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Climate change induced molting mismatch? Mountain hare abundance reduced by duration of snow cover and predator abundance

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Abstract. In northern latitudes, species that have adapted to snow cover by molting and changing pelage color will be particularly vulnerable to climate change, as predation levels may increase due to a mismatch with background coloration. Here, we investigated the synergistic effect of mammalian generalist predators (red fox *Vulpes vulpes* and pine marten *Martes martes*) and the duration of snow cover on the abundance of a winter-adapted species, the mountain hare (*Lepus timidus*). We analyzed 12 yr of data from 622 snow tracking lines in southeast Norway along a gradient in annual duration of snow-covered ground. The mountain hare abundance index was positively related to the generalist predator abundance index, probably due to a combined numerical and functional response of the predators. The mountain hare abundance index was negatively associated with a short duration of snow cover, and this effect was stronger in areas with a high predator abundance index. Hence, we demonstrated a causal link between the mountain hare abundance index, predators, and the duration of snow cover. We expect declining mountain hare densities in the future caused by interactive effects of reduced duration of snow-covered ground, potentially increasing generalist predator densities and the limited ability of mountain hares to adapt to the climate change-induced molting mismatch.

Key words: climate change; coloration mismatch; generalist predators; index lines; molting; mountain hare; pelage color; pine marten; red fox; snow tracking.

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Introduction

Species are currently experiencing pronounced changes in their physical environment due to increasing temperatures and altered patterns of precipitation. In line with this, human-induced climate change is considered a major driver of declining species diversity worldwide (Walther et al. 2002, Parmesan 2006). The increase in temperature, coupled with increasing precipitation and a reduction in duration of snow cover, may have large impacts on boreal ecosystems through changes in species distribution, community structure, ecosystem dynamics, and the physiology and behavior of individuals (Walther et al. 2002, Post et al. 2009, Elmhagen et al. 2015).

In Fennoscandia, the mountain hare (*Lepus timidus*) has declined significantly over the past decade (Kauhala and Helle 2007, Pedersen and Pedersen 2012, Elmhagen et al. 2015), and it was evaluated to be "near threatened" by the Norwegian Red List in 2015 (Henriksen and Hilmo 2015). Pedersen and Pedersen (2012) present several hypotheses of why the mountain hare population in Norway has declined, of which climate change and increased predation are two of them. Species that have physiological adaptations to snow cover such as molting and changing pelage color will be particularly vulnerable to predation if there is a mismatch between pelage color and background coloration (Litvaitis 1991, Berteaux et al. 2004). Under a scenario of a warmer climate, the duration of the mismatch may increase if changes in the period of snow cover are too rapid to be counteracted by phenotypic plasticity or rapid evolution in time of molting (but see Berteaux et al. 2004). Furthermore, a study of snowshoe hares (*Lepus americanus*) showed that timing of molting is a trait with a relatively small degree of phenotypic plasticity (Zimova et al. 2014), which implies that adaptations to climate change would require natural selection and microevolution on physiological or behavioral traits. Accordingly, the mountain hare is a boreal species that we expect will be negatively affected by such a mismatch leading to increased predation risk from generalist predators such as red fox (*Vulpes vulpes*) and pine marten (*Martes martes*). Here, we investigate the synergistic effect of generalist predators and the duration of snow cover in a winter-adapted species, the mountain hare. We utilize 12 yr of snow tracking data of mountain hares, red fox, and pine marten from southeast Norway, along a gradient in annual duration of snow-covered ground from less than three to more than six months. Despite this being a relatively short timeframe for detecting effects of predation and climate change, we utilize the spatiotemporal variation in generalist predation pressure, as well as the spatiotemporal variation in the number of days with snow cover as a proxy for the general trend of an increase in generalist predators and a warming climate. We predict a lower abundance index of mountain hares in areas with a short duration of snow-covered ground due to a longer period of mismatch between pelage and background coloration. Furthermore, we expect a stronger negative effect of this mismatch in areas where the generalist predator abundance index is high due to increased predation risk.

Methods

Study area

Hedmark County (27,400 km^2) is situated in the boreal zone with some areas of alpine tundra at higher elevations (Fig. 1). The human population density averages 7.1/km^2 and is highest in the southern areas (data from www.ssb.no). Elevation ranges from 140 m asl in the south to a maximum of 2180 m asl in the north. In the south, the land is covered by a mosaic of forests and agricultural

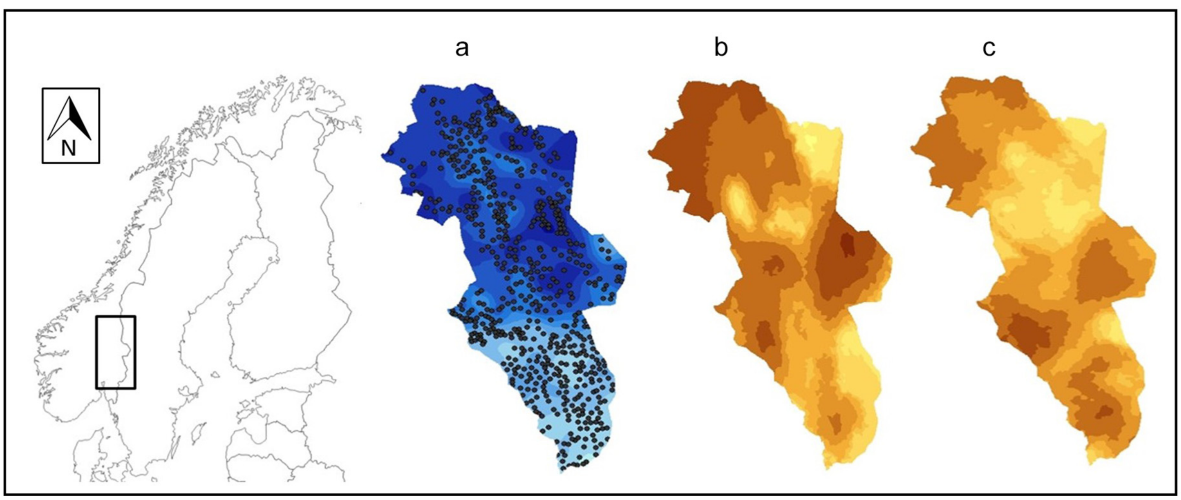

Fig. 1. Left panel: location of the study area in Norway (62° N, 12° E). Right three panels: extrapolated data of (a) number of snow-days in winter in Hedmark County, Norway (darkest > 190 d, lightest < 90 d); dots mark the center of the 622 snow tracking lines. Number of tracks per km along snow tracking lines/days since last snowfall for (b) mountain hare abundance index (darkest > 2, lightest < 0.2) and (c) generalist predator abundance index (darkest > 2, lightest < 0.2). The data are mean values from the years 2003 to 2014.

fields. Moving towards the north, human population density declines, and the land is dominated by forests and alpine areas. There is a trend of a reduction in primary productivity as you move from the west to the east within Hedmark County (Moen et al. 1999). In the central part of the study area, average annual precipitation was 628 mm, and the temperature averaged −9.1°C in January and +15.5°C in July during the period of our study (2003–2014; data from www.met.no). However, mean annual temperatures decrease with increasing latitude and altitude, which is reflected by a gradient in the duration of snow cover from south to north (Fig. 1).

Data

As part of a program aimed at monitoring Eurasian lynx (*Lynx lynx*) in Hedmark County, the Hedmark Chapter of the Norwegian Association of Hunters and Anglers have carried out annual track counts along 3 km long snow transect lines in January each year in the period 2003–2014. The transect lines were surveyed once per year when snow conditions were favorable for identifying species' tracks (i.e., 2–5 d after a fresh snowfall). The transect line density is 3–4 lines per 100 km^2 (Tovmo and Brøseth 2011), and a total of 622 different lines have been surveyed (Fig. 1a), varying from 281 to 484/yr. Tracks of all species have been recorded including mountain hare, red fox, and pine marten (Data S1). The snow tracking indices first and foremost reflect spatiotemporal activity and distribution patterns of the different species. Due to the pronounced interspecific differences in movement patterns and distances, we do not attempt to compare relative abundance among species. We did not include lynx tracks in our analyses as these were only sporadically encountered in the study area. Indeed, lynx abundance in the area is low with a mean of 28 lynx in Hedmark County over the past 3 yr (Brøseth et al. 2016), corresponding to a density of approximately one lynx per 1000 km^2. Further, mountain hares are not the main prey for Eurasian lynx, being found in approximately 20% of scat samples (Odden et al. 2006). Hence, we assumed that lynx had a marginal effect on the abundance of mountain hares. The red fox, on the other hand, is the main predator of both adult and juvenile mountain hares, accounting for 40% of the total mortality (Dahl 2005).

The Norwegian Water Resources and Energy Directorate have provided models with extrapolated historical snow data at a 1-km^2 resolution (www.senorge.no). For the center point of the 622 transect lines, we extracted the number of days for each of the years 2003–2014 with snow cover >5 cm, and used this in our model as number of snow-days in winter (Data S1).

Statistical analysis

Snow tracking indices were calculated as the numbers of tracks per km transect divided by the number of days since last snowfall. In the analyses, we used tracks recorded in January year t together with the number of days with snow cover (snow-days) in year $t-1$, to reflect the population response to the snow conditions of the previous year. We utilized linear mixed-effects models. We included the log-transformed mountain hare track index (year t) as a dependent variable and snow-days (year $t-1$), the red fox track index (year t), the pine marten track index (year t), and the generalist predator track index (pine marten and red fox summed, year t) as independent variables. Transect line ID entered the models as a random term. First, we selected the most parsimonious model using Akaike information criterion values, and then, we tested whether adding abiotic variables such as year, latitude, and longitude would increase the fit of the model. Altitude was excluded as explanatory variable as it was highly correlated with latitude (Pearson's correlation: 0.833, $t = 109.24$, $P > 0.001$). All explanatory variables were standardized following Gelman and Hill (2007). The data were analyzed using R version 3.2.3 (R Development Core Team 2015). The maps with predicted average number of days with snow cover (Fig. 1a) and track densities of mountain hares (Fig. 1b) and generalist predators (Fig. 1c) in Hedmark County were produced using ordinary kriging analyses in ArcGis version 10.3 (ESRI 2014). Here, we interpolated track indices and the average snow cover duration based on average values per transect from the whole period of study.

Results

The mean duration of snow cover across all transect lines in Hedmark County varied

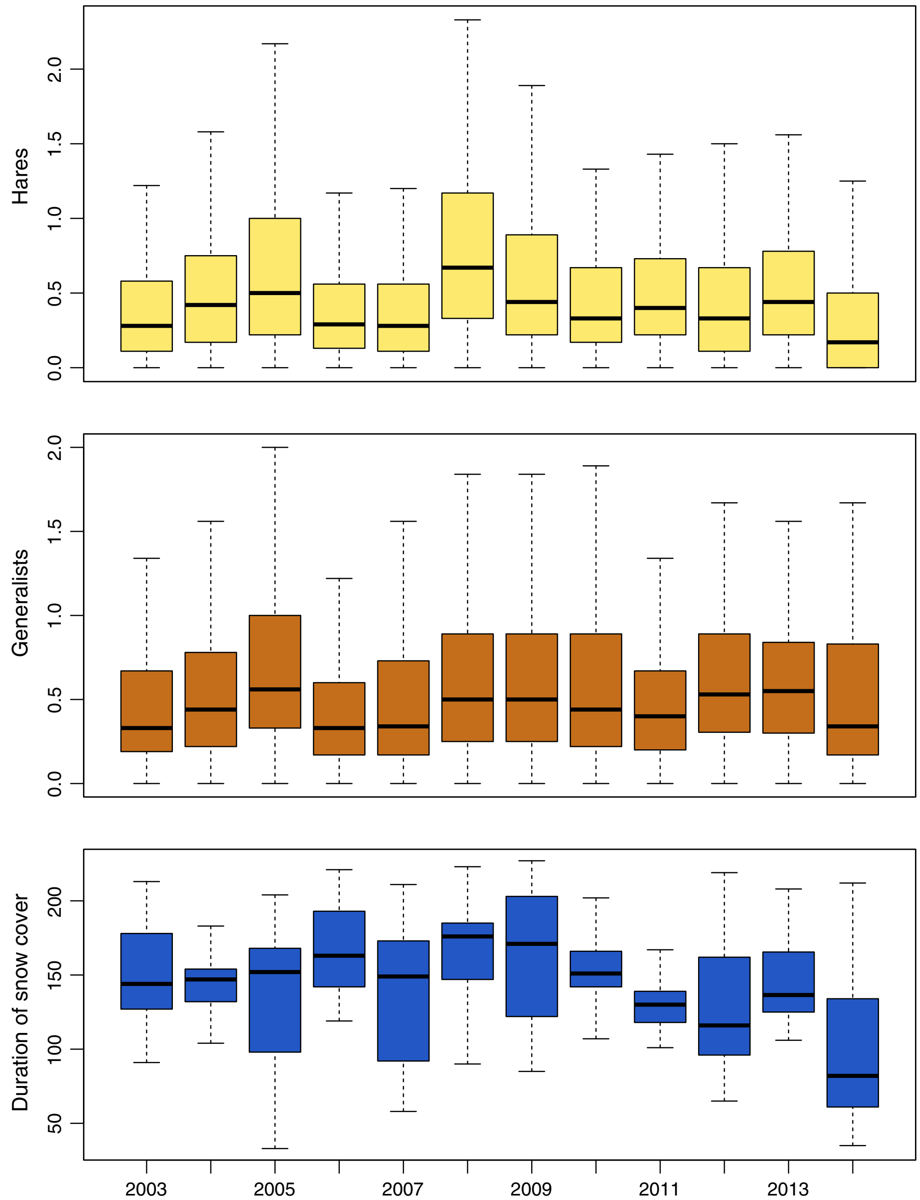

Fig. 2. Temporal variation in number of mountain hare and generalist predator tracks per km along snow tracking lines/days since last snowfall, and duration of snow cover in Hedmark County from 2003 to 2014. Outliers are excluded from the box plot.

markedly among years, ranging from 99 d in 2014 to 165 d in 2006, with an average duration of 144 d (Figs. 1a, 2). Furthermore, there was also a considerable spatial variation in the snow cover over the study area pooled over years with less than three months of snow cover in the south, to more than six months of snow cover in the north (Fig. 1a). Across all transect lines and years, the duration of snow cover ranged from a minimum of 33 d to a maximum of 227 d. The number of generalist predator and mountain hare tracks varied considerably (Figs. 1b, c, 2), averaging 0.62 predator tracks/km (max: 7.00, min: 0.00) and 0.59 mountain hare tracks/km

Table 1. Ranking of the best linear mixed-effects models explaining the number of mountain hare tracks.

Model†	Parameter estimates‡	AIC	ΔAIC	*w*§
M1	$-0.77 \pm 0.02I + 0.68 \pm 0.03R + 0.38 \pm 0.03S + 0.21 \pm 0.05R \times S$	11,519.15	132.05	0.000
M2	$-0.78 \pm 0.02I + 0.65 \pm 0.03R + 0.39 \pm 0.03S$	11,539.01	151.91	0.000
M3	$-0.78 \pm 0.02I + 0.62 \pm 0.03R$	11,710.28	323.18	0.000
M4	$-0.77 \pm 0.02I + 0.38 \pm 0.03M + 0.23 \pm 0.03S - 0.11 \pm 0.05M \times S$	11,985.64	598.54	0.000
M5	$-0.78 \pm 0.02I + 0.36 \pm 0.03M + 0.29 \pm 0.03S$	11,988.51	601.41	0.000
M6	$-0.78 \pm 0.02I + 0.37 \pm 0.03M$	12,078.63	691.53	0.000
M7	$-0.78 \pm 0.02I + 0.32 \pm 0.03S$	12,183.87	796.77	0.000
M8	$\mathbf{-0.77 \pm 0.02\mathit{I} + 0.71 \pm 0.02\mathit{G} + 0.36 \pm 0.03\mathit{S} + 0.19 \pm 0.04\mathit{G} \times \mathit{S}}$	**11,403.49**	**16.39**	**0.000**
M9	$-0.78 \pm 0.02I + 0.69 \pm 0.02G + 0.37 \pm 0.03S$	11,419.79	32.69	0.000
M10	$-0.77 \pm 0.02I + 0.70 \pm 0.02G$	11,582.2	195.10	0.000
M11	$-0.78 \pm 0.02I$	12,289.28	902.18	0.000
M8A	$-0.77 \pm 0.02I + 0.71 \pm 0.02G + 0.36 \pm 0.03S + 0.01 \pm 0.02Y + 0.19 \pm 0.04G \times S$	11,405.35	18.25	0.000
M8B	$-0.78 \pm 0.02I + 0.71 \pm 0.02G + 0.30 \pm 0.03S + 0.14 \pm 0.04\mathrm{La} + 0.19 \pm 0.04G \times S$	11,392.54	5.44	0.062
M8C	$\mathbf{-0.78 \pm 0.02\mathit{I} + 0.70 \pm 0.02\mathit{G} + 0.33 \pm 0.03\mathit{S} - 0.16 \pm 0.04Lo + 0.19 \pm 0.04\mathit{G} \times \mathit{S}}$	**11,387.1**	**0**	**0.938**

† Variables "year," "latitude," and "longitude" were added to the most parsimonious model (M8) to check for increased model fit.

‡ Parameter estimates (±SE). Number of mountain hare tracks per km and days since snowfall (log-transformed) as dependent variables. Intercept (*I*) independent variables are the number of red fox tracks (*R*), pine marten tracks (*M*), generalist predator tracks (*G*: sum of pine marten and red fox tracks), days of snow cover year $t - 1$ (*S*), year (*Y*), latitude (La), and longitude (Lo). The two most parsimonious models with and without spatiotemporal variables, respectively, in bold font.

§ Akaike information criterion (AIC) weights.

(max: 13.33, min: 0.00). We compared 11 candidate models in order to explain the spatiotemporal variation in the number of mountain hare tracks along snow tracking lines (Table 1). The most parsimonious model (M8) included the duration of snow cover during the preceding year, the number of generalist predator tracks (red fox and pine marten summed), and the interaction between these terms (Table 1, Fig. 3). When including year, latitude, and longitude to model M8, we found that adding longitude increased model fit (Table 1). There seems to be an east–west gradient in number of mountain hare tracks, with more tracks in the west (Fig. 1b). We found a positive correlation between mountain hares and generalist predators (Fig. 3). Moreover, the number of mountain hare tracks was positively associated with the length of the period of snow cover (Fig. 3). The interaction term showed that the negative effect of a short duration of snow cover is dependent on the abundance of generalist predators; that is, pronounced negative effects on the mountain hare population are expected in areas with a high abundance of generalist predators (Fig. 3).

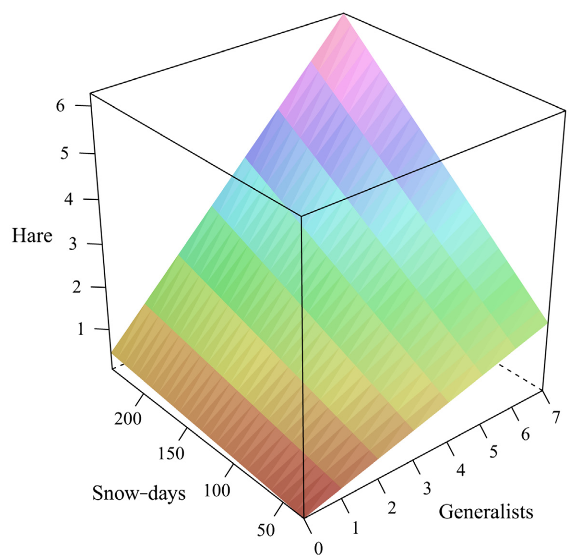

Fig. 3. Predicted values of number of mountain hare tracks per km transect and days since last snowfall (Hare). Explanatory variables were days of annual snow cover the preceding year (snow-days), and number of generalist predator tracks per km transect and days since last snowfall (generalists). Calculated using non-standardized raw data.

Discussion

We found a positive correlation between the abundance indices of generalist predators and mountain hares. This pattern may be caused by (1) generalist predators tracking the spatiotemporal variation in mountain hare abundance through a numerical and/or a functional response; that is, that predator densities increase (through immigration or reproduction) in areas rich in mountain hares, or (2) that individual predators focus their activity in areas rich in mountain hares. Although we cannot differentiate between these two mechanisms, the consequence for mountain hares is probably higher predator encounter rates and increased mortality risk.

Furthermore, the negative correlation between mountain hare abundance index and the duration of snow cover shown in our study may be explained by a higher mortality among hares in areas with less snow during winter due to a mismatch between pelt and background coloration (Zimova et al. 2016). This explanation is supported by the apparent synergetic effect between snow cover and generalist predator abundance index. According to our best model, a reduction in the duration of snow cover had a negligible effect in areas with a low abundance index of generalist predators. There may be a tradeoff between food availability and predation risk (Rehnus et al. 2016), with areas of short duration of snow cover yielding high availability of food plants during winter. However, if this effect is present in the current study, this would rather camouflage any effect of predation than explain them.

There is a higher mountain hare abundance index in the west compared to the east of Hedmark County; we speculate that this could be explained by a decrease in productivity from west to east (Moen et al. 1999), leading to less favorable mountain hare habitat.

There are several signs of mountain hares being able to adapt to reduced snow cover duration. First, the Irish hare (*Lepus timidus hibernicus*) does not molt to white winter pelage. Second, there are pelage morphs of Norwegian mountain hares which do not turn completely white, but rather have a light bluish gray winter pelage (Pedersen and Pedersen 2012). However, our study suggests that mountain hares may not be able to adapt fast enough to cope with the rapid climatic changes, leading to less snow cover. This could be caused by either a low phenotypic plasticity in the mountain hares or a low capability of contemporary evolution (evolutionary adaptations observable over the course of decades; Berteaux et al. 2004). Irrespective of the cause, the consequence is a decline in the mountain hare abundance. Our study concurs with recent research conducted on snowshoe hares, where there is a mismatch in seasonal coat color due to decreased snow cover duration (Mills et al. 2013) and low phenotypic plasticity (Zimova et al. 2014). This leads to high fitness costs due to reduced survival, potentially causing population declines (Zimova et al. 2016). In our study, we show that a negative impact of reduced snow cover is closely linked to generalist predator abundance. In the future, a negative impact of a mismatch in coat coloration may be amplified by an increase and range expansion of generalist predators, with the red fox in particular (Elmhagen et al. 2015) causing a reduced density and distribution of the mountain hare. Indeed, from modeling of ecogeographical variables and predicted climate change, Acevedo et al. (2012) found that the mountain hare in Europe is expected to decrease to 30% of its current distribution by 2080. Furthermore, the mountain hare is expected to experience a poleward shift as a consequence of climate change (Leach et al. 2015). Also, in snowshoe hares, Sultaire et al. (2016) found a northward movement of their southern range in response to climate change, rather than land-use change. Our results also suggest a possible mechanism for the observed decline in other color-changing species in the boreal and arctic, such as the willow ptarmigan (*Lagopus lagopus*) and rock ptarmigan (*Lagopus muta*). Future research should aim at investigating the relationship between mountain hares, snow and generalist predators further by evaluating the actual mismatch between background coloration and predation risk. This study highlights future management challenges when it comes to mountain hares, as the duration of snow cover is reduced through climate change, an option of monitoring mountain hare populations is lost. Rehnus and Bollmann (2016) suggest sampling of DNA from mountain hare fecal pellets as a method of estimating population size in mountain hares, which is an expensive but efficient method of population monitoring. An alternative approach that is under development in Norway is the use of camera traps for monitoring of the mountain hare and other wildlife (www.viltkamera.nina.no).

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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1722/full