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Climate change and the race for survival:

exploring the effects of climate change on the phenology and distribution of native mountain hares *(Lepus timidus)* and invasive European hares *(Lepus europaeus)*

PhD in Applied Ecology and Biotechnology
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Abstract

Species that live in seasonally changing environments often evolve adaptations to their environment. Seasonal moulting between winter and summer coats is an adaptation to seasonal snow cover that is expressed by multiple mammal and bird species. It has a critical impact on survival as individuals that are mismatched against their background have either an increased risk of being predated or decreased probability of catching prey. Species' coat phenology can be negatively affected when climate change induced reductions in snow cover duration and extent result in moult timing not matching snow appearance and disappearance. Additionally, abnormal winter and summer snow conditions can result in animals being mismatched when they time moulting correctly.

In Paper I, I used camera trap observations collected across an environmental gradient to create a Bayesian multinomial logistic regression model that estimated the correlation between mountain hare (*Lepus timidus*) moult timing and altitude, latitude, and climate zone. In Paper II, I developed a generalised additive model (GAM) that estimated the correlation between these environmental variables and the probability of mountain hares being mismatched. In Paper III, I used camera trap and citizen science observations in conjunction with environmental and climatic data to create species distribution models. These models were used to map the current distribution, current suitable habitat, and future suitable habitat of white mountain hares (*Lepus timidus timidus*), heath hares (*Lepus timidus sylvaticus*), and European hares (*Lepus europaeus*).

Altitude, latitude, and climate zone correlated with mountain hare moult timing. Hares living at increased altitudes and latitudes moulted later in the spring and earlier in the autumn than their low altitude and latitude conspecifics. Mountain hares inhabiting areas with continental climates moulted earlier in the spring and later in the autumn than hares living in areas with coastal climates. These environmental variables also correlated with the probability of mountain hares being mismatched against their background. Mountain hares inhabiting inland areas at high altitudes and latitudes with continental climates were mismatched less throughout the year than their low altitude and latitude conspecifics in coastal regions. The species distribution models indicated that white mountain hares are distributed across Norway, heath hares are limited to Norway’s southeast and southwest coastal regions and European hares occupy the south-east corner next to the Swedish border. White mountain hare future suitable habitat was predicted to decrease in area whereas heath hare and European hare habitat is expected to expand. This is likely to increase inter-specific interactions and competition.

Sammendrag

Arter som lever i miljøer med store forskjeller mellom årstidene utvikler ofte tilpasninger til miljøet sitt. Å bytte mellom sommer- og vinterdrakt er en tilpasning til sesongavhengig snødekke som finnes hos flere pattedyr- og fuglearter. Dette har stor innvirkning på overlevelse fordi individer som har et misforhold mellom draktfarge og farge på omgivelsene enten har høyere risiko for predasjon eller lavere sannsynlighet for å fange byttedyr. En arts draktfenologi kan bli påvirket negativt når reduksjon i lengden på snøsesongen og utbredelsen av snø som følge av klimaendringer resulterer i at draktskifte ikke samsvarer med når snøen er til stede. I tillegg kan unormale snøforhold i løpet av snøsesongen resultere i misforhold mellom drakt og farge på omgivelsene når dyr skifter drakt til riktig tid.

I artikkel I brukte jeg kamerafelleobservasjoner samlet inn langs en miljøgradient til å lage en bayesisk multinomisk logistisk regresjonsmodell som estimerte korrelasjonen mellom tidspunktet for draktskifte hos skogshare (*Lepus timidus*) og høyde over havet, breddegrad, og klimasone. I artikkel II utviklet jeg en generalisert additiv modell (GAM) som estimerte korrelasjonen mellom disse miljøfaktorene og sannsynligheten for at det er misforhold mellom skogsharens drakt og farge på omgivelsene. I artikkel III brukte jeg observasjoner fra kamerafeller og folkeforskning til å lage artsspesifikke utbredelsesmodeller som kartla nåværende utbredelse, nåværende egnet habitat, og framtidig egnet habitat for hvit skogshare (*Lepus timidus timidus*), blåhare (*Lepus timidus sylvaticus*), og sørhare (*Lepus europaeus*).

Høyde over havet, breddegrad, og klimasone korrelerte med tidspunktet for skogsharens draktskifte. Harer som levde høyere opp og ved høyere breddegrader skiftet drakt senere om våren og tidligere på høsten enn sine artsfeller lengre ned og ved lavere breddegrader. Harer i innlandsklima skiftet drakt tidligere om våren og senere på høsten enn harer i kystklima. Disse klimafaktorene korrelerte også med sannsynligheten for at harene hadde misforhold mellom drakt og farge på omgivelsene. Innlandsharer i høyden ved høyere breddegrader hadde sjeldnere misforhold mellom drakt og farge på omgivelsene enn kystharer i lavlandet ved lavere breddegrader. Utbredelsesmodellene indikerte at hvite skogsharer er utbredt over hele Norge, at blåharer er begrenset til Norges sørøstlige og sørvestlige kystområder, og at sørharer lever i den sørøstlige delen av Norge langs grensen til Sverige. Modellene forutsier at arealet egnet habitat for hvit skogshare vil reduseres i framtiden, mens mengden egnet habitat for blåhare og sørhare antas å øke. Dette vil sannsynligvis øke mengden interspesifikke interaksjoner og konkurranse.

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Paper II

Stokes, A. W., T. R. Hofmeester, N. H. Thorsen, J. Odden, J. D. C. Linnell, M. Zimova, L. S. Mills, and S. Pedersen. 2023. Mountain hare (*Lepus timidus*) coat colour mismatch is greatest in areas that have experienced the largest climate change induced reductions in the number of snow days. *Manuscript*

Paper III

Stokes, A. W., T. R. Hofmeester, N. H. Thorsen, J. Odden, J. D. C. Linnell, and S. Pedersen. 2023. Current distribution and the impact of climate change on the future suitable habitat of two morphs of the native mountain hare, and the non-native European hare in Norway. *Manuscript*

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Introduction

1.1 Phenological adaptations to seasonally changing environments

Numerous species that inhabit seasonally changing environments, such as from snow accumulation to snow melt and from summer to winter, evolve adaptations to their local environment. These adaptations often involve timing life history events, such as flowering (Amasino and Michaels 2010), migration (Fryxell and Sinclair 1988), breeding (Lincoln and Short 1980), and moulting (reviewed in Zimova et al. 2018), to account for seasonal environmental changes.

These life history events are often timed using photoperiod (Temte 1994, Bradshaw and Holzapfel 2007, Amasino and Michaels 2010), either in isolation or in combination with other environmental cues including nutrient availability (Menassol et al. 2012), snow cover (Watson 1963, Flux 1970), precipitation (Mu et al. 2021) and temperature (Watson 1963, Jackes and Watson 1975, Hairston and Kearns 1995, Larkin et al. 2001). The timing of life events that are primarily controlled by photoperiod should remain relatively stable from year to year as photoperiod is constant between years in specific locations. This means that life events can be mistimed when seasonal changes occur either early or late. In response, plants and animals that inhabit areas typified by considerable environmental variation often display more phenotypic variation than their conspecifics that inhabit more environmentally stable areas (Ashmore and Janzen 2003, Villellas et al. 2014, Kreyling et al. 2019).

1.2 Seasonal coat colour change

Seasonal coat colour change, which occurs when species moult from a dark coat in the summer to a white coat in the winter, is an adaptation to seasonally changing environments that has evolved in at least 21 bird and mammal species (Mills et al. 2018, Zimova et al. 2018). It is primarily controlled by photoperiod (reviewed in Zimova et al. 2018) but is also affected other environmental variables, including temperature (Rothschild 1942, Watson 1963) and snow cover (Watson 1963, Flux 1970, Watson 1973). Seasonal coat colour change occurs in both prey species, including mountain hares (*Lepus timidus*) and snowshoe hares (*Lepus* *americanus*), and predatory species, such as Arctic foxes (*Vulpes lagopus*) and least weasels (*Mustela nivalis*), providing multiple advantages. Winter white coats are longer, denser and provide better insulation than summer brown coats in a variety of species including Arctic fox (Underwood and Reynolds 1980) and snowshoe hare (Grange 1932, Lyman 1943). Regional variation has been observed, with the coats of snowshoe hares inhabiting high latitudes providing better insulation than those of their low latitude conspecifics (Gigliotti et al. 2017). Seasonal coat colour change also increases camouflage against animals' background in both winter and summer (Wallace 1879, Cott 1940, Merilaita and Lind 2005).

For adaptive coat colouration to provide optimal benefit, the transition between coats should match the timing of snow appearance and disappearance as well as matching snow conditions within the winter and summer periods. Climate change leading to snow disappearing within the winter period could result in an animal that accurately times moulting still being mismatched within the winter season. Strong selection pressure is likely to be applied against animals that do not match their seasonal coat to their local conditions (Zimova et al. 2016, Pedersen et al. 2017). Failing to adapt moult phenology to climate change has led to declining distribution and population size in rock ptarmigan (Imperio et al. 2013), snowshoe hares (Diefenbach et al. 2016, Sultaire et al. 2016), and mountain hares (Pedersen et al. 2017). As seasonal coat colour change is primarily controlled by photoperiod (reviewed in Zimova et al. 2018), it is likely that species that express this adaptation will be negatively affected by climate change that affects snow cover duration and extent.

1.3 Species distribution is affected by climate change and non-native species

Species distributions are strongly affected by climate change, leading to both expansion and contraction of different species' distributions (Pearson et al. 2013, Elmhagen et al. 2015, Brown et al. 2016). As the Earth warms, species that are adapted to cold climates move towards higher altitudes (Moritz et al. 2008, Elsen et al. 2020) and latitudes (Thomas and Lennon 1999, Hastings et al. 2020), leading to extirpation from parts of their distribution and increased extinction risk (Elsen et al. 2020). These habitats can be colonised by generalist species that are adapted to more temperate climates (Parmesan and Yohe 2003, Caravaggi et al. 2017). Generalist species frequently expand their distribution more quickly than specialists, often resulting in competing specialist species experiencing range declines and increased areas of sympatry (Platts et al. 2019, Schai-Braun et al. 2021). Climate change also facilitates the establishment of non-native species that are adapted to the changed environmental conditions (Dukes and Mooney 1999, Hellmann et al. 2008, Walther et al. 2009), leading to interactions between native and non-native species (Dukes and Mooney 1999, Caravaggi et al. 2017).

Non-native generalist species tend to be more successful than specialists after introduction as they exploit wider niches (Duncan et al. 2003, Blackburn et al. 2009). There is some evidence that non-native species that occupy similar niches to native species are more likely to naturalise successfully (Diez et al. 2009, Divisek et al. 2018) but, other studies have reported contradictory results (Jiang et al. 2010). When native and non-native species occupy similar niches, competition for resources, such as space and food, often occurs, which can lead to the native species' distribution decreasing (Mooney and Cleland 2001, Bøhn et al. 2008). Hybridisation between non-native and native species is likely to occur when the two species are closely related. This can lead to a process called 'extinction by hybridisation and introgression' (Rhymer and Simberloff 1996), which can occur when the population of purebred individuals decreases below the number needed for replacement (Wolf et al. 2001). Therefore, the introduction of non-native species can result in native species being extirpated from parts of their distribution and increasing extinction risk (Dukes and Mooney 1999, Huxel 1999, Butchart et al. 2010).

1.4 Move, adapt, or die

Species that are negatively affected by environmental disturbances can respond in three ways; move to a more suitable habitat, adapt to the environmental stressors, or become extinct (Levins 1969, Aitken et al. 2008, Corlett and Westcott 2013). In some cases, the rate of climate change outpaces species' dispersal speed (Pearson 2006, Chen et al. 2011, Nathan et al. 2011). Additionally, moving to higher altitudes can result in populations being unable to migrate due to a lack of suitable habitat at lower altitudes (Opdam and Wascher 2004). Species can adapt to stressors through evolution, phenotypic plasticity, or a combination of both. These factors interact as they both have genetic components (Scheiner 1993, Ghalambor et al. 2007).

Numerous phenological adaptations to climate change have been recorded leading to life history events, including migration and breeding, occurring earlier in spring (Walther et al. 2002, Jenni and Kery 2003, Parmesan and Yohe 2003). But, adaptation often occurs more slowly than needed to track environmental change (Both and Visser 2001, Zimova et al. 2014). Failure to adapt to environmental change inevitably increases extinction risk.

1.5 Study organisms: white mountain hares, heath hares, and European hares

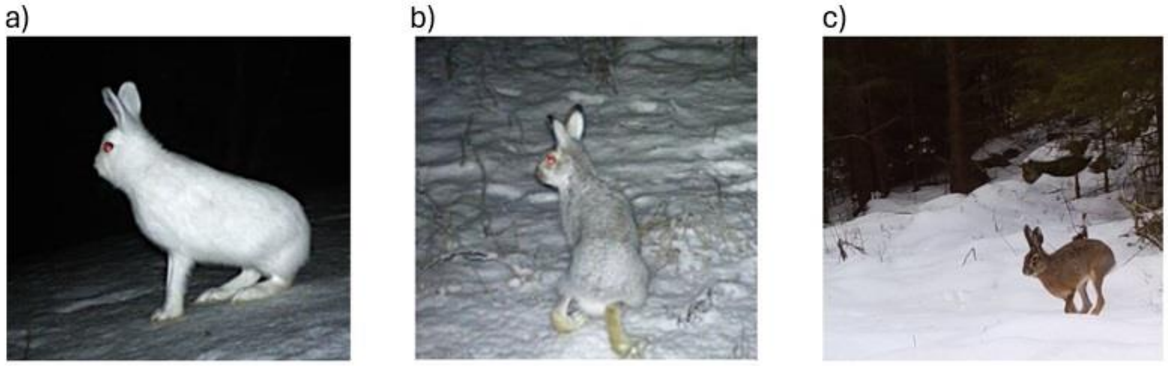

Figure 1. (a) White mountain hare, (b) heath hare, and (c) European hare in winter photographed by SCANDCAM camera traps (https://viltkamera.nina.no).

In this thesis, I focused on three study organisms, white mountain hares (*Lepus timidus timidus*), heath hares (*Lepus timidus sylvaticus*), and European hares (*Lepus europaeus*). I used mountain hare as an umbrella term for all mountain hare subspecies. Excluding the Irish subspecies (*Lepus timidus hibernicus*), mountain hares display a seasonal coat colour throughout their range (Mills et al. 2018). White mountain hares moult from brown in summer to white in the winter (Figure 1.a) whereas heath hares moult from brown in the summer to a light grey, bluish colour during the winter (Figure 1.b). Heath hares' bluish coat is thought to be an adaptation to milder winters experienced in the south of Norway (Barth 1891). It could provide superior camouflage to the white mountain hares' coat in areas with inconsistent snow cover. Alternatively, it could be a bet hedging strategy that enables heath hares to survive in areas that experience variable within season and between year snow conditions. This may enable mountain hares to mitigate some of the negative impacts of coat colour mismatch caused by reductions in snow cover. Mountain hares are generalist herbivores distributed across Europe and Asia spanning from the Faroe Islands in the west to Japan in the east (Angerbjorn and Flux 1995). They are native to Norway and inhabit most of the country with their range varying from sea level to over 1,600 meters above sea level (m.a.s.l.), which is above the tree line. They tend to prefer dense shrubs and forests that provide food and refuge from predators (Hiltunen et al. 2004, Bisi et al. 2013).

European hares are generalists that are native to mainland Europe and Asia (Flux and Angerman 1990). They do not express seasonal coat colour change, retaining their brown coats year-round (Figure 1.c). Within Norway, they are a non-native species that expanded into the south-east after being released into Sweden in the 1800s (Thulin 2003 and references within). They are a beneficiary of climate change, which has resulted in their territory expanding in Ireland (Caravaggi et al. 2017) and Fennoscandia (Thulin 2003, Jansson and Pehrson 2007). They typically inhabit lowland and agricultural habitats (Kamieniarz et al. 2013) but, their distribution has reduced in some areas due to agricultural intensification (Smith et al. 2005). Ensuring that a high proportion of set-asides are present within agricultural areas reduces population decline by increasing leveret survival rate (Schai-Braun et al. 2020).

1.6 Knowledge gap and objectives

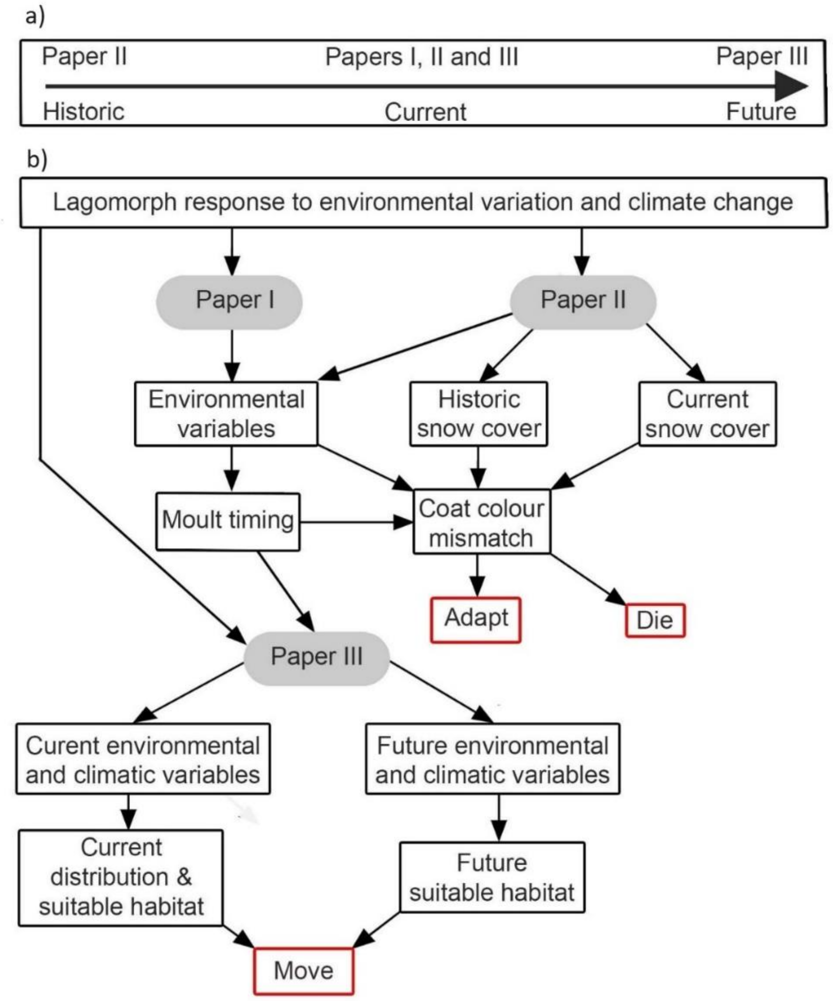

Figure 2. (a) Timeline of which period each paper addresses. (b) Connection between the papers, the datasets used in my analysis, and how they interact with the move, adapt, or die framework (Figures designed by Allan Stokes and drawn by David Stokes).

Numerous studies have investigated moult timing in snowshoe hares, which are native to North America, and various other mammal and bird species (reviewed in Zimova et al. 2018). However, before this study, mountain hare moult timing had not been studied in Norway. Additionally, this project represents the first time that moult timing and seasonal coat colour mismatch have been estimated over an entire country. Most moult timing literature focuses on mismatch that occurs within the two moulting seasons. In my second paper, I expanded on this by investigating mismatch across the entire year in addition to within the moulting period. Before this study, mountain hare hunting bag reports had been conducted within Norway (Pedersen and Pedersen 2012). Additionally, mountain hare and European hare distribution had been described on a Europe wide scale (Acevedo et al. 2012). But, fine scale distribution studies within Norway had not been conducted. Therefore, this thesis represents the first occasion on which white mountain hares, heath hare and European hare current distribution and future suitable habitat has been estimated exclusively within Norway. The time-periods investigated in each paper and how the analysis links together between papers is illustrated in Figure 2. I investigated the following research questions in my papers:

Paper I: I investigated the correlation between environmental variables (altitude, latitude, and climate zone) and spatial and temporal variation in moult timing. I predicted that mountain hares inhabiting areas characterised by high altitudes, high latitudes and continental climates would keep their winter white coats for longer than their conspecifics inhabiting areas characterised by low altitudes, low latitudes, and coastal climates. This was based on inland areas at high altitudes and latitudes experiencing greater historical snow cover duration. I also predicted that moult timing would vary more in spring than in autumn as this pattern was reported in previous studies conducted on snowshoe hares (Mills et al. 2013, Zimova et al. 2014) and least weasels (Atmeh et al. 2018).

Paper II: I built on the research conducted in Paper I by using the moult timing predictions to investigate the correlation between the environmental variables used in Paper 1 and the probability of mountain hares being mismatched across Norway. I predicted that the probability of mismatch would be greatest in coastal regions at low elevations and latitudes as these areas have experienced the largest reductions in the number of snow days (Hanssen-Bauer et al. 2017). I also predicted that mismatch recorded during the entire year, hereafter referred to as *cumulative mismatch*, would be greatest in areas that have experienced the largest reductions in the number of snow days.

Paper III: I estimated the current distribution and future suitable habitat of white mountain hares, heath hares and European hares. I predicted that the current distribution of white mountain hares would be spread across the majority of Norway, heath hares would be limited to the lower half of Norway, particularly along the coast, and that European hares would be limited to the southeast corner next to the Swedish border. For future suitable habitat, I predicted that white mountain hare suitable habitat would contract whereas heath hare and European hare habitat would expand. These predictions were based on current observational data and my estimations of how each study organism would react to a warming climate.

Methods

2.1 Study area and observation data (Papers I, II and III)

All three studies within this project utilised images obtained from camera traps deployed by the SCANDCAM project across Norway between 58° N to 69° North (Figures 3.a and 4, Table 1). The cameras were deployed across an environmental gradient in a grid pattern with approximately one camera trap per 50 km^2 grid cell. The camera traps were positioned to maximise the probability of observing lynx (*Lynx lynx*) and other politically sensitive species, resulting in site selection not being randomised. All camera trap images that I used in this thesis are stored on the SCANDCAM website (https://viltkamera.nina.no).

Both mountain hares and European hares, which can hybridise (Gustavsson 1971, Schroder et al. 1987), are present in the study area. The species identification protocol described in Smith et al. (2018) was used to differentiate between the species with hares being classified as either mountain hares or European hares. I excluded observations from the analysis if it was not possible to determine the species observed. Therefore, hybrids were excluded from the data used in this thesis.

For Papers I and II, I used all images containing mountain hares that were identified at 678 camera trap locations (Figure 3.a and Table 1). I modified the scale from Zimova et al (2020) where hares were classified as (a) white if they had ≥90% white fur, (b) brown if they had ≤10% white fur and (c) moulting if they had any other proportion of white fur. I subset the data into two datasets covering the spring and autumn moulting periods. Observations recorded between the 1st and 212th ordinal day of the year (1st January to 31st July in non-leap years) were defined as 'spring'. All other ordinal days were defined as 'autumn'.

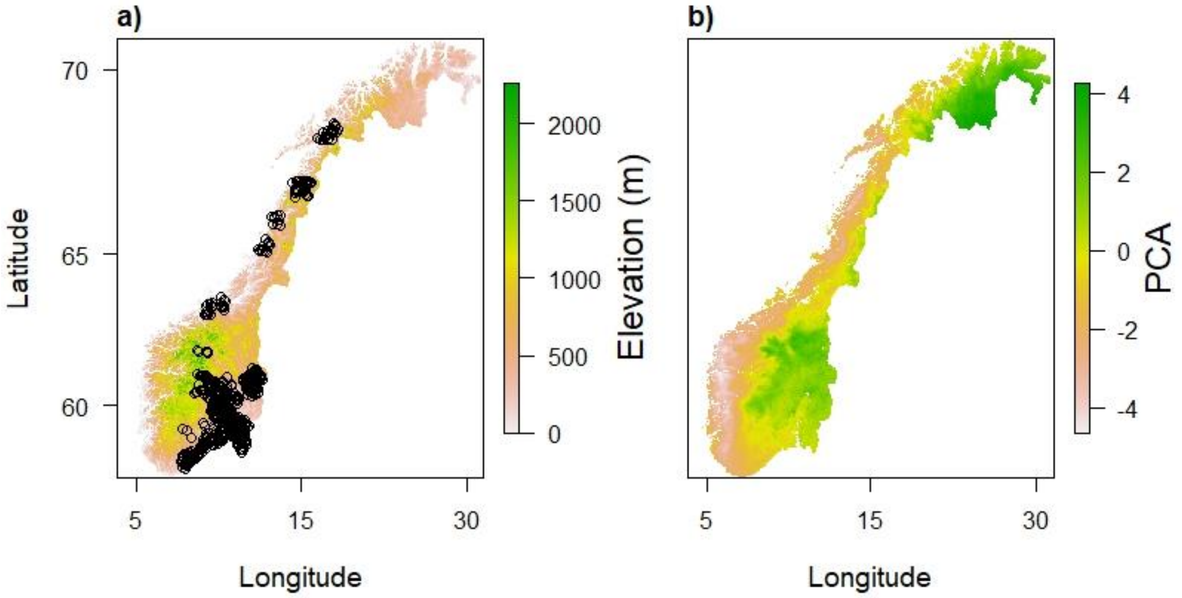

Figure 3. (a) Digital elevation model with the location of 678 camera traps that recorded observations used in Papers I and II. The cameras were deployed by the SCANDCAM project at altitudes between 0 and 841 meters above sea level (m.a.s.l.) and between 58° N and 69° N. (b) Climate zone as a continuous variable, used as an environmental variable in Papers I and II.

For Paper III, additional camera trap images were classified. This expanded the data collection date range and the area over which data was collected (Figure 4 and Table 1). To increase the area containing observations, I used mountain hare and European hare citizen science observations reported to the Norwegian Species Observation Service (www.artsobservasjoner.no) platform (accessed 24th August 2023). I used observations containing an image that had been validated by a third-party expert.

Next, I subset the mountain hare observations into white mountain hare and heath hare datasets. As it is only possible to differentiate between white mountain hares and heath hares when they express their winter coats, I used the model developed in Stokes et al. (2023) (model described in section 2.3.1) to determine the dates on which mountain hares were estimated to have moulted to either >50% white or blue in each location. I then used these dates to subset the camera trap and citizen science mountain hare observations. I discarded observations where it was not possible to determine hare species and colour. I did not subset European hare images as they can be identified throughout the year.

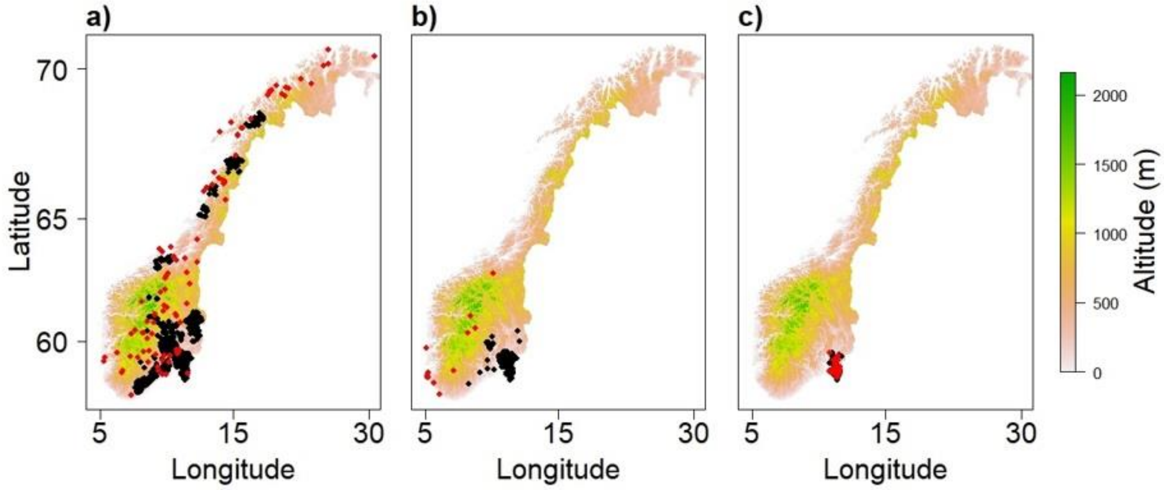

Figure 4. Location of camera trap (black circles) and citizen science (red circle) observations for (a) white mountain hares, (b) heath hares and (c) European hares used in Paper III. I thinned the data to one observation per species per 1 km^2 cell (see section 2.3.3).

Traditional surveying techniques, such as live trapping and fitting radio collars, are typically labour intensive, limiting the geographical area covered and the amount of data collected (De Bondi et al. 2010). Camera traps are a cost effective and time efficient data collection method that enable continuous, long-term monitoring over large areas that would be impractical to observe using other methods (Moruzzi et al. 2002, Vine et al. 2009, De Bondi et al. 2010). Therefore, they are often used to monitor elusive, wide-ranging species that are challenging to survey (Griffiths and Schaik 1993, Burton et al. 2015). Camera traps have been used to study species distribution, abundance, phenology, and behaviour (Tape and Gustine 2014, Burton et al. 2015, Caravaggi et al. 2017, Zimova et al. 2019). However, they have limited ability to observe fine-scale behavioural traits. For example, it was not possible for me to use this dataset to analyse microhabitat selection. More localised monitoring methods, such as VHF and GPS collaring, would facilitate researching similar traits (Smith et al. 2018).

Table 1. Range of values at which both camera trap and citizen science data were obtained for all study organisms across all papers.

	Papers I and II	Paper III	
	Camera trap	Camera trap	Citizen science
Observation date range	10th January 2011 to 25th June 2019	25th November 2010 to 6th April 2022	19th February 2005 to 30th June 2023
Altitude range (m.a.s.l.)	0 to 841	0 to 841	0 to 1,408
Latitude (° North)	58 to 69	58 to 69	58 to 71
Climate zone	−2.68 to 2.86	NA	NA

2.2 Explanatory variables (Papers I, II, and III)

2.2.1 Environmental variables (Papers I, II and III)

I obtained latitude based on camera trap locations and citizen science sightings information logged on www.artsobservasjoner.no. I extracted the altitude of each observation from a digital elevation model (DEM) with a 50 m^2 resolution (Figure 3.a) (Korsnes 2018). Climate zone as a continuous variable with a 1 km^2 resolution was mapped by Bakkestuen et al. (2008) (Figure 3.b). A negative value correlated to a coastal climate and a positive value correlated to a continental climate. Hereafter, I used the climate zone map to standardise the resolution and grid cell layout of all explanatory variables and maps.

2.2.2 Snow data (Paper II)

I used two snow datasets based on interpolated weather station data from www.senorge.no. I defined a snow day as any day where the depth of snow was ≥ 5 cm. I chose this depth as the ground is still visible when the snow depth is < 5 cm (Pedersen et al. 2017). The first snow dataset, hereafter referred to as the *climate change* dataset, was composed of two maps containing the average number of snow days from 1959 to 1988 and from 1989 to 2018 across

Norway. I could not include an earlier 30-year period as www.senorge.no records start in 1957. I calculated variation in the number of snow days by subtracting the two maps from each other. The second snow dataset, referred to as the *weather* dataset, contained snow depth data for every camera trap location in every ordinal day from 2011 to 2018.

2.2.3 Historic and future climatic variables (Paper III)

Shared Socioeconomic Pathways (SSPs) were defined as climate change scenarios by the IPCC 2021 climate change report (Masson-Delmotte et al. 2021). I used a moderate climate change prediction (SSP370) for all analysis. I used climatic and environmental variables to predict the current distribution, current suitable habitat, and future suitable habitat of all three study organisms. Current distribution was defined as the area that these organisms currently inhabit. Suitable habitat was defined as the area containing habitat they could potentially inhabit.

To this end, I used BIOCLIM (www.worldclim.org) historic (1970 – 2000) and future (2061 – 2080 and 2081 – 2100) climatic variables that are relevant to my study species, such as annual precipitation and temperature of the coldest month (Table 3). I also used CHELSA (https://chelsa-climate.org) historic (1981 – 2010) and future (2041 – 2070 and 2071 – 2100) snow cover days data. For the current estimates, I paired the 1970 – 2000 BIOCLIM data with the 1981 – 2010 CHELSA data. For the future predictions, I paired 2061 – 2080 BIOCLIM predictions with 2041 – 2070 CHELSA predictions (hereafter referred to as *medium-term* predictions) and 2071 – 2100 CHELSA predictions with 2081 – 2100 CHELSA predictions (hereafter referred to as *long-term* predictions).

I used www.copernicus.eu land use data (accessed 24th August 2023) to create two maps containing the proportion of each cell covered by either forest or agricultural land. These variables were chosen as they are relevant to my study organisms. I kept these variables constant when predicting future habitat suitability as land use is determined by political decisions which I cannot predict.

Estimating the current distribution of European hares within Norway is challenging as they are expanding into suitable habitat they have not had sufficient time to colonise. Therefore, models that predict current suitable habitat could give estimates that are significantly greater than their current distribution. To account for this, I included latitude and longitude variables to spatially constrain results when estimating the current distribution of all study organisms.

2.2.4 Bias file (Paper III)

I created a bias file to address sampling biases in my observation data. I included all camera trap locations, including those that did not record hare observations. When estimating citizen science observer effort, I assumed an equal probability of reporting all land mammals. I downloaded all terrestrial mammal sightings using the same selection criteria and date range used for hare observations. I subset the dataset retaining a maximum of one camera trap observation and one citizen science observation per 1 km^2 cell. I gave cells containing both observation types a value of 2, cells containing one observation type a value of 1, and all other cells a value of 0.1.

2.3 Data analysis

2.3.1 Variation in moult timing and coat colour mismatch (Papers I and II)

I created Bayesian models, called the *moult timing models* (model 1), to estimate the probability of mountain hares being white, brown, or moulting in both “spring” and “autumn” from 2011 to 2019 (Paper I). I used the camera trap observations as the response variable and ordinal day, elevation, latitude, and climate zone as explanatory variables (Table 3). I also included a year specific intercept to enable analysis of the results from individual years and camera trap locations as a random intercept.

Next, I used the moult timing results in conjunction with the weather dataset to estimate when hares were mismatched against their background at each camera trap location on every day between 2011 and 2018 (Paper II). I excluded 2019 as the observation dataset did not include the entire year (Table 1). I classified hares as white when the probability of being white was greater than the probability of being brown and vice versa. This enabled me to account for mismatch occurring when hares were moulting as well as when they were white or brown. I used the weather dataset to classify white hares as mismatched when snow depth at camera trap locations was < 5 cm and brown hares as mismatched when snow depth was ≥ 5 cm.

I obtained a measure of the probability of mismatch by summing the number of years in which hares were mismatched on each ordinal day at each camera trap location, giving a count between 0 and 8. I used this value to derive a probability estimate between 0 and 1. Next, I created a generalised additive model (GAM), called the *probability of mismatch model* (model 2), using the probability of mountain hares being mismatched as the response variable and ordinal day, latitude, elevation, and climate zone as explanatory variables (Table 3).

2.3.2 Cumulative mismatch (Paper II)

I created a generalised linear mixed model (GLMM), called the *cumulative mismatch model* (model 3), to analyse the correlation between *cumulative mismatch* (average days mismatch per year) and change in the number of snow days at each camera trap location. For the response variable, I used the weather dataset in conjunction with the moult timing estimates to find the average number of days hares were mismatched per year per location (Table 3). For the explanatory variable, I used the climate change dataset to find the change in the number of snow days per year per location. I included year and camera trap location as random intercepts. When plotting the results, I included partial residuals rather than data points as they control for the effects of year and camera trap location (Figure 10).

2.3.3 Distribution and suitable habitat model selection (Paper III)

I used the MaxEnt software (Phillips et al. 2017) to model white mountain hare (model 4), heath hare (model 5), and European hare (model 6) current distribution, current suitable habitat, and future suitable habitat. I used MaxEnt as it can explain non-linear relationship, use presence only data, such as citizen science observations, and make predictions using climate change predictions (Elith et al. 2010, Khosravi et al. 2016). I thinned the dataset to one observation per species per 1 km^2 grid cell to reduce the impact of sampling bias (Kramer-

Schadt et al. 2013) (Figure 4 and Table 2). After subsetting and thinning the observations, a total of 642 camera trap locations and 164 citizen science locations were used in the models. I then used the ENMeval package (Muscarella et al. 2014) to find the model with the best test statistics for each study organism. See table 3 for the variables included in each organisms' model.

Table 2. Number of camera trap and citizen science observations after thinning the dataset to one observation per organism per cell. One cell contained both European hare camera trap and citizen science observations. All other cells contained one observation type per organism.

	Mountain hare	Heath hare	European hare
Camera trap observations	579	144	31
Citizen science observations	99	13	54
Observations used in final analysis	678	157	84

2.3.4 Modelling distribution and future suitable habitat (Paper III)

I called MaxEnt within R, fitting current distribution and current suitable habitat models for all study organisms. I used the bias file to generate 10,000 random background points that estimated sampling bias and ran all models for 20 replications with 2,000 iterations per replication. Next, I used the current suitable habitat models in conjunction with the climate change predictions to predict the medium and long-term future suitable habitat. For each map, I estimated the proportion of Norway containing suitable habitat by calculating the area where the training omission rate threshold was > 10%. Omission rate is the proportion of test locations falling within cells that are predicted as unsuitable habitat (Phillips et al. 2006). I interpreted the model results using binary maps, which enabled calculating the area of suitable habit.

I completed all data analysis using R versions 4.1.3 for Paper I and 4.3.2 for Papers II and III (R Core Team 2022). I used the *raster* (Hijmans 2023), *GGPLOT2* (Wickham 2016), and *jtools* (Long 2022) packages for plotting figures.

Table 3. Explanatory variables contained in each model used for this thesis. The model number is given in brackets. The current distribution models contain latitude and longitude in addition to the variables listed.

	Model name and number					
Variable name and units	Moult timing (model 1)	Probability of mismatch (model 2)	Cumulative mismatch (model 3)	White mountain hare suitable habitat (model 4)	Heath hare suitable habitat (model 5)	European hare suitable habitat (model 6)
Ordinal day	✓	✓	NA	NA	NA	NA
Altitude (m.a.s.l.)	✓	✓	NA	✓	✓	✓
Latitude (°N)	✓	✓	NA	NA	NA	NA
Climate zone	✓	✓	NA	NA	NA	NA
Snow days (climate change)	NA	NA	✓	NA	NA	NA
Snow days (weather)	NA	NA	✓	NA	NA	NA
Year	✓	NA	✓	NA	NA	NA
Location	✓	NA	✓	NA	NA	NA
Max temp warmest month (°C)	NA	NA	NA	NA	✓	NA
Min temp coldest month (°C)	NA	NA	NA	✓	✓	✓
Annual precipitation (mm)	NA	NA	NA	NA	✓	✓
Snow cover days (CHELSA)	NA	NA	NA	NA	✓	✓
Agriculture	NA	NA	NA	✓	NA	✓
Forest	NA	NA	NA	✓	NA	NA

3 Results and Discussion

3.1 Observation and snow data

After cleaning the dataset used for Papers I and II, I obtained 7,554 spring and 2,525 autumn observations giving a total of 9,979 mountain hare observations at 678 camera trap locations between 2011 and 2019 (Table 1). The large difference between the number of samples obtained in autumn and spring could be explained by increased activity during mating season (Pettigrew et al. 2021). The number of observations collected each year increased as the number of camera traps deployed increased. Therefore, results obtained in later years are more reliable and have narrower credible intervals than those obtained in earlier years (Figure 7).

Between 1959 to 1988 and 1989 to 2018 the camera trap locations experienced a reduction of between 4 and 57 snow days. This is consistent with patterns observed over most of the northern hemisphere (Derksen and Brown 2012, Kunkel et al. 2016).

3.2 Spatial and temporal variation in moult timing (Paper I)

Altitude, latitude, and climate zone correlated with mountain hare moult timing (Figure 5, model 1). There was strong support for the probability of mountain hares keeping their winter white coats for longer with increasing with altitude (Figure 5.a) and latitude (Figure 5.b) in both spring and autumn. There was weak support for mountain hares keeping their winter white coats for longer in coastal climates (Figure 5.c).

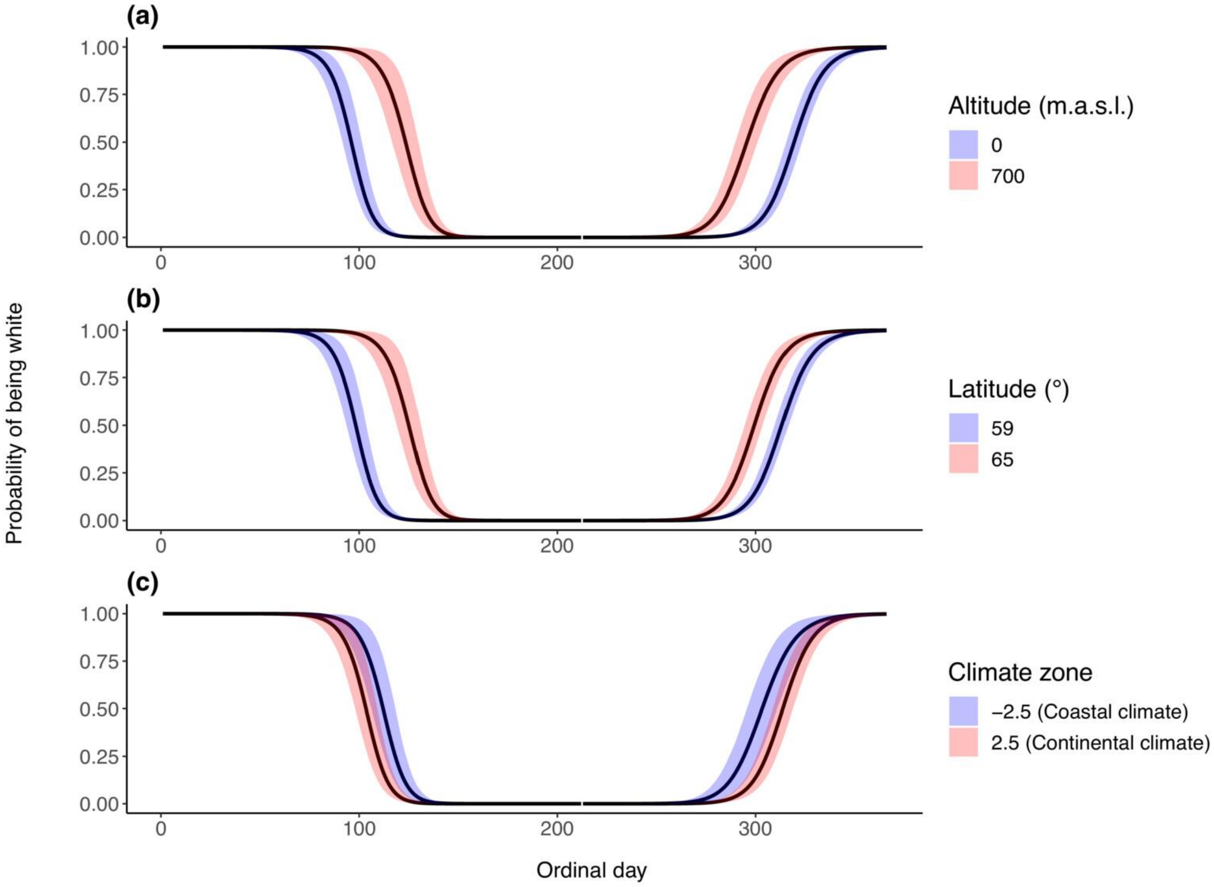

Figure 5. The probability of mountain hares being white compared to the combined probability of being brown or moulting at different (a) altitudes, (b) latitudes, and (c) climate zones. The solid lines represent the probability of being white and the shaded areas represent the 95% credible intervals. In each plot, the two variables not being tested were set to the mean values.

There was considerable variation in mountain hare moult timing across Norway (Figure 6, model 1). Starting in spring (Figure 6.a), hares along the south and southwest coast moulted first from white to brown. Hares in the far north and mountainous regions were the last to moult (Figure 6.b and c). The pattern reversed in autumn with hares in the far north and mountainous regions moulting from brown to white before hares in other regions (Figures 6.e and f). The contradiction between hares in coastal climates keeping winter white coats for longer than their inland conspecifics (Figure 5.c) and hares in southerly coastal regions moulting first in spring and last in autumn illustrates climate zone’s weak effect size.

The altitude (Figure 5.a) and latitude (Figure 5.b) results correlated with my hypotheses, likely due to increased historical snow cover duration in these areas. Similar findings were reported in other studies investigating the impact of elevation on mountain hare moult timing (Watson 1963) and latitude on snowshoe hare moult timing (Grange 1932). However, a different study found no evidence of snowshoe hare moult timing varying during autumn (Zimova et al. 2019). The climate zone result, which contradicted my hypothesis, may be confounded by all camera traps north of 63° N being close to the coast (Figure 3.a). Additionally, climate zone had a reasonably strong correlation with altitude and latitude, which could result in some of the variation explained by climate zone being accounted for by the other variables.

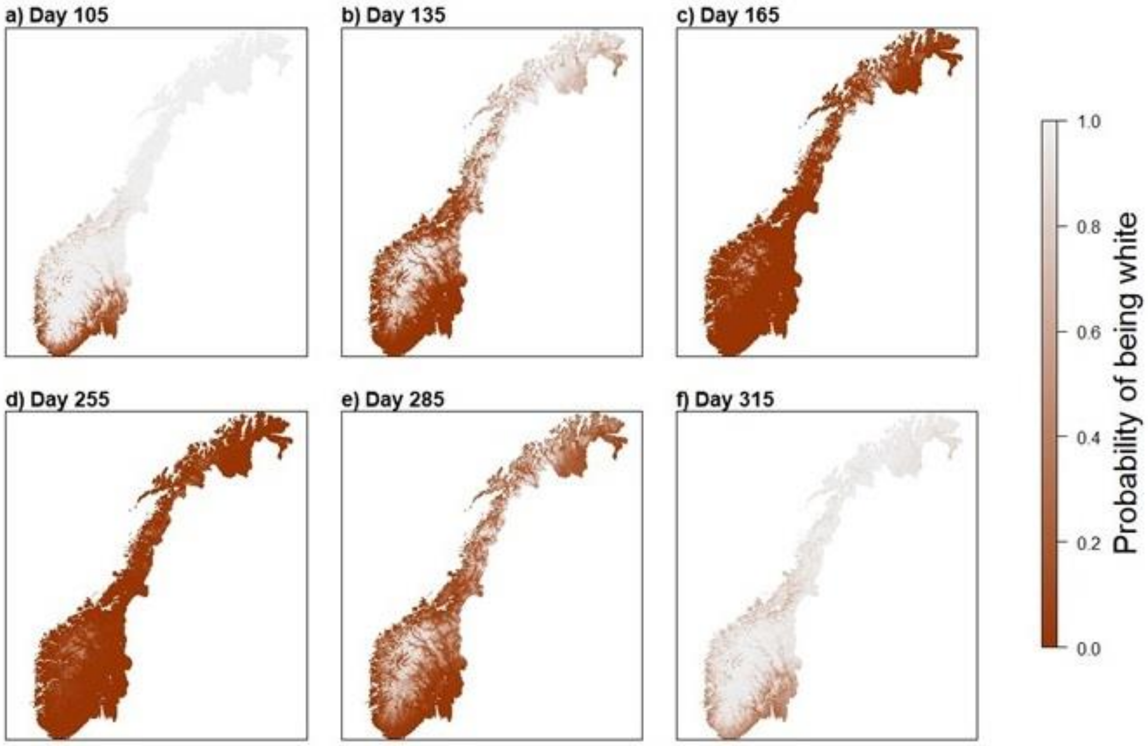

Figure 6. The probability of mountain hares being white relative to the probability of being brown or moulting across Norway on days (a) 105 (15th April), (b) 135 (15th May), (c) 165 (14th June), (d) 255 (12th September), (e) 285 (12th October) and (f) 315 (11th November). Results for areas not covered with camera traps should be interpreted with caution as they are based on extrapolation. All maps have a 1 km^2 resolution.

3.3 Between year variation in moult timing (Paper I)

There was some between year variation in moult timing in both spring and autumn (Figure 7, model 1). During the spring moult, there were several years in which the grey bars, representing the start of moulting, did not overlap between years. A similar pattern was observed with the brown bars, representing the end of spring moulting. During the autumn moult the brown bars, representing the start of moulting, and the grey bars, representing the end of moulting, overlapped between years. The non-overlapping CIs during spring suggest there is some phenotypic variation but, the effect size is small. This is consistent with photoperiod, which does not vary between year, being the main variable affecting moult timing (reviewed in Zimova et al. 2018). I hypothesised that adaptive behavioural responses, such as manually removing fur, could account for this variation (Stokes et al. 2023).

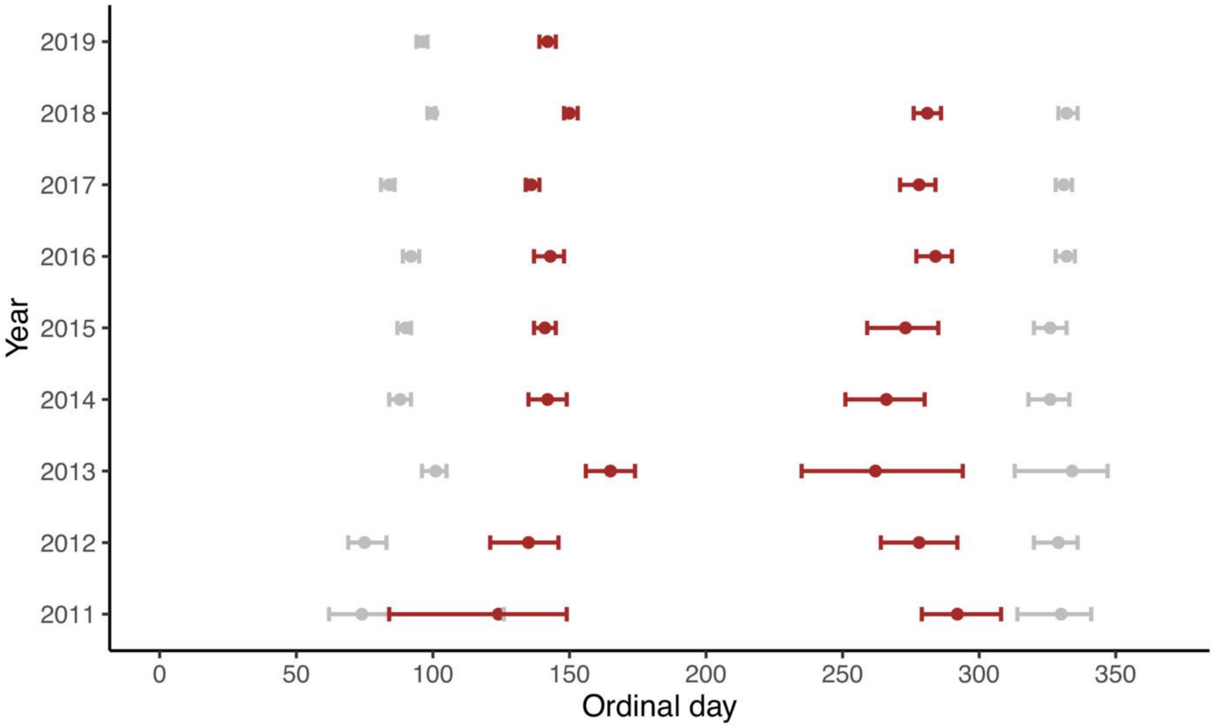

Figure 7. Between year variation with 95% credible intervals for spring and autumn mountain hare moult timing. Grey bars represent the day on which hares are 90% white (10% moulting or brown). Brown bars represent the day on which hares are 90% brown (10% moulting or white).

3.4 Spatial and temporal variation in coat colour mismatch (Paper II)

There was a strong correlation between all environmental variables and the probability of being mismatched (Figure 8, model 2). Mountain hares living at high altitudes (Figure 8.a) and latitudes (Figure 8.b) in continental areas (Figure 8.c) were less likely to be mismatched against their backgrounds throughout the year than their conspecifics inhabiting lower altitudes and latitudes in coastal areas. The probability of mountain hares being mismatched peaked during the autumn moult (Figure 8). It remained above 0 throughout the winter, increased during the spring moult before decreasing to 0 during the summer. The duration of the spring moult was considerably longer than the autumn moult, which has also been observed in stoats (*Mustela erminea*) (Rothschild 1942), but the probability of being mismatched was lower during the spring moult. This suggests there is greater variation in spring moult timing, which is consistent with previous research conducted on multiple species (Mills et al. 2013, Zimova et al. 2014, Atmeh et al. 2018, Stokes et al. 2023). Hares remaining mismatched for longer during the spring moult could contradict my earlier hypothesis that increased variation in spring moult timing could be an adaptation to varying snow conditions. Analysis conducted on a finer scale is needed to shed further light on this topic.

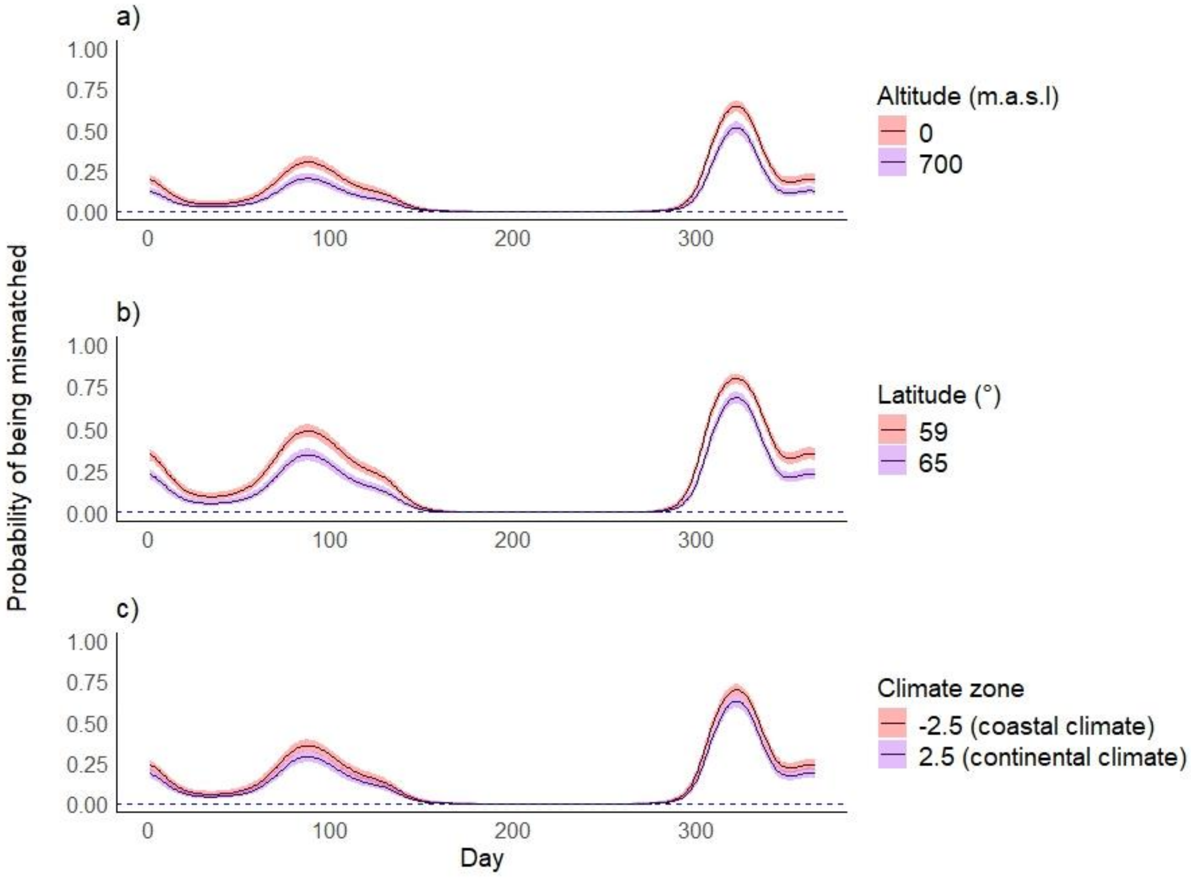

Figure 8. The probability of hares being mismatched against their environment varied with (a) altitude, (b) latitude, and (c) climate zone. When plotting a specific variable, the other two variables were set to their mean value. The solid lines represent the probability of being mismatched and the shaded areas represent the 95% confidence intervals.

On Day 45, the probability of mountain hares being mismatched against their background was close to 0 across large parts of Norway (Figure 9.a, model 2). However, it was above 0 along the west coast, in the mountains in the southwest, and in the far north. At the start of the spring moult, the probability of being mismatched was mostly above 0, particularly along the west coast and in the far north next to the Finland border (Figure 9.b). The probability of being mismatched was 0 across all Norway during the summer (Figure 9.d). The mismatch probability reached its highest level across all of Norway during the autumn moult (Figure 9.e) before decreasing during winter (Figure 6.f).

The results obtained near the Finnish border in the far north were surprising as the probability of being mismatched is relatively low in surrounding areas (Figure 9.b c, and f). This should be treated with caution as the model is predicting outside of the area in which observations were collected (Figure 3.a). In the absence of an evolutionary response, the probability of mountain hares being mismatched throughout the year is likely to increase as the number of snow days within Norway is expected to decrease by 2100 (Hanssen-Bauer et al. 2017). Mismatched mountain hares are likely to be at increased risk of predation, putting them under strong selection pressure (Pedersen et al. 2017). Phenotypic variation in response to decreased snow days has observed in mountain hares (Zimova et al. 2020b) and snowshoe hares (Kumar et al. 2020) but, did not occur at the pace of environmental change.

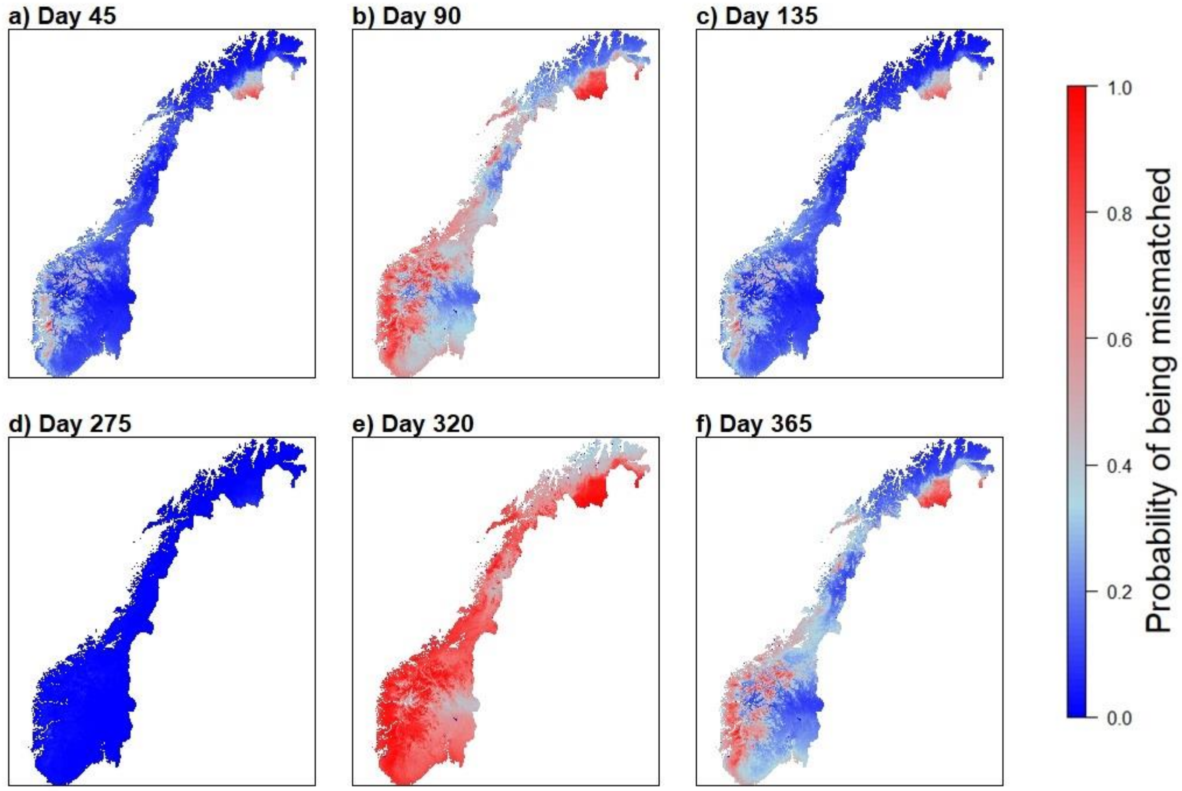

Figure 9. Probability of mountain hares being matched against their background on ordinal day (a) 45 (14th February), (b) 90 (30th March), (c) 135 (14th May), (d) 275 (2nd October), (e) 320 (16th November), and (f) 365 (31st December). Results for areas without camera traps should be interpreted with caution as they are based on extrapolation. All maps have a 1 km^2 resolution.

3.5 Cumulative mismatch (Paper II)

Greater cumulative mismatch was observed in mountain hares inhabiting regions with significant reductions in the number of snow days compared to those in areas with smaller reductions (Figure 10, model 3). This indicates that mountain hares are failing to track the negative effects of climate change. This is consistent with previous research on mountain hares (Zimova et al. 2020b), snowshoe hares (Zimova et al. 2014, Kumar et al. 2020), and least weasels (Atmeh et al. 2018). Additionally, cumulative mismatch was greater than the reduction in the number of snow days across all camera trap locations.

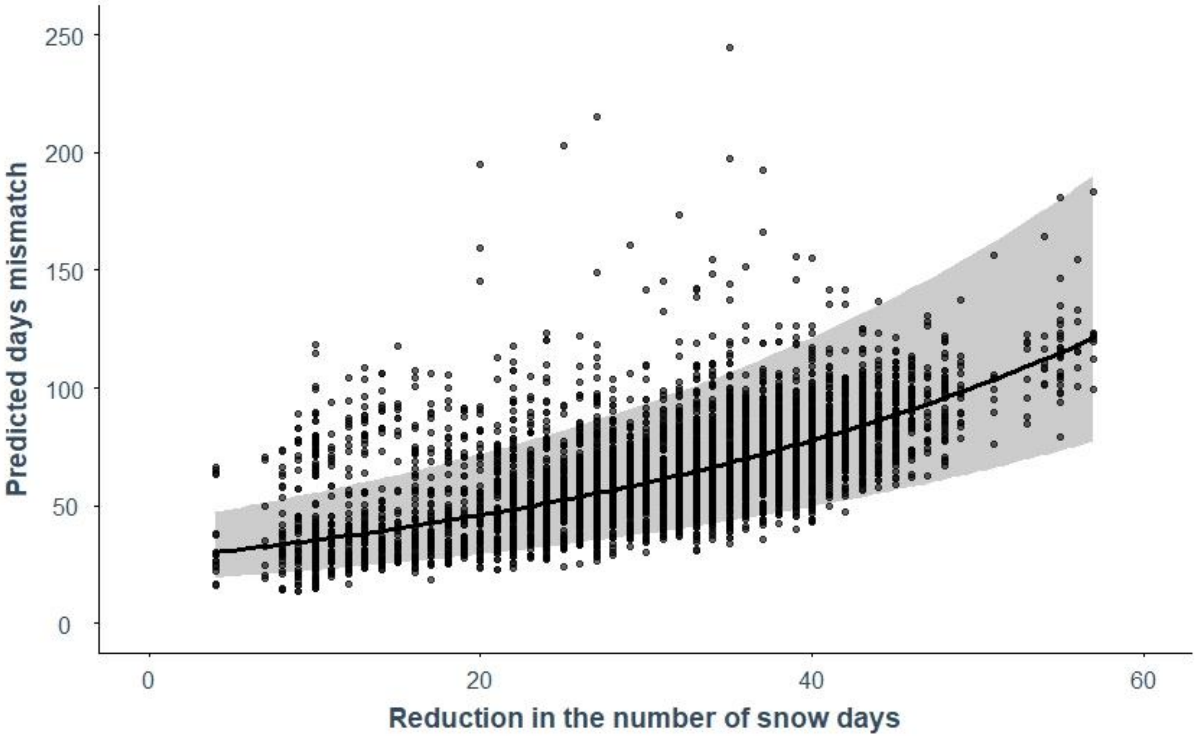

Figure 10. The number of days cumulative mismatch increases as the reduction in the number of snow days increases. The shaded area represents the 95% confidence intervals and the dots are partial residuals. There is a non-linear relationship as I back transformed to the original scale before plotting.

3.6 Current distribution and current suitable habitat (Paper III)

The variables included in the MaxEnt models varied between the different study organisms (Table 3). As some variables had a minimal effect on model performance, I referenced the three most important variables from each study organisms' suitable habitat model.

White mountain hare habitat suitability (model 4) had a positive relationship with forest, a negative relationship with altitude, and a curved relationship with minimum temperature of the coldest month, peaking at around -10°C. The positive correlation between habitat suitability and forest cover may result from dense vegetation offering refuge from predators (Thirgood and Hewson 1987, Hewson and Hinge 1990). The negative association with altitude is likely to result from a lack of vegetation at high altitude areas within Norway. White Mountain hare current distribution covered 33.7% of Norway (Figure 11.a) and current suitable habitat covered 38.5% (Figure 11.d). This is an underestimation of the suitable area as hunting bag records confirm that mountain hares inhabit areas in the far north and southwest mountains that have been classified as unsuitable habitat (Pedersen and Pedersen 2012). The limited number of observations along the coast, in the southwest mountains, and in the far north likely resulted in suitable habitat being classified as unsuitable. Including observations recorded during the entire year and citizen science observations without photos would reduce this issue but, would prevent differentiating between sub-species and increase risk of observer error.

Heath hare habitat suitability (model 5) had a curved relationship with the number of snow days, peaking around 150 days, a negative relationship with annual precipitation, and a curved relationship with minimum temperature of the coldest month, peaking around -6°C. The higher optimal temperature in the heath hare model compared to the white hare model could result from temperature's impact on snow cover duration. Heath hare current distribution (Figure 11.b) was limited to Norway's southeast and along the southern coast covering 6.6% of the country. These areas have fewer snow days than inland areas supporting the hypothesis that their winter coat is an adaptation to milder winters (Bergengren 1969). Heath hare suitable habitat (Figure 11.e) covers 9.8% of Norway with most additional suitable habitat spread around Trondheim.

European hare habitat suitability (model 6) had a curved relationship with the number of snow days, peaking around 120 days, a negative relationship with annual precipitation, and a curved relationship with minimum temperature of the coldest month, peaking around -5°C. As observations were collected in the northern tip of European hare range (Acevedo et al. 2012), sampling bias could affect optimal climatic conditions predicted by our model. Including observations recorded further south could result in the model predicting that European hares prefer milder climates. In other parts of their range, between 40 and 60 snow days (Pikula et al. 2004, Kudryavtseva and Smirnov 2012) and temperatures over 4°C (Marboutin and Hansen 1998) are optimal, indicating that these results are caused by sampling the northern tip of their distribution. European hare current distribution was limited to 1.3% of Norway in the southeast next to the Swedish border (Figure 11.c). Suitable habitat area increased to 3.2% of Norway expanding around the Oslo fjord and a few isolated areas south of Trondheim (Figure 11.f).

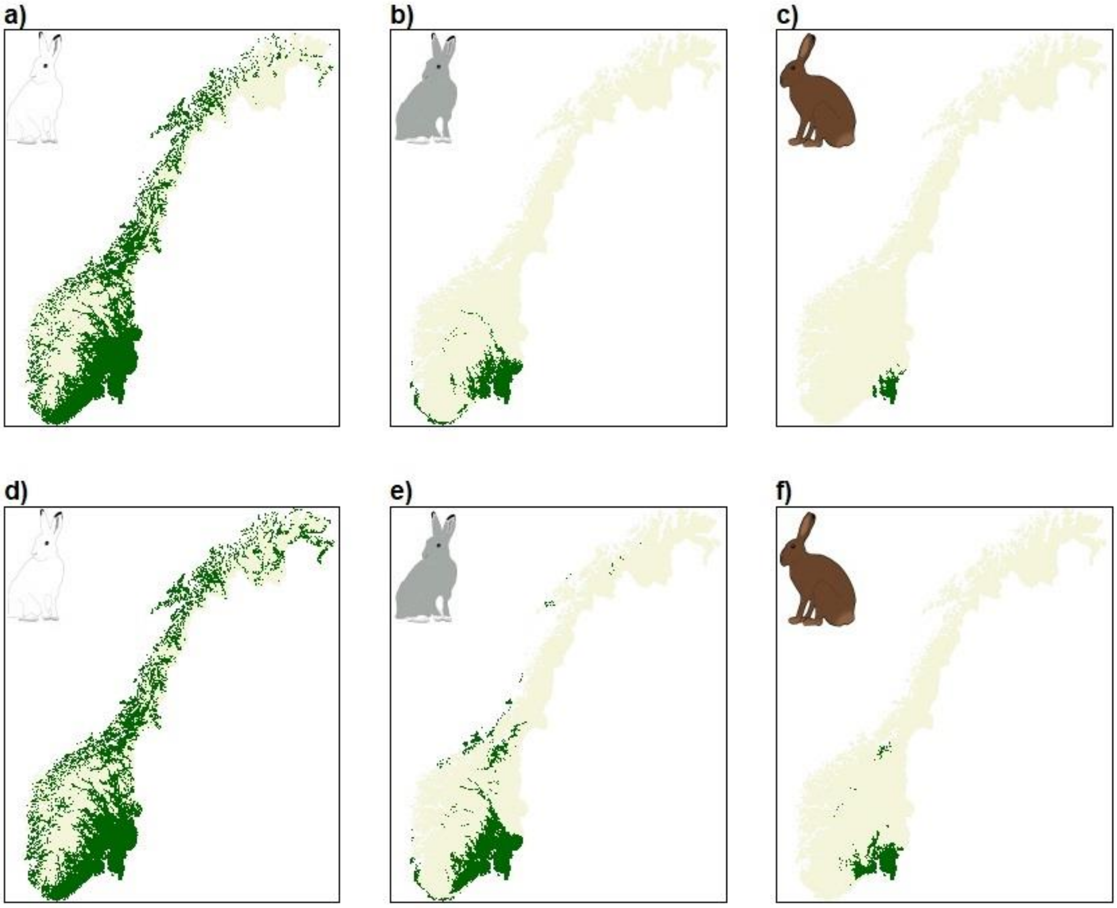

Figure 11. The current distribution of (a) white mountain hare, (b) heath hares, and (c) European hares. The suitable habitat of (d) white mountain hares, (e) heath hares, (f) European hares. All maps have a 1 km^2 resolution. The green cells represent the current distribution and suitable habitat.

3.7 Future suitable habitat (Paper III)

White mountain hare suitable habitat area within Norway contracted towards the east and north under the climate change scenarios, decreasing to 30.3% of Norway under the medium-term prediction (Figure 12.a) and 25.2% under the long-term prediction (Figure 12.d). Land use and altitude were assumed to remain constant. Therefore, minimum temperature of the coldest month was solely responsible for change in white mountain hare future suitable habitat (Table 3). The snow season is expected to decrease between one and seven months by 2100 with coastal regions most affected (Hanssen-Bauer et al. 2017). This is likely to increase coat colour mismatch, which will further increase predation selection pressure (Marcström et al. 1989, Pedersen et al. 2017).

Conversely, heath hare suitable habitat area increased to 29.7% under the medium-term prediction (Figure 12.b) and 35.3% under the long-term prediction (Figure 12.e) with their suitable habitat expanding north along the Swedish border. European hare suitable habitat also increased to 10.1% under the medium-term prediction (Figure 12.c) and 13.7% (Figure 12.f) under the long-term prediction. Most of the increase was between Oslo and Trondheim but there was also some suitable habitat in the far north.

It is unlikely that either European hares or heath hares will colonise Norway's far north without human intervention as there are large areas of unsuitable habitat between this area and their current distribution. The area that European hares currently inhabit was unsuitable under both medium and long-term predictions (Figure 12.c and f). Our dataset represents the northern tip of European hares' distribution. Therefore, including observations recorded in milder climates could result in this area being predicted as suitable. A similar issue may have resulted in the heath hare model underestimating suitable habitat along the west coast (Figure 12.b and e).

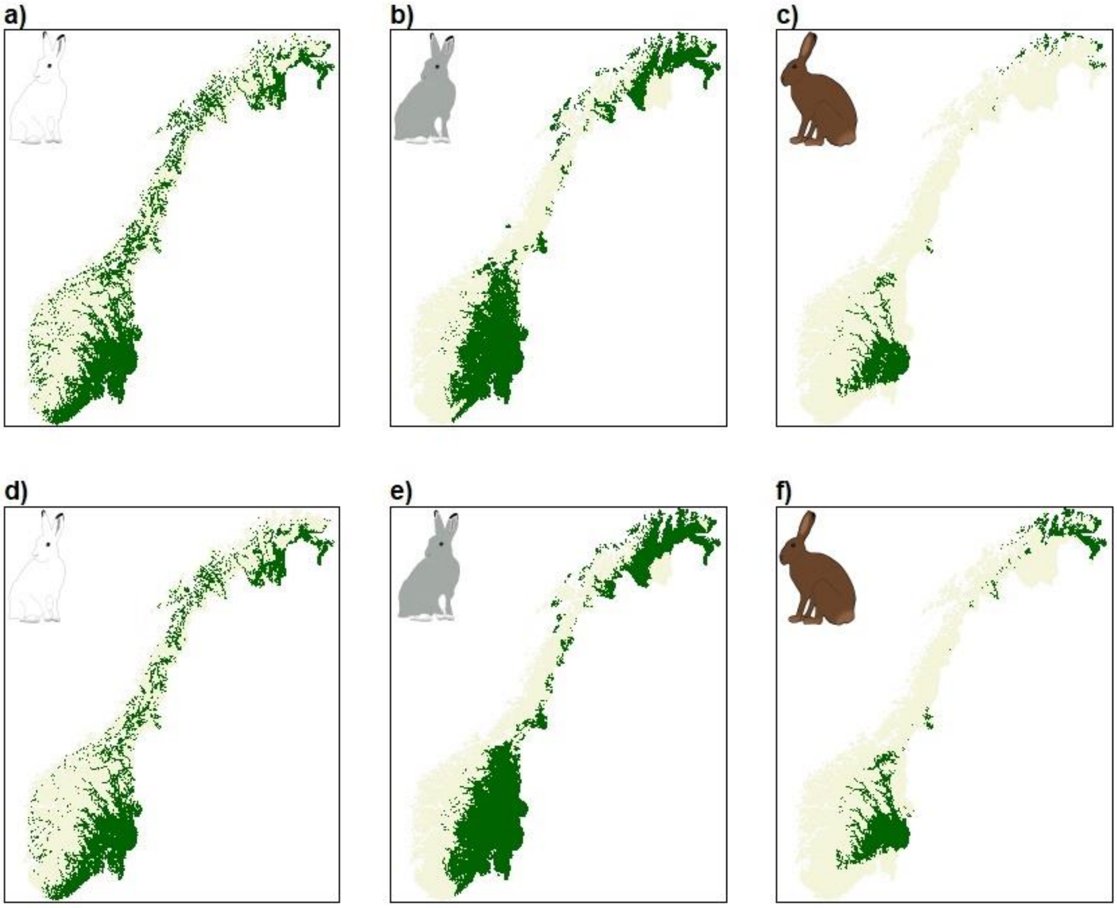

Figure 12. Medium-term suitable habitat under moderate (SSP370) climate change predictions for (a) white mountain hare, (b) heath hares, and (c) European hares. The long-term suitable habitat under moderate climate change predictions for (d) white mountain hares, (e) heath hares, (f) European hares. All maps have a 1 km^2 resolution. The green cells represent the suitable habitat.

4 General Discussion

4.1 Local adaptation in mountain hare moult timing (Paper I)

Mountain hare moult timing has adapted to local environmental conditions by varying along altitudinal, latitudinal, and climatic gradients (Figures 5 and 6). Large differences in moult timing were expressed over short geographical distances, particularly around Norway's southwest mountainous regions. (Figure 6) This indicates that geneflow between these regions is insufficient to dilute local adaptation.

Regional variation in moult timing could result from population level phenotypic variation, individual level phenotypic plasticity, or a combination of both. As I did not monitor specific individuals, it was not possible to quantify the relative importance of either factor. Moult timing showed evidence of weak population level phenotypic variation in spring but not in autumn (Figure 7), matching patterns observed in least weasels (Atmeh et al. 2018) and snowshoe hare (Mills et al. 2013, Zimova et al. 2014). The variation observed in this study is unlikely to match climate change induced reductions in future snow cover, which will decrease survival probability (Zimova et al. 2016). Behavioural responses to mismatch are possible but, the evidence within the literature is limited. One study observed snowshoe hares modifying patch selection in response to coat colour mismatch (Litvaitis 1991) whilst other studies failed to confirm these findings (Zimova et al. 2014, Zimova et al. 2020a).

4.2 Spatial and temporal variation in coat colour mismatch

Regional variation in moult timing was insufficient to adapt to the reduction in the number of snow days calculated between two 30-year periods used in this study (1959-1988 and 1989 and 2018). Cumulative mismatch was largest in areas that experienced the greatest reductions in the number of snow days (Figure 10), indicating that mountain hares are failing to adapt to climate change. Other studies have found similar results in Scottish mountain hares (Zimova et al. 2020b), least weasels (Atmeh et al. 2018), and snowshoe hares (Zimova et al. 2014, Kumar et al. 2020). Additionally, the number of days mismatch was greater than the reduction in the number of snow days, suggesting that mountain hare coat colour is adapted to a climate that existed before www.senorge.no snow records began in 1957. This illustrates how shifting baseline syndrome, which occurs when observers assume that the conditions they studied are the baseline (Pauly 1995), can affect studies using relatively recent climate data.

Mountain hares along Norway's coast were mismatched throughout large parts of the winter as well as during the moulting seasons (Figure 9). Therefore, hares inhabiting coastal areas that timed the spring and autumn moult correctly would still be mismatched against their environment. There was a very high probability of mismatch in the far north next to the Finnish border throughout large parts of the year. This result should be viewed with caution as the model is extrapolating outside the range over which observation data was collected (Figure 3.a)

4.3 Long term impact of coat colour mismatch

Increased predation risk on mismatched mountain hares leads to reduced population density (Pedersen et al. 2017). Snow cover duration within Norway is expected to decrease by 2100, particularly in coastal regions (Hanssen-Bauer et al. 2017), indicating that mountain hares that do not move or adapt will be exposed to increased selection pressure. There are several avenues by which mountain hares could adapt to their changing environment. Heath hares' winter coat, which is hypothesised to be an adaptation to milder climates (Barth 1891), could enable them to expand their current distribution (Figure 4.b and 11.b) along Norway's coast. Additionally, Irish mountain hares (*Lepus timidus hibernicus*) do not express seasonal coat colour variation (Mills et al. 2018), indicating that Norwegian mountain hares have the genetic potential to evolve a similar adaptation.

Many species cannot evolve quickly enough to track anthropogenic climate change with one study claiming than the rate of change in some species would need to be 10,000 times quicker than currently observed (Quintero and Wiens 2013). However, there are numerous examples of rapid evolutionary change, known as evolutionary rescue (Gonzalez et al. 2013), occurring in response to anthropogenic stressors. After being introduced to Australia in 1935, the length of cane toads' (*Bufo marinus*) legs increased, leading to a fivefold increase in the distance travelled each year (Phillips et al. 2006). Additionally, European rabbits (*Oryctolagus cuniculus*) rapidly evolved adaptations to myxomatosis (*Myxoma virus*), resulting in the case fatality rate dropping from 90% to 23% in seven years (Marshall and Fenner 1958, Marshall and Douglas 1961).

4.4 Species distribution and habitat suitability models

The absence of snow cover days from the white mountain hare model (Table 3) was surprising as the negative impact of coat colour mismatch on survival probability is well documented (Zimova et al. 2016, Pedersen et al. 2017). This likely results from white mountain hare observations being obtained in coastal regions (Figure 4.a) which did not experience snow cover. As MaxEnt uses presence only data, the model selection process did not detect any negative impacts that coat colour mismatch may have on abundance. Despite this, it is likely that further decreases in snow cover duration and extent will increase predation risk (Pedersen et al. 2017).

The heath hare suitable habitat model predicted that habitat north of Trondheim is currently suitable (Figure 11.e). This was not supported by observational data (Figure 4.b) but was supported by reports from hunters (S Pedersen, personal conversations). Therefore, spatially constraining the current distribution model prevented MaxEnt from predicting to areas lacking observation data but, also prevented it from predicting to suitable habitat that is likely to be occupied. This highlights that MaxEnt predictions that are not spatially constrained predict the occurrence of suitable habitat, which may be different to current distribution. Researchers using MaxEnt need to account for this to ensure that their methodology is tailored to their research questions.

The European hare future suitable habitat predictions (Figures 12.c and f) indicate that the area they currently occupy (Figure 11.c) will become unsuitable. This likely results from the observation data used representing the northern tip of their distribution (Acevedo et al. 2012). Including data from southern Sweden and other more temperate parts of European hares' distribution could result in the future habitat suitability models predicting that this area will remain suitable and Norway's southern coastline also becoming suitable.

The increase in area of both heath hare and European hare future suitable habitat (Figure 12) could result in Norway becoming a refuge for both organisms. Agricultural intensification is resulting in European hare distribution decreasing (Santilli et al. 2014). Additionally, competition with European hares is leading to heath hares being extirpated from parts of their Swedish distribution (Thulin et al. 2021).

4.5 Interspecies interactions

Interspecies interactions are likely to increase as the overlap between the study organisms' suitable habitats increase under both medium and long-term climate change predictions (Figure 12). Areas where mountain hares and European hares occur in sympatry tend to be unstable (Thulin 2003 and references within) with European hares often outcompeting mountain hares (Jansson and Pehrson 2007, Reid 2011, Caravaggi et al. 2014, Schai-Braun et al. 2023). This often results in mountain hare distribution contracting to higher elevations (Thulin 2003, Reid 2011, La Morgia et al. 2023). Mountain hares create forms in denser forests when living in sympatry with European hares (Thulin 2003 and references within), which could reinforce white mountain hares' positive relationship with forest land use.

The overlap in distribution is likely to increase hybridisation between mountain hares and European hares. This may negatively affect mountain hares as male European hares express mate guarding behaviour (Holley 1986). This behaviour has not been observed in male mountain hares (Hewson 1990). Additionally, hybrids are more likely to mate with European hares than with mountain hares in large parts of their shared distribution (Levänen et al. 2018, Schai-Braun et al. 2023). However, bidirectional hybridisation was observed within Ireland (Reid et al. 2022). Unidirectional hybridisation could lead to purebred mountain hares experiencing 'extinction by hybridisation' (Rhymer and Simberloff 1996), resulting from their population density decreasing and losing parts of their range to hybrids (Thulin and Tegelström 2002, Thulin et al. 2006). Hybrids are likely to inhabit the altitudinal area between European hares and mountain hares (Schai-Braun et al. 2023).

5 Management implications

The mountain hare population has declined within Fennoscandia over the past 20 years (Pedersen and Pedersen 2012, Elmhagen et al. 2015) resulting in it being classified as “near threatened” in the 2015 Norwegian Red List (Henriksen and Hilmo. 2015). White mountain hare, heath hare, and European hare distribution is decreasing in parts of their respective ranges (Thulin 2003, Schmidt et al. 2004, Thulin et al. 2021) with heath hares extirpated from most of Skåne County, Sweden (Thulin 2003). Therefore, there is a need for management strategies than aim to conserve these organisms and their habitats.

Norway could act as a refuge for all three organisms. However, this will likely negatively impact white mountain hares and heath hares as their distributions typically reduce in size when in direct competition with European hares (Caravaggi et al. 2014, Schai-Braun et al. 2023). As European hares are a non-native species, it is debatable whether their continued expansion within Norway should be encouraged. At present, both mountain hares and European hares are hunted within Norway with hunting regulations being identical for both species (Lovdata 2009, 2021, 2022). Relaxing regulations to allow European hare hunting throughout a greater proportion of the year could limit their expansion within Norway.

As previously discussed, the proportion of a cell containing forest was positively correlated with white mountain hare habitat suitability. Management decisions that maintain or increase this land use type could conserve white mountain hares within Norway and protect them from the expected increase in European hare distribution.

6 Personal reflections

The dataset that I have used contains huge amounts of data relative to that which most researchers use. However, if the SCANDCAM project was not limited by financial and political constraints deploying camera traps across all of Norway in a randomised grid pattern would improve data quality. The quality of the moult timing maps (Figure 6), probability of being mismatched maps (Figure 9), and the current distribution and suitable habitat maps (Figure 11) would be improved by cameras along the south-west coast, in the far north and in the mountains in the south.

In hindsight, there are many things that I would do differently if I started again. There were several data analysis dead ends that cost considerable time and effort. For example, I abandoned an R package that is no longer maintained as it failed to produce consistent results. Switching to a heavily cited package that is regularly maintained resolved this issue.

Defining if mountain hares were matched against their background during the moulting period was challenging as it is difficult to say if they're mostly white, mostly brown, or neither. Additionally, there could be variation between white mountain hares and heath hares. I am open to ideas on other methods for resolving this problem.

7 Future studies

There are several ways in which my work could be expanded on in the future. Variation in moult timing can result from individual phenotypic plasticity, population level phenotypic variation or a combination of both. In Paper I, I observed weak variation in spring moult timing. It was not possible for us to disentangle the relative effects of phenotypic variation and plasticity as individual mountain hares were not monitored. At the time of writing, my supervisor, Simen Pedersen, is fitting GPS collars to mountain hares. Multi-year data gathered from tagged hares could enable us to study individual phenotypic plasticity.

In Paper II, I compare current moult timing patterns with current and historic snow patterns. It is not possible to compare historic moult timing patterns to historic snow patterns as camera trap images were not collected prior to 2011. Maintaining the SCANDCAM camera network will enable future researchers to study how moult timing patterns change over time. Comparing current moult timing patterns to those present in the future would shed more light on the rate at which mountain hares are adapting to climate change.

The probability of mismatch GAM (model 2) developed for Paper II used interpolated snow data collected by weather stations with a 1 km^2 resolution. The model shows that mountain hares are mismatched throughout the year in parts of Norway's southwest. It was not possible to use this data to determine if mountain hares reduce the impact of mismatch by selecting small patches containing snow. However, camera trap images could be used to gain a measure of whether hares choose to spend more time in areas where they are matched against their background. Additionally, Simen Pedersen is hoping to establish a captive population in Evenstad that could be used to test this hypothesis by using direct observation data.

Other Maxent studies investigating mountain and European hares have attempted to model interactions between the species (see Bisi et al. 2015). Although I discussed interspecies interactions in Paper III, I did not formally test how the study organisms may affect each other. Bisi et al (2015) tackled this problem by including a map containing the competitors' current distribution within their MaxEnt models. European hares' limited distribution within Norway means that this method is unlikely to work with the current dataset. Future studies could use this methodology if European hare distribution increases in line with my predictions. Hybridisation between mountain hares and European hares is likely to become increasingly common within Norway as European hare distribution increases. Therefore, analysis of its impact will become increasingly important.

Additionally, I planned to investigate if mountain hare activity patterns varied depending on whether they were matched against their environment. Unfortunately, this was abandoned due to a lack of time. A master’s student is planning to study this topic and I would like to be involved after my PhD has finished.

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Dissertation articles

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RESEARCH ARTICLE

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Altitude, latitude and climate zone as determinants of mountain hare (*Lepus timidus*) coat colour change

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Abstract

Local adaptation to annually changing environments has evolved in numerous species. Seasonal coat colour change is an adaptation that has evolved in multiple mammal and bird species occupying areas that experience seasonal snow cover. It has a critical impact on fitness as predation risk may increase when an individual is mismatched against its habitat's background colour. In this paper, we investigate the correlation between landscape covariates and moult timing in a native winter-adapted herbivore, the mountain hare (*Lepus timidus*), throughout Norway. Data was collected between 2011 and 2019 at 678 camera trap locations deployed across an environmental gradient. Based on this data, we created a Bayesian multinomial logistic regression model that quantified the correlations between landscape covariates and coat colour phenology and analysed among season and year moult timing variation. Our results demonstrate that mountain hare moult timing is strongly correlated with altitude and latitude with hares that live at higher latitudes and altitudes keeping their winter white coats for longer than their conspecifics that inhabit lower latitudes and altitudes. Moult timing was also weakly correlated with climate zone with hares that live in coastal climates keeping their winter white coats for longer than hares that live in continental climates. We found evidence of some among year moult timing variation in spring, but not in autumn. We conclude that mountain hare moult timing has adapted to local environmental conditions throughout Norway.

KEYWORDS
lagomorph, moult, phenology, phenotypic trait, subarctic

TAXONOMY CLASSIFICATION
Applied ecology, Evolutionary ecology, Global change ecology, Zoology

1 | INTRODUCTION

For species living in seasonal environments (e.g. from summer to winter or from dry to wet season) local adaptations to annually changing environmental conditions may evolve. Numerous species have evolved to time their life history events to match these changes in local seasonal conditions (Bradshaw & Holzapfel, 2007; Williams et al., 2015). To time these phenological events, one reliable 'zeitgeber' is daylength or photoperiod (Gwinner, 2003; Hofman, 2004), either on its own or in combination with other variables, such as temperature (Jackes & Watson, 1975; Larkin et al., 2001; Watson, 1963) and snow cover (Flux, 1970; Watson, 1963; Zimova et al., 2014).

Many animal species use photoperiod to time breeding (Coppack & Pulido, 2004; Dawson et al., 2001; Goldman, 1991; Gwinner, 1996b), moulting (Bissonnette & Bailey, 1944; Lesher & Kendeigh, 1941; Lyman, 1943), migration (Gwinner, 1996a) and other life history events. As photoperiod remains constant between years at specific locations, between year variation in local conditions could result in photoperiod timed phenological events being mistimed against the local environment. Fluctuations in environmental variables, such as precipitation (Villellas et al., 2014) and temperature (Ashmore & Janzen, 2003; Kreyling et al., 2019), can result in increased within-species phenotypic variation in a variety of plant and animal species when compared to individuals of the same species that live in more stable habitats. Consequently, synchrony in phenological timing of individuals within a population is expected to increase with climate stability.

Animals occupying areas that are seasonally covered by snow live in environments that change from dark in summer to white in winter. As a predator avoidance strategy, at least 21 species have adapted seasonal changes in colouration of fur and feather (Mills et al., 2018; Zimova et al., 2018), which provides camouflage in both a winter white and summer dark landscapes (Cott, 1940; Merilaita & Lind, 2005; Wallace, 1879). To provide optimal camouflage, the timing of coat colour change should be synchronised with the period of continuous snow cover. Mismatched timing of coat colour change is linked to range contractions and population declines in several species including snowshoe hares (*Lepus americanus*) (Diefenbach et al., 2016; Sultaire et al., 2016), mountain hares (*Lepus timidus*) (Acevedo et al., 2012; Pedersen et al., 2017), rock ptarmigan (*Lagopus muta*) (Imperio et al., 2013) and white-tailed ptarmigan (*Lagopus leucura*) (Wang et al., 2002), showing the importance of synchronising moult timing to habitat conditions. However, snow conditions might not be stable from year to year, and there might be seasonal differences in the predictability of the appearance and disappearance of snow. In autumn, there are usually multiple snowfalls with interspersed thawing events that completely remove snow cover. In spring, snow disappearance is more likely to be permanent until the following autumn. Therefore, snow cover is likely to be more stable in spring compared to autumn.

Snowshoe hares that occupied higher altitudes and latitudes expressed winter coats for a longer time than their low latitude (Grange, 1932, but see Zimova et al., 2019) and altitude conspecifics (Holmgren et al., 2001; Nowak et al., 2020; Zimova, Giery, et al., 2020). Also, increased snow cover in continental areas is likely to result in hares living in these areas keeping their winter coats for longer than hares in coastal areas. Snowshoe hares (Zimova et al., 2014) and least weasels (*Mustela nivalis nivalis*; Atmeh et al., 2018) exhibit some phenotypic variation in moult timing in parts of their distribution during the spring moult, when transitioning from white to brown, but not during the autumn moult when transitioning from brown to white. Therefore, seasonal coat colour change is expected to be a more synchronised process in spring, in both start and end date, compared to autumn. This could result in increased among year variation in spring moult timing compared to autumn moult timing. This is the first long-term study over a geographical area large enough to test these predictions.

Mountain hares express seasonal coat colour change in most of their range, except the subspecies (*L. t. hibernicus*) found in Ireland (Mills et al., 2018). It is a generalist herbivore inhabiting boreal and alpine areas that occupy a wide range of climatic, latitudinal and altitudinal gradients, experiencing large variations in winter snow cover duration. They have a circumpolar distribution spread across Europe and Asia from Britain, Ireland and the Faroe Islands in the west to Japan in the east (Angerbjorn & Flux, 1995). They are native to Norway and are found throughout the country with their distribution ranging from sea level to around 1600 m, which is above the tree line. Coastal areas in the south and south-west of Norway experience relatively short snow cover duration compared to inland areas and areas in the north (Schuler et al., 2006) with coastal areas in the south and south-west receiving as little as 1 month of snow cover per year (Tallaksen et al., 2018). Additionally, coastal areas experience greater between-year variation in the depth and extent of snow cover than inland areas (www.senorge.no).

Here we provide the first quantitative study of mountain hare moult timing variation using 9 years of data collected at 678 camera locations along an extensive geographic gradient in Norway. Proximate factors such as temperature, snow cover and forest cover may affect moult timing. However, in this first attempt to explain moult timing variation in Norwegian mountain hares, we focused on large-scale geographic gradients in altitude, latitude and climate, which may be the ultimate causes of moult timing variation. We utilised a Bayesian multinomial logistic regression model to study (1) how moult timing varied along broad-scale geographical gradients in altitude, latitude and climate and (2) how moult timing varied among years and seasons. First, we used altitude, latitude and climatic zone, distinguishing between coastal and continental climates, as indicators of local geographical conditions we predicted that hares living at high altitudes and latitudes and in continental climates would keep their winter white coats for longer than their conspecifics at low altitudes and latitudes and in coastal climates. Second, based on previous snowshoe hare and least weasel studies, we predicted that moult timing would be more synchronised among individuals in spring, resulting in reduced population-level variation in moult start and end, compared to autumn. Third, we predicted larger among year variation in the timing of moult in spring compared to autumn.

2 | METHODS

2.1 | Data collection

We utilised images from camera traps (Figure 1) that were deployed by the SCANDCAM project (www.viltkamera.nina.no) to monitor the Eurasian lynx (*Lynx lynx*) (Hofmeester et al., 2021). Camera traps were deployed in multiple study areas in an extensive grid with approximately one camera per 50 km^2 grid cell (Figure 2). We selected

FIGURE 1 Mountain hares in (a) white, (b) moulting and (c) brown coat colour stage captured by camera traps deployed in Norway by the SCANDCAM project (© NINA).

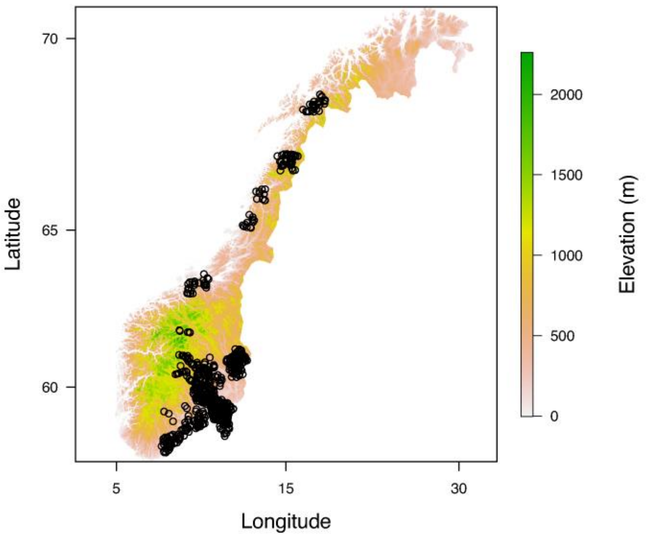

FIGURE 2 The location of 678 camera trap sites that recorded a mountain hare observation during 2011–2019 (black circles). The camera traps were deployed across an environmental gradient within Norway by the SCANDCAM project, with latitudes varying between 58° N and 69° N and altitudes varying between 0 and 841 m above sea level.

all mountain hare records from the period between 10 January 2011 and 25 June 2019. Images containing mountain hares were recorded at 678 locations across Norway (Figure 2), spanning a latitudinal gradient from 58° N to 69° N and altitudes from 0 to 841 m above sea level and climate zone PCA values were between −2.68 (coastal climate) and 2.86 (continental climate). To reduce pseudo-replication, we discarded observations recorded within 60 min of the previous observation. Mountain hares and invasive European hares (*Lepus europaeus*), which are also present in south-eastern Norway (Viken County), were differentiated using the species descriptions contained in Smith et al. (2018). When mountain hares were identified, we estimated the proportion of the hares' coat (excluding the long white belly) which was white. We classified moulting stage into three categories modified from Zimova, Barnard, et al. (2020). (1) Hares with ≥90% white fur were classified as 'white', (2) hares with ≤10% white fur were classified as 'brown' and (3) all other hares were classified as 'moulting'. All images were accessed on www.viltkamera.nina.no and were visually classified by one of two observers. They were quality-controlled whenever the observer was uncertain of the classification.

2.2 | Covariates

We divided the year into two seasons, 'spring' and 'autumn'. Spring was defined as ordinal days 1–212 (1 January to 31 July in non-leap years) and autumn for the rest of the year. Ordinal day 212 was chosen as all mountain hares had moulted to their summer brown coats by this date and had not started moulting back to winter white. Altitude and latitude were extracted based on camera trap positions. We obtained altitude from a digital elevation model (DEM) with 50 m^2 resolution (Korsnes, 2018) (Appendix S1a) using the *raster* package's (Hijmans, 2022) extract function. We obtained climate zone as a continuous variable with a resolution of 1 km^2 from Bakkestuen et al. (2008) (Appendix S1b). We converted climate zone vector data to a raster using the *fasterize* (version 1.0.4) package (Ross, 2020). Bakkestuen et al. (2008) mapped climate zones by conducting principal component analysis (PCA) using terrain data, climatic data, hydrological data and geological data. A positive PCA value indicates a continental climate whereas a negative value indicates a coastal climate.

2.3 | Data analysis

We created two models, one for spring and one for autumn. We used multinomial logistic regression to estimate the probability of a hare being in moult category *i* (white, moulting or brown) on each ordinal day *d*. We included year *k*-specific intercepts to test if moult timing varied between years. The model used the following equation:

$$p(y=i)=\frac{e^{\alpha_{ik}+\beta_{1i}\times d+\beta_{2i}\times a_j+\beta_{3i}\times l_j+\beta_{4i}\times c_j+s_{ij}}}{1+\sum_{m=1}^{i-1}e^{\alpha_i+\beta_{1i}\times d+\beta_{2i}\times a_j+\beta_{3i}\times l_j+\beta_{4i}\times c_j+s_{ij}}}$$

where *d* is ordinal day, and a_j, l_j and c_j, respectively, are the altitude, latitude and climate zone at camera site *j* (as adapted from Zimova, Giery, et al., 2020; Zimova et al., 2019). Parameters β_{1-4j} represent the slopes for the different covariates. We included a category *i* and year *k* specific intercept α_{ik} as well as a site-specific random intercept s_{ij} to account for repeated observations per camera site. The brown category was set to 0 in both spring and autumn models to provide a baseline for comparison with the moulting and white categories.

We implemented the models in a Bayesian framework using JAGS (Denwood, 2016) called from R V4.1.3 (R Core Team, 2022) with the *jagsUI* package (version 1.5.2) (Kellner, 2021). We standardised altitude, latitude and climate zone (mean = 0, SD = 1) before running the models. Ordinal day was included as an explanatory covariate to enable estimation of the probability of a hare being white, brown or moulting between coats on specific days of the year. We checked for collinearity between the covariates using both the variance inflation factor (VIF) and Pearson correlation coefficient. For every covariate combination, the Pearson values were below 0.6 (Appendix S2) and VIF values were below 2.0 (Appendix S3).

We used uninformative, normally distributed priors with a mean of 0 and precision of 0.01 for all slopes and the year *k*-specific intercepts. For the site *s* random intercept, we used a mean of 0 and a standard deviation defined as a vague prior with a uniform distribution between 0 and 100. We ran the models with three chains all thinned by 100 for 120,000 iterations, with a burn-in of 60,000 iterations. We confirmed model convergence using traceplots and the Gelman-Rubin convergence statistic (R-hat) (Brooks & Gelman, 1998) with all variables used in the final models having R-hat values of 1.10 or less. Additional models, in which the dataset was subset to only include cameras located south of 61° N, were used to test if model performance was affected by camera trap placement north of this latitude. The results were consistent with those obtained using the full dataset indicating that camera placement north of 61° did not affect model performance.

We produced all figures using the *ggplot2* (Wickham, 2016), *raster* (Hijmans, 2022) and *cowplot* (Wilke, 2020) packages. When plotting the correlation between the explanatory variables and moult timing (Figures 3 and 5), the variables not being manipulated were set to the mean value. Figures 3 and 4 give the probability of being white compared to the combined probability of being brown or moulting.

3 | RESULTS

Between 2011 and 2019 a total of 9979 mountain hare observations were obtained at 678 camera trap locations (Figure 2 and Appendix S4). Of these observations, 7454 were recorded in 'spring' and 2525 were recorded in 'autumn'. The number of camera traps deployed across Norway increased throughout the study period, leading to an increase in the number of observations obtained in each year (see Appendix S5 for location of traps that recorded observations in each year).

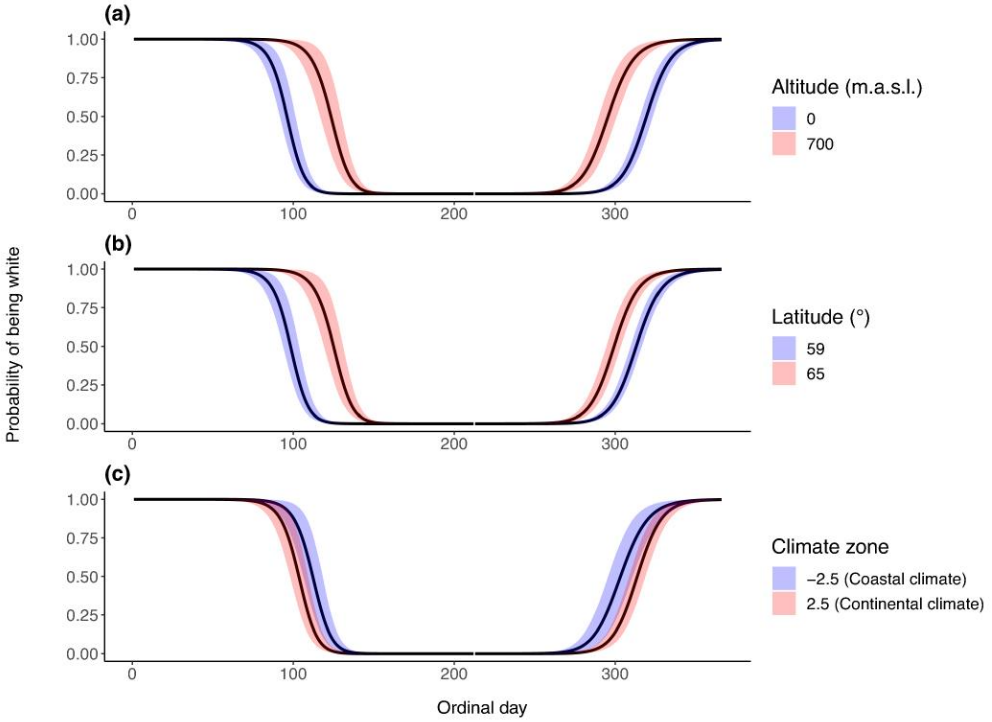

FIGURE 3 Timing of spring and autumn moult giving the probability of mountain hares being white compared to the combined probability of being brown or moulting at different altitudes (a), latitudes (b) and climate zones (c). Solid lines represent the predicted probability of being white and shaded areas indicate the 95% credible intervals. Figures use the mean of all intercepts included in the final models. The explanatory variables not plotted in each graph were set to the mean value.

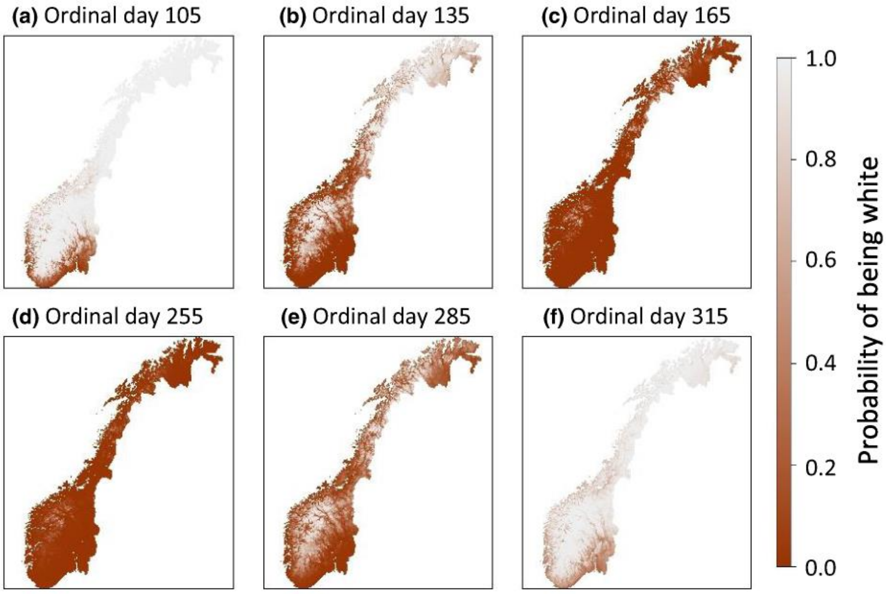

FIGURE 4 Prediction maps with a resolution of $1\times1\,\text{km}^2$ giving the probability of mountain hares being white compared to the combined probability of being brown or moulting across Norway on ordinal days (a) 105 (15th April), (b) 135 (15th May), (c) 165 (14th June), (d) 255 (12th September), (e) 285 (12th October) and (f) 315 (11th November). The probability of being white was predicted using the model output and the environmental covariates contained in every cell. See Appendix S6 for an animated map containing every ordinal day.

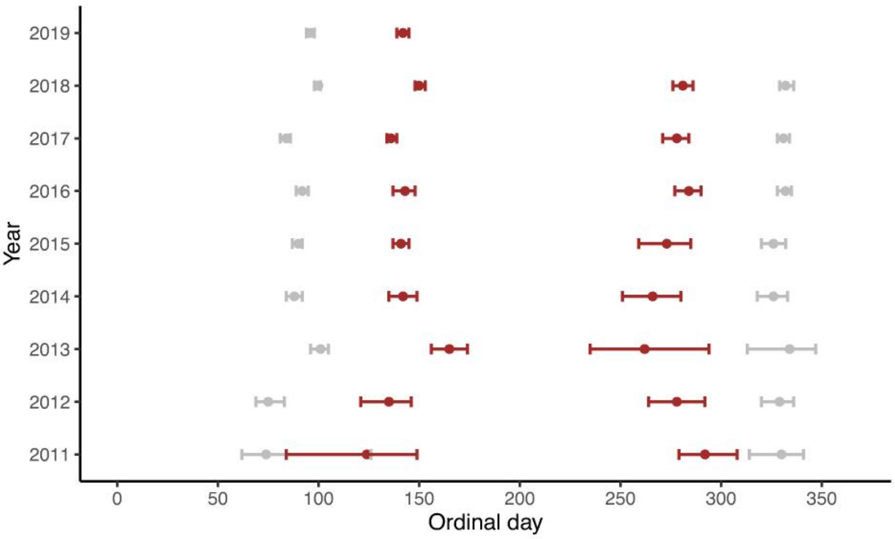

FIGURE 5 Between year intercepts with 95% CI for spring and autumn at mean altitude (257 m), latitude (61° N) and climatic zone. Grey dots with 95% CI represent the mean ordinal day on which 90% of hares are white (10% brown or moulting). Brown dots with 95% CI represent the mean ordinal day on which 90% of hares are brown (10% white or moulting). The supplemental information contains sample sizes (Appendix S4), number of days between the midpoints (Appendix S7) and intercept beta values (Appendix S8).

The results from our models indicate that all three explanatory covariates, altitude, latitude and climate zone, correlated with moult timing in spring and autumn with none of the 95% credible intervals (CI) overlapping 0. We found strong evidence for hares keeping their winter white coats for a longer duration at increased altitudes and latitudes (Figure 3a,b). The probability of being white increased with altitude in spring ($\beta_{2,\text{white}}=1.492$, 95% (CI) = 1.309–1.673; Figure 3a) and in autumn ($\beta_{2,\text{white}}=0.870$, 95% CI = 0.639–1.117; Figure 3a). Similarly, the probability of being white increased with latitude in spring ($\beta_{3,\text{white}}=2.472$, 95% CI = 2.265–2.672; Figure 3b) and in autumn ($\beta_{3,\text{white}}=0.642$, 95% CI = 0.443–0.844; Figure 3b). Climate zone had the smallest effect size in both spring and autumn. The probability of being white decreased with an increasingly inland climate (increasing PCS values) in both spring ($\beta_{4,\text{white}}=-0.335$, 95% CI −0.510 to −0.163; Figure 3c) and autumn ($\beta_{4,\text{white}}=-0.287$, 95% CI −0.525 to −0.053; Figure 3c).

The 50% probability of being white occurred 27 days earlier in spring and 23 days later in autumn at sea level, compared to 700 m above sea level (Figure 3a). Also, the 50% probability of being white occurred 27 days earlier in spring and from brown to white 14 days later in autumn at 59° N compared to 65° N (Figure 3b). Additionally, the 50% probability of being white occurred 9 days earlier in spring and 11 days later in autumn in inland climates compared to coastal climates (Figure 3c).

Mountain hare moult timing varied across mainland Norway (Figure 4). Starting in mid-winter moving into spring, there was a travelling wave of moulting moving from lower to higher altitudes and latitudes (see Appendix S6 for animated map containing every ordinal day). The opposite effect was observed in autumn. The altitudinal and latitudinal moult timing gradients show that hares that inhabit mountainous areas and the north of Norway kept their winter white coats for longer than their conspecifics that inhabit low altitude and latitude areas. The model output indicates that mountain hares in coastal areas moult later in spring and earlier in autumn (Figure 3c). The prediction maps show that hares in southern Norway's coastal areas moult earlier in spring and later in autumn (Figure 4a,f), indicating that the effect of latitude is stronger than the effect of climate zone. This is consistent with the climate zone effect size being smaller than those of altitude and latitude. Predictions for areas outside of camera trap locations (Figure 2) should be interpreted with care as these results are extrapolated.

Timing of spring and autumn moults varied slightly between years (Figure 5). From 2013 onwards the 95% CIs are consistently narrower in spring than in autumn, which probably results from increased sample sizes in spring (Appendix S4). For the spring intercepts, multiple years have non-overlapping CIs for 90% white, which signifies the start of spring moulting, and 90% brown, which signifies the end of spring moulting. For example, 2013 does not overlap with 2014 and 2017 does not overlap with 2018. For the autumn intercepts, the brown CIs, signifying the start of autumn moulting, overlapped in most years. The CIs for 90% white, signifying the end of autumn moulting, overlapped in all years. The time taken for moulting in spring to finish, represented by the number of days between 90% of hares being white and 90% of hares being brown, ranged between 46 days in 2019 and 64 days in 2013 and 2018 (Appendix S7). The time taken for moulting to occur in autumn ranged between 38 days in 2011 and 72 days 2013. The autumn result should be viewed with caution as 2011 and 2013 had limited sample sizes (Appendix S4).

4 | DISCUSSION

We used camera trap by-catch observations to provide the first quantitative assessment of how large-scale environmental variables correlate with mountain hare moult timing. As predicted, hares at higher altitudes and latitudes moulted later, from white to brown, in spring and earlier, from brown to white, in autumn, keeping their winter white coats for longer when compared to their lowland and low latitude conspecifics. Contrary to our prediction, we found support for a slightly later spring moult and earlier autumn moult in areas characterised by coastal climates rather than inland climates, resulting in hares that live in areas with coastal climates keeping their winter white coats for longer than their inland conspecifics.

The unexpected correlation between climate zone and moult timing (Figure 3c) could result from variation explained by climate zone also being partially explained by altitude (Pearson correlation coefficient > 0.5 in both seasons) and latitude (Pearson correlation coefficient < −0.3 in both seasons; Appendix S2). Additionally, all camera traps north of 63° N are close to the coast (Figure 2) which may confound results. However, in southern Norway there is a coastal to continental moult timing gradient shown in the prediction maps (Figure 3a,f) indicating that the model has captured a correlation between moult timing and climate. Furthermore, it is likely that there will be increased variability in moult timing in coastal climates as there is increased among year variation in snow cover and duration compared to continental climates (www.senorge.no).

The altitude (Figure 3a) and latitude (Figure 3b) results are likely due to an expectation of longer snow cover duration at increased altitudes and latitudes. These results are consistent with previous studies of other mountain hare populations and other lagomorph species, which found that increased elevation correlated with mountain hares keeping their winter coats for longer (Watson, 1963) and increased latitude correlated with snowshoe hares keeping their winter white coats for longer (Grange, 1932). However, Zimova et al. (2019) found no evidence of autumn moult timing variation in snowshoe hares. Additionally, in spring, hares that lived at high latitudes moulted to brown earlier than conspecifics at lower latitudes. The correlations between moult timing and altitude and latitude indicate that mountain hare populations have adapted to local conditions, suggesting that gene flow between populations is insufficient to dilute local adaptations. This is particularly true for altitude as this variable can change significantly over a short geographic distance.

The non-overlapping CIs between some years in the spring moult (Figure 5) indicate that there is some between year phenotypic variation. However, the between year difference in moult timing is small, which is consistent with photoperiod rather than climate being the main driver of mountain hare moult timing (reviewed in Zimova et al., 2018). This is consistent with similar studies conducted on snowshoe hares (Mills et al., 2013; Zimova et al., 2014) and least weasels (Atmeh et al., 2018), which found evidence of between year phenotypic variation in spring, but not in autumn. The limited moult timing variation may reduce fitness as an inability to change moulting patterns in response to among year variation in snow extent and duration will increase camouflage mismatch and, consequently, decrease survival probability (Zimova et al., 2016). We hypothesise that behavioural responses to mismatch, such as micro-habitat patch selection, changed diurnal activity patterns or manually removing winter fur during the spring moult, could occur. Evidence of snowshoe hares modifying their behaviour in response to being mismatched is limited with one study suggesting that hares exhibit patch selection in response to pelage colour variation (Litvaitis, 1991) whilst one other study found no evidence of behaviour modification (Zimova et al., 2014). We are not aware of these hypotheses being investigated in mountain hares.

Moult timing variation could result from population-level phenotypic variation, individual-level phenotypic plasticity or a combination of both factors. As our methodology did not facilitate monitoring specific individuals, we could not disentangle the relative importance of population and individual-level variation. Observations were obtained at specific locations in multiple years (Appendix S9). This makes it likely that some individuals were recorded in multiple years, increasing the probability of individual phenotypic plasticity influencing results. We obtained three times as many observations in spring compared to autumn (Appendix S4), which is probably caused by increased hare activity patterns during the mating season (Pettigrew et al., 2021) and the spring dataset containing observations for 58 more days. This resulted in the intercept CIs (Figure 5) being larger in autumn than in spring.

Understanding the role that environmental characteristics have on moult timing is vital when assessing the impact that climate change may have on species that express a seasonal coat colour change. Our study sites span 1300 km and 11 latitudinal degrees (58° N to 69° N), from sea level to 841 m above sea level making this is the first study that investigates moult phenology over a large, continuous climatic gradient spanning three biomes (temperate forest, boreal forest and alpine tundra). Analysing the correlation between the explanatory variables and mountain hare moult timing will enable us to predict how the species will react to climate change-induced reductions in snow cover extent and duration. Future studies could also conduct fine-scale analysis of the climate variables, including temperature and snow cover, that correlate with moult timing. We plan to investigate these issues in future papers.

AUTHOR CONTRIBUTIONS

Allan W. Stokes: Formal analysis (lead); methodology (equal); visualization (lead); writing – original draft (lead); writing – review and editing (equal). **Tim R. Hofmeester:** Conceptualization (supporting); formal analysis (supporting); methodology (equal); visualization (supporting); writing – review and editing (equal); funding aquisition (supporting). **Neri H. Thorsen:** Formal analysis (supporting); methodology (equal); visualisation (supporting); writing – review and editing (equal). **John Odden:** Conceptualisation (supporting); methodology (equal); visualisation (supporting); Writing – review and editing (equal); funding aquisition (supporting); funding aquisition (equal). **John D. C. Linnell:** Conceptualisation (supporting); methodology (equal); visualisation (supporting); writing – review and editing (equal). **Simen Pedersen:** Conceptualization (lead); funding acquisition (lead); methodology (equal); writing – review and editing (equal).

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CONFLICT OF INTEREST STATEMENT

We confirm that there are no conflicts of interest.

DATA AVAILABILITY STATEMENT

The dataset used for analysis including phenotypic and environmental data and the location where the observations were collected: Figshare, DOI: 10.6084/m9.figshare.22560340.

PERMISSION TO REPRODUCE MATERIALS

None.

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SUPPORTING INFORMATION

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

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2

Mountain hare (*Lepus timidus*) coat colour mismatch is greatest in areas that experienced the largest climate change induced reductions in snow cover duration

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Abstract

Seasonal coat colour variation has evolved in multiple bird and mammal species as an adaptation to environments that experience seasonal snow cover. Climate change induced reductions in the duration and extent of seasonal snow cover can apply strong selection pressure on phenological life events, including seasonal coat colour variation. This results in animals that do not match their background being at a selective disadvantage. In this paper we investigate the impact of climate change induced reductions in the number of snow days on the probability of mountain hares (*Lepus timidus*) being mismatched against their environment. We collected data between 2011 and 2019 at 678 camera trap locations spread across an environmental gradient between 58° N and 69° N. Using this data in conjunction with snow depth data collected over two 30-year periods (1959-1988 and 1989-2018), we created a generalised linear mixed model that predicted the correlation between the number of days mismatch and the reduction in the number of snow days. We found that the number of days mismatch was greatest in areas that have experienced the largest reductions in the number of snow days and that the number of days mismatch was greater than the reduction in the number of snow days. We also created a generalised additive model that predicted the probability of mountain hares being mismatched against their background. Our results indicated that the probability of coat colour mismatch correlated with environmental variables. Hares that inhabit higher altitudes and latitudes in areas with continental climates being mismatched against their background less than their low altitude and latitude conspecifics that inhabit regions with coastal climates. The effects of seasonal coat colour mismatch were greatest around Norway's coastal regions, particularly in the south. We conclude that climate change has negatively affected the probability of mountain hares' coat colour matching their background.

Introduction

Species that live in seasonally changing environments often evolve phenological adaptations, including synchronised breeding (Goldman 1991, Coppack and Pulido 2004), migration (Gwinner 1996), and moulting (Lesher and Kendeigh 1941, Lyman 1943), tailored to variation in their local environment. These circannual traits are often timed using photoperiod (Gwinner 2003, Hofman 2004) in combination with other environmental variables, including temperature (Watson 1963, Jackes and Watson 1975) and snow cover (Watson 1963, Flux 1970). Both prey and predator species may evolve adaptive colouration that camouflages them against their environment (Cott 1940, Merilaita and Lind 2005, Stevens and Merilaita 2009) resulting in predator prey relationships applying strong selection pressure on this trait (Stevens and Merilaita 2009).

Seasonal coat and plumage colour change from summer brown to winter white is an adaptation to environments that are snow free in summer and snow covered in winter. This trait has evolved in at least 21 bird and mammal species (Mills et al. 2018, Zimova et al. 2018), reducing the probability of these species being detected (Zimova et al. 2016). Moulting between summer and winter coats has been confirmed as being mainly controlled by photoperiod in various species, including Siberian hamsters (*Phodopus sungorus*), Syrian hamsters (*Mesocricetus auratus*) (Duncan and Goldman 1984, Paul et al. 2007), snowshoe hares (Lyman 1943) and least weasels (*Mustela nivalis*) (Bissonnette and Bailey 1944). Seasonal coat colour mismatch, which occurs when animals' coats do not match the colour of their environment, transpires when seasonal variation in snow cover duration and extent does not match the species moult timing (Mills et al. 2013). Additionally, in areas where temperatures are close to 0°C, winter precipitation that historically fell as snow may fall as rain (Kapnick and Hall 2011, Ombadi et al. 2023). This leads to reduced snow cover, which can result in animals being mismatched within a season even if they successfully synchronise moulting with the transition between seasons.

Climate change can lead to mismatch between environmental conditions and phenological life events (Parmesan and Yohe 2003, Kharouba et al. 2018). Modifying the timing of phenological events, such as hibernation (Ozgul et al. 2010), reproduction (Reale et al. 2003), migration (Both and Visser 2001), and moulting (Zimova et al. 2014), are common adaptations to a changing climate (Forrest and Miller-Rushing 2010, Visser et al. 2010). Cold adapted species may respond by moving towards the poles (Parmesan et al. 1999, Sirois-Delisle and Kerr 2018) and to higher altitudes (Colwell et al. 2008, Bisi et al. 2015). This can result in these species being extirpated from parts of their range (Aitken et al. 2008, Pohl et al. 2023), and eventual extinction (Pounds et al. 1999, Thomas et al. 2004).

Mountain hares moult between summer and winter coats, except for the Irish mountain hare (*Lepus timidus hibernicus*), which maintains a brown coat year-round (Mills et al. 2018). We previously found that Norwegian mountain hare moult timing varies considerably across latitudinal and elevational gradients (Stokes et al. 2023). Hares at high altitudes and latitudes moulted to summer brown earlier in spring and winter white later in autumn, compared to their low altitude and elevation conspecifics. We also found that there was some evidence of moult timing phenotypic variation in spring but not in autumn, which is consistent with research conducted on other moulting species (Zimova et al. 2014, Atmeh et al. 2018). Mountain hares are distributed across Eurasia from the Faroe Islands in the west to Japan in the east (Angerbjorn and Flux 1995). The Norwegian population's seasonal moult is likely to be under strong selection pressure as lagomorph mortality rate is strongly linked to predation (Marcström et al. 1989, Zimova et al. 2016, Pedersen et al. 2017). This is particularly likely in

Norway's coastal regions, which have been strongly affected by climate change induced reductions in snow cover (Hanssen-Bauer et al. 2017).

In this paper, we used nine years of data collected between 2011 and 2019 by 678 camera traps spread across a large geographic and climatic gradient in Norway from 58° N to 69° N in conjunction with current and historic interpolated snow data collected from 1959 to 2019. We aimed to provide a quantitative study investigating how mountain hare moult timing and coat colour mismatch has been affected by climate change over a 60-year period. We investigated coat colour mismatch due to moult timing phenology and mismatch caused by snow conditions during winter and summer. We investigated (1) the effect of climate change induced reductions in the number of snow days on coat colour mismatch accumulated throughout the year, hereafter referred to as *cumulative mismatch*. (2) Whether this impact is larger during the spring or autumn moulting period, hereafter referred to as *phenological mismatch*, and (3) how the probability of mismatch is affected by environmental variables. We predicted that coat colour mismatch would be greatest in areas that have experienced the largest reductions in the number of snow days, that mismatch would be greater in autumn than in spring, and that the probability of mismatch would be greater for hares that live in coastal areas at lower latitudes and elevations.

Methods

Hare data and moult timing predictions

In this study, we used images that were collected between 10th January 2011 and 25th June 2019 by 678 camera traps deployed across Norway (Figure 1). The cameras were deployed between 58° N to 69° N and between 0 and 841 meters above sea level by the SCANDCAM project (https://viltkamera.nina.no). We discarded mountain hare images that were recorded within 60 minutes of the previous image to limit the number of observations obtained by repeatedly sampling the same hare multiple times. After cleaning the data, we had 9,979 observations. All images are publicly available on (https://viltkamera.nina.no) and were classified by one of two observers.

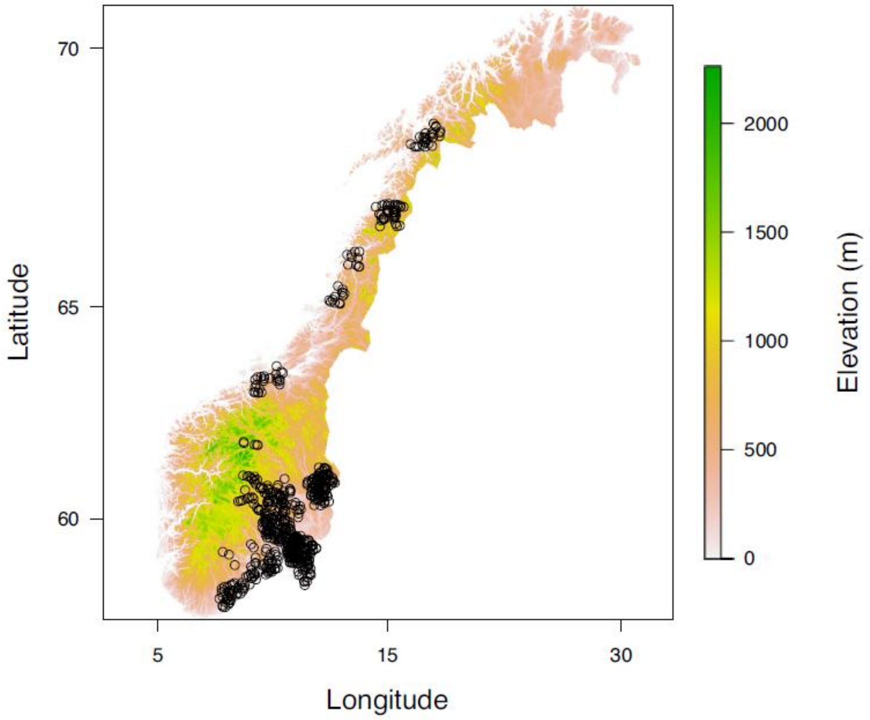

Figure 1. Location of 678 camera traps that recorded mountain hare observations (black circles). The cameras were deployed between 0 and 841 meters above sea level and between 58° N and 69° N by the SCANDCAM project.

Snow data

We used two snow datasets with 1 km^2 resolution based on interpolated data from weather stations across Norway from www.senorge.no (access date = 17 October 2023). We used the first dataset as a measure of climate change and the second as a measure of weather. We defined a snow day as snow depth being ≥ 5 cm as the ground is still visible when snow cover is < 5 cm (Pedersen et al. 2017).

First, we created the *climate change* dataset to obtain a measure of how climate change has affected the number of snow days. To this end, we created two 1 km^2 rasters containing 30-year averages (1959 - 1988 and 1989 - 2018) of the number of snow days per year (Suppl 1). It was not possible to include an earlier 30-year period as 1957 is the earliest year www.senorge.no has available data. We calculated the difference between the two rasters to determine change in the average number of snow days (Suppl 2). Secondly, we created the *weather* dataset, which contained snow depth at every camera trap location for every ordinal day between 2011 and 2019. We used this dataset to determine when hares were mismatched and to create an index of the start and end of winter (see below).

Additional environmental data

Finally, we obtained environmental covariates for each camera trap location. We extracted latitude based on each cameras' geographic location. We used the extract function in the raster (Hijmans 2023) package to extract the elevation of each camera trap from a digital elevation model (DEM) with a 50 m^2 resolution (Korsnes 2018) (Suppl 3.a). We also obtained climate zone with a 1 km^2 resolution as a continuous variable from (Bakkestuen et al. 2008), who estimated climate zone using principle component analysis (PCA) with climatic data, hydrological data and geological data, and terrain data (Suppl 3.b). We used *fasterize* (version 1.0.4) (Ross 2020) to convert it from vector to a raster.

Data analysis

This paper builds on Stokes et al (2023) in which we used these camera trap images to create Bayesian multinomial logistic regression models that predicted mountain hare moult timing across Norway between 2011 and 2019. These models predicted the correlation between the probability of mountain hares being in a specific coat colour category (white, brown, or moulting) based on elevation, latitude, and climate zone. In the current paper, we used the results from these models to predict the probability of hares being either white or brown at each camera trap location on every ordinal day between 2011 and 2018. We did not include 2019 as the last observation used in the model was recorded on 25th June 2019, resulting in the model not predicting for the entire year. We classified hares as being white when the probability of being white was greater than the probability of being brown and vice versa. This enabled us to estimate mismatch that occurred within the moulting seasons. We used the weather dataset to classify white hares as mismatched when snow depth was < 5 cm and brown hares as mismatched when snow depth was ≥ 5 cm.

We studied how cumulative mismatch at the camera trap locations correlated with a reduction in the number of snow days by fitting a generalised linear mixed model using the glmmTMB package (Brooks et al. 2017) (Figure 2). For the response variable, we used the weather dataset in conjunction with moult timing estimates taken from the Stokes et al. (2023) model to find the average number of days hares were mismatched per year at each camera trap location. For the explanatory variable, we used the climate change dataset to find the change in the number of snow days at each camera trap location. We included camera trap location and year as random intercepts. Due to the use of count data, we specified the response variable as a Poisson distribution, which we modelled through a log link function.

To study how phenological mismatch correlated with reduction in snow days, we used two generalised linear mixed models; one for spring moult (white to brown) and one for autumn moult (brown to white). We created an index of winter end and start by defining the end of winter as the last day in which there were seven continuous snow days and winter start as the first day in which there were seven continuous snow days. These definitions resulted in some camera trap locations not experiencing winter. To account for this, we set the winter end date to the earliest ordinal day on which the end of winter was recorded. Next, we set the winter start date to the latest ordinal day in which the start of winter was recorded. This meant that locations that did not experience winter had the most extreme winter start and end dates recorded. For the first model, the response variable was the difference in days between the start of spring moult and end of winter (hereafter referred to as *spring asynchrony*). For the second model, the response variable was the difference in days between the start of autumn moult and the start of winter (hereafter referred to as *autumn asynchrony*). A positive number meant that moulting started after snow disappearance in spring and before snow appearance in autumn. A negative number meant the opposite. For both models we used reduction in the number of snow days (climate change dataset) as the explanatory variable and location and year as random intercepts. We assumed a normal distribution, used an identity link function, and fitted the models using the glmmTMB package (Brooks et al. 2017).

We used the mismatch estimates obtained using the weather dataset to estimate spatial and temporal variation in the probability of mountain hares being mismatched against their background at every camera trap location on every day between 2011 and 2018. For each day and location, we assigned a value of 1 if a hare was mismatched and a value of 0 if it was matched. We then summed the values for each ordinal day and location giving a value between 0 and 8, which represented the number of years in which hares were mismatched against their background between 2011 and 2018. We used this value to obtain a measure of probability between 0 and 1 representing the probability of hares being mismatched against their background on each day at every camera trap location. We created a generalised additive model (GAM) in the mgcv R package (Wood 2017), using the probability of being mismatched as the response variable and ordinal day, elevation, latitude, and climate zone as explanatory covariates. A cyclic smooth was used for ordinal day. We standardised elevation, latitude, and climate zone (mean = 0, SD =1). We smoothed all environmental variables limiting the number of knots (k) to 20 using default splines settings. We limited knots, which are the breakpoints in the smooth function, to 20 to prevent over-fitting the model. We fitted the model with a binomial distribution. When plotting model results (Figure 4), we chose different values for our explanatory variables, 0 and 700 m meters above sea level (m.a.s.l.) (altitude), 59 and 65° N (latitude), and -2.5 and 2.5 (climate zone), representing environmental variation present at camera trap locations.

We completed all data analysis using R version 4.3.2 (R Core Team 2022). We used the *GGPLOT2* (Wickham 2016), *cowplot* (Wilke 2020), *jtools* (Long 2022), and *raster* (Hijmans 2023) packages to produce all figures. We plotted partial residuals (Figures 2 and 3) to control for variation caused by the random intercepts (camera trap location and year) (Fox and Weisberg 2018).

Results

Spatial and temporal variation in predicted number of days of mismatch

The camera trap locations experienced a decline of between 4 and 57 snow days (mean = 31 days, standard deviation = 37.5) between the two 30-year averages (1959-1988 and 1989-2018). Some parts of Norway, particularly in the far north, experienced an increase in the number of snow days (Suppl 1 and 2) but, these regions were not covered by camera traps.

When investigating if hares were able to adapt their moult phenology to climate change, we found that the number of days of cumulative mismatch increased as snow cover duration decreased over the 60 year period, (intercept = 3.08, SE = 0.0820, $p < 0.0001$) (Figure 2). The slope estimate for the difference in the number of snow days was 0.262.

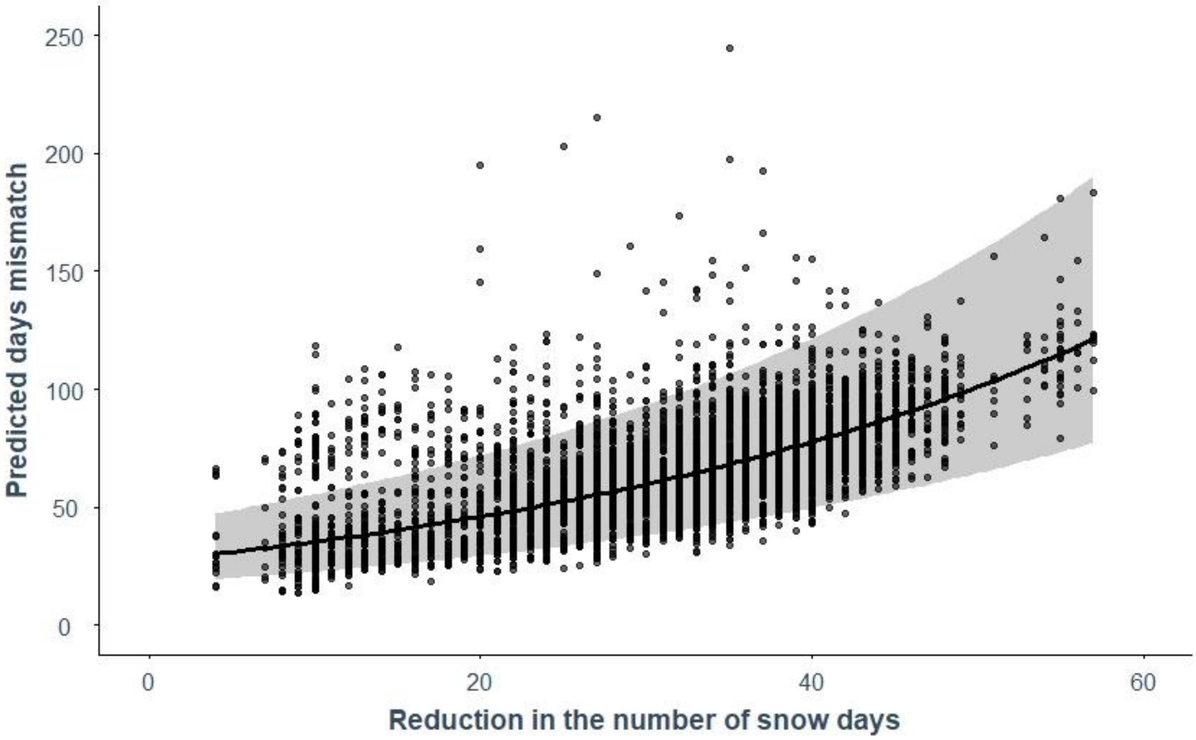

Figure 2. Number of days of cumulative mismatch increased with increasing effects of climate change, illustrated by reduction in snow days. The shaded area represents the 95% confidence intervals and the dots represent the partial residuals. We back transformed the results to the original scale before plotting, resulting in a non-linear relationship.

Moult timing compared to the start and end of winter

When investigating if hares could adapt their moult timing to reduced number of snow days, we found that phenological mismatch increased as snow cover duration decreased (Figure 3). Spring asynchrony increased as the reduction in snow days increased (estimate = 0.871, SE = 0.0712, $p < 0.0001$) (Figure 3.a). The gap between winter end and spring moult end was greater for hares inhabiting areas that experienced large snow day reductions compared to their conspecifics living in areas that experienced a smaller reduction in the number of snow days. Autumn asynchrony also increased as the reduction in the number of snow days increased (estimate = 0.743, SE = 0.0457, $p < 0.0001$) (Figure 3.b). The gap between winter moult end and winter start was greater for hares inhabiting areas that experienced large snow day reductions compared to their conspecifics living in areas that experienced smaller reductions in the number of snow days.

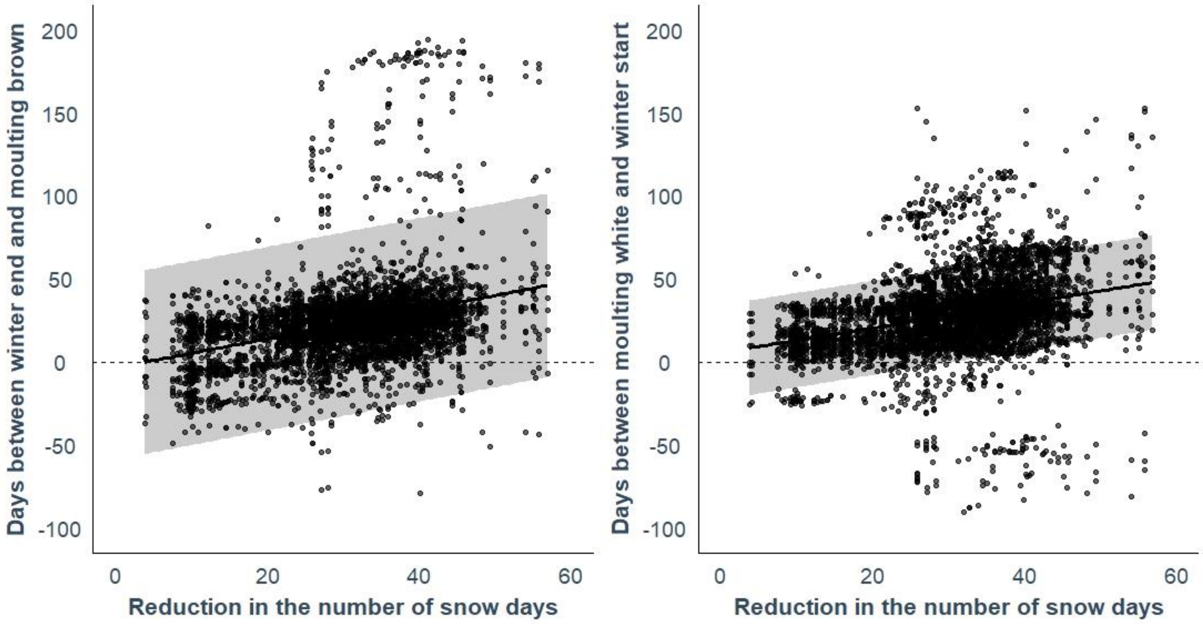

Figure 3. The predicted difference between (a) spring moult end and end of winter compared to the reduction in snow days and (b) winter start and autumn moult end compared to reduction in snow days. For spring moult, negative numbers indicate that spring moulting finished before winter end and positive numbers indicate moulting finished after winter end. For the autumn moult, positive numbers indicate that moult finished before winter start and negative numbers indicate that moulting finished after winter start. The shaded areas represent the 95% confidence intervals and the dots represent the partial residuals.

Correlation between environmental variables and probability of being mismatched

We found temporal and spatial variation in the probability of mountain hares being mismatched across Norway (Figures 4 and 5, see Suppl 4 for an animated map containing every ordinal day). The model used to analyse correlation between environmental variables and the probability of hares being mismatched explained 63.7% of the deviance. The highest probabilities of being mismatched occurred during the autumn moult (Figure 4 and 5.e). The probabilities of being mismatched remained larger than 0 throughout winter, increased during the spring moult before dropping to 0 during the summer (Figure 4). Hares that lived at 700 meters above sea level had a lower probability of being mismatched throughout the winter and moulting periods than those that lived at sea level ($p < 0.0001$) (Figure 4.a). Hares that lived at 65° N had a lower probability of being mismatched against their environment throughout the winter and moulting periods than those that lived at 59° N ($p < 0.0001$) (Figure 4.b). Finally, hares that lived in inland areas (positive climate zone) had a lower probability of being mismatched throughout the winter and moulting periods than those living in coastal areas (negative climate zone) ($p < 0.0001$) (Figure 4.c).

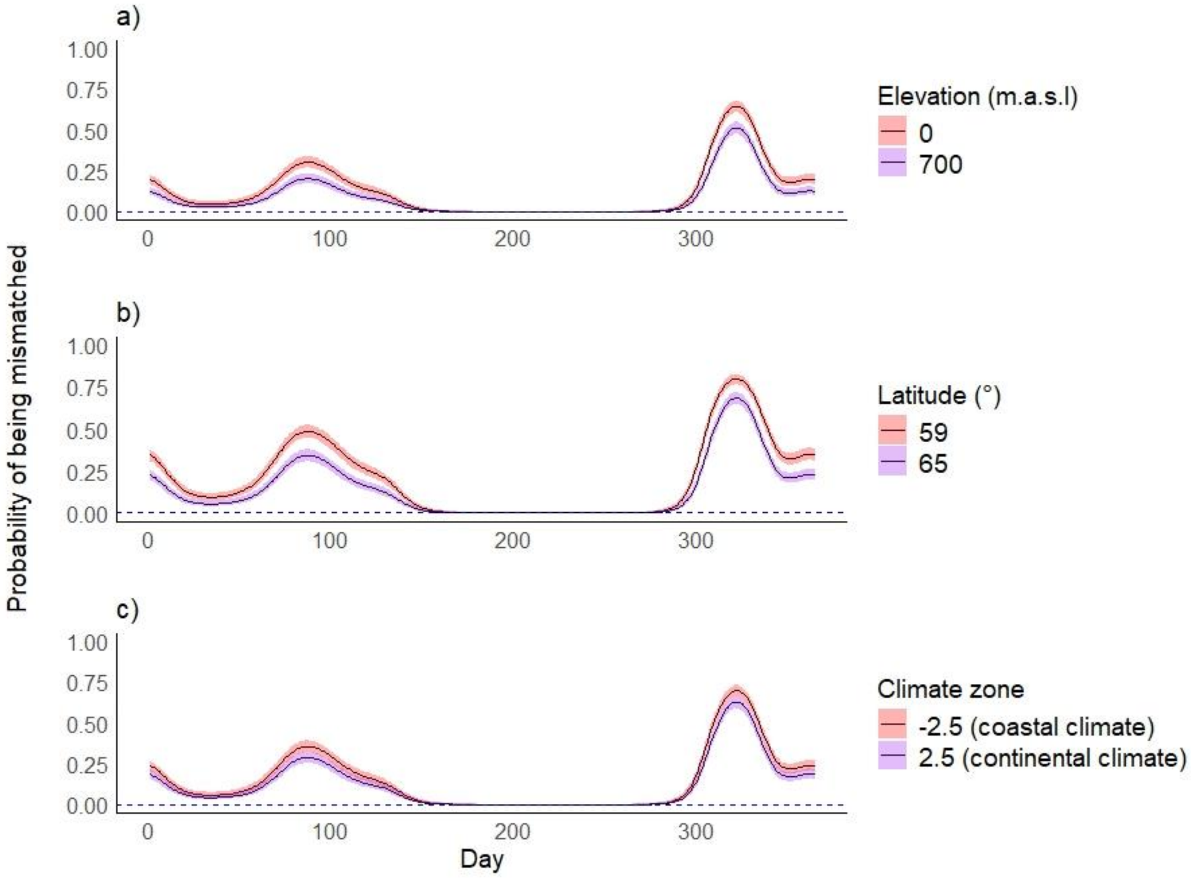

Figure 4. Variation in the probability of hares being mismatched against their environment at different (a) altitudes, (b) latitudes, and (c) climate zone indexes. When plotting the respective panels, the other two environmental variables were set to their mean value. The number of knots for each variable were limited to 20 to prevent over-fitting.

At the start of the year, hares across large parts of Norway had a mismatch probability of 0 (Figure 5.a). There were patches where the probability was greater than 0 along the west coast, southwest mountains, and the far north next to the Finnish border. The mismatch probability increased to above 0 across all of Norway during the spring moult (Figures 5.b and c) before decreasing to 0 during the summer (Figure 5.d). The mismatch probability reached its highest level across all of Norway during the autumn moult (Figure 5.e) before decreasing during the winter (Figure 5.f). Mismatch probability tended to be highest throughout the year in the southwest coastal regions remaining above 0 throughout the autumn, winter, and spring.

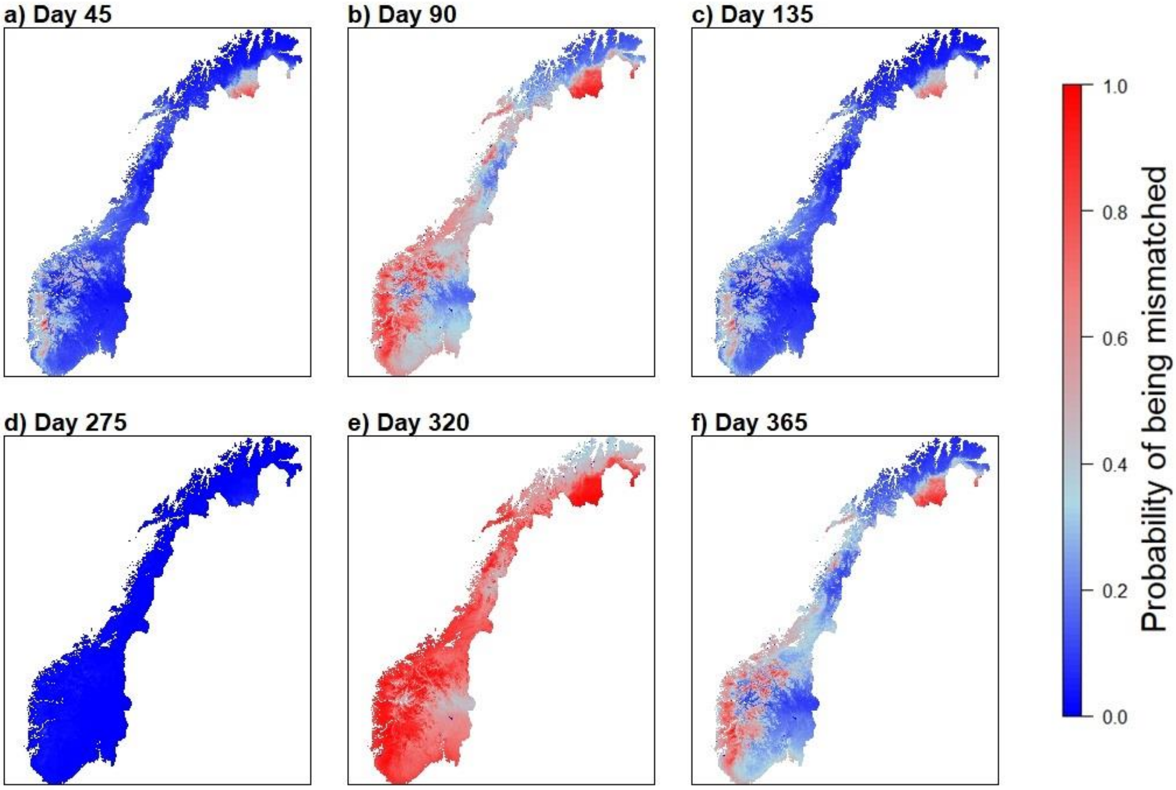

Figure 5. The probability of hares being mismatched against their environment across Norway on 1 km^2 grid on ordinal days (a) 45 (14th February), (b) 90 (30th March), (c) 135 (14th May), (d) 275 (2nd October), (e) 320 (16th November), and (f) 365 (31st December). Our GAM predicted the probabilities of being mismatched using environmental variables contained in every cell. See Suppl 4 for an animation containing every day of the year.

Discussion

In this paper, we quantified how lagomorph coat colour mismatch correlated with 60-years of climate change data. We also investigated lagomorph mismatch within the winter and summer seasons as well as within the moulting period. We used camera trap observations in combination with current and historical snow data, collected over a 60-year period, to analyse how current mountain hare coat colour mismatch compares to change in snow conditions. We found that mountain hares spend a considerable number of days mismatched against their environments in parts of their distribution. The number of days spent mismatched was generally highest in areas that experienced a large reduction in snow days relative to historical records.

The number of snow days decreased across most of Norway between 1959 and 2018 (Suppl 2), following trends seen across the northern hemisphere (Derksen and Brown 2012, Kunkel et al. 2016). Hares inhabiting areas characterised by large decreases in the number of snow days experienced more days of cumulative mismatch (Figure 2), indicating that mountain hares are failing to track climate change. This is consistent with previous studies on mountain hares (Zimova et al. 2020) and other mammals that express seasonal coat colour change, including snowshoe hares (Zimova et al. 2014, Kumar et al. 2020), and least weasels (Atmeh et al. 2018). It is likely that our study system was affected by climate change before snow records began in 1957. This is evidenced by the number of days of mismatch being greater than the reduction in the number of snow days throughout the sampled area (Figure 2). Therefore, mountain hare moult timing is likely to have evolved to fit snow patterns pre-dating 1959. This indicates that shifting baseline syndrome (Pauly 1995) may affect this and other studies using historical data to investigate the effects of climate change.

Spring and autumn asynchrony were correlated with reduced snow days, resulting in phenological mismatch being greatest in areas that experienced the largest reductions in the number of snow days (Figure 3). The confidence intervals were considerably wider in the spring moult than in the autumn, indicating that there is a wider range in the gap between end of spring moult and end of winter compared to end of autumn moult and the start of winter. Previous studies on a variety of moulting species have found greater variation in spring moult dates than autumn moult dates (Zimova et al. 2014, Atmeh et al. 2018, Stokes et al. 2023), which may correlate with this result.

Elevation, latitude, and climate zone all had the expected effect on the probability of hares being mismatched against their environment (Figure 4). Hares that inhabited low elevations and latitudes in coastal areas were mismatched against their background for longer than hares in the rest of Norway (Figures 4 and 5). They were worse at tracking snow patterns in these areas, possibly due to greater reductions in the number of snow days (Suppl 2.a). Historically, these areas have experienced precipitation falling as snow (www.senorge.no). Climate change induced state changes, which result in an increase in the amount of precipitation falling as rain (Trenberth 1998, Ombadi et al. 2023), has led to a significant reduction in the number of snow days (Suppl 2.a). The probability of being mismatched was at its highest during the autumn moult across all environmental variables. The duration of mismatch during the autumn moult was considerably shorter than the spring moult, which has been observed in stoats (*Mustela erminea*) (Rothschild 1942). This could also correlate with increased variation in the spring moult (Zimova et al. 2014, Atmeh et al. 2018, Stokes et al. 2023). The reasons for increased variation in spring moult timing are still unclear. Increased predation during spring could lead to more phenotypes being expressed. Alternatively, it could result from behavioural responses, such as manually removing fur during the spring moult, that aim to reduce coat colour mismatch. To our knowledge these hypotheses have not been tested. The duration of mismatch being longer during the spring moult could contradict the hypothesis that increased moult timing variation during spring is an adaptive response that reduces coat colour mismatch. The probability of being mismatched stayed above 0 throughout both moulting periods and the winter, particularly in southwest coastal areas, contrasting with 0 probability of being mismatched during the summer (Figures 4 and 5). Surprisingly, there was a high probability of hares being mismatched in Norway’s far north next to the Finnish border both early (Figure 5.a) and late (Figure 5.f) in the year. This area experiences between 160 and 260 snow days a year (Suppl 1) and has seen an increase in the number of snow days over the last 60 years (Suppl 2). This result should be treated with caution as our model is predicting far outside the range of our data (Figure 1). In the absence of an evolutionary response, the probability of mismatch is likely to further increase as Norway is predicted to see further decreases in the number of snow days, particularly in coastal regions, by 2100 (Hanssen-Bauer et al. 2017).

Mismatched mountain hares are thought to be under strong selection pressure caused by predation (Pedersen et al. 2017). Phenotypic variation in response to climate change induced variation in snow conditions have been recorded in mountain hares (Zimova et al. 2020) and snowshoe hares (Kumar et al. 2020) but, these responses were insufficient to keep pace with changing conditions. Additionally, many species may not be able to evolve at the pace needed to adapt to climate change induced environmental variation. For example, a study of over 500 tetrapod clades found that the rate of evolutionary change needed to be 10,000 times faster than what currently occurs (Quintero and Wiens 2013). However, rapid evolutionary responses have been documented in various species including elephants (*Loxodonta africana*)

(Campbell-Staton et al. 2021), midwife toads (*Alytes muletensis*) (Moore et al. 2004) and European rabbits (*Oryctolagus cuniculus*) (Marshall and Douglas 1961).

Fast evolutionary change, referred to as evolutionary rescue (reviewed in Gonzalez et al. 2013), may enable recovery before extinction occurs. There is significant variation in mountain hare moult timing phenology within Norway (Stokes et al. 2023), which could facilitate a fast evolutionary response. Additionally, the mountain hare subspecies *Lepus timidus sylvaticus*, which is found along Norway's south coast (Stokes et al, in prep), moults to a bluish grey coat in winter. This is thought to be an adaptation to reduced number of snow days experienced in milder winter climates (Barth 1891). This subspecies could be well concealed despite having a high probability of being mismatched (according to our definition) during the winter and moulting periods. Additionally, Irish mountain hares (*Lepus timidus hibernicus*) do not moult to a winter white coat (Mills et al. 2018), indicating that sufficient selection pressure could result in Norwegian mountain hares evolving a similar adaptation. Individual hares could mitigate the negative impact of being mismatched through behavioural changes, such as microhabitat selection and minimising diurnal activity. There is some evidence of snowshoe hares selecting patches based on coat colour variation (Litvaitis 1991) but, subsequent studies have failed to find supporting evidence (Zimova et al. 2014, Kumar et al. 2020). So far, this has not been tested on mountain hares.

Understanding how mountain hares and other moulting species are evolving in response to environmental variation is critical for understanding the impact that climate change has on moulting species. Our study represents the first time this has been studied over the scale of an entire country with data collection spanning 11 latitudinal degrees. At present, we are limited to analysing how current moult timing correlates with current and historical snow patterns as we do not have camera trap records prior to 2011. Our results suggest that mountain hares' seasonal coat colour phenology is not evolving at the speed needed to track climate change. Maintaining the SCANDCAM camera trap network for a considerable amount of time would facilitate analysis of the rate of evolutionary response.

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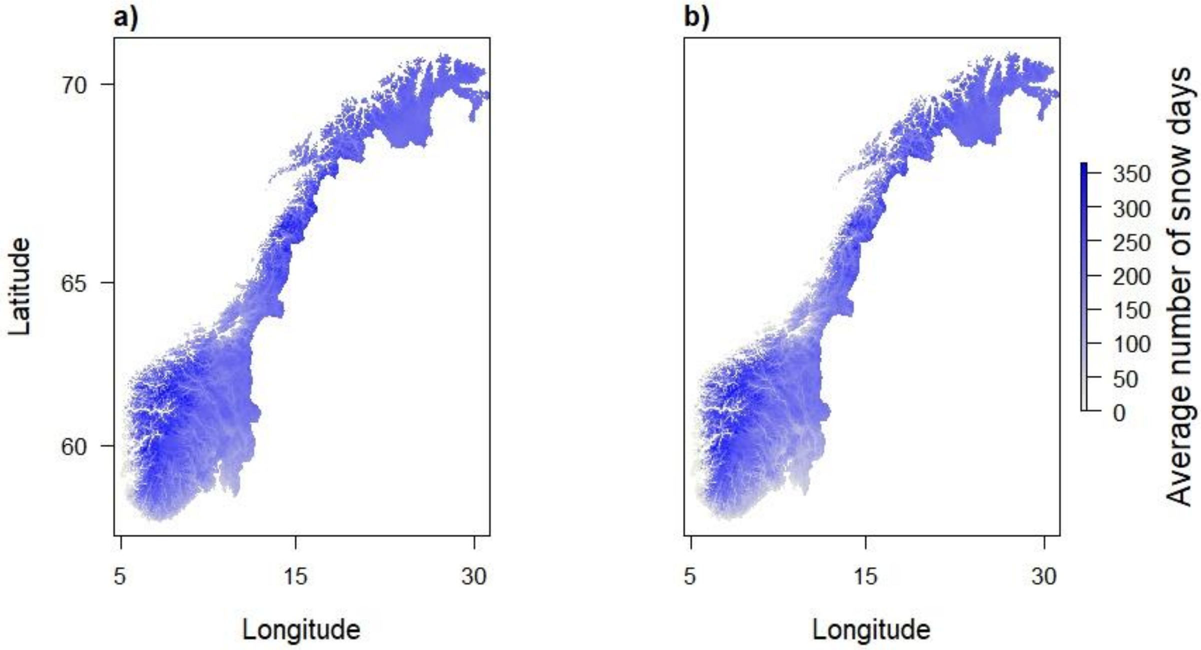
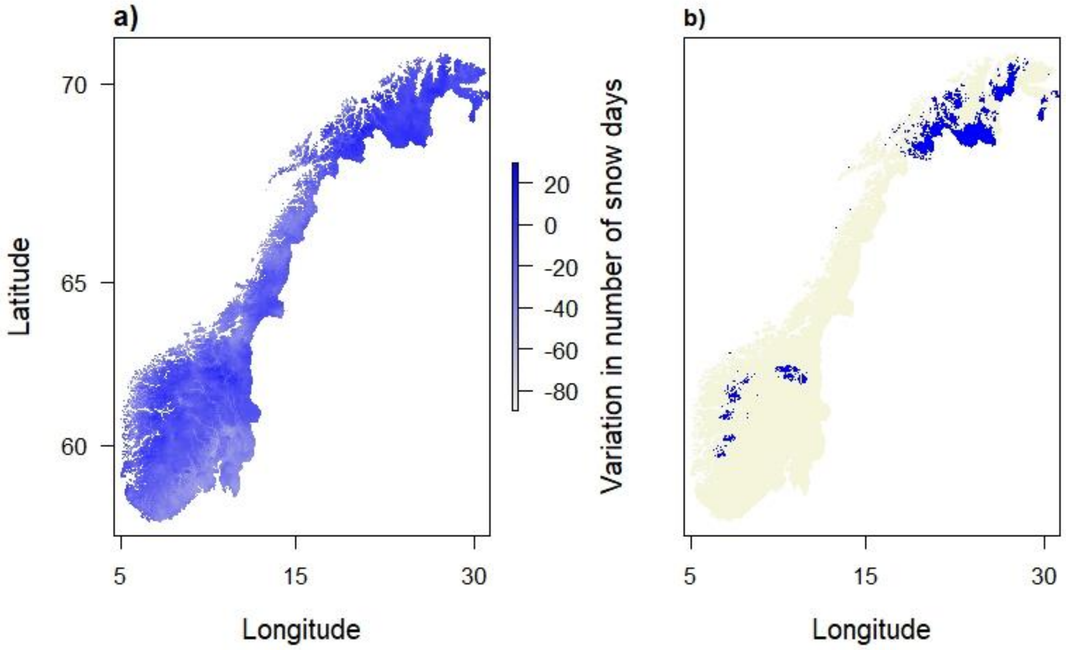
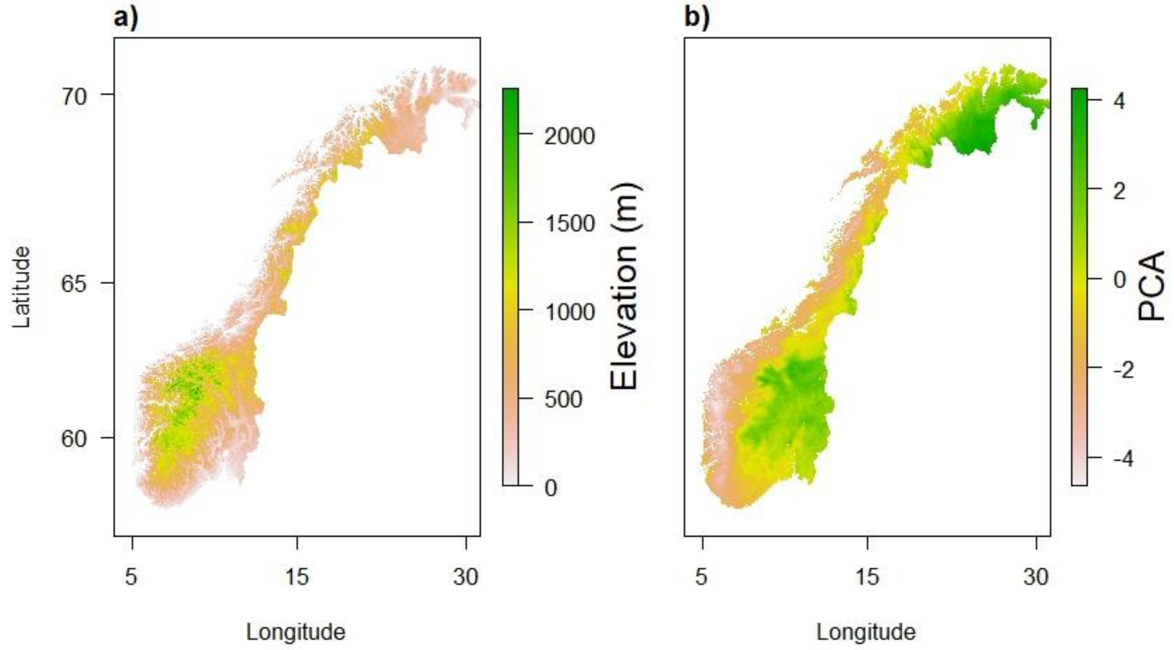
Supplementary information



Suppl 1. The average number of snow days per year from (a) 1959 to 1988 and (b) 1989 to 2018. The maps contain interpolated data collected by weather stations spread across Norway.



Suppl 2. (a) The change in the average number of snow days per year between 1959 to 1988 and 1989 to 2018. (b) Binary output showing areas where the average number of snow days per year have increased in blue and decreased in beige.



Suppl 3. (a) Digital elevation model (DEM) containing the elevation across Norway (Korsnes 2018) and (b) Climatic zones across Norway with negative values representing coastal climates and positive values representing continental climates (Bakkestuen et al 2008).

Animation will be included as a video file when submitted to a journal.

Suppl 4. The probability of hares being matched against their environment on every ordinal day of the year across all of mainland Norway. Results outside of areas covered by camera traps should be treated with caution as they are extrapolated by our model.

3

Current distribution and the impact of climate change on the future suitable habitat of two morphs of the native mountain hare, and the non-native European hare in Norway

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Abstract

Climate change is leading to the suitable habitat of numerous species moving away from current and historical locations. White mountain hares (*Lepus timidus timidus*) moult from brown in summer to white in winter, as an adaptation to snowy winter conditions. Heath hares (*Lepus timidus sylvaticus*) moult from brown in summer to a bluish grey colour in winter, hypothesised to be an adaptation to variable winter conditions. European hares (*Lepus europaeus*) maintain a brown coat year-round. European hares are colonising Norway after being introduced into Sweden in the 19th century. We used citizen science and camera trap observations in conjunction with environmental and climatic variables to map these three organisms' current distribution and current and future suitable habitat within Norway. Forest cover, altitude, and minimum temperature of the coldest month influenced white mountain hare distribution. Minimum temperature of the coldest month, snow cover days, and annual precipitation influenced heath hare and European hare distribution. We also explored potential changes in the areas of suitable habitat under multiple climate change scenarios. Our results suggest that white mountain hare distribution covers most regions within Norway, heath hares occupy southern regions, and European hares are limited to the southeast corner

next to the Swedish border. Under climate change predictions, white mountain hare suitable habitat area will contract eastwards and northwards. Conversely, heath hare and European hare suitable habitat area is expected to expand northwards, resulting in interspecies interactions becoming more common. White mountain hares are likely to come under increased pressure both from climate change and European hare expansion.

Introduction

Climate change strongly affects species distribution, leading to the expansion and contraction of different species' distributions (Elmhagen et al. 2015, Brown et al. 2016, Caravaggi et al. 2017). Cold weather adapted species inhabiting areas affected by temperature increases are likely to shift their distribution towards the poles (Hastings et al. 2020) and to higher altitudes (Moritz et al. 2008), leading to extirpation from parts of their former range and potential extinction (Pounds and Crump 1994, Thomas et al. 2004, Thomas et al. 2006). Species adapted to more moderate climates may be able to expand their territory by moving into the vacated areas (Caravaggi et al. 2017, Hastings et al. 2020), which can increase interactions between native and non-native species (Caravaggi et al. 2017).

Non-native species often out compete and hybridise with native species, leading to native species being extirpated from parts of their historic range (Bradford 1991) and, in some cases, extinction (Rhymer and Simberloff 1996, Huxel 1999, Butchart et al. 2010). Generalist species have a higher likelihood of successful naturalisation following introduction than specialists, due to their ability to utilise broader ecological niches. (Duncan et al. 2003, Blackburn et al. 2009). Additionally, non-native species can interact with other anthropogenic disturbances, such as climate change which may make conditions more suitable for invading species (Rahel and Olden 2008, Flory et al. 2022).

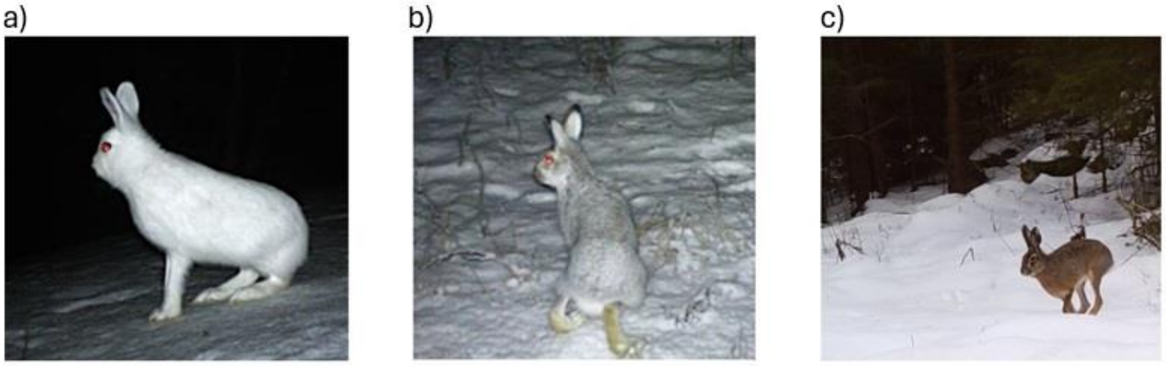

Figure 1. SCANDCAM camera trap images of (a) white mountain hare, (b) heath hare, and (c) European hare in winter.

Mountain hares are native to Norway where they are affected by climate change (Stokes et al. In prep). In future, they could also be affected by expansion of the non-native, temperate climate adapted European hare. The mountain hare (nominal subspecies: [*Lepus timidus timidus*]) (hereafter referred to as 'white mountain hare') is a cold adapted, generalist lagomorph that inhabits Fennoscandia, Russia, and northern parts of Asia (Angerbjorn and Flux 1995). They are present throughout Norway with their distribution ranging from sea level to above the tree line. They moult from brown in the summer to white in the winter (Figure 1.a). The heath hare (*Lepus timidus sylvaticus*) is a mountain hare sub-species that is also native to Norway. In this paper, we use the term 'mountain hare' as an umbrella term for both subspecies**.** Heath hares moult from brown in the summer to bluish grey in the winter (Figure 1.b) (Thulin et al. 1997). Heath hares were originally described in Norway by Barth (1891) as an adaptation to the milder climates of the southwestern Norwegian coast. Its moult strategy indicates that it is still a cold adapted species but, it may be able to better tolerate warmer climates with more inconsistent snow conditions than the white mountain hare.

European hares (*Lepus europaeus*) maintain a brown coat all year round (Figure 1.c) and are native to mainland Europe and central Asia (Flux and Angerman 1990). They have a large range across Europe with Fennoscandia's southern tip representing their most northerly distribution. European hares are a non-native, temperate weather adapted species that expanded into the south-east of Norway after being released into Sweden in the late 19th century (Thulin 2003 and references within). They out-compete (Reid 2011, Thulin et al. 2021) and hybridise (Jansson and Pehrson 2007, Levänen et al. 2018, Pohjoismäki et al. 2021) with mountain hares in parts of their shared range. This can result in mountain hares being pushed to higher altitudes (Schai-Braun et al. 2023). At present, European hares are dependent on anthropogenic habitats within Fennoscandia (Pohjoismäki et al. 2021) but, there is some indication that they are adapting to forested areas (Jansson and Pehrson 2007). Snow cover is likely to be critically important to all three study organisms with a decrease in snow cover duration and extent negatively affecting white mountain hares and favouring heath hares and European hares (Schmidt et al. 2004, Jansson and Pehrson 2007). Obtaining an accurate estimate of these organisms' current distribution and future change in habitat suitability will help inform management decisions.

In this study, we used Maxent to analyse which environmental and climatic variables affected the current distribution of our study organisms within Norway. Building on the premise that these distributions are in part linked to climate, we explored how habitat suitability might change under optimistic, moderate, and extreme climate change scenarios. We analysed the relative importance of these variables to investigate which were most likely to affect species distribution and habitat suitability. Specifically, we investigated (1) the current distribution and suitable habitat of white mountain hares, heath hares, and European hares and (2) the predicted future suitable habitat under various climate change predictions for our three study organisms. We defined current distribution as the area that the study organisms currently inhabit and suitable habitat as the area of the environment that it is possible for them to inhabit. This distinction was necessary as European hares are expanding into parts of Norway that they have not had time to colonise. For current distribution, we predicted that white mountain hares would be spread across the majority of Norway, heath hares would be limited to Norway's lower coastal regions, and European hares would be constrained to Norway's south-east. Secondly, we predicted that under future climate change scenarios, white mountain hare suitable habitat would contract further north and away from the coast whereas heath hare and European hare suitable habitat would expand further north and inland with the outcomes being more pronounced under more severe predictions.

Methods

Empirical data collection

In this study, we used a combination of citizen science and camera-trap observations of hares collected in Norway (Table 1 and Figure 2). Camera traps were deployed by the SCANDCAM project (https://viltkamera.nina.no) primarily to monitor Eurasian lynx (*Lynx lynx*) (Hofmeester et al. 2021). Citizen science observations, which were included to increase the range of geographic areas covered, were accessed on the Norwegian Species Observation Service (www.artsobservasjoner.no) platform (accessed 24th August 2023). This website enables people to enter their own observations and upload photographic evidence (Koch et al. 2023). We accessed all hare observations that contained an accompanying photograph and that had been validated by a third-party expert. We used the criteria described in Smith et al (2018) to visually confirm if the organism was a mountain hare or European hare. Since white mountain hares and heath hares can only be differentiated when expressing their winter coats, we manually checked wintertime images to determine if the hares' coats were white or blue in winter. We used spatial predictions of mountain hare moult timing from Stokes et al (2023) to determine when the probability of mountain hares being white or blue was ≥ 50%. We used these cut-off dates to manually check mountain hare subspecies. We included all European hare observations as they can be identified throughout the year. We discarded the observation if it was not possible to determine hare species or colour.

Table 1. Range of environmental values at which both camera trap and citizen science data were obtained for all study organisms.

	Camera trap	Citizen science
Altitude range (meters)	0 to 941	0 to 1,408
Latitude (° North)	59 to 69	58 to 71
Date range observations were obtained over	25th November 2010 to 6th April 2022	19th February 2005 to 30th June 2023

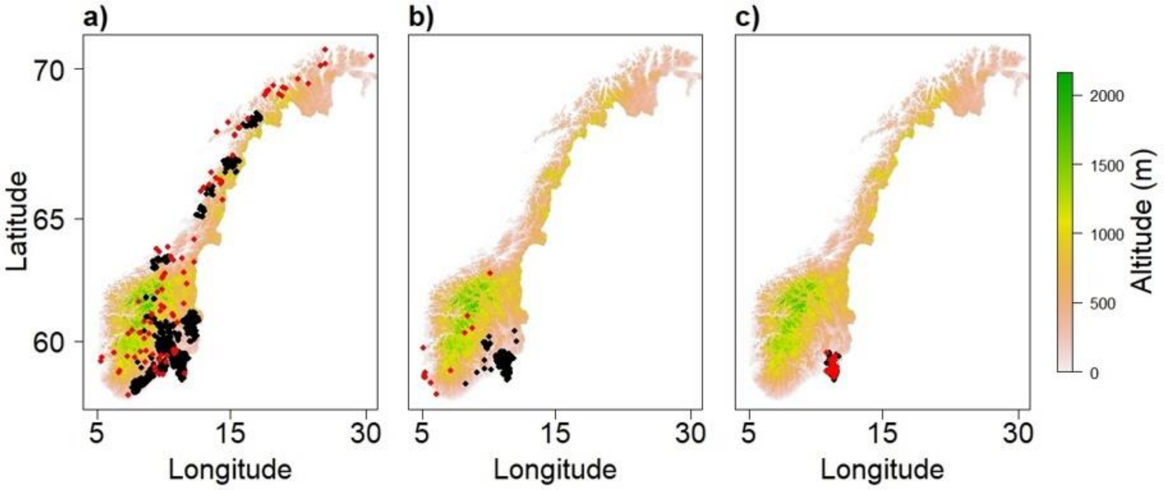

Figure 2. Location of camera trap (black circles) and citizen science observations (red circles) used in a) mountain hare b) heath hare and c) European hare models over a digital elevation model.

Variable selection

We used environmental and current and future climatic variables to predict hare distribution and habitat suitability. The IPCC 2021 climate change report defined Shared Socioeconomic Pathways (SSPs) as climate change scenarios (Masson-Delmotte et al. 2021). SSP126 is an optimistic scenario, SSP370 is a moderate scenario, and SSP545 is an extreme scenario.

We used 2.5 seconds (approximately 1 km^2) historical BIOCLIM files (1970 to 2000) (accessed 20th August 2023) and SSP126, SSP370 and SSP585 climate change predictions for 2061 to 2080 and 2081 to 2100 created by the EC-Earth3-Veg model (EC-Earth 2019) (accessed 1st December 2023 on www.worldclim.org. We selected the environmental data that we thought was biologically relevant (Table 2) and discarded all other variables.

We also used SSP126, SSP370 and SSP585 2.5 seconds CHELSA (https://chelsa-climate.org) snow cover days data (accessed 1st December 2023), defined as “the number of days on which the ground is covered with snow” (Brun et al. 2022). We used historical snow data from 1981 to 2010 and future snow predictions from 2041 to 2070 and 2071 to 2100. We paired the 1981 to 2010 snow data with the 1970 to 2000 BIOCLIM data, 2041 to 2070 snow predictions with

2061 to 2080 BIOCLIM predictions (hereafter referred to as *medium-term predictions*) and 2071 to 2100 snow cover predictions with 2081 to 2100 BIOCLIM predictions (hereafter referred to as *long-term predictions*). Finally, we mapped land use using a 2.5 second land cover raster from (www.copernicus.eu) (access date 24th August 2023). We created two rasters containing the proportion of agricultural and forest land cover categories (Suppl 1 and 2). We discarded all other land use categories as we assumed they were not biologically relevant (Table 2). When predicting future habitat suitability, we assumed that land usage would be constant over time as land use changes depend on political and societal decisions, which are challenging to predict.

We used the terra package (Hijmans 2023) to clip all climatic and environmental rasters to Norway's extent and reprojected them to the 1 km^2 grid used in Stokes et al (2023). We used the variance inflation factor (VIF) to test if all variables were collinear and discarded a variable if the VIF was greater than 5 (James et al. 2013). For example, we discarded annual mean temperature due to it being collinear with both minimum monthly temperature and maximum monthly temperature. When predicting current distribution, we included latitude and longitude to spatially constrain species distribution. This was necessary as European hares are currently expanding across Norway, leading to Maxent predicting this species in areas it has not had time to colonise.

Model selection

We used Maxent (Phillips et al. 2017) to model (1) the current distribution, (2) current habitat suitability, and (3) future habitat suitability for the three study organisms. We chose Maxent due to its ability to process "presence only" data and analyse non-linear relationships (Phillips et al. 2006). We thinned the data so that there was one observation per 1 km^2 grid cell, which reduces the effect of sampling bias (Kramer-Schadt et al. 2013), and discarded observations recorded in locations where explanatory variables were not available. Next, we used the ENMeval package (Muscarella et al. 2014) to produce test statistics for all combinations of the selected climatic variables, four regularisation multipliers (0.25, 0.5, 1, 2), and all combinations of the product, linear, and quadratic features classes. We used the spatial block cross-validation method with default latitude and longitude settings, which is recommended for processing spatially auto-correlated data (Roberts et al. 2016) and temporally projecting models, such as when predicting future climate change effects (Wenger and Olden 2012). We excluded models with omission rates greater than 10% as this indicates that the model is over-fitted (Muscarella et al. 2014). Next, we selected the model with the lowest Akaike’s information criteria (AIC) (Akaike 1974). We also checked the area under the curve (AUC) to ensure that the selected models had values > 0.8 as this signifies that the model should produce good predictions (Araújo et al. 2005). AUC can produce misleading results so it should not be used in isolation (Lobo et al. 2007).

Table 2. Environmental variables included in the model selection process with justification for their inclusion.

Variable	Justification	Units
Max. temperature warmest month	The proportion of juveniles in European hare populations was positively correlated with July temperature (Smith et al. 2005).	°Celsius
Min. temperature coldest month	The proportion of breeding female European hares positively associated with January temperature (Smith et al. 2005).	°Celsius
Annual precipitation	Increased precipitation was negatively associated with European hare density (Smith et al. 2005)	mm year^{-1}
Altitude	European hares occupy lower altitudes than mountain hares in the Alps (Schai-Braun et al. 2023). European hares gain altitude more quickly than mountain hares in response to climate change (*Lepus timidus varronis*) (Schai-Braun et al. 2021).	Meter
Snow cover days	Causal link between mountain hare abundance and snow cover duration (Pedersen et al. 2017)	Days year^{-1}
Agriculture and grassland	Frequency of mountain hares decreases as frequency of grassland increases (Schai-Braun et al. 2023). European hare abundance increased with arable land (Smith et al. 2005).	% of cell
Forest	Mountain hares primarily inhabit mixed forests but, can also colonise other forested areas (reviewed in Angerbjörn & Flux 1995). Mountain hares prefer ligneous foliage over grasses (Schai-Braun et al. 2020).	% of cell

Bias file

Bias files, which account for biased sampling techniques, are commonly used to account for sampling bias when using presence-only data. We included all camera trap locations, including those that had not recorded hare observations in our bias file. To obtain an estimate of reporting effort for the citizen science data, we downloaded all validated terrestrial mammal sightings containing an image from the Norwegian Species Observation Service (accessed 24th August 2023). We sub-sampled the citizen science and camera trap observations using the date range used for determining mountain hare morph. We assumed that the presence of a citizen science terrestrial mammal sighting with a photograph gave a good proxy for the time that people spent in the field reporting, assuming that people that submitted a photograph of a different terrestrial mammal would have reported a hare if they had photographed one. See Suppl 3 for a list of included species. We combined the camera trap and citizen science datasets and randomly subset the observations so that there was a maximum of one citizen science observation and one camera trap observation per grid cell. Cells containing camera traps that did not record hare observations were also included in the bias file. Next, we created a raster where we gave cells containing no observations a value of 0.1, cells containing camera trap or citizen science observations a value of 1, and cells containing both citizen science and camera trap observations a value of 2 (as per Kramer-Schadt et al. 2013). We projected the bias file to the same 1 km^2 resolution used for the environmental and climate variables.

Modelling

We called Maxent version 3.4.3 within R (version 4.3.2, R Core Team 2022) using the dismo package (Cobos et al. 2019). We used the bias file to generate 10,000 background points which gave an estimate of the sampling bias. We used the ‘cloglog’ link function to run all models as it is the most appropriate method for estimating presence probabilities (Phillips et al. 2017). The models were run for 20 bootstrapped replications with each replication having a maximum of 2,000 iterations and using a training to test ratio of 80/20. We estimated permutation importance (Table 4 and Suppl 4) and performed jackknife analysis (Suppl 5) to estimate the impact each variable had on model performance. We fitted current distribution and current suitable habitat models for all study organisms then used the current suitable habitat models create medium and long-term predictions under SSP126, SSP370 and SSP585 climate change predictions. We estimated the area of suitable habitat in each map by calculating the proportion of cells where the habitat suitability had a training omission rate threshold greater than 10%. We interpreted the results as a binary output as our main aim was to determine the area of current and future suitable habitat.

Results

Data collection

After we had thinned our data to one observation per cell, we had a total of 754 camera trap and 166 citizen science hare observations (Table 3). For European hares, we had one pair of citizen science and camera trap observations in the same grid cell. We did not observe citizen science and camera trap observations in the same grid cell in our white mountain hare and heath hare datasets. White mountain hare observations were spread out over the majority of mainland Norway, heath hare observations were limited to the south of Norway, and European hare observations were made exclusively in the south-east close to the Swedish border (Figure 2).

Table 3. Number of cells containing either citizen science or camera trap observations after data cleaning. We thinned the dataset to one observation per study organism per cell before running the models. Only one cell containing European hare observations had both citizen science and camera trap observations.

	Mountain hare	Heath hare	European hare
Camera trap observations	579	144	31
Citizen science observations	99	13	54
Observations used in final analysis	678	157	84

Model settings and performance

The ΔAIC, AUC, and omission rate statistics indicated that the selected models for all study organisms performed well and should give accurate predictions (Suppl 6). The European hare model with the lowest AIC was excluded due to having an omission rate > 10%. The model with second lowest AIC had a ΔAIC value < 2, indicating that it performed equally as well as the discarded model (Muscarella et al. 2014).

The variables included in the best fitting models varied between study organisms (Table 4). For white mountain hares, habitat suitability increased with the proportion of forest cover (permutation importance = 44.4%, figure 3.a) and decreased with altitude (permutation importance = 32.2%, figure 3.b). There was a polynomial relationship with minimum temperature of the coldest month with the optimum value being around -10°C (permutation importance = 12.7%, Figure 3.c).

For heath hares, habitat suitability had a polynomial relationship with the number of snow cover days with the optimum value being around 150 days (premutation importance = 41.6%, Figure 3.d). Habitat suitability had a positive relationship with annual precipitation (premutation importance = 14.9%, Figure 3.e) and a polynomial relationship with minimum temperature of the coldest month with the optimum value being around -6°C (premutation importance = 36.7%, Figure 3.f).

Table 4. The relative importance of each explanatory variable to habitat suitability. See Suppl 4 for the importance of each variable to current distribution.

Variable	White mountain hare permutation importance (%)	Heath hare permutation importance (%)	European hare permutation importance (%)
Max temp warmest month	NA	4.3	NA
Min temp coldest month	12.7	36.7	25.9
Annual precipitation	NA	14.9	27.6
Altitude	32.2	2.6	7.9
Snow cover days	NA	41.6	38.0
Agriculture	10.7	NA	0.6
Forest	44.4	NA	NA

For European hares, habitat suitability had a polynomial relationship with the number of snow days with the optimum value being around 120 days (premutation importance = 38.0%, Figure 3.g) and increased with annual precipitation (premutation importance = 27.6%, Figure 3.h). It and a polynomial relationship with the temperature of the coldest month with the optimum value being around -5°C (premutation importance = 25.9%, Figure 3.i).

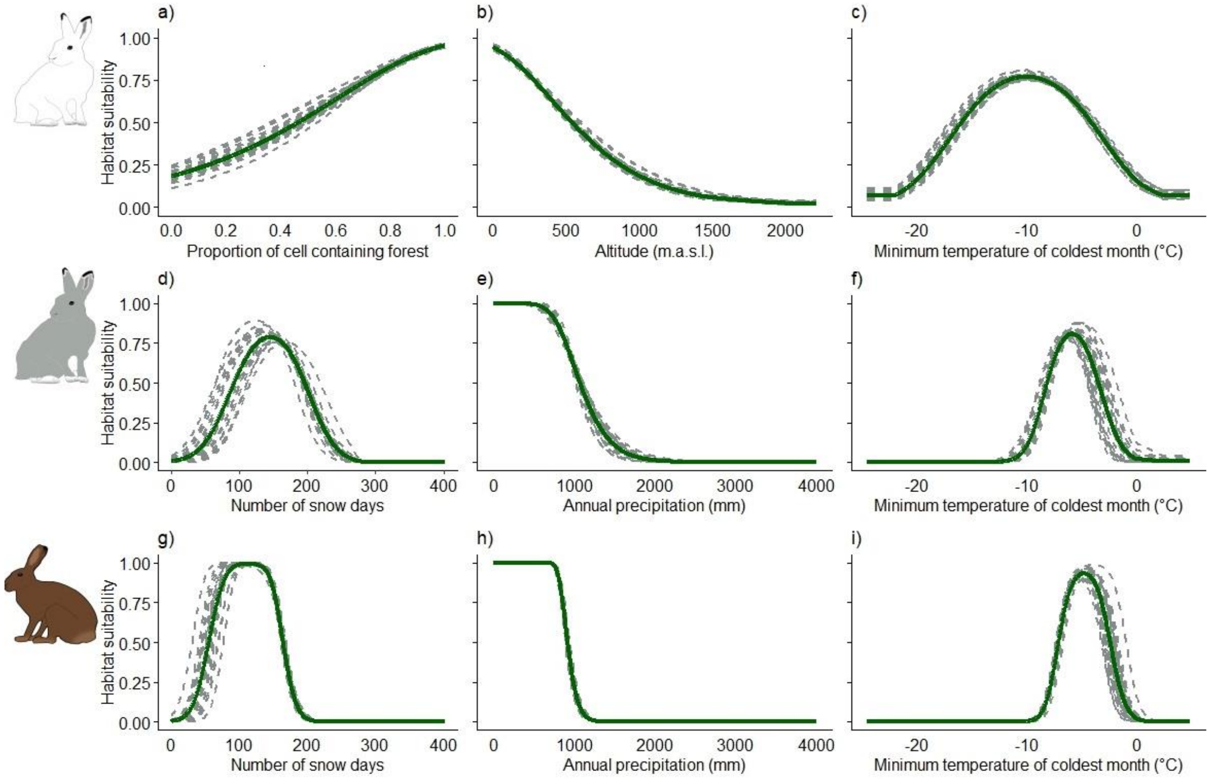

Figure 3. The marginal response curves of our study organisms' three most important explanatory variables. White mountain hare: (a) forest land use, (b) altitude, and (c) minimum temperature of the coldest month. Heath hare: (d) number of snow days, annual precipitation and (f) minimum temperature of the coldest month. European hare: (g) number of snow days, (h) annual precipitation, and (i) minimum temperature of the coldest month. The solid green lines are the average values across 20 replications. The dashed grey lines represent the individual runs.

Current distribution, current suitable habitat, and future suitable habitat

Our models predict that white mountain hare current distribution (Figure 4.a) and suitable habitat (Figure 4.d) is spread across Norway. White mountain hare suitable habitat contracts eastwards and northwards under SSP126 (Suppl 7.a and d), SSP370 (Figures 5.a and d), and SSP585 (Suppl 8.a and d) climate change predictions. The effect is greatest under SSP585 predictions indicating that white mountain hares will be negatively affected most by severe climate change (Table 5).

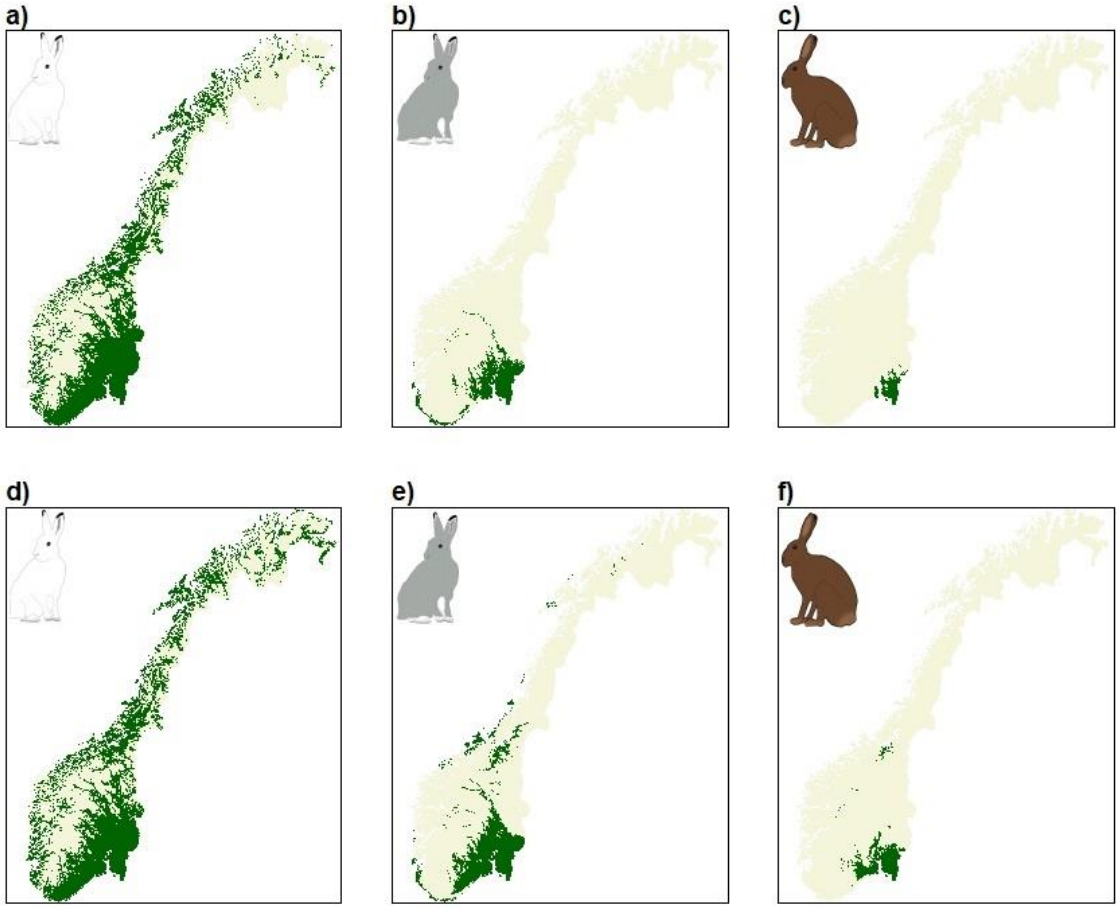

Figure 4. Estimated current distribution of (a) white mountain hare, (b) heath hare, and (c) European hare with green cells representing the current distribution. Estimated current suitable habitat of (d) white mountain hare, (e) heath hare, and (f) European hare with green cells representing suitable habitat. The map is projected at 1 km^2 resolution across Norway using a 10% omission rate threshold.

Heath hare current distribution is limited to the south of Norway (Figure 4.b). The current suitable habitat spreads further north with small patches of suitable habitat being present past 69° north (Figure 4.e). Their suitable habitat expands considerably under SSP126 (Suppl 7.b and e), SSP370 (Figures 5.b and e) and SSP585 (Suppl 8.b and e) climate change predictions with most of the areas around Norway’s eastern border containing suitable habitat. Heath hare suitable habitat area expands the most under SSP370 predictions indicating that moderate climate change is most beneficial for them (Table 5).

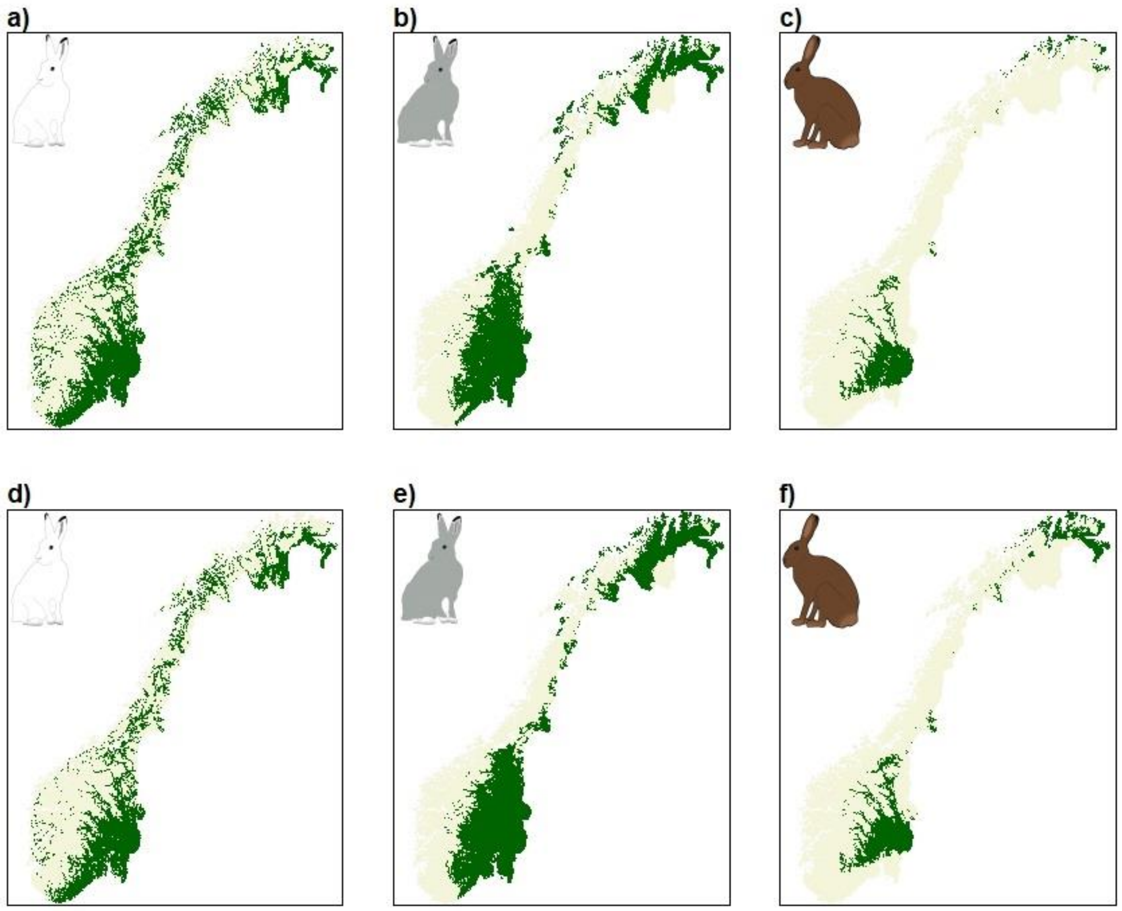

Figure 5. Medium term suitable habitat predictions under SSP370 climate change predictions for (a) white mountain hare, (b) heath hare, and (c) European hare. Long term suitable habitat predictions under moderate (SSP370) climate change predictions for (d) white mountain hare, (e) heath hare, and (f) European hare. The map is projected at 1 km^2 resolution across Norway using a 10% omission rate threshold. Green cells represent suitable habitat.

The current European hare distribution map indicates that they are currently isolated to Norway's south-east corner next to the Swedish border (Figure 4.c). The model predicts that there are small areas containing suitable habitat for European hares west of the Oslo-fjord. There is no observation data confirming their presence in these areas (Figure 2). The current habitat suitability model predicts that there is a small patch of suitable habitat in the middle of Norway near Trondheim (Figure 4.f). Under SSP126 (Suppl 7.c and f), SSP370 (Figures 5.c and f) and SSP585 (Suppl 8.c and f) climate predictions European hare suitable habitat expands further north resulting in suitable habitat area increasing (Table 5). Our model predicts that the area that they currently inhabit will become unsuitable.

Table 5. Variation in the proportion of Norway that covered by our study organisms' current distribution, current suitable habitat, and future suitable habitat under multiple climate change predictions. Each proportion was calculated using the 10% omission rate threshold.

	White mountain hare habitat (%)	Heath hare habitat (%)	European hare habitat (%)
Current distribution	33.7	6.6	1.3
Current suitable habitat	38.5	9.8	3.2
SSP126 medium-term	34.8	22.3	8.9
SSP126 long-term	34.8	22.3	7.5
SSP370 medium-term	30.3	29.7	10.1
SSP370 long-term	25.2	35.3	13.7
SSP585 medium-term	28.5	30.1	9.2
SSP585 long-term	17.2	30.1	15.1

Discussion

In this paper, we used camera trap and citizen science observations in conjunction with climatic and environmental variables to map the current distribution, current suitable habitat, and future suitable habitat of white mountain hares, heath hares, and European hares. We also analysed which variables affected our study organisms' current and future habitat suitability. Our current distribution predictions indicated that white mountain hares are spread across regions within Norway, heath hares are limited to the coastal regions of Norway's lower half, and European hares are limited to the lower south-east corner. Our future predictions indicate that white mountain hare suitable habitat will contract towards the east whereas heath hare and European hare suitable habitat will expand northwards resulting in the three organisms coming into increased contact.

Current distribution and suitable habitat

Although our maps indicate that white mountain hares are spread across a large proportion of Norway, we think that the models under-predict their current distribution (Figure 4.a) and suitable habitat (figure 4.d) along Norway's south-west coast, central mountainous region and in the far north. These discrepancies are likely to be a result of a lack of samples obtained in these areas (Figure 2). Expanding the citizen science observations to include validated sightings without image confirmation and including observations recorded when the hares are brown would mitigate this issue. However, it would increase the probability of observer error and prevent us from identifying subspecies. Mapping of hunting bag reports have confirmed that mountain hares are present in parts of Norway's far north and the southwest mountains, which our model has classified as unsuitable habitat (Pedersen and Pedersen 2012). White mountain hares may prefer forested environments, which were the most important factor determining habitat suitability (Figure 3.a and Table 4), as they provide refuge from predators and harsh weather conditions (Bisi et al. 2013). Scottish mountain hares have been observed using heather for this purpose (Thirgood and Hewson 1987, Hewson and Hinge 1990) and snowshoe hares spend more time in closed canopy forests than in open areas where there is an increased predation risk (Griffin and Mills 2009). We found a negative relationship between habitat suitability and altitude (Figure 3.b). This could result from decreased food and shelter availability as forest cover is absent from high altitude areas in Norway (Suppl 1.b). Additionally, as European hares are limited to Norway's southeast corner (Figure 4.c) there is likely to be limited interspecies competition pushing mountain hares to higher altitudes. The model did not include snow cover days even though other studies have found that it has a strong impact on mountain hare abundance (Pedersen et al. 2017). This likely results from white mountain hare observations being recorded in cells along Norway's south and west coast that experienced zero snow cover days (Suppl 9). Additionally, our models were based on presence only data that did not account for abundance.

The heath hare current distribution model indicates that they are spread along Norway's southwest coast and in the southeast (Figure 4.b), supporting the hypothesis that their blue coat is an adaptation to the milder and shorter winters found in these areas (Barth 1891, Bergengren 1969). The current suitable habitat model predicts suitable habitat along the coastline north of Trondheim (Figure 4.e), which is supported by reports from hunters (S Pedersen, personal conversations). Therefore, including latitude and longitude prevented our model overpredicting distribution but, also prevented it from predicting to areas lacking observation data. The large difference in the minimum temperature of the coldest month that heath hares (Figure 3.f) can tolerate compared to white mountain hares (Figure 3.c) may result from temperature's impact on the number of snow days. It is hypothesised that the heath hares' winter coat is less dense than the white mountain hares' coat but, we are not aware of this being tested.

The European hare current distribution model slightly over-estimated their range west of the Oslo fjord (Figure 4.c), which is not supported by observational data (Figure 2). This is likely due to the close geographic proximity and similar habitat either side of the fjord. Suitable habitat expands north and west of the Oslo fjord along with small patches between Oslo and Trondheim (Figure 4.f). This contradicts Acevedo et al (2012), who predicted suitable habitat along Norway's south coast. This may result from our dataset representing the northern tip of European hares' current distribution (Acevedo et al. 2012). Including data from southern parts of their distribution characterised by a temperate climate could result in our model predicting this area as suitable habitat. It is likely that European hares will colonise areas surrounding the Oslo fjord relatively quickly as European hares introduced into Ireland had a radial range expansion rate of 0.73 km year^{-1}, resulting in their distribution expanding threefold from 2005 to 2012-13 (Caravaggi et al. 2014). The polynomial correlation between snow cover days and European hare habitat suitability (Figure 3.g) likely arises from all cells containing observations experiencing between 121 and 164 snow days (Suppl 9). At present, European hares have not had time to colonise areas of Norway that do not experience snow days. Other studies found that European hare population density was highest between 40 and 60 snow cover days (Pikula et al. 2004, Kudryavtseva and Smirnov 2012), suggesting that a lower number of snow days is optimal. The negative correlation with annual precipitation (Figure 3.h) is consistent with other studies that found that European hare population density is negatively associated with annual precipitation, which may result from high precipitation negatively affecting leverets (Hackländer et al. 2002). European hares' polynomial response to minimum temperature of the coldest month (Figure 3.i) is likely to result from minimum temperature in cells containing observations ranging between -7.6°C and -4.4°C (Suppl 9). Increased average winter temperature positively affected European hare survival with the highest survival rate occurring at over 4°C (Marboutin and Hansen 1998), indicating that including samples from more temperate parts of their distribution would result in higher optimal temperature. These variables can interact with low winter temperature and high spring precipitation leading to increased leveret mortality rate and increased disease spread (Hackländer et al. 2002, Rödel and Dekker 2012).

Suitable habitat under climate change scenarios

As we predicted, the suitable habitat area of white mountain hares decreased under all SSP climate change scenarios with greater reductions occurring under the more severe scenarios (Table 5). Similar predictions have been described in other countries including Ireland, Sweden, and Finland (Hof et al. 2012, Caravaggi et al. 2017) with their Europe wide distribution predicted to decrease to between 30 and 72% of its range by 2080 (Acevedo et al. 2012). Given our assumption that altitude and land usage remained constant, the change in future habitat suitability results from minimum temperature of the coldest month increasing. This variable increases under all climate change scenarios with the largest increases occurring under the more extreme predictions (Suppl 10). Depending on the severity of climate change and location within Norway, the snow season is predicted to be between one and seven months shorter by 2100 compared to current snow patterns, with the largest reductions appearing in coastal regions (Hanssen-Bauer et al. 2017). This is likely to affect white mountain hares as it will increase coat colour mismatch, which negatively impacts mountain hares (Zimova et al. 2020). Additionally, reduced snow depth negatively affects mountain hares' ability to reach shrub level foliage during winter (Pehrson 1983). This suggests that white mountain hares could be particularly vulnerable to state changes, which occur when climate change pushes temperatures above 0°C leading to precipitation falling as rain rather than snow (Trenberth 1998, Ombadi et al. 2023).

The future suitable habitat of both heath hares and European hares is expected to expand under all climate change scenarios with heath hares range expansion being largest under SSP370 predictions and European hare range expansion being greatest under SSP585 predictions (Table 5). There are large geographical distances between heath hare and European hare southern and northern suitable habitats making it unlikely that they could colonise these areas without human interference (Figure 5, Suppl 7 and 8). Currently, European hares occupy Norway's southeast corner. Our model predicts that this area will be unsuitable under the climate change predictions (Figure 5, Suppl 7 and 8). We think that this is caused by sampling the northern tip of European hares' distribution (Acevedo et al. 2012) and that including observations from temperate regions within their distribution would alleviate this issue. A similar issue may prevent the heath hare model predicting suitable habitat along Norway's south-west coast (Figure, Suppl 7 and 8). As Norway represents the most westerly part of heath hares' range it is not possible to control for this by including more data.

Species interactions

Our future predictions indicate that there will be significant overlap in the ranges of our study organisms under all climate change scenarios (Figure 5, Suppl 7 and 8). Areas of sympatry tend to be transitory after European hare introduction (reviewed in Thulin 2003) with most studies indicating that European hares outcompete mountain hares (Jansson and Pehrson 2007, Reid 2011, Caravaggi et al. 2014, Schai-Braun et al. 2023). Mountain hares living in sympatry with European hares maintain forms in denser forest further away from open fields than their allopatric conspecifics (Thulin 2003 and references within) and have a less varied diet (Wolfe et al. 1996, Dingerkus and Montgomery 2001), indicating that mountain hares are outcompeted for resources. Acevedo et al. (2012) argued that mountain hares can outcompete European hares when they have similar population densities but, are outcompeted when European hare population density is higher. The combination of climate change and competition with European hares often results in mountain hare distribution moving to higher altitudes after a period of sympatry (Thulin 2003, Reid 2011, La Morgia et al. 2023).

Conclusion

Our results indicated that forests were critical to white mountain hare distribution. Additionally, dense forest cover provides refuge for mountain hares, helping them to avoid predators and direct competition with European hares. Therefore, conservation efforts could focus on maintaining forest cover. At present, our European hare and heath hare models suffer from issues relating to our observations being obtained in the northern part of their distributions. Including observations obtained in south Sweden could help to alleviate these issues. Although European hare distribution is reducing in parts of their native range it is debatable whether they should be allowed to expand into Norway. Both mountain hares and European hares are hunted within Norway with identical regulations for both species (Lovdata 2009, 2021, 2022). As European hares are a non-native species, implementing a more liberal hunting season could be used as a measure of population control, potentially decreasing competition with mountain hares. Our future predictions indicate that our study organisms will come into increased contact, leading to increased interactions. Future studies could focus on the resulting interspecies interactions.

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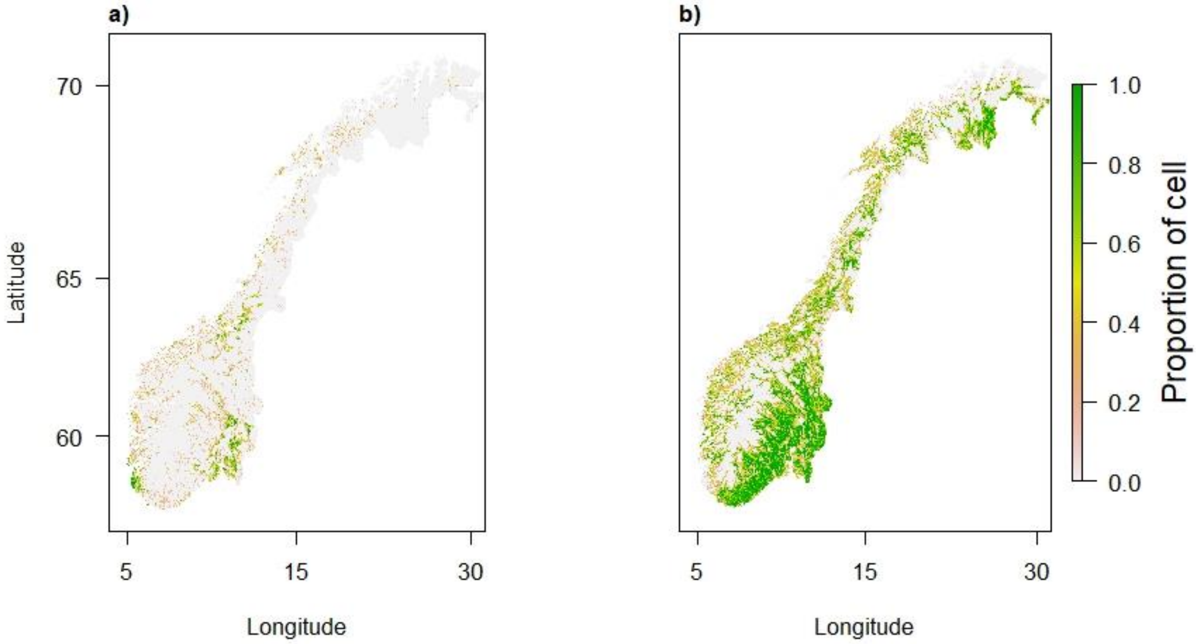
Supplemental information



Suppl 1. Proportion of each cell containing (a) agriculture and (b) forest land types.

Suppl 2. All land use categories included in the agriculture and forest land use rasters.

Agriculture	Forest
Non-irrigated arable land	Broad-leaved forest
Pastures	Coniferous forest
Complex cultivation patterns	Mixed forest
Land principally occupied by agriculture, with significant areas of natural vegetation	Sclerophyllous vegetation
Natural grasslands	Transitional woodland-shrub

Suppl 3. Scientific and common names of the species included in the bias file. Where the full species name was not provided, the genus name is given.

Scientific name	Common name
Alces alces	Eurasian elk
Alces alces alces	European elk
Apodemus	Mouse or rat
Apodemus flavicollis	Yellow-necked field mouse
Apodemus sylvaticus	European woodmouse
Arvicola amphibius	Eurasian water vole
Barbastella barbastellus	Western barbastelle
Canis aureus	Golden jackal
Capreolus capreolus	Western roe deer
Castor fiber	Eurasian beaver
Cervus elaphus	Red deer
Chiroptera	Bats
Crocidura russula	White-toothed shrew
Dama dama	Fallow deer
Eptesicus nilssonii	Northern bat
Erignathus barbatus	Bearded seal
Erinaceus europaeus	Western European hedgehog
Lemmus lemmus	Norway lemming
Lepus europaeus	European hare
Lepus timidus	Mountain hare
Lutra lutra	Eurasian river otter
Martes martes	European pine marten
Meles meles	Eurasian badger
Micromys minutus	European harvest mouse
Microtus	Meadow voles
Microtus agrestis	Short-tailed field vole
Microtus levis	East European vole

Microtus oeconomus	Root vole
Mus musculus	House mouse
Mustela erminea	Ermine
Mustela nivalis	Least weasel
Mustela putorius	European polecat
Myodes glareolus	Bank vole
Myodes rufocanus	Gray red-backed vole
Myodes rutilus	Northern red-backed vole
Myopus schisticolor	Wood lemming
Myotis brandtii	Brandt's bat
Myotis daubentonii	Daubenton's bat
Myotis mystacinus	Whiskered bat
Neomys fodiens	Eurasian water shrew
Neovison vison	American mink
Nyctalus noctula	Noctule
Nyctereutes procyonoides	Raccoon dog
Odobenus rosmarus	Walrus
Ondatra zibethicus	Muskrat
Oryctolagus cuniculus	Rabbit
Ovibos moschatus	Muskox
Pipistrellus nathusii	Nathusius's pipistrelle
Pipistrellus pygmaeus	Soprano pipistrelle
Plecotus auritus	Brown big-eared bat
Rangifer tarandus	Reindeer
Rangifer tarandus platyrhynchus	Svalbard reindeer
Rangifer tarandus tarandus	Mountain reindeer
Rattus norvegicus	Norway rat
Sciurus vulgaris	Eurasian red squirrel
Sicista betulina	Northern birch mouse
Sorex araneus	European shrew
Sorex isodon	Even-toothed shrew

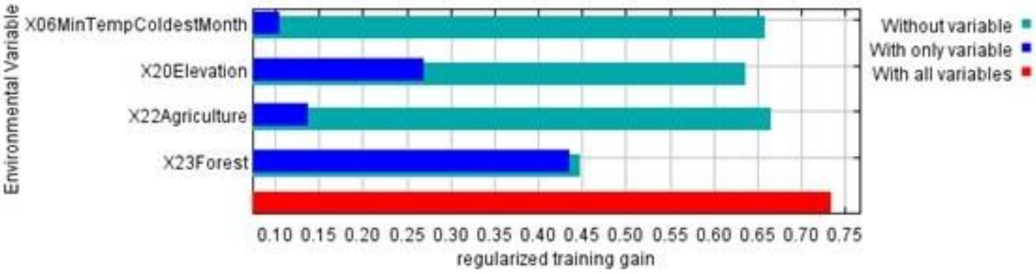
Sorex minutus	Eurasian pygmy shrew
Sus scrofa	Pig
Vespertilio murinus	Particolored bat
Vulpes vulpes	Red fox

Suppl 4. The relative importance of each explanatory variable, including latitude and longitude, to current distribution.

Variable	White mountain hare permutation importance (%)	Heath hare permutation importance (%)	European hare Permutation importance (%)
Max temp warmest month	NA	1.7	NA
Min temp coldest month	15.3	18.2	10.8
Annual precipitation	NA	7.6	8.8
Altitude	37.5	24.5	0.0
Snow cover days	NA	4.3	0.2
Agriculture	3.9	NA	0.4
Forest	17.4	NA	NA
Latitude	10.4	1.7	59.1
Longitude	15.5	4.6	20.6

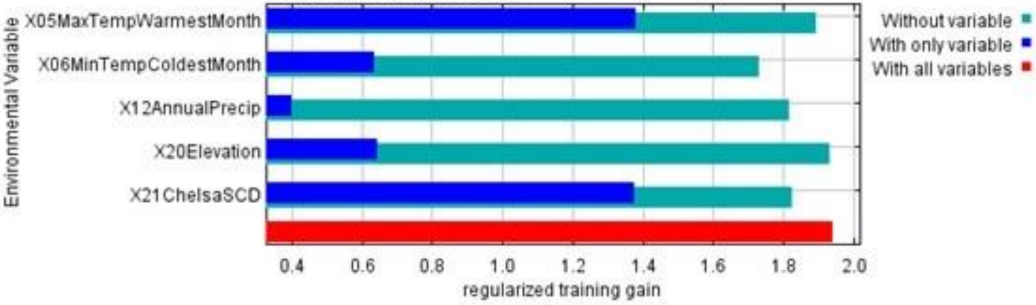
a)

Jackknife of regularised training gain for white mountain hare (*Lepus timidus timidus*)



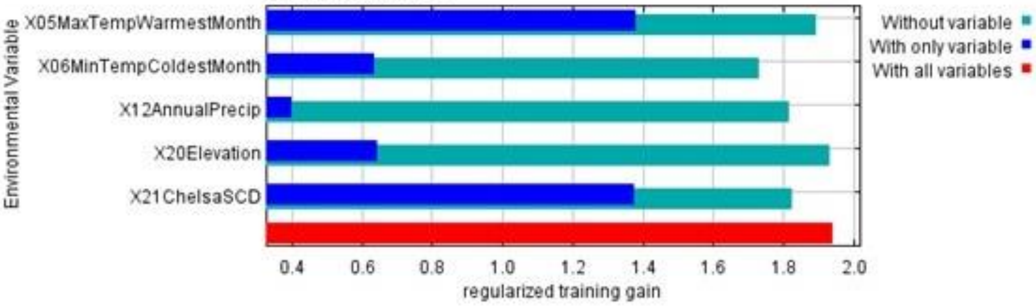
b)

Jackknife of regularised training gain for heath hare (*Lepus timidus sylvaticus*)



c)

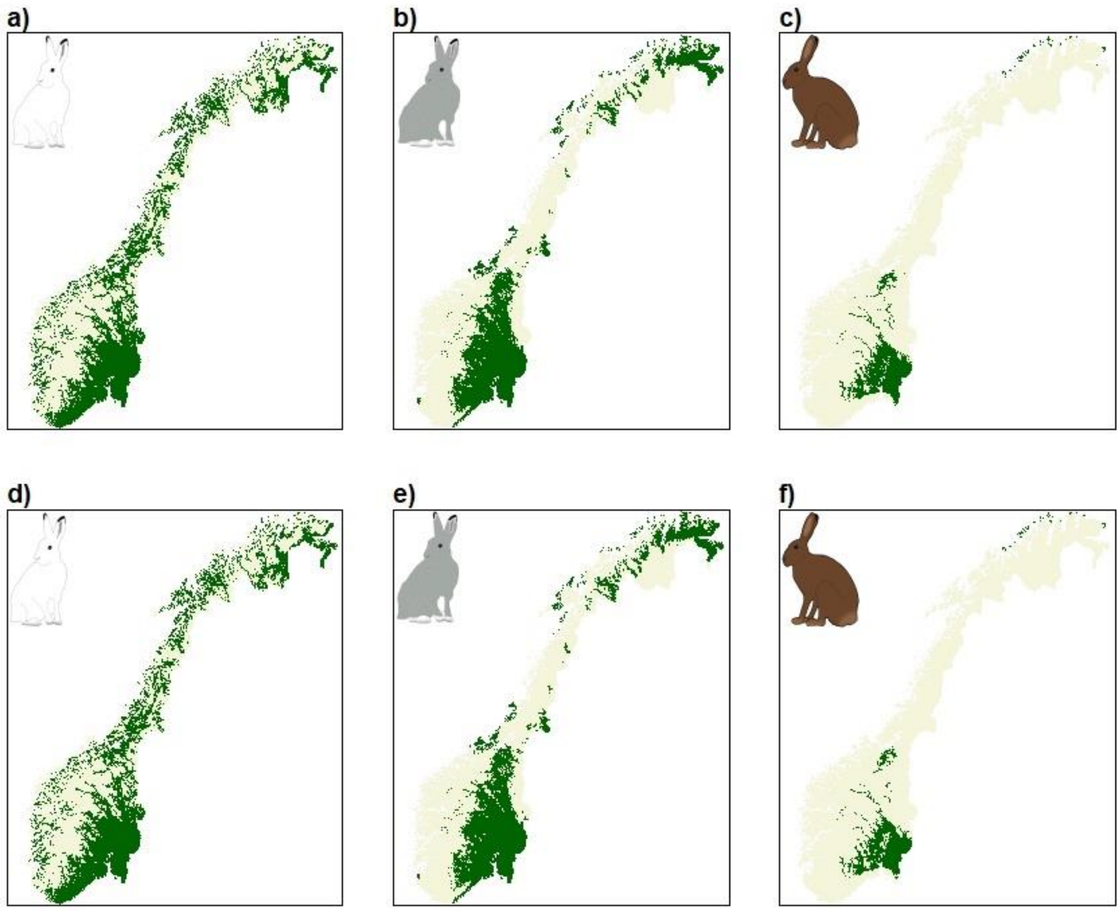
Jackknife of regularised training gain for European hare (*Lepus europaeus*)



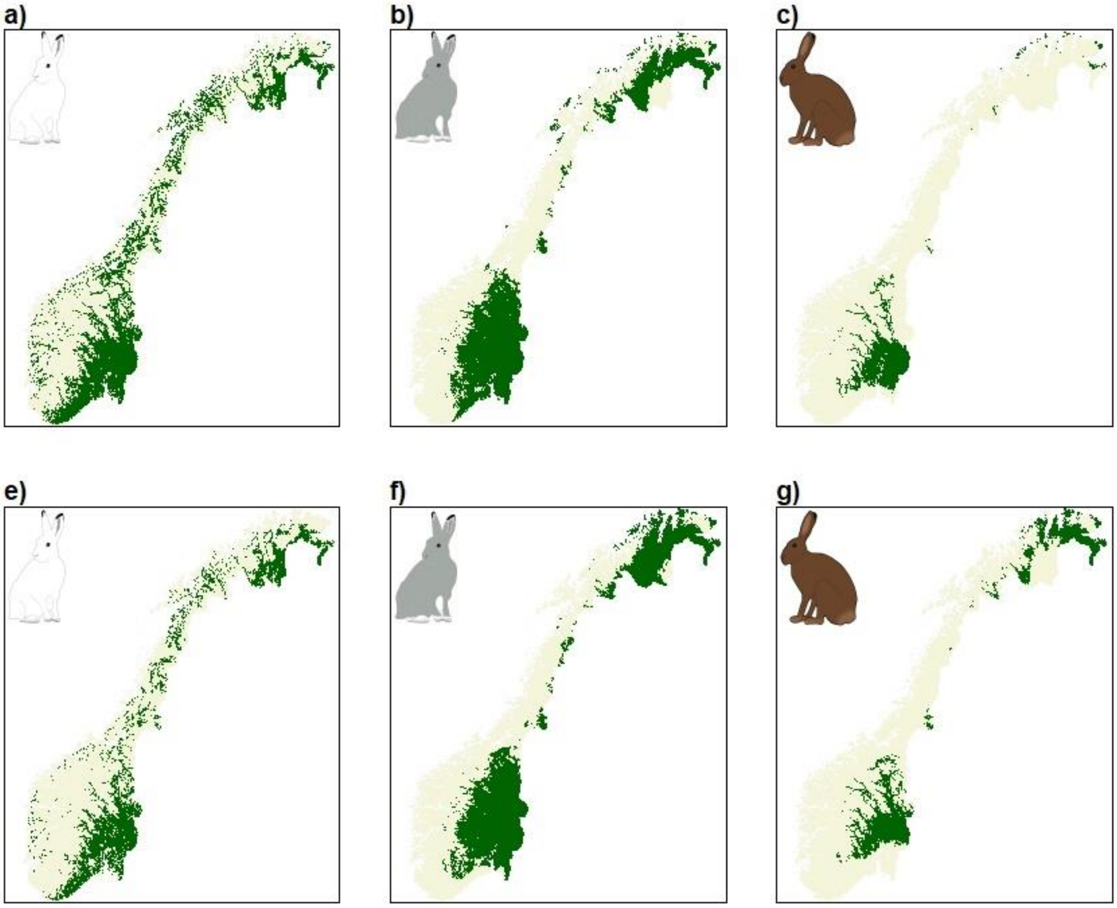
Suppl 5. Jackknife analysis illustrating the relative and combined importance of variables included in the suitable habitat models for (a) white mountain hares, (b) heath hares and (c) European hares.

Suppl 6. Test statistics for each study organisms' model of best fit. All statistics were generated by the ENMevaluate function within the ENMeval package (Muscarella et al. 2014).

	White mountain hare	Heath hare	European hare
AIC	15,949	3,274	1,522
AUC	0.852	0.959	0.990
Omission rate (10%)	0.099	0.096	0.059
Regularisation multiplier	2	0.25	0.25
Feature classes	Linear, quadratic, and product	Linear, quadratic, and product	Linear, quadratic, and product



Suppl 7. Medium-term suitable habitat predictions under SSP126 climate change predictions for (a) white mountain hare, (b) heath hare, and (c) European hare. Long-term suitable habitat predictions under SSP126 climate change predictions for (d) white mountain hare, (e) heath hare, and (f) European hare. The map is projected at 1 km^2 resolution across Norway using a 10% omission rate threshold.



Suppl 8. Medium-term suitable habitat predictions under SSP585 climate change predictions for (a) white mountain hare, (b) heath hare, and (c) European hare. Long-term suitable habitat predictions under SSP585 climate change predictions for (d) white mountain hare, (e) heath hare, and (f) European hare. The map is projected at 1 km^2 resolution across Norway using a 10% omission rate threshold.

Suppl 9. The mean and range of all variables included in model selection within cells that contain observations of our study organisms.

	White mountain hare	Heath hare	European hare
Maximum temperature of warmest month (°C)	19.1 (9.7 – 21.9)	20.2 (14.5 – 21.3)	20.5 (19.8 – 21.6)
Minimum temperature of coldest month (°C)	-8.0 (-16.0 – -1.1)	-6.6 (-12.1 – 0.4)	-6.0 (-7.6 – -4.4)
Annual precipitation (mm)	925 (407 – 2,434)	861 (619 – 1,930)	816 (749 – 902)
Snow cover days	184 (0 – 348)	152 (0 – 263)	148 (121 – 164)
Agriculture (%)	12.6 (0 – 100)	18.1 (0 – 95)	40.5 (0 – 99)
Forest (%)	70.8 (0 – 100)	70.7 (0 – 100)	45.0 (0 – 99)

Suppl 10. Mean and range of all environmental variables included in models under historical records and future predictions. The values were extracted from the raster files used to create our models.

		SSP126		SSP370		SSP585	
	Current	Medium term	Long term	Medium term	Long term	Medium term	Long term
Maximum temperature of warmest month (°C)	15.9 (1.8 – 22.5)	18.6 (5.2 – 25.3)	18.8 (5.6 – 25.7)	19.9 (6.5 – 26.7)	21.3 (7.8 – 27.7)	20.5 (7.4 – 27.4)	22.7 (8.8 – 28.7)
Minimum temperature of coldest month (°C)	-9.7 (-22.2 – 2.4)	-6.7 (-17.4 – 4.3)	-6.7 (-17.7 – 4.4)	-5.3 (-15.9 – 5.2)	-4.0 (-14.7 – 6.2)	-4.8 (-15.2 – 5.5)	-2.4 (-12.8 – 7.3)
Annual precipitation (mm)	1,104 (317 – 3,708)	1,215 (358 – 4,120)	1,213 (359 – 4,092)	1,240 (368 – 4,185)	1,299 (385 – 4,458)	1,268 (370 – 4,318)	1,355 (400 – 4,695)
Snow cover days	234 (0 – 365)	191 (0 – 365)	193 (0 – 365)	172 (0 – 365)	146 (0 – 365)	182 (0 – 365)	136 (0 – 365)

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Many species have evolved adaptations that enable them to survive in seasonally changing environments. Moulting from brown in the summer to white in winter is an adaptation to seasonally changing snow cover that is expressed by mountain hares *(Lepus timidus)*. It has a critical impact on survival probability as animals that are mismatched against their background are at increased risk of being predated. Climate change induced variation in snow fall and snow melt can result in hares moulting at the wrong time of year.

My results indicated that mountain hares that lived at high altitudes and latitudes kept their winter white coats for longer than their low altitude and latitude conspecifics. Additionally, hares living in areas with coastal climates kept their winter white coats for longer than those in areas with continental climates. Between two 30-year periods (1959 – 1988 and 1989 – 2018), climate change led to a reduction of between 4 and 57 snow days at the camera trap locations. Mountain hares inhabiting areas that experienced the largest reductions in the number of snow days experienced the greatest numbers of days of coat colour mismatch. The number of days mismatch was greater than the reduction in the number of snow days, indicating that mountain hares are adapted to environmental conditions that existed before snow records began in 1957.

White mountain hare *(Lepus timidus timidus)* suitable habitat was predicted to contract across Norway by 2100 under a range of climate change predictions. Conversely, heath hare *(Lepus timidus sylvaticus)* and European hare *(Lepus europaeus)* suitable habitat will expand along Norway’s east border.