interactions could still be more important at the warmer edge of its
438 distribution.

439 Our analyses suggest that predator-mediated interactions become even more important in
440 the colder regions of boreal ecosystems, contrary to the classic view that species interactions are
441 more important at the warmer edge of species' distributions. The role of predator-mediated
442 interactions along a climatic gradient are more generally likely to depend on the diet breadth of
443 predators and availability of different prey types. Rodent cycles – regarded as the heartbeat of boreal
444 ecosystems - cause changes in prey availability that lead to predator-mediated interactions for
445 alternative prey species. Long-term dampening of the rodent cycles that is predicted to arise due to
446 climate change is likely to have widespread repercussions for the dynamics of many species in the
447 boreal, especially ground-nesting birds such as the willow ptarmigan.

448

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456

457

458 *Data availability*

459 The ptarmigan dataset (for different geographic regions) is freely available via GBIF [53-55]. The
460 subset used for the analysis of this paper, along with the rodent data, are available at Dryad (link
461 here XXX).

462

463 *Competing interests*

464 The authors have no competing interested to declare.

465

466 *Author contributions*

467 EBN and HCP designed the line-transect sampling protocols and helped to develop and maintain the
468 Hønsøfuglportalen system. DB developed the research questions, with contributions from EBN. DB
469 conducted the statistical analyses. DB wrote the first draft of the manuscript and all coauthors
470 helped to refine the hypotheses and develop the manuscript.

471

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