Research

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Lack of phenological shift leads to increased camouflage mismatch in mountain hares

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Understanding whether organisms will be able to adapt to human-induced stressors currently endangering their existence is an urgent priority. Globally, multiple species moult from a dark summer to white winter coat to maintain camouflage against snowy landscapes. Decreasing snow cover duration owing to climate change is increasing mismatch in seasonal camouflage. To directly test for adaptive responses to recent changes in snow cover, we repeated historical (1950s) field studies of moult phenology in mountain hares (*Lepus timidus*) in Scotland. We found little evidence that population moult phenology has shifted to align seasonal coat colour with shorter snow seasons, or that phenotypic plasticity prevented increases in camouflage mismatch. The lack of responses resulted in 35 additional days of mismatch between 1950 and 2016. We emphasize the potential role of weak directional selection pressure and low genetic variability in shaping the scope for adaptive responses to anthropogenic stressors.

1. Introduction

Recent climate change has already subjected wild populations to large changes in environmental conditions [1]. Failure of populations to sufficiently track these changes will result in local declines and extinctions [2,3]. Some populations have responded adaptively via phenotypic plasticity and/or evolution [4–7]. However, others have failed to track climate change or seem to have responded in non-adaptive ways [8–10]. Predicting population responses to climate change remains challenging, in part because many interacting factors determine future trajectories of inherently complex natural systems [11]. Yet, understanding whether and how populations will respond to climate change is one of the most urgent challenges facing biologists [12].

In response to climate change, snow cover duration is decreasing in many parts of the Northern Hemisphere [13,14], and consequently imposing changing and potentially novel selection pressures on organisms adapted to seasonally changing environments [15]. A diverse group of birds and mammals moult from summer dark to winter white coat annually to increase crypsis against snow [16,17]. While weather, especially temperature, can fine tune the phenology of those moults each year, changing daylength is the principal driver of the moults across taxa [16,18]. As snow duration declines owing to climate change, colour moulting species become increasingly mismatched with their background [19]. Field studies indicate that mismatch in seasonal coat colour and snow presence or absence has negative individual and population consequences via increased predator-induced mortality [20–25]. For example, snowshoe hares (*Lepus americanus*) experience 7–14% decreased

Table 1. Historical and present study sites in northeast and central Scotland, average elevation at the sites in metres above sea level, years when surveys were carried out, latitude and longitude.

region	site	elev.	survey years	lat.	long.
historic surveys					
Angus Glens	Glen Esk high	610	1957–1961	56.957	−2.839
Angus Glens	Glen Esk low	270	1957–1961	56.943	−2.835
Deeside/Strathdon	Corndavon	450	1951, 1955, 1957–1959	57.068	−3.234
Deeside/Strathdon	Glen Muick	380	1958–1959	57.022	−3.046
Deeside/Strathdon	Punchbowl	310	1957–1959	56.860	−2.730
Deeside/Strathdon	Roar Hill	450	1958–1959	57.129	−2.999
current surveys					
Highland	Findhorn high	640	2016	57.235	−4.136
Highland	Findhorn low	430	2016	57.206	−4.102
Deeside/Strathdon	Lecht	730	2015–2016	57.193	−3.240

weekly survival when mismatched against their background [23,24]. Given this strong selection against mismatch, persistence of colour moulting species will require adaptation to future changes in global snow cover [26,27].

Climate-mediated phenotypic plasticity, described in several colour moulting species, can, theoretically, buffer against camouflage mismatch [16,19]. However, previous studies that investigated plasticity in response to climate change showed that current levels of plasticity are insufficient to prevent mismatch; snowshoe hares and least weasels (*Mustela nivalis*) became mismatched during years with fewer days of snow cover [18,19,22,28]. This suggests that adaptive evolution of moult phenology and/or moult plasticity—evolutionary rescue [27,29]—may be crucial for the persistence of colour moulting species. Whether evolutionary shifts in moult phenology (e.g. shifts in the photoperiodic response) or plasticity (e.g. shifts in the sensitivity to temperature) can occur is unknown. However, existing intrapopulation variation in moult phenology and strong selection favouring cryptic coloration suggest evolutionary rescue is possible [23,30].

Historical phenological studies provide some of the only opportunities to test whether organisms have already responded to climate change. Unfortunately, such datasets are extremely rare for moult phenology. Fortunately, Watson [31] and Flux [32] described seasonal moult of wild mountain hares (*Lepus timidus scoticus*) in the northeast and central highlands of Scotland over spring and autumn seasons during the 1950s and 1960s. To our knowledge, this effort represents the longest-running systematic historical survey of moult phenology in any species. These studies documented intrapopulation variation in hares' moult phenology each year and population-level phenotypic plasticity in response to ambient temperature, especially in the spring [31,32]. The adaptive capacity of mountain hares to mitigate camouflage mismatch via phenotypic plasticity is unknown, however. Similarly, the selective costs of camouflage mismatch in the highly managed Scottish Highlands have not been investigated; but based on insights gained from the study of other populations [33] and other colour moulting species [22,23], extant Scottish mountain hares may have avoided increases in camouflage mismatch via adaptive shifts in response to widespread reductions in snow cover [34].

In this study, we assessed the potential of a wild population of a common, seasonally colour moulting species to adaptively track climate change. We took advantage of the detailed historical surveys of mountain hare moult phenology in the Scottish Highlands to examine population responses to decreasing snow cover over the past 65 years. First, we quantified current population mean moult phenologies and tested whether they have shifted since the 1950s. We hypothesized that mountain hares should have shifted moult phenologies in ways that reduce camouflage mismatch by moulting to white winter fur later in the autumn and to brown summer fur earlier in the spring. Second, we quantified population-level phenotypic plasticity to examine whether it contributes to any potential shifts in mean phenology. Third, we quantified historical and present-day frequency of mismatch as measures of species vulnerability to future environmental change. We end with general conclusions on some key considerations when predicting adaptive responses of wild populations to climate change.

2. Methods

(a) Study areas
Historical surveys were carried out at six sites in the northeast and central highlands of Scotland, UK, from 1951 to the end of 1961 [31,32]. We were unable to resurvey the same sites owing to changes in land management, access restrictions to private land and loss of mountain hares from some historic sites [35]. We, therefore, surveyed different sites with comparable topography, land management practices and vegetation type. The current sites were located in the upland areas of the northeast and central highlands of Scotland and spanned a similar elevational range as the historical sites (table 1; electronic supplementary material, table S1). All historic and current sites were dominated by dwarf heath and subalpine plant communities, common vegetation type of the Scottish uplands and represent the habitat type preferred by mountain hares in the geographical area [36].

(b) Field surveys
We followed the original historical field survey methods [31,32]; one surveyor walked along a predetermined route (*ca* 3–6 km

long). Hares were detected as they were either flushed (moved) in response to the surveyor or in reaction to other hares, or less frequently, as the surveyor thoroughly scanned the surroundings with binoculars. Hares are largely inactive during the day and the majority of hares were detected as they flushed. Our experience and that reported in the literature is that hares tend not to flush until an observer is very close to them, or unless disturbed by other fleeing hares; therefore, the large majority of detections were within less than 50 m of the observer [37]. For all hares detected within 200 m of the observer which provided a clear view that allowed coat colour to be assessed, we recorded coat colour (described below). Surveys were repeated twice a month (October–January and March–June) for a total of 5–11 surveys per season in 2016 at the two Findhorn sites and 2015 and 2016 at the Lecht site, giving eight year–season–site combinations (electronic supplementary material, table S1). Surveys were always undertaken in clear and dry conditions so as to reduce the possible effects of weather on detecting hares. The risk of repeat observations of the same individuals within a survey was minimized by visually monitoring flushed individuals as far as possible. Each survey was completed within a single 4–5 h session.

(c) Moult phenology

We recorded, and where possible photographed, the coat colour for each observed hare using the moult score protocol developed by Watson [31]. Each hare was ranked in one of five colour categories; DD (completely dark), D (mostly dark), LD (half-dark and half-white), L (mostly white) or LL (completely white) by the surveyor. Observations accompanied by photographs (greater than 80%) were later verified by a single observer (electronic supplementary material, figure S1). Historical surveys at one site used a slightly different method [32] to determine the five colour categories (=colour was scored independently for seven body parts and averaged), but interchangeability of the two scoring methods was confirmed by the site's observer (J. Flux 2015, personal communication) and by agreement with records from similar dates and sites [31]. Finally, to reduce potential bias between observers and to simplify parameter estimation, we reduced the initial five categories into three: white (LL, L), moulting (LD) and brown (D, DD) for all analyses (electronic supplementary material, figure S1).

(d) Statistical analyses

We used R (v. 3.5.2; R Core Team 2016) for all statistical analyses.

(i) Climate variables and analysis

To characterize climate in the study region, we calculated temperature and snow cover variables over the past 65 years. The mean seasonal temperature, tavg was calculated for each year from 1950 to 2016 using gridded 5×5 km resolution monthly average temperature (Met Office UKCP09) [38] at each study site. The seasons were defined as spring (1 March–31 May) and autumn (1 September–30 November) and encompassed the main periods when hares underwent moults. Days with snow cover (snow days) were summed for each season of each year; for 1960–2011, snow days were those days when snow cover was present at a site (snow water equivalent greater than 0 mm) based on daily gridded 5×5 km resolution data [39]. Because this dataset became unavailable after 2011, for 2012–2016, snow days were defined by days when snow cover was present at a site (grid cells were greater than 50% snow covered) based on daily 1.5×1.5 km resolution data [40]. We combined the two snow datasets to span the entire period of interest and verified the compatibility of the two datasets by comparing period of overlap (2000–2011; electronic supplementary material,

figure S2). Next, we calculated for each year and site 25th percentile of snow days in the autumn and 75th percentile of snow days in the spring, as indices for early autumn and late spring snow days, respectively. Lastly, we calculated the number of transitions as the number of changes between snow cover presence and absence at each site by summing the number of times snow days were followed by days without snow and vice versa each year and season. The resulting number of transitions is a measure of environmental stochasticity with snow cover repeatedly falling and melting multiple times during each season. All snow variables were calculated for the main snowfall periods in Scotland; spring snowfall (1 March–31 May), autumn snowfall (1 October–31 December) and autumn-to-spring snowfall period (snow season, 1 October–31 May).

Although high-resolution snow data do not exist for Great Britain prior to 1960, we assumed that the 1950s data were comparable to the 1960s and used the 1960s data as a proxy to calculate historical mismatch. We validated this assumption by comparing number of snow days during 1951–1960 and 1961–1970 which were collected during the Snow Survey of Great Britain [41]. Only records from stations lying within 40 km of any of our study sites and that recorded daily snow cover for at least 6 years during both decades ($n = 7$) were included in the comparison. We found no difference between the number of snow days during the entire snow season (here referring to the period 1 October–31 May) between the two decades using a Wilcoxon rank-sum test with continuity correction ($p = 0.45$, $W = 1684$).

Changes in mean temperature, number of snow days, number of snow transitions and timing of early autumn and late spring snow were quantified using mixed effects models. The mean seasonal temperature, number of snow days, number of transitions and the 25th or 75th percentile snow dates were used as response variables, year as a fixed effect and site as a random effect using the *lmer* function from the *lme4* [42] package in R [43].

(ii) Moult phenology

We developed a hierarchical multinomial logistic regression analysis within a Bayesian framework to describe moult phenology and its phenotypic plasticity [18]. For all models, we estimated the probability of a hare colour y being in colour category i at site j on a Julian day d as

$$\Pr(y = i) = \frac{e^{\alpha_i + \beta 1_i * d + s_{i,j}}}{1 + \sum_{k=1}^{i-1} e^{\alpha_i + \beta 1_i * d + s_{i,j}}}.$$

Coat colour was treated as a categorical variable, such that a hare on day d was either brown (p_{brown}), white (p_{white}) or moulting (p_{moult}) and $\Sigma(p_{1:3, j,d}) = 1$. Site was coded as a random covariate $s_{i,j}$ to reflect the hierarchical structure of the dataset and admit repeat measures. α_i was the intercept and $\beta 1_i$ was the effect of Julian day on the probability of being either brown, white or moulting. Autumn and spring moults were modelled separately. Hereafter, we refer to this model without additional covariates as the basic model.

To compare moult phenology between the time periods, we combined colour observations from all years and sites in one dataset and added a fixed effect of time period $\beta 2_i$ (1950s or 2010s) on the probability of being in a certain colour category to the basic model. We used the estimated probabilities to derive approximate dates when hares initiated and completed the moults as 'initiation' and 'completion' dates during each time period. Autumn initiation was specified as the first Julian day when the mean $p_{brown} < 0.9$ and completion date when the mean $p_{white} > 0.9$; the opposite condition was used to estimate the spring dates (i.e. initiation$_d$ $p_{white} < 0.9$ and completion$_d$ $p_{brown} > 0.9$).

Next, we investigated the role of phenotypic plasticity in moult phenology in response to ambient temperature.
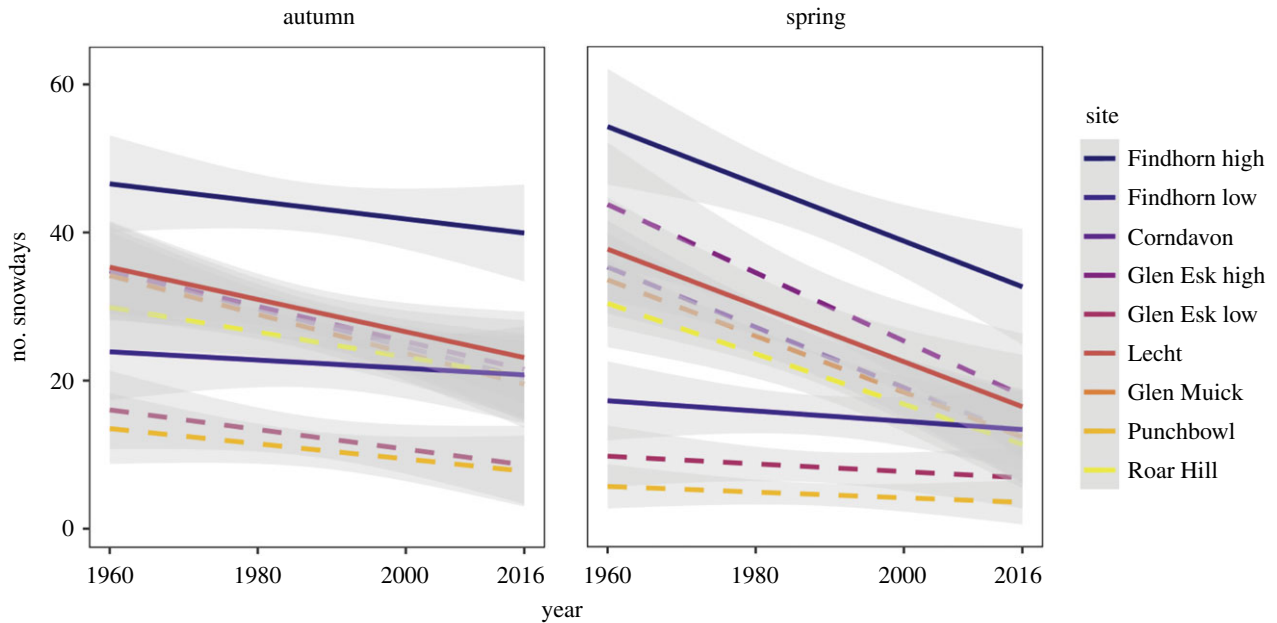
Figure 1. Number of snow days during the autumn- and spring snowfall season at the study sites between 1960 and 2016. Coloured lines show linear regression slopes for each site with 95% confidence intervals depicted in grey. Solid (dashed) lines indicate sites used in current (historical) surveys. (Online version in colour.)

Because ambient temperature is thought to moderate mountain hare moult phenology [31,32], and thereby improve a model's ability to detect differences between time periods, we constructed an additional set of models with temperature as an additional covariate ($tavg_{j,e}$). $tavg_{j,e}$ was the average seasonal temperature at site j during year e and was added as a fixed effect $\beta 3_i$ to the basic model containing time period $\beta 2_i$ described above. We standardized tavg to have a mean of 0 and s.d. of 1. Additionally, to explicitly test the effect of tavg, we constructed a univariate model with a single fixed effect $\beta 3_i$ ($tavg_{j,e}$). The resulting $\beta 3_i$ coefficients were the slopes of reaction norms of the probabilities of being brown ($\beta 3_{brown}$) or white ($\beta 3_{white}$) on tavg.

For all models, we obtained posterior distributions of all parameters along with their 95% credible intervals (CRI) using Markov chain Monte Carlo implemented in JAGS (v. 4.0.1), which we called using the R2jags package [44]. Model convergence was assessed using the Gelman–Rubin statistic, where values less than 1.1 indicated convergence [45]. We generated three chains of 300 000 iterations after a burn-in of 150 000 iterations and thinned by three. Parameters α_i, $\beta 1_i$ and $\beta 3_i$ received a vague prior of N(0, 0.001), while $\beta 2_i$ and the standard deviation of random effect $s_{i,j}$ received uniform priors of U(−10, 10) and U(0, 100), respectively.

(iii) Phenotypic mismatch

To examine the occurrence of mismatch between hare winter coat colour and snow-free ground between 1951 and 2016, we calculated the number of days of mismatch at each site each year and season. Mismatch occurred on days when hares were white and snow was absent at each site. We defined white hares when the mean $p_{white} > 0.6$ based on the basic model, as this threshold would include completely (LL) and mostly white (L) hares (electronic supplementary material, figure S1) and is consistent with previous studies [18,19]. To test for increase in the mismatch over the 60+ years of climate change, we ran a univariate linear mixed model with mismatch days as the response variable, year as a fixed effect and site as a random effect. Finally, to explore the sensitivity of the definition of white threshold, we repeated the analysis with an alternative threshold at mean $p_{white} > 0.9$.

3. Results

(a) Climate change

Temperature increased and snow cover duration decreased for all sites and seasons over the 1950–2016 period, while snow stochasticity did not change. Seasonal average temperature (tavg) increased by a mean (±s.d.) of 0.17 (±0.018)°C decade^{-1} during spring and 0.13 (±0.016)°C decade^{-1} during autumn ($p \ll 0.001$; electronic supplementary material, figure S3). This led to increases in average seasonal temperature of 1.15°C in the spring and 0.84°C in the autumn between 1950 and 2016. The number of snow days decreased during both seasons by a mean of −2.79 (±0.33) days decade^{-1} in spring, and −1.72 (±0.30) days decade^{-1} in autumn ($p \ll 0.001$; electronic supplementary material, figure S4) and by a mean of −6.52 (±0.68) snow days decade^{-1} for the entire snow season ($p \ll 0.001$; figure 1). This led to an average decline of 37.14 days of annual snow cover at our sites between 1960 and 2016. Next, we found that the mean date of early autumn snow occurs about 4 days later (0.069 ± 0.033 days, $p = 0.038$) and the late spring snow now occurs about 7 days earlier (−0.12 ± 0.039, $p = 0.0031$) since the 1960s (electronic supplementary material, figure S6). Finally, we found no change in stochasticity of snow, measured by the number of transitions between bare ground and snow cover during the entire snow season ($\beta = -0.018$, s.e. = 0.014, $p = 0.17$) or autumn seasons ($\beta = -0.0075$, s.e. = 0.0078, $p = 0.33$). In the spring, there was a significant decrease in the number of transitions ($\beta = -0.029$, s.e. = 0.0063, $p \ll 0.001$), although this effect size is small (1.63 fewer transitions between 1960 and 2016), probably owing to the confounding effect of the decreasing number of springtime snow days (electronic supplementary material, figures S4 and S5).

(b) Moult phenology

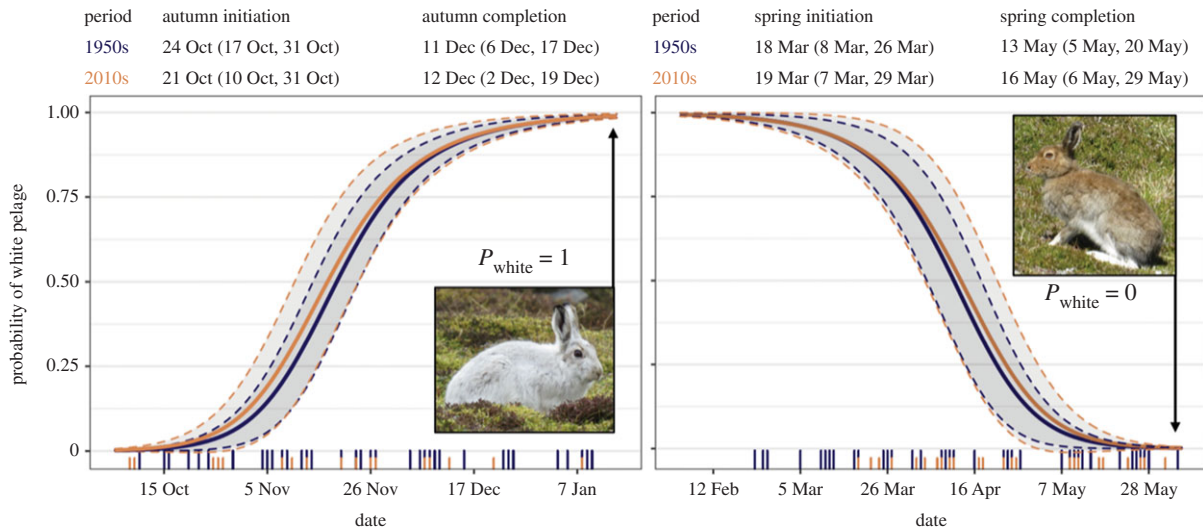We did not detect any significant shifts in spring or autumn moult phenology between 1951 and 2016 (table 2a,b). The

period	autumn initiation	autumn completion		period	spring initiation	spring completion
1950s	24 Oct (17 Oct, 31 Oct)	11 Dec (6 Dec, 17 Dec)		1950s	18 Mar (8 Mar, 26 Mar)	13 May (5 May, 20 May)
2010s	21 Oct (10 Oct, 31 Oct)	12 Dec (2 Dec, 19 Dec)		2010s	19 Mar (7 Mar, 29 Mar)	16 May (6 May, 29 May)

Figure 2. Similar mean mountain hare moult phenologies during 1950s and 2010s in the highlands of Scotland. Solid lines depict predicted probabilities of being white over time based on the basic model including seasonal average temperature tavg. The shaded areas and dashed lines show 95% credible intervals (CRI) and the perpendicular hash marks along the x-axis depict survey dates, colour coded for each time period. Photographs show mountain hares when probability of being in white pelage is 100% (left) and 0% (right). Dates above plots indicate the mean initiation and completion dates and CRIs. (Online version in colour.)

Table 2. Absence of shifts in moult phenology from 1951 to 2016 and some phenotypic plasticity in mountain hares in the highlands of Scotland in autumn and spring. (Mean effect sizes and 95% credible intervals (CRI) estimates for slopes for models including (a) time period only, (b) time period and seasonal average temperature (tavg), and (c) tavg only. $\beta2_i$ indicates the effect of time period and $\beta3_i$ indicates the effect of seasonal temperature tavg on the probability of brown ($\beta3_{brown}$) and white ($\beta3_{white}$). Asterisks indicate CRIs not overlapping zero.)

(a)	$\Pr(y = i) = \alpha_i + \beta1_i \times \text{day} + \beta2_i \times \text{time period}_j + s_{i,j}$			
	moult season	$\beta2_{brown}$	$\beta2_{white}$	
	autumn	−0.62 (−2.12, 0.89)	0.62 (−0.26, 1.56)	
	spring	−0.23 (−0.83, 0.35)	0.01 (−1.00, 1.00)	
(b)	$\Pr(y = i) = \alpha_i + \beta1_i \times \text{day} + \beta2_i \times \text{time period}_j + \beta3_i \times \text{tavg}_{j,e} + s_{i,j}$			
	moult season	$\beta2_{brown}$	$\beta2_{white}$	$\beta3_{brown}$	$\beta3_{white}$
	autumn	−0.34 (−1.68, 1.00)	0.06 (−0.68, 0.92)	0.25 (−0.05, 0.54)	−0.46* (−0.71, −0.20)
	spring	−0.37 (−1.56, 0.60)	−0.05 (−1.30, 0.93)	1.00* (0.87, 1.14)	−0.78* (−0.92, −0.64)
(c)	$\Pr(y = i) = \alpha_i + \beta1_i \times \text{day} + \beta3_i \times \text{tavg}_{j,e} + s_{i,j}$			
	moult season			$\beta3_{brown}$	$\beta3_{white}$
	autumn			0.270 (−0.018, 0.554)	−0.456* (−0.676, −0.288)
	spring			1.005* (0.870, 1.144)	−0.766* (−0.906, −0.627)

effect of the time period covariate on the probabilities of being brown ($\beta2_{brown}$) or white ($\beta2_{white}$) overlapped zero for both seasons in models with (table 2b), or without seasonal temperature (tavg; table 2a, figure 2). Next, mean population moult initiation dates did not differ significantly between moult phenology of the 1950s and 2010s in spring or autumn as indicated by the overlapping 95% CRI (figure 2); hares initiate autumn moults in late October (mean Julian date = 296) and spring moults around mid-March (mean Julian day = 78). Similarly, the estimated completion dates have not changed between the two time periods for either season with spring moults completing in mid-May (mean Julian day = 135) and autumn moults in mid-December (mean Julian day = 345; figure 2).

We found evidence for phenotypic plasticity in response to annual variation in temperature tavg (table 2b,c). In the spring,

the effect of tavg ($\beta3_i$) was significant, indicating that moults were delayed during colder springs. This resulted in up to a 20 day difference in the mean population completion dates between some springs. In the autumn, tavg had a significant effect only on the probability of being white ($\beta3_{white}$, table 2c), with non-significant shifts towards earlier initiation and completion of the moult during colder autumns.

(c) Phenotypic mismatch

Estimated mismatch in coat colour increased between 1950 and 2016 at all sites and seasons. The increases were steepest over the entire snow season (1 October–31 May) ($\beta_{Year} = 0.52$, $p \ll 0.001$) and evident when moulting seasons were considered separately (autumn $\beta_{Year} = 0.14$, $p \ll 0.001$; spring $\beta_{Year} = 0.18$, $p \ll 0.001$; figure 3). Since the 1960s, from when
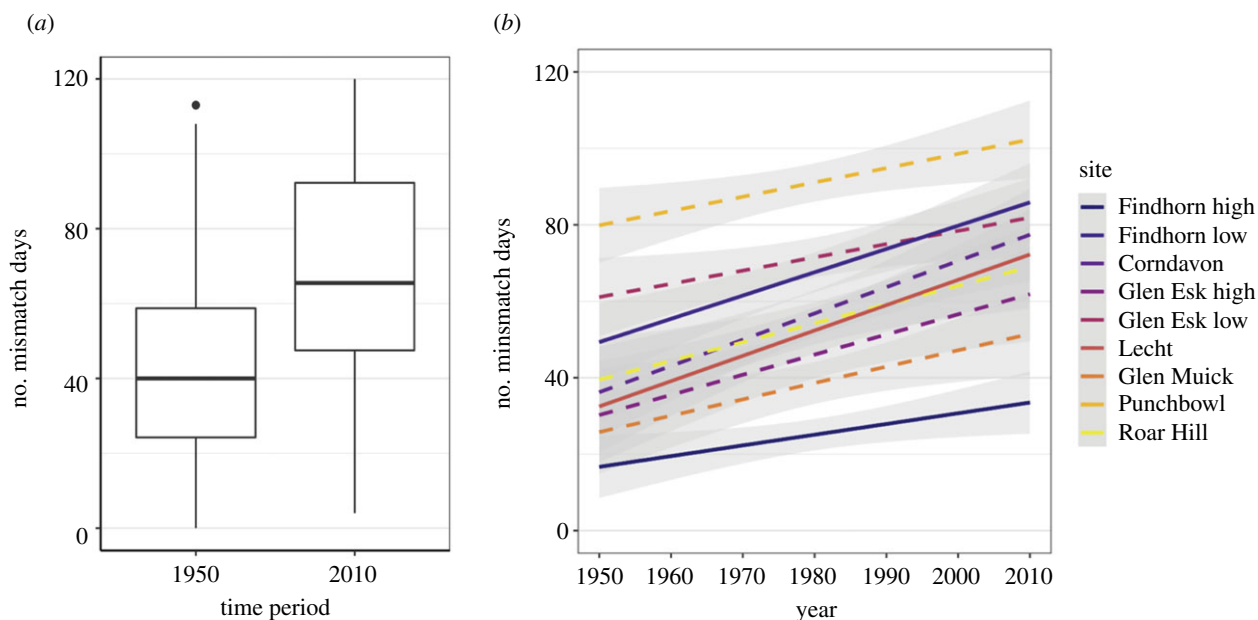
Figure 3. Estimated number of days when white mountain hares would be found mismatched against snowless background from 1950 to 2016 in the highlands of Scotland. The number of mismatch days is calculated over the entire snow season (1 October–31 May) for each year. (a) Boxplots show the number of mismatch days in the 1950s and 2010s. Horizontal lines within the boxes denote the medians, boxes the first and third quartiles, whiskers extend to the largest and smallest value within 1.5 × the interquartile range and the point represents an outlier. (b) Coloured lines show linear regression slopes for each site with 95% confidence intervals depicted in grey. Solid (dashed) lines indicate sites used in current (historical) surveys. (Online version in colour.)

gridded snow data are available, the regression slopes translate to 29.7 more days with white hares (mean $p_{white} > 60\%$) against snowless background than in the 2010s, with an additional 5.2 days when data are extrapolated to the 1950s (figure 3b). Across all the sites, the mean number mismatch days increased from 44.3 (s.d. = 24.8) days during 1950s and 1960s to 69.9 (s.d. = 30.1) during the 2010s (figure 3a). The results were similar when an alternative mismatch threshold (=mean $p_{white} > 90\%$) was used (electronic supplementary material, table S2).

4. Discussion

Across the northeast and central highlands of Scotland seasonal temperatures have increased and the number of snow days has declined since the 1950s; a trend seen across the Northern Hemisphere [13,14]. Despite the directionality and large magnitude of the observed climate shift documented here, our results suggest that moult phenology did not track the shortening snow seasons to prevent camouflage mismatch. Further, temperature-mediated phenotypic plasticity in moult phenology was detectable, but insufficient to prevent camouflage mismatch. Altogether, this resulted in 35 additional days of phenotypic mismatch whereby mostly white hares inhabited snowless backgrounds. As snow cover is expected to decline by up to additional 50% by 2100 across Scotland [34], mountain hares in the Scottish uplands are very likely to experience further phenotypic mismatch in the future.

The lack of sufficient adaptive phenological responses in mountain hares was unexpected for two main reasons. First, phenotypic plasticity has been commonly documented across taxa in a range of traits [46,47] and some plasticity in moult phenology has been observed in several seasonally colour moulting species [16,18,28]. Yet, the observed levels

of plasticity were apparently insufficient to prevent increases in camouflage mismatch—a finding consistent with field studies of snowshoe hares over shorter time periods [18,28,48]. Second, strong natural selection against camouflage mismatch has been documented in other colour moulting species [22–24] and negative population consequences of mismatch were found in mountain hares in Norway [33]. Therefore, evolutionary shifts in moult phenologies are a plausible, if not expected, response to reduced snow cover. Given that these two components of adaptive capacity are so widely observed, our results provide a striking contrast to evidence for adaptive shifts observed in other systems [22,23,27]. Multiple factors may have contributed to the lack of shifts in moult phenology in mountain hares. In the next paragraphs, we discuss the potential contributions of environmental stochasticity, potentially low genetic variance and attenuation of selection pressure against camouflage mismatch in Scotland. We also discuss how the increasing duration of camouflage mismatch in mountain hares might influence these populations in the future.

Adaptive tracking of decreasing snow cover could be slowed or stalled if temporally varying selection pressures prevent the generation of stable optimal phenotypes via phenotypic plasticity or evolutionary adaptation [49,50]. The climate of Scotland's highlands is extremely variable and unpredictable in time and space, subjecting mountain hares to high environmental stochasticity. Although temperature exerts major control over snow cover and depth in Scotland, snowfall is often associated with frontal systems and a cold winter does not necessarily mean a snowy one [51]. Indeed, hares experience high variability in snow cover during each winter, with an average of 14.2 snow cover transitions per winter during our study period. However, the high stochasticity in climate has not increased over the past 60 or more years (electronic supplementary material, figure S5), so environmental

stochasticity seems unlikely to be a primary inhibitor of recent adaptive responses.

For moult phenology or its plasticity to evolve by natural selection, sufficient heritable genetic variation must exist in the trait and population must be large enough that selection is not overwhelmed by genetic drift [52,53]. Circannual phenological traits often have a heritable basis [54,55], and the genetic basis for winter colour *per se* (i.e. winter dark versus white morphs) has been determined for some populations of snowshoe hares [56] and mountain hares [57]. The genetic basis, and response to selection, of moult timing and rate (phenology) has not yet been described, but is similarly likely to be affected by genetic architecture, gene expression and the disruptive effect of genetic drift in small populations [58–60]. Genetic drift owing to small population size may be relevant in this case because recent (i.e. since 1990s) population reductions have been reported for some areas in the northeast and central highlands of Scotland [35,61]. Furthermore, although genetic variation in Scotland populations is unknown, some evidence suggests it is lower than in other mountain hare populations in Europe [62,63]. However, without better information on genetic variance in Scottish hares, we cannot infer whether it might have contributed to the lack of response in moult phenology.

We believe a primary contributing factor for the apparent lack of phenological shifts in mountain hares in Scotland is attenuation of selection pressure. Natural selection for cryptic coloration is one of the strongest drivers of adaptive evolution [64,65], with examples including peppered moths (*Biston betularia*) in Great Britain [66], mice inhabiting light-coloured substrates [67], and seasonal colour moults in birds and mammals [16]. However, relaxed selection (i.e. reduced effect of phenotypic trait on fitness) can lead to a loss of functional traits or diminished phenotypic plasticity [68,69]. The main adaptive advantage of the winter white moult is predator avoidance (thermoregulatory properties are overwhelmingly controlled by changes in hair length and density, not hair colour; Zimova *et al*. [16]). Therefore, evolutionary shifts in moult timing would require directional selection imposed by predation.

In Scotland, mountain hares are prey for a range of species including red fox (*Vulpes vulpes*), wild cat (*Felis silvestris*), otter (*Lutra lutra*) and golden eagle (*Aquila chrysaetos*) [70,71]. However, in the northeast and central highlands of Scotland, mountain hares are associated with heather-dominated moorlands managed for commercial shooting of red grouse (*Lagopus lagopus scoticus*) [36,72]. Predator numbers and diversity are severely depressed across these lands owing to legal and illegal predator control over the last century [61,73,74]. Thus, the relatively low predator-induced mismatch costs would be expected to relax natural selection against mismatch in these areas relative to regions with more intact predator communities such as in Norway [33] or Montana, USA [23]. Given the highly altered selection regime on intensively managed moorlands, camouflage mismatch might have little-to-no fitness costs for mountain hares in our study system, now and in the recent past.

If attenuated predation risk is the main contributing factor to what we suggest is a relatively static moult phenology, we expect that a return of predation pressure could lead to negative population consequences. For example, if generalist predators were to increase in response to land use or policy changes, the accumulated duration of camouflage mismatch could threaten hare population persistence. This 'latent maladaptation' is, therefore, worth considering when assessing the species vulnerability to climate and land use change [35,75]. Irrespective of any potential increase in predator numbers, we recommend management efforts that favour evolutionary rescue (i.e. large connected populations that harbour high genetic diversity; [27,29]) to achieve evolutionary resilience and long-term persistence in the face of future biotic and abiotic changes [76]. This recommendation is especially relevant for the mountain hare populations in the northeast and central highlands of Scotland, where there is evidence of local population declines [35,61] and additional stressors related to game bird management and woodland/forestry expansion [77,78].

Two potential limitations of our study are worth noting. First, for analyses, we collapsed moult observations into three categories, which may decrease resolution of initiation and completion dates. Second, we only had 2 years of 'current' hare moult phenology, making it difficult to eliminate the possibility of plasticity in moult phenology that may manifest at other temperatures. Future studies that include additional years and sites of observations will help elucidate Scottish mountain hares' capacity to respond to a wider range of conditions under current and future climate.

For at least 21 species across the Northern Hemisphere, seasonal coat colour has been shaped directly by climate [27]. The general consensus is that as decreasing snow duration continues to cause winter white animals to be found against dark snowless backgrounds, evolutionary change will be necessary to mitigate the negative effects of increasing camouflage mismatch [19,23,27]. However, here we found little evidence that moult phenology in mountain hares in Scotland has changed despite directional climate change over the past 60 or more years. While more study is necessary to understand the full extent of phenotypic plasticity and why it appears moult phenology has not shifted in response to environmental change, we suggest that relaxed selection for camouflage, potentially coupled with low genetic variance, would be consistent with our findings. If true, we expect that the fitness consequences of climate change will ultimately depend on the strength of selection pressures such as predation. Altogether, our findings underscore that wildlife adaptive responses to anthropogenic stressors will ultimately depend on both abiotic and biotic conditions.

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