

Local climate determines vulnerability to camouflage mismatch in snowshoe hares

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Abstract

Aim: Phenological mismatches, when life-events become mistimed with optimal environmental conditions, have become increasingly common under climate change. Population-level susceptibility to mismatches depends on how phenology and phenotypic plasticity vary across a species' distributional range. Here, we quantify the environmental drivers of colour moult phenology, phenotypic plasticity, and the extent of phenological mismatch in seasonal camouflage to assess vulnerability to mismatch in a common North American mammal.

Location: North America.

Time period: 2010–2017.

Major taxa studied: Snowshoe hare (*Lepus americanus*).

Methods: We used > 5,500 by-catch photographs of snowshoe hares from 448 remote camera trap sites at three independent study areas. To quantify moult phenology and phenotypic plasticity, we used multinomial logistic regression models that incorporated geospatial and high-resolution climate data. We estimated occurrence of camouflage mismatch between hares' coat colour and the presence and absence of snow over 7 years of monitoring.

Results: Spatial and temporal variation in moult phenology depended on local climate conditions more so than on latitude. First, hares in colder, snowier areas moulted earlier in the fall and later in the spring. Next, hares exhibited phenotypic plasticity in moult phenology in response to annual variation in temperature and snow duration, especially in the spring. Finally, the occurrence of camouflage mismatch varied in space and time; white hares on dark, snowless background occurred primarily during low-snow years in regions characterized by shallow, short-lasting snowpack.

Main conclusions: Long-term climate and annual variation in snow and temperature determine coat colour moult phenology in snowshoe hares. In most areas, climate change leads to shorter snow seasons, but the occurrence of camouflage mismatch varies across the species' range. Our results underscore the population-specific susceptibility to climate change-induced stressors and the necessity to understand this variation to prioritize the populations most vulnerable under global environmental change.

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adaptation, camouflage mismatch, climate change, latitudinal gradient, phenological mismatch, phenotypic plasticity, range edge, snow, snowshoe hares

1 | INTRODUCTION

As a result of anthropogenic climate change, plant and animal populations are increasingly confronting environmental conditions different from the ones to which they are adapted. Organisms occupying seasonal environments have evolved mechanisms for the timing of their life cycles (i.e., phenology) to match with optimal environmental conditions and resources at their location (Bradshaw & Holzapfel, 2007; Williams, Henry, & Sinclair, 2015). When phenology and favourable environmental conditions become asynchronized, organisms can suffer negative fitness costs (Both, Bouwhuis, Lessells, & Visser, 2006; Lane, Kruuk, Charmantier, Murie, & Dobson, 2012; Post & Forchhammer, 2008; Senner, Stager, & Sandercock, 2017; Zimova, Mills, & Nowak, 2016). Such phenological mismatches are becoming increasingly common under climate change (Cohen, Lajeunesse, & Rohr, 2018; Parmesan & Yohe, 2003; Thackeray et al., 2010), which in the absence of adaptive responses could lead to population declines and local extinctions (Visser & Gienapp, 2019). Thus, there is a pressing need to understand the degree to which climate change leads to phenological mismatches and the capacity of wild populations to withstand attendant fitness costs.

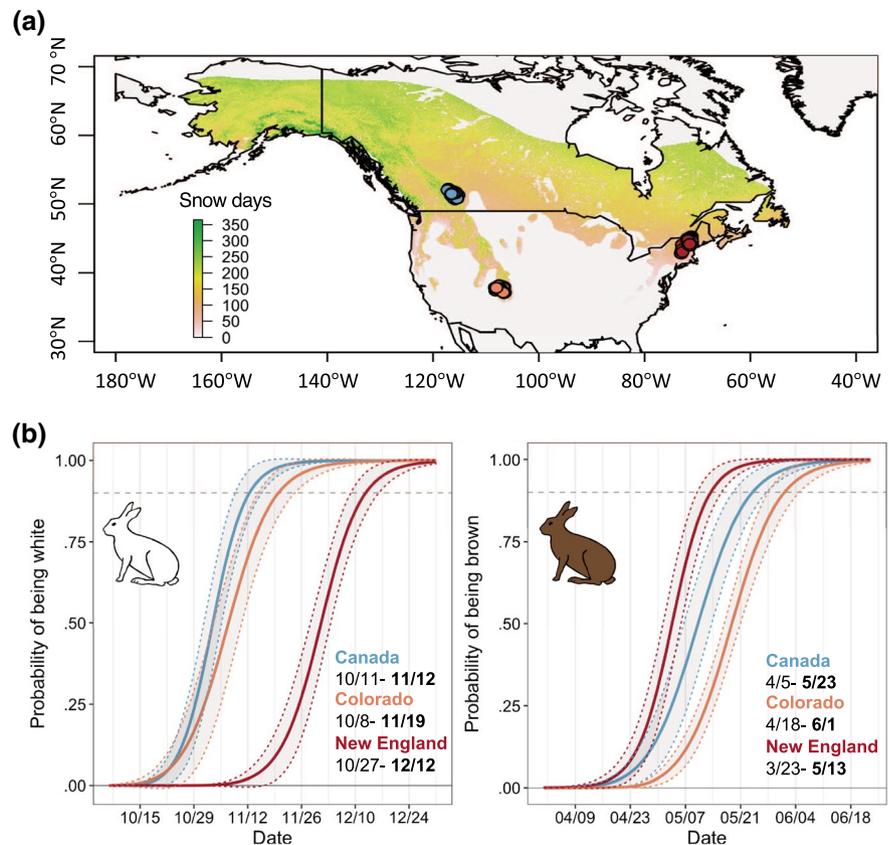
Understanding the variation in phenology and its environmental drivers is fundamental for assessing current and future species' vulnerability to phenological mismatches. For the majority of traits in plants and animals in temperate regions, photoperiod serves as the principal cue for phenology, with temperature and other environmental factors exerting lesser influence (Bradshaw & Holzapfel, 2007; Hofman, 2004). Because photoperiod, latitude and climate covary across most species' ranges, variation in phenology is often distributed along latitudinal gradients. Northern populations typically experience harsher and colder climates that correspond with later initiation of spring and earlier initiation of fall events compared to southern populations (Bradshaw & Holzapfel, 2007; Hut, Paolucci, Dor, Kyriacou, & Daan, 2013). However, latitude may not be a reliable predictor of phenology for two reasons. First, the covariance between latitude and climate is imperfect when other geographic factors such as elevation also affect climatic conditions (Chuine, 2010; Visser, Caro, Oers, Schaper, & Helm, 2010). Secondly, species show year-to-year in situ variation in phenological traits in response to annual variation in climate. This temporal phenological variation is referred to as 'population-level' phenotypic plasticity, and is different from between-individual level phenotypic plasticity (Gienapp & Brommer, 2014; Phillimore, Hadfield, Jones, & Smithers, 2010). Overall, both spatial and temporal variation in phenology may have

consequences for susceptibility to phenological mismatch on both the local population and broader species levels.

Seasonal coat colour moult, a key phenological trait, has received increased attention as a trait shaped by climate. Across the Northern Hemisphere, 21 species of mammals and birds change coat or plumage colour from brown in the summer to white in the winter to match snow-covered landscapes (Mills et al., 2018; Zimova et al., 2018). As with other phenological traits, photoperiod serves as the principal cue for moult phenology, with some evidence that year-to-year variation in winter weather modulates the progression of moult (Hofman, 2004; Zimova et al., 2018). However, decreasing duration of snow cover due to climate change (Choi, Robinson, & Kang, 2010; Kunkel et al., 2016; Vaughan et al., 2013) may result in phenological mismatch, whereby winter white animals become colour mismatched against dark, snowless backgrounds (Mills et al., 2013). Field studies indicate that mismatch in seasonal coat colour and snow presence or absence leads to high fitness costs due to increased predator-induced mortality (Atmeh, Andruszkiewicz, & Zub, 2018; Zimova et al., 2016) and may have already contributed to range contractions for several species including *Lagopus* and *Lepus* spp. (Diefenbach, Rathbun, Vreeland, Grove, & Kanapaux, 2016; Imperio, Bionda, Viterbi, & Provenzale, 2013; Pedersen, Odden, & Pedersen, 2017; Sultaire et al., 2016).

The snowshoe hare (*Lepus americanus*), a key prey species of the boreal forest of North America (Krebs, Boonstra, Boutin, & Sinclair, 2001), exhibits seasonal colour moults in the majority of its range (Gigliotti, Diefenbach, & Sheriff, 2017; Mills et al., 2018; Nagorsen, 1983). Because of their broad distribution (Figure 1a), hares inhabit a large range of environmental conditions, making them an ideal species for investigating variation in moult phenology and camouflage mismatch. In the only two areas where moults have been recently investigated in relation to climate change (i.e., Montana and Wisconsin, USA), phenotypic plasticity is not sufficient to prevent camouflage mismatch (e.g., Mills et al., 2013; Wilson, Shipley, Zuckerberg, Peery, & Pauli, 2018). For example, hares in Montana experience about a week of mismatch annually whereby hares are in the wrong coat colour in relation to their background (i.e., white hares on snowless background or brown hares on snow; Mills et al., 2013; Zimova, Mills, Lukacs, & Mitchell, 2014; Zimova et al., 2016). Because hares rely heavily on their camouflage for survival, mismatch has strong negative fitness costs (i.e., 7–12% reduced weekly survival) that in the absence of evolutionary shifts and under projected snow declines would be sufficient to cause steep population declines and local extinction (Wilson et al., 2018; Zimova et al., 2016). To date, no study has evaluated the phenological drivers and camouflage

FIGURE 1 Camera site locations and snowshoe hare moult phenologies and moult dates in the Canada, Colorado and New England study areas. (a) Snowshoe hare range (downloaded from www.iucnredlist.org) is coloured and shaded by the mean annual number of snow days (Dietz, Kuenzer, & Dech, 2015). Coloured points represent the 448 remote-camera trap sites. (b) Bold lines depict predicted probabilities of being in the final colour category (white in the fall, brown in the spring) over time. The dashed lines show 95% credible intervals. The horizontal dashed lines at .90 intersect with population means to identify moult completion dates. Population mean moult initiation and completion dates are depicted as a date range in the bottom right corners, with the completion dates in bold. The predicted probabilities and dates were estimated for each season and population based on the model without covariates [Colour figure can be viewed at wileyonlinelibrary.com]



mismatch across the heterogeneous snowshoe hare range in a unified analytical framework.

To understand snowshoe hare vulnerability to camouflage mismatch, we quantified the spatial and temporal variation in colour moult phenology, phenotypic plasticity, and the occurrence of camouflage mismatch across three disjunct, climatically and geographically distinct populations. First, we hypothesized that the spatial variation in moult phenology would be determined by latitude and local climate. We tested two predictions: (a) populations in more northern sites moult earlier in the fall and later in the spring, (b) populations in colder and snowier sites moult earlier in the fall and later in the spring. Second, we hypothesized that hares exhibit temperature- and snow-mediated phenotypic plasticity in moult phenology and we predicted that moults occur earlier in fall and later in spring during colder and or snowier years. Third, we quantified the occurrence of camouflage mismatch for each population in spring and fall and assessed which snowshoe hare populations may be the most vulnerable to camouflage mismatch now and under future climate change.

2 | MATERIALS AND METHODS

2.1 | Study areas

Our analysis integrated three regional monitoring studies in North America: the Canadian Rockies, the San Juan Mountains in Colorado, and northern New England (Figure 1a). Together, these areas

encompass wide latitudinal, altitudinal and habitat variation across the distributional range of snowshoe hares (Table 1). Our northernmost study area in the Canadian Rockies included three national parks (Banff, Yoho and Kootenay National Parks) and was characterized by rugged, forested mountainous regions with a long snow season. This area is located within a homogeneous boreal habitat at the core of the snowshoe hare distribution range (Cheng, Hodges, Melo-Ferreira, Alves, & Mills, 2014). The southernmost study area was located in the San Juan Mountains of south-west Colorado; an isolated patch of high-elevation southern boreal forest near hares' southern range boundary. The northern New England study area, also near the southern edge of hare distribution, encompassed portions of the Green Mountains in Vermont and the White Mountains in New Hampshire. This area stretched across a transition zone between the northern hardwood and boreal forests and had, on average, the mildest climate of the three areas. Major hare predators in all areas included coyotes (*Canis latrans*), red fox (*Vulpes vulpes*), Canada lynx (*Lynx canadensis*), bobcats (*Lynx rufus*), martens (*Martes* spp.), weasels (*Mustela* spp.), northern goshawks (*Accipiter gentilis*) and great-horned owls (*Bubo virginianus*). The study area in Canada also had wolves (*Canis lupus*) and grizzly bears (*Ursus arctos*).

2.2 | Camera trapping design

We obtained our snowshoe hare phenology data as by-catch photos from three long-term independent studies of forest carnivores.

TABLE 1 Geospatial and long-term climate details regarding the camera trap networks in the study areas. Number of camera sites and independent coat colour observations are given separately for each season and area (across all years and areas the number of independent camera sites totaled 448). Other metrics include mean values across all camera sites within a study area with standard deviation in parentheses. Long-term mean minimum (tmin) and maximum (tmax) temperature and snow season duration are based on 1980–2009 period

| Study area | Latitude (degrees) | Elevation (m) | Fall | | | Spring | | | Snow season (days) | Snow season (days) | | |
|-------------|--------------------|-------------------|------------------|----------|--------------|--------------|--------------------|------------------|--------------------|--------------------|-------------|----------------|
| | | | Camera sites (n) | Obs. (n) | tmin (°C) | tmax (°C) | Snow season (days) | Camera sites (n) | | | Obs. (n) | tmin (°C) |
| Canada | 51.38 (0.33) | 1,850.98 (266.20) | 98 | 967 | -5.41 (1.33) | 5.22 (1.86) | 93.08 (10.93) | 91 | 921 | -6.62 (1.68) | 5.17 (2.33) | 168.69 (18.18) |
| Colorado | 37.63 (0.30) | 3,200.79 (215.46) | 110 | 322 | -4.68 (1.09) | 9.70 (1.78) | 72.83 (6.91) | 183 | 1,705 | -7.24 (1.28) | 8.03 (1.71) | 155.70 (11.07) |
| New England | 44.54 (0.51) | 627.18 (284.59) | 65 | 486 | 0.25 (0.89) | 10.61 (1.63) | 52.07 (7.30) | 105 | 1,122 | -3.44 (0.93) | 8.35 (1.84) | 125.01 (12.49) |

A combination of motion-triggered camera models was used across the sites, but all produced comparable high-quality images during the day and night. The camera spacing differed between regions, but at any given time the minimum distance between cameras was > 1 km; grid sizes varied by study area (10 km × 10 km in Canada, 4 km × 4 km in Colorado and 2 km × 2 km in New England). Each camera site was stationary and remained within a grid cell for a minimum duration of 1 year. We combined all observations for the cameras that were moved between years within < 1 km distance and assigned them an average latitude, longitude and elevation. The 1-km threshold was chosen because it far exceeds average individual hare seasonal movement and home range size at all three areas (Hodges, 1999; Ivan, 2011; Mills et al., 2005).

2.3 | Coat colour monitoring

Coat colour was visually estimated from the by-catch hare photographs by one observer, following a standardized protocol for colour classification and image quality filtering (Zimova et al., under review). Briefly, hares were classified as (a) white when > 90% of the body (excluding belly and feet) was white, (b) brown when < 10% of the body was white, and (c) moulting for all other instances. As per previously developed classification methods (Zimova et al., 2014), we excluded the feet and belly colour as these stay white all year in all three areas (Grange, 1932). Because hares cannot be individually identified from photos, we considered photos spaced by > 24 hr as independent events, unless different individuals were distinguishable (e.g., two hares in one photo, a hare in a different moult stage recorded within 24 hr).

In Canada, 121 cameras operated from September 2011 to November 2016, yielding 1,888 independent coat colour observations. In Colorado, 206 cameras operated from September 2010 to June 2011 and from January 2014 to August 2017, yielding 2,027 independent observations. In New England, 121 cameras operated from January 2014 to January 2018, yielding 1,608 independent observations.

2.4 | Statistical analysis

We used R (version 3.4.3; R Core Team, 2016) for all statistical analyses.

2.4.1 | Climate variables

To characterize annual and long-term climate conditions at each camera site, we prepared a set of temperature and snow cover variables relevant to moult phenology (Mills et al., 2018; Zimova et al., 2018). Annual minimum (tmin) and maximum (tmax) temperature during spring and fall were calculated for each year of monitoring (2010–2017) at each camera site using daily gridded 1 km × 1 km

resolution data (Daymet; Thornton et al., 2018). We used the same dataset to calculate mean seasonal t_{min} and t_{max} during the 30-year period 1980–2009 to describe long-term climate at each camera site. The seasons were defined as spring (1 March–31 May) and fall (1 September–30 November), because at all areas the majority of moulting occurs during those months.

We used modelled snow water equivalent (SWE) to quantify the duration of the continuous snow season and the total number of snow days for the spring and fall. For the years of monitoring (2010–2017), we used daily gridded 1 km \times 1 km resolution data by Snow Data Assimilation (hereafter SNODAS; Barrett, 2003). Because SNODAS is unavailable prior to 2000, we used daily gridded 6 km \times 6 km resolution data (Livneh et al., 2015) to describe the mean long-term snow conditions during the 30-year period (1980–2009). The duration of spring snow season each year was calculated as the number of days between 1 January and snowmelt date, that is, the first day when snow is absent (SWE = 0) at a camera site for a minimum of 7 days. Fall snow season was estimated as the number of days following the summer (i.e., the longest snowless period at each camera site each year), between snow onset date (i.e., first day when SWE > 0 for a minimum of 7 days) and 31 December. We used the 7-day buffers to discard spurious early spring snowmelts followed by further extended snow season and to account for spurious snow flurries in the fall. The total number of snow days was calculated as the sum of days with SWE > 0 from 1 January to 31 August for the spring and from 1 September to 31 December for the fall.

2.5 | Moulting phenology

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

$$p(y=i) = \frac{e^{\alpha_i + \beta 1_i * d + s_{ij}}}{1 + \sum_{k=1}^{i-1} e^{\alpha_k + \beta 1_k * d + s_{ij}}} \quad (1)$$

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 $\Sigma(p_{1:3, j, d}) = 1$. Camera site was coded as a random covariate s_{ij} to reflect the hierarchical structure of the dataset and allow for repeated measurements. 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. Fall and spring moults were modelled separately.

2.5.1 | Spatial variation in moulting phenology

First, to quantify average moulting phenology of each population (Canada, Colorado, New England), we combined colour observations from all years at that area and ran the model separately for each. We used the estimated probabilities to derive approximate dates when

hares initiated and completed their moults as 'initiation' and 'completion' dates at each area. Fall start was specified as the first Julian day when mean $p_{brown} < .9$ and end date when mean $p_{white} > .9$; the opposite condition was used to estimate the spring dates (i.e., start when $p_{white} < .9$ and end when $p_{brown} > .9$).

Next, to test the effect of local environmental covariates on phenology, we combined colour observations from all years and populations in one dataset and constructed a set of univariate models. Each model included a single fixed effect of an environmental covariate $\beta 2_i$ on the probability of being brown, white or moulting. The environmental covariates were latitude, elevation, and the 30-year long-term temperature and snow conditions (i.e., t_{min} and t_{max} , duration of snow season) in spring and fall during each season at each camera site. We used univariate models to avoid problems associated with multicollinearity as most environmental covariates were highly correlated (Pearson correlation coefficients > |.60|; Supporting Information Table S1). To facilitate comparisons between models, all covariates were standardized to a mean of 0 and SD of 1.

The resulting β coefficients represented the increase in the probability of being in a certain colour category on the multinomial-logit scale for every one-unit (SD) change in the covariate. We considered a covariate to have a significant effect on moulting phenology when the resulting β coefficients' 95% credible intervals (CRIs) did not overlap zero. Because we were not interested in quantification of the effect size per se, but rather on the direction and the relative sizes of the different covariates, we did not convert the coefficients to normal scale. We primarily focused on the covariate effects on probability of the season's final colour (i.e., $\beta 2_{white}$ in the fall, $\beta 2_{brown}$ in the spring) not the initial colour or moulting colour category, in part to simplify the reporting of results. Furthermore, because photoperiod is known to strongly control the hormonal cascade that triggers the moulting, we expected the effects of climate to be more apparent in the final rather than the initial stage of the moulting (i.e., follicle stimulation and hair growth initiation versus the appearance of the newly grown hairs and shedding of the old hairs; Zimova et al., 2018). Finally, in most cases, the significance or absolute effect size of initial and final colour probabilities were similar (all β coefficients shown in Supporting Information Tables S2 and S3).

2.5.2 | Temporal variation in moulting phenology

Next, to test the effect of annual variation in temperature and snow season duration, we constructed an alternative set of univariate models. Each model included a single fixed effect of climate covariate $\beta 2_i$ on the probability of being in a certain colour category to avoid multicollinearity issues (Supporting Information Table S1). The covariates included mean annual t_{min} , t_{max} , and duration of snow season in spring and fall at each camera site. The resulting $\beta 2_i$ coefficients were the slopes of reaction norms of the climate covariates on probabilities of being brown ($\beta 2_{brown}$) or white ($\beta 2_{white}$).

For all models, we obtained posterior distributions of all parameters along with their 95% CRIs using Markov chain Monte Carlo

(MCMC) implemented in JAGS (version 4.0.1), which we called using the R2jags package (Su & Yajima, 2012). Model convergence was assessed using the Gelman–Rubin statistic, where values < 1.1 indicated convergence (Gelman & Rubin, 1992). We generated three chains of 300,000 iterations after a burn-in of 150,000 iterations and thinned by three. Parameters α_i , β_{1_i} and β_{2_i} received a vague prior of $N(0, 0.001)$, and the standard deviation of random effect $s_{i,j}$ received a uniform prior of $U(0, 100)$.

2.5.3 | Camouflage mismatch

Camouflage mismatch was calculated based on the daily presence or absence of snow and the modelled coat colour at each camera site. Snow was present at a camera site when SWE > 0, and absent when SWE = 0, based on daily gridded 1 km × 1 km resolution data (SNODAS, for validation of dataset see Sirén et al., 2018). Next, we defined white hares as when mean $p_{\text{white}} \geq 60\%$ and brown hares as $p_{\text{brown}} > 60\%$ as these thresholds included mostly white or brown hares, respectively, when compared to observations. The camera days with brown and white hares were calculated using colour probabilities from the models that included the best annual climate predictor (effect sizes in Table 3) in order to account for inter-annual variation in phenology.

To quantify the annual frequency of camouflage mismatch within each population, we calculated the number of days at all camera sites (camera days) when the colour of hares would either match or mismatch against the background colour. ‘White mismatch’ occurred on days when hares were white and snow was absent at the site. ‘Brown mismatch’ occurred on days when hares were brown and snow was present (Mills et al., 2013). ‘Match’ occurred on days when hares were white (brown) and snow was present (absent). The proportion of white mismatch occurrence, for example, was calculated as the count of all camera days when hares would experience white mismatch, divided by the total number of camera days (i.e., number of camera sites at each area multiplied by the total number of days in a season). We calculated the mismatch occurrence for two 4-month periods when mismatch might occur at all three study areas; 1 February–31 May (spring) and 1 September–31 December (fall). All proportions were multiplied by 100 for interpretation in %.

3 | RESULTS

3.1 | Spatial variation in moult phenology

Snowshoe hare moult phenology varied across the three study areas (Figure 1). In the fall, populations in Colorado and Canada initiated fall moults in early October, with some evidence that hares in Canada moulted faster (32 days total) than hares in Colorado (42 days; Figure 1b). The hare population in New England initiated fall moults almost 3 weeks later and took the longest to complete the moults (46 days). In the spring, hares in New England initiated the

white-to-brown moults first, in late March, followed almost 2 weeks later by populations in Canada and 4 weeks later by the southernmost population in Colorado. The Colorado population took the shortest to complete the transitions (44 days versus 48 and 51 days in Canada and New England, respectively) and became brown only 2 and 3 weeks later than the populations in Canada and New England, respectively (Figure 1b).

Variation in moult phenology between populations did not follow the north–south latitudinal gradient as predicted. Among populations, latitude had a significant effect on the spring moult phenology, but the effect was negative; hares at higher (i.e., northern) latitudes became brown earlier than hares in lower latitudes (Table 2). In the fall, latitude had no effect on moult phenology (Table 2). Local climate and elevation were strong predictors of moult phenology and

TABLE 2 Effect of latitude, elevation and long-term climate covariates on snowshoe hare moult phenology. Mean effect sizes and 95% credible interval (CRI) estimates for slopes for univariate models including data from all years and populations combined. Betas indicate effects of covariates on the probability of the moult’s final colour category ($\beta_{2_{\text{brown}}}$ in the spring, $\beta_{2_{\text{white}}}$ in the fall). Snow is the duration of continuous snow season (days), tmax and tmin are the mean minimum and maximum temperature (°C) in springs and falls during 1980–2009. Asterisks indicate CRIs not overlapping 0. Values reflect standardized data

| Covariate | Fall $\beta_{2_{\text{white}}}$ | Spring $\beta_{2_{\text{brown}}}$ |
|-----------|---------------------------------|-----------------------------------|
| Latitude | 0.566 (−0.136, 1.293) | 0.689* (0.376, 1.012) |
| Elevation | 2.165* (1.450, 3.033) | −1.325* (−1.631, −1.039) |
| Snow | 0.446 (−0.214, 1.123) | −0.809* (−1.143, −0.492) |
| tmax | −1.855* (−2.479, −1.288) | 0.776* (0.440, 1.123) |
| tmin | −2.370* (−2.894, −1.909) | 1.280* (0.998, 1.579) |

TABLE 3 Effect of annual temperature and snow season duration on moult phenology in snowshoe hares. Betas are the slopes of reaction norms β_2 (= mean effect size of annual climate covariate) and their 95% credible intervals (CRIs) on the probability of the moult’s final colour category. Snow is the duration of continuous snow season (days), tmax and tmin are the mean minimum and maximum temperature (°C) in spring and fall each year during 2010–2017. Asterisks indicate CRIs not overlapping zero. Values reflect standardized data

| Covariate | Fall $\beta_{2_{\text{white}}}$ | Spring $\beta_{2_{\text{brown}}}$ |
|-------------|---------------------------------|-----------------------------------|
| Snow annual | 1.466* (1.009, 1.929) | −1.627* (−1.969, −1.303) |
| tmax annual | −2.070* (−2.850, −1.432) | 1.587* (1.208, 2.003) |
| tmin annual | −2.344* (−2.943–1.845) | 1.273* (0.921, 1.655) |

always in the predicted direction in both seasons; earlier fall and later spring moults were associated with sites that are generally colder, snowier and located at higher elevations. Elevation and long-term minimum temperature had the strongest effect on moult phenology in both seasons (Table 2).

3.2 | Temporal variation in moult phenology

We found evidence of population-level temperature- and snow-mediated plasticity in moult phenology. All annual temperature and snow covariates affected moult phenology in the predicted direction; moults occurred later in the spring and potentially earlier in the fall during colder and or snowier years (Table 3). In the spring, this annual variation in temperature and snow duration resulted in 2- to 3-week differences in mean population initiation and completion dates between some years in Canada and New England (Figure 2). In contrast, we found no significant differences between spring initiation and completion dates in the Colorado population. Furthermore, we did not detect any differences in the fall moult phenology start or end dates in any population (Supporting Information Figure S3).

3.3 | Camouflage mismatch

The occurrence of camouflage mismatch varied between study areas and years (Figure 3, Supporting Information Figure S1, Table 4). White mismatch (white hare against snowless background) was relatively infrequent at all sites and occurred only during low snow years in New England and Colorado. Hares in New England experienced the highest frequency of white mismatch during both seasons (Table 4), with the highest proportions of camera days with white mismatch in fall 2015 (15%) and in spring 2016 (9%); seasons with 37–40 fewer snow days

than observed during 1980–2009 (Figure 3). Brown mismatch was rare in the New England population, with the exception of fall 2016, with 6% brown mismatch (Supporting Information Figure S1). Snowshoe hares in Colorado had lower proportions of white mismatch days than in New England but reached 7% in the fall of 2016, which had a very short snow season (Figure 3). In the springs, brown mismatch was more common than white mismatch in Colorado (Table 4). In Canada, white

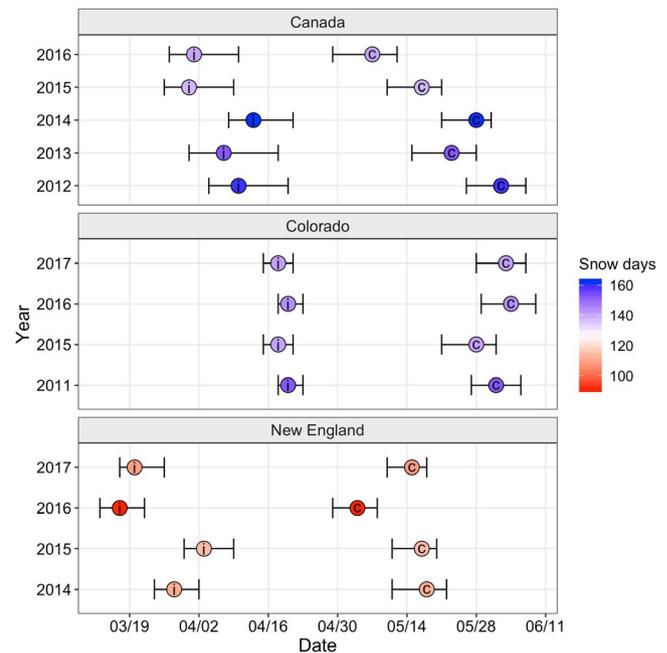


FIGURE 2 Estimated annual spring moult initiation (i) and completion (c) dates in the studied hare populations in Canada, Colorado and New England. Points show mean date estimates and are coloured by the annual duration of spring snow season (in days). Horizontal lines show 95% credible intervals (CRIs; overlapping CRIs identify same dates) [Colour figure can be viewed at wileyonlinelibrary.com]

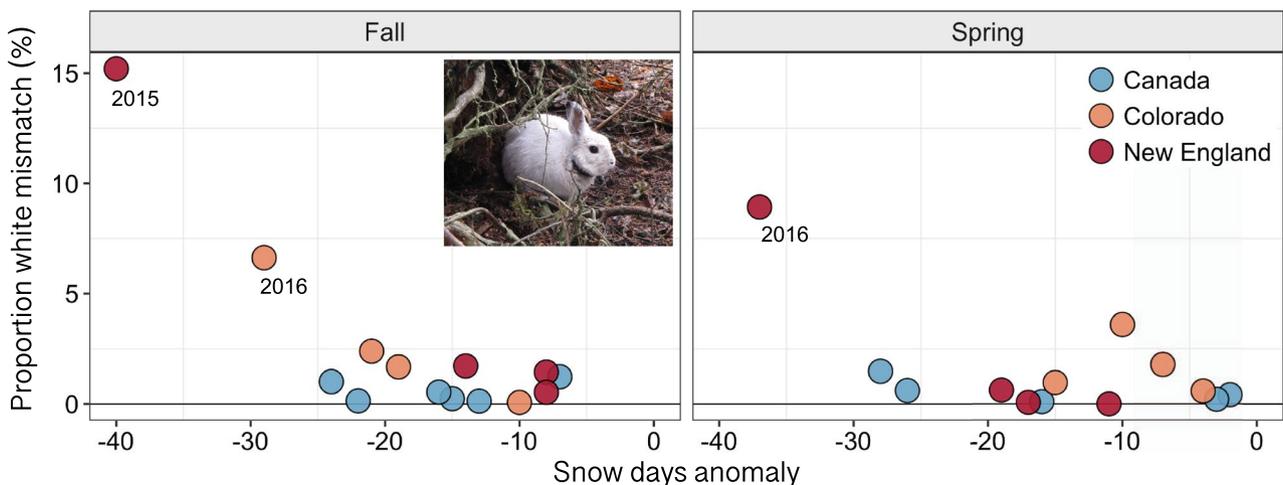


FIGURE 3 Annual proportions of camera days with white mismatch occurrences plotted against anomalies in the number of snow days each season in Canada, Colorado and New England. Study area-specific anomaly in the number of snow days was calculated for each year as the difference between the mean number of snow days during each season and the mean number of snow days during 1980–2009 at all camera sites. Seasons when hares experienced very high white mismatch are marked by the year inscriptions. Photo depicts white mismatched hare [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 4 Modelled mean percent of camera days with white and brown mismatch at each study area. Mean percent were calculated based on annual estimates (Canada: six falls and five springs, Colorado and New England: four springs and four falls). Standard deviations are given in parentheses

| | Canada | | Colorado | | New England | |
|--------|-------------|--------------|-------------|-------------|-------------|-------------|
| | White | Brown | White | Brown | White | Brown |
| Spring | 0.56 (0.55) | 11.96 (4.31) | 1.74 (1.34) | 6.39 (0.68) | 2.41 (4.36) | 0.98 (0.73) |
| Fall | 0.55 (0.47) | 9.54 (3.60) | 2.69 (2.80) | 1.11 (0.66) | 4.72 (7.00) | 2.42 (2.68) |

mismatch was very rare, exceeding 1% in only three out of the nine seasons of monitoring (Figure 3), but brown mismatch was frequent (Table 4, Supporting Information Figure S1).

4 | DISCUSSION

Using by-catch photographs from remote camera traps, we quantified the spatial and temporal variation in snowshoe hare moult phenology and camouflage mismatch across nearly the full range of environmental conditions experienced by the species. To our knowledge, this is the first study to evaluate these processes at such resolution in any seasonally moulting species. First, local climate conditions were the main drivers of spatial and temporal variation in moult phenology; hares in colder and snowier sites and in higher elevations moult later in the spring and earlier in the fall. Second, hare populations exhibited temperature- and snow-mediated plasticity in moult phenology; we found strong evidence of later spring- and suggestive evidence of earlier fall-moults during colder and or snowier years. Third, the occurrence of camouflage mismatch varied in space and time, but white mismatch was more common in areas characterized by shallow, short-lasting snowpack. Finally, because areas with shallow snowpack are expected to face the steepest declines in snow cover duration (Lute, Abatzoglou, & Hegewisch, 2015; Ning & Bradley, 2015), we conclude that hares occupying those southern edge portions of their range are the most vulnerable to camouflage mismatch under current and future climate change.

4.1 | Local climate drives variation in moult phenology

Our analysis based on 448 camera sites and spanning over 15 degrees of latitude showed that local climate influenced moult phenology in snowshoe hares (Figure 1). Mean phenology in both seasons structured strongly along elevational, temperature, and snow cover gradients. Similar findings were described for other phenological traits across taxa (e.g., migration, reproduction and hibernation) where phenology correlated with local variation in climate (e.g., Duursma, Gallagher, & Griffith, 2018; Fielding, Whittaker, Butterfield, & Coulson, 1999; Sheriff et al., 2011; While & Uller, 2014). As for seasonal colour moult phenology, local climatic factors have been previously described to determine phenology in colour moulting species including snowshoe hares (Grange, 1932; Zimova

et al., 2014), mountain hare (Watson, 1963), stoats (Feder, 1990) and rock ptarmigan (Salomonsen, 1939), although all were examined over relatively small spatial scales or conclusions were based on opportunistic observations and low sample sizes. Likewise, for multiple colour moulting species, the global distribution of genetically determined winter brown and winter white coat colour morphs is driven by variation in snow cover duration (Mills et al., 2018).

We found no evidence that moult phenology variation was distributed along a latitudinal (i.e., north-south) gradient. While the effects of climate and elevation were strong in both seasons, the effects of latitude were not detected in the fall and in the opposite direction than expected in the spring (i.e., during the spring moult, the probability of being brown increased with latitude, Table 2). We think that the positive effect of latitude in the spring was driven by spatial variation in climate; the southernmost study area, Colorado, was as cold as the northernmost area. Although our study lacked the spatial coverage to give a definite conclusion on the role of latitude in moult phenology variation, we showed that latitude alone cannot predict moult phenology across a species range. Future studies that include more replicates across the latitudinal gradient will help elucidate the interacting effects of latitude and local environmental conditions on seasonal moult phenology.

4.2 | Phenotypic plasticity in response to temperature and snow

We found that annual temperature and snow affect the moult phenology of snowshoe hares. However, this variation resulted in differences in population moult initiation and completion dates between years only in the spring (Figure 2). For example, hares in Canada became brown 21 days earlier in spring 2016, which was on average 2.9°C warmer (tmin) with a snow season 22 days shorter than spring 2014 (Figure 2 and Supporting Information Figure S2). Similar difference was observed between the same 2 years in New England, where the 2.4°C higher tmin and 21-day shorter snow season in spring 2016 than in 2014 corresponded with 11- and 14-day advances in moult initiation and completion dates, respectively (Figure 2 and Supporting Information Figure S2). In contrast, we did not detect any differences between the spring moult phenologies in the Colorado population during all years of monitoring (Figure 2). However, annual temperature and snow season length were less variable in Colorado than in the other two study areas (Supporting Information Figure S2). For example, the 11-day difference in snow duration and 1.3°C difference in

tmin between the two most extreme springs (2011 and 2015) might not have been sufficient to observe significant differences between phenology dates (Figure 2). To determine whether hares in Colorado have lower phenotypic plasticity or whether this finding was caused by lower inter-annual variation will require analyses of additional years across a wider range of climatic conditions.

We found some evidence for population-level phenotypic plasticity in the fall moult phenology (Table 3), but we did not detect significant differences between initiation or completion dates in any study area (Supporting Information Figure S3). Lower phenological plasticity in the fall than in the spring was previously described in least weasels and connected to lower variation in the fall than in the spring temperatures (Atmeh et al., 2018). In this study, the lower inter-annual variation in climatic conditions might have similarly contributed to the seasonal variation in plasticity in some cases (e.g., low variation in tmax in fall in Canada; Supporting Information Figure S2). However, in most cases, the inter-annual variation in temperature and snow at our study areas was comparable between spring and fall seasons (Supporting Information Figure S2). For example, snow season duration differed by up to 44 days and tmax by 2.3°C between the most extreme falls in New England (2015 and 2016; Supporting Information Figure S2), yet we observed no differences between moult phenology dates (Supporting Information Figure S3). Furthermore, low plasticity in the fall and a similar level of phenotypic plasticity in the spring as observed here were previously described

for individual snowshoe hares in the Rocky Mountains in Montana (i.e., 2–3 weeks in the spring; Mills et al., 2013; Zimova et al., 2014). However, in this study, the number of independent snowshoe hare colour observations was lower during the falls than in the springs at most of the sites (Table 1), which may have resulted in reduced statistical power to detect differences during this season.

Finally, we note that the methodology prevented phenology monitoring of the same individuals – and their fates – over multiple years. Therefore, we were unable to investigate to what extent natural selection against camouflage mismatch might have contributed to the observed differences in temporal variation moult phenology. Specifically, during the few very short snow duration years, natural selection might have removed highly mismatched individuals from the population and contributed to the observed shift in the phenological distribution. Quantifying the relative importance of natural selection and individual plasticity on population-level responses in phenology will require intensive field studies with tagged individuals over multiple years.

4.3 | Spatial variation in camouflage mismatch

We observed high variation in the number of snow days each year but, overall, snow cover duration has decreased over the last 30 years in all three areas (Supporting Information Figure S4; Fassnacht, Venable,

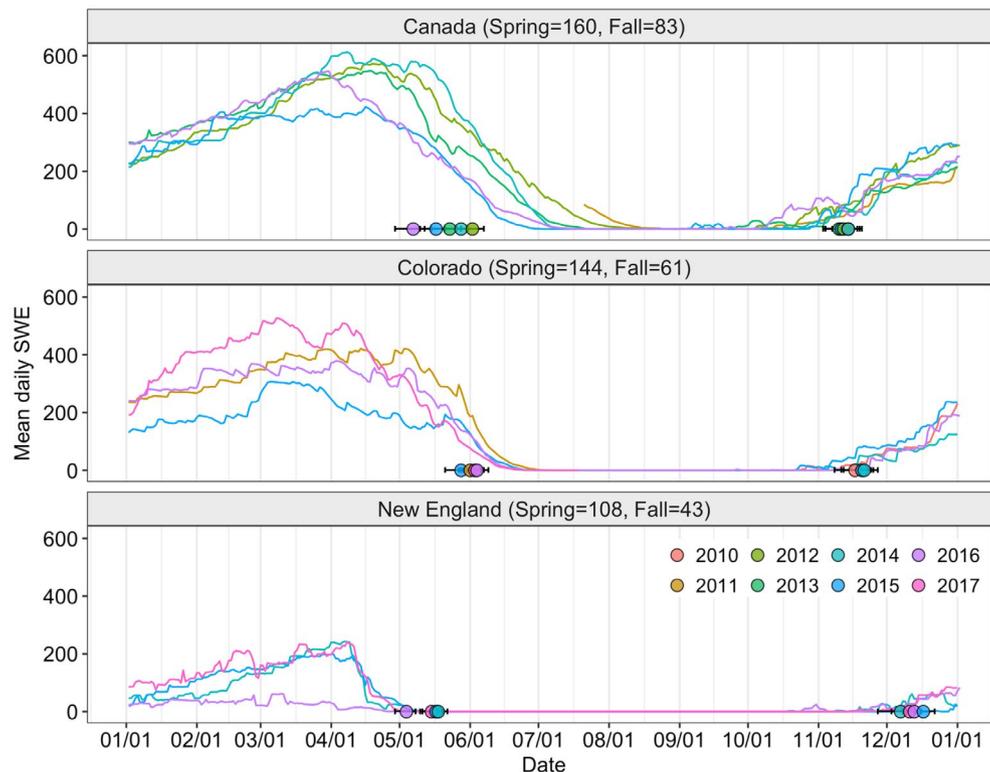


FIGURE 4 Mean daily snow water equivalent (SWE; mm) at the remote camera sites for the years of moult phenology monitoring. Coloured circles along the x axes indicate the population mean moult completion dates for each year, with spring moults on the left and fall moults on the right. Mean number of snow days for years of monitoring is given in facet titles for spring and fall [Colour figure can be viewed at wileyonlinelibrary.com]

McGrath, & Patterson, 2018; Harpold et al., 2012; Kunkel et al., 2016; Mote, Li, Lettenmaier, Xiao, & Engel, 2018; Ning & Bradley, 2015). The declines in snow cover manifested differently in each population, however. In the Canadian population, white mismatch was very low each year, while the number of snow days ranged from 1 to 28 fewer days than observed on average during 1980–2009 (Figure 3). This is likely due to the very deep, long-lasting snowpack in the study area (Table 1, Figure 4). For example, during the years of monitoring, spring snow season ended on average on 9 June (Figure 4), more than 2 weeks after hares finished their white-to-brown moults (i.e., moults initiated on 5 April and completed on 23 May; Figure 1b). Yet, annual snow season duration in the Canadian Rockies is predicted to decrease by about 1 month by the end of the century (Pomeroy, Fang, & Rasouli, 2015). Those predictions would advance average snowmelt to about 2 weeks prior to when hares become fully brown. Although increase in white camouflage mismatch will likely occur in very short snow years, based on our results a mean decrease of snow season by 1 month will unlikely lead to dramatic increases in the frequency of white hares on snowless background (see Figure 3).

In contrast, hares in Colorado and New England are much more vulnerable to white camouflage mismatch. For both populations, the proportion of white mismatch increased rapidly with fewer snow days, especially once the snow days anomaly exceeded 21 days (Figure 3). Beyond this 3-week threshold, hares began to experience elevated white mismatch (i.e., 15% in fall and 9% in spring in New England; 7% in fall in Colorado). This suggests that phenotypic plasticity in moult phenology is insufficient to buffer against the snow declines in those marginal areas where snow season is already short (Table 1, Figure 4). To contrast the New England study area with the previous example from Canada, the continuous snow season ended on average on 18 April (Figure 4) but hares underwent spring moults from 23 March to 13 May (Figure 1b). Therefore, with mean snowmelt occurring before hares are halfway through the moult, early snowmelt years (e.g., 2016 seasonal snow melted on 1 April; Supporting Information Figure S2) result in steep increases in white mismatch.

Based on our results, in the absence of evolutionary shifts in phenology, snowshoe hares in New England and Colorado will suffer drastic increases in white mismatch over the next century. In the Colorado study area, the frequency of low snow years is expected to increase and the annual snow season to decrease by 20–50 days (for comparison see mismatch in fall 2016, Figure 3) by mid-century (Lute et al., 2015). Similarly, in many parts of New England, snow cover duration is predicted to shorten from the current 5 months to 3 months by 2100 (Ning & Bradley, 2015). Under such projections, hare in both study areas will by the end of the century routinely experience the same amount of mismatch as they experienced during the very low snow years of fall 2016 in Colorado and 2015 in New England.

The pattern observed with white mismatch was somewhat mirrored by that of brown mismatch. In both seasons in New England and during the fall in Colorado, white mismatch was more frequent than brown mismatch as snow cover was more likely to be absent

when hares were white than vice versa (Figure 4). In contrast, during springs in Canada and Colorado, hares experienced long periods when they had already moulted to summer brown pelage, but snow was still present on the ground (Figure 4). Furthermore, the onset of snow during fall often occurred prior to hares completing their brown-to-white moults in Canada. Overall, the relatively high occurrence of brown camouflage mismatch, despite the recorded snow declines, was unexpected. Eventually, however, as climate change will continue to lead to shorter snow duration across most of the snowshoe hare range (Danco, DeAngelis, Raney, & Broccoli, 2016; Easterling et al., 2017; Fyfe et al., 2017), the occurrence of brown mismatch will decrease.

The relative fitness costs of white versus brown mismatch are unknown, but we suspect that white mismatch has a higher survival cost than brown mismatch based on our experience in the field, while locating radio-collared hares. First, brown animals and objects (e.g., branches, tree trunks, brown animals) are relatively common year-round, but white animals and objects are rare outside of winter. Perhaps due in part to this frequency difference in the two mismatch types, a white hare against a snowless background appears far more conspicuous than a brown hare resting on snow. Previous quantifications of survival costs were carried out for 'absolute mismatch', that is both white and brown mismatch combined (Wilson et al., 2018; Zimova et al., 2016). Nonetheless, as documented here and elsewhere (Wilson et al., 2018; Zimova et al., 2016), white mismatch is already high in some populations and will increase under climate change (Mills et al., 2013). Therefore, fitness costs of white and brown mismatch should be quantified to inform conservation efforts, notably in situ management actions that foster evolutionary rescue, or genetic rescue by assisted gene flow of individuals with pre-adapted moult phenologies or winter coat colour (Mills et al., 2018).

Understanding the spatial and temporal variation in phenological traits is critical for understanding the impact of climate change and species' adaptive potential to environmental stressors. Here, we showed that snowshoe hare moult phenology is determined by local climate, but populations vary in their susceptibility to camouflage mismatch. Snowshoe hares responded to annual variation in temperature and snow via some adjustments in moult phenology, but the buffering effects of phenotypic plasticity were diminished in populations distributed along the southern edge of their range. In those areas, characterized by mild climate and shallow, short-lived snowpack, climate change mediated snow declines led to higher phenological mismatch. Therefore, hares occupying southern, marginal areas will in the absence of rapid evolution experience steep increases in camouflage mismatch, as those areas are expected to experience the largest declines in snow cover duration (Fyfe et al., 2017; Ning & Bradley, 2015), consistent with theoretical expectations of range contraction (Sirén & Morelli, 2019). More generally, our results underscore that populations vary in their susceptibility to environmental stressors and management efforts should consider this intraspecific variation to identify populations most vulnerable under global environmental change (Hampe & Petit, 2005; Nadeau, Urban, & Bridle, 2017).

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DATA ACCESSIBILITY

The data used in this study are available at datadryad.org (<https://doi.org/10.5061/dryad.k98sf7m35>).

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BIOSKETCH

Marketa Zimova is a postdoctoral researcher interested in the effects of global environmental change on wild populations. The majority of her work aims to understand species adaptive potential to climate change and to yield useful information that can guide conservation and management decisions necessary for maintaining biodiversity. The research team includes scientists from the United States and Canada who study climate change and the ecology and evolutionary biology of wild organisms.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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