

Camouflage mismatch in seasonal coat color due to decreased snow duration

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Most examples of seasonal mismatches in phenology span multiple trophic levels, with timing of animal reproduction, hibernation, or migration becoming detached from peak food supply. The consequences of such mismatches are difficult to link to specific future climate change scenarios because the responses across trophic levels have complex underlying climate drivers often confounded by other stressors. In contrast, seasonal coat color polyphenism creating camouflage against snow is a direct and potentially severe type of seasonal mismatch if crypsis becomes compromised by the animal being white when snow is absent. It is unknown whether plasticity in the initiation or rate of coat color change will be able to reduce mismatch between the seasonal coat color and an increasingly snow-free background. We find that natural populations of snowshoe hares exposed to 3 y of widely varying snowpack have plasticity in the rate of the spring white-to-brown molt, but not in either the initiation dates of color change or the rate of the fall brown-to-white molt. Using an ensemble of locally downscaled climate projections, we also show that annual average duration of snowpack is forecast to decrease by 29–35 d by midcentury and 40–69 d by the end of the century. Without evolution in coat color phenology, the reduced snow duration will increase the number of days that white hares will be mismatched on a snowless background by four- to eightfold by the end of the century. This novel and visually compelling climate change-induced stressor likely applies to >9 widely distributed mammals with seasonal coat color.

phenotypic plasticity | snow downscaling | rhythm | phenological mismatch | threshold trait

Shifts in annual timing of life history events are a common response of plant and animal populations to climate change (1, 2). In many cases, these phenological shifts span multiple trophic levels, creating mistiming as animal reproduction (3), hibernation emergence (4, 5), or migration (6) become detached from peak timing of food or habitat structure (7). The consequences of such mismatches are difficult to link to specific outcomes under future climate change because the multitrophic level responses have complex underlying climate drivers that are often confounded by other anthropogenic stressors.

A much more direct phenological mismatch could occur for the nine or more widely distributed mammal species that molt seasonally from brown to white so that coat color tracks the presence of snow (Fig. 1). A decrease in the number of days with seasonal snow on the ground is one of the temperate region's strongest climate change indicators (8, 9). Because the circannual seasonal color polyphenism is likely regulated by photoperiod (10), an inflexible pattern of coat color change in the face of shortened snow seasons would presumably lead to increased mismatch between a winter white coat and a nonsnowy background. In the same way that cases of mismatch in animal camouflage are high profile (11), seasonal coat color mismatch produces a striking visual metaphor for direct effects of climate change (Fig. 2). This novel form of phenological mismatch due to climate change also leads to immediate implications for fitness and population persistence because coat color matching in mammals is known to be a critical form of crypsis from visually hunting predators (12).

We investigated whether current levels of plasticity in the initiation or rate of coat color change would be able to reduce mismatch between the seasonal coat color and an increasingly snow-free background expected in the future. Our target organism was wild snowshoe hares (*Lepus americanus*), a member of the most widespread genus showing seasonal coat color change (Fig. 1). Snowshoe hares are a key prey item in northern North America food webs and an essential prey for the US threatened Canada lynx (*Lynx canadensis*), making it an appropriate focal species for understanding functional mismatches among interacting species under climate change (13). Both individual behaviors and population dynamics of hares are overwhelmingly shaped by predation, which comprises 85–100% of mortality in different regions and different years (14). For example, hares move less and die more when illuminated to predator under a full moon on snow (15), and they tend to avoid risky canopy gaps within closed forests (16). At the population level, differences in adult survival in different stand structure types are sufficient to dampen population cycles in their southern range (17, 18).

The pervasive influence of predation on hares implies strong selection on their cryptic coloration (19) and against sustained seasonal mismatch in coat color (17, 20). Indeed, naturalists have long noted the remarkable concordance between phenology of hare seasonal coat color change and the presence of snow across elevational, latitudinal, and seasonal gradients (21–23).

Although local adaptation to reduced snow through natural selection is possible for any trait enduring a phenological mismatch, the most immediate adaptive solution to minimize seasonal color mismatch is through plasticity (3, 6, 24). For example, male rock ptarmigan (*Lagopus mutus*) exhibit behavioral plasticity to reduce conspicuousness by soiling their white plumage after their mates begin egg laying in spring, a phenomenon likely underlain by tradeoffs between sexual selection and predation risk (25). A more direct avenue for plasticity to reduce mismatch when confronted by reduced snow duration would arise from plasticity in the initiation date or the rate of the seasonal coat color molts. It is not known how much plasticity exists in these traits, nor how much seasonal color mismatch is expected in the future as snow cover lasts a shorter time in the fall and spring.

An evaluation of plasticity in response to changing snow conditions requires that the seasonal coat color trait be exposed to a wide range of snowpacks representative of past extremes and applicable to the future. We took advantage of a serendipitous triplet of consecutive winters (2010–2012) at our US Northern

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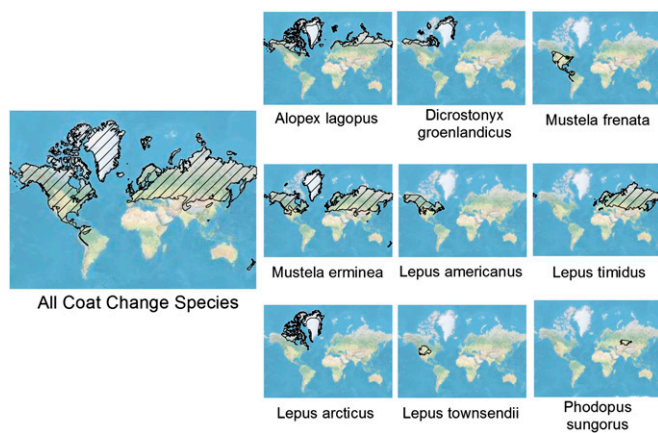


Fig. 1. Seasonally color changing species around the world. Geographical distributions of nine mammal species with seasonal coat color changes from brown to white in at least some populations. Species include Arctic fox (*Alopex lagopus*), collared lemming (*Dicrostonyx groenlandicus*), long-tailed weasel (*Mustela frenata*), stoat (*Mustela erminea*), snowshoe hare (*Lepus americanus*), mountain hare (*Lepus timidus*), Arctic hare (*Lepus arcticus*), white-tailed jackrabbit (*Lepus townsendii*), and Siberian hamster (*Phodopus sungorus*). Additional species with seasonal coat color change (e.g., least weasel; *Mustela nivalis*) are not shown. Maps derived from International Union for Conservation of Nature redlist metadata (www.iucnredlist.org/technical-documents/spatial-data#mammals).

Rockies study site in western Montana that spanned among the shortest and longest snow years in the recent past. We monitored 148 different snowshoe hares over the study period (43 different hares in 2010, 63 in 2011, and 58 in 2012), using radiotelemetry to locate hares weekly to quantify coat color phenology and the snow around each hare (*Materials and Methods*). The percentage of white color of hares and the percentage of snow cover within 10 m of each hare were quantified in 20% increments with a standardized protocol of observation and photographs. We classified animals that just initiated or nearly completed the molt as 5% or 95% white; rate of molt was based on the number of days between the initiation date and completion date. A hare was considered mismatched when the contrast between its coat color

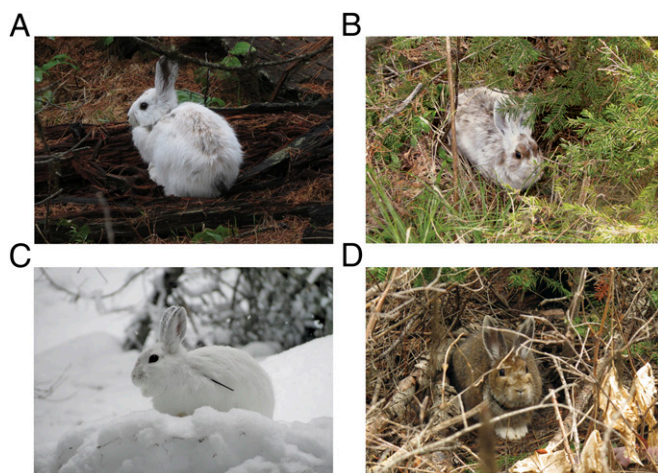


Fig. 2. Types of contrast between seasonal coat color and snow background. Radiocollared snowshoe hares from this study showing (A) 100% contrast (mismatch), (B) 60% contrast (mismatch), (C) 0% contrast (no mismatch), and (D) 0% contrast (no mismatch).

and background was at least 60% [mismatch = (hare % white – ground % white) \geq 60%].

We used a repeated-measures change point analysis (26) to estimate the population mean initiation and completion dates of hare coat color change for each of the 3 y (*Materials and Methods*). Bayesian credible intervals (analogous to frequentist confidence intervals) for the initiation and completion date of both spring and fall color molts were derived from the change point analysis, providing explicit statistical tests across years of the population reaction norm for initiation and rate of coat color change. Further, we used the model to test for other potential modifiers of the circannual coat color rhythm, including temperature, percent snow around hares, and sex.

To quantify how these 3 y differed in snow cover and how they compared with the recent past and expected future, we developed ecologically relevant downscaled snow duration and temperature models applicable to our study area (*Materials and Methods*). We modeled daily snow water equivalent (SWE) at our site for the recent past (1970–1999) and present (2010, 2011, and 2012) using a locally calibrated temperature-index snow model (27). The daily temperature and precipitation values needed to drive the model were estimated using a topographically informed interpolation of surrounding weather station observations (28). To quantify the rates of seasonal cooling and warming in the 3 y, we calculated a cumulative sum of degree days below 0 °C in the fall (September–December) and above 0 °C in the spring (March–June). Annual snow season duration was calculated as the longest annual period of temporally continuous snow cover from July to June.

To assay prospective snow conditions at our study site, we next drove the snow model using a change factor approach that perturbs observed interpolated weather station data for our site using an ensemble of climate projections. A total of 19 different climate models from the fifth phase of the Coupled Model Intercomparison Project (CMIP5) were used under two representative concentration pathways (RCPs) experiments including medium-low (RCP4.5) and high (RCP8.5) forcings (Table S1). Projected changes in average monthly temperature and precipitation, downscaled to our sites, were summarized and examined for two future 30-y time periods (“mid-century” for 2030–2059; “late-century” for 2070–2099) relative to a recent (1970–1999) baseline. The snow model was then driven separately for each of the 19 models and RCP scenarios producing a total of 38 different outcomes for both mid- and late-century (Fig. S1).

Results and Discussion

The three sampled years (2010, 2011, and 2012) spanned the range of snowpacks for the recent past (1970–1999 baseline) in terms of both number of days with snow on the ground (Fig. 3A) and SWE (Fig. 3B). Furthermore, the range of SWE across these years included the expected mean for the mid-century and for one of the two late-century forcing scenarios (Fig. 3B). Collectively, the retrospective and prospective snow modeling confirms that the three winters we sampled exposed the color polyphenism to drastic differences in snow amount and duration that approached the extremes of the recent past and to a lesser extent the future. These field conditions provided a powerful test, for a natural population, of the potential for plasticity in the circannual rhythm of coat color molt to reduce camouflage mismatch between white hares and increasingly brown backgrounds in the fall and spring.

Across these 3 y with vastly different snow conditions, the initiation date of the color molts was fixed both in the fall and spring (overlapping Bayesian confidence intervals among annual initiation dates across the 3 y; Fig. 4A and Fig. S2), consistent with a photoperiod driver for this circannual trait (2). Also, the rate of coat color change (number of days between initiation and

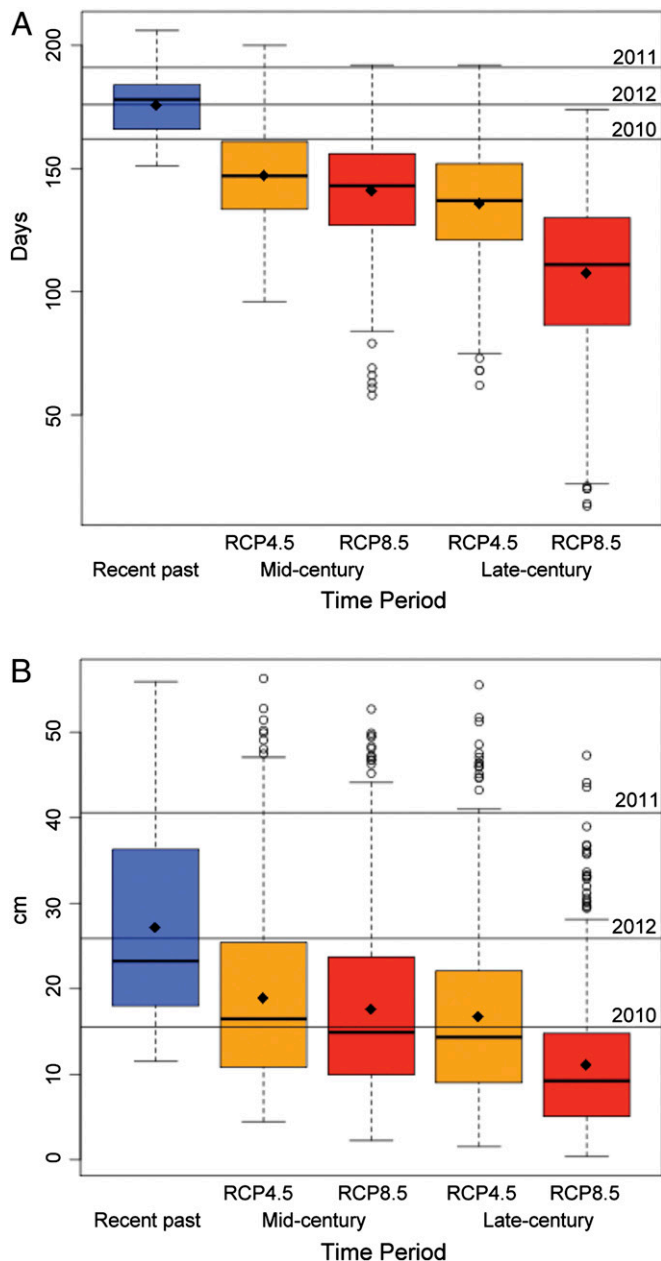


Fig. 3. Modeled baseline and future snow conditions. *(A)* Length of the main snow season for the three observation years (black horizontal lines) and boxplots of snow season length for the recent past (1970–1999) baseline (blue shading) and future time periods (mid-century, 2030–2059; late-century, 2070–2099) and emissions scenarios (orange shading, RCP4.5; red shading, RCP8.5). Future boxplots represent entire population of results from 19-member climate model ensemble. Bold horizontal lines are the median, and diamonds are the mean. *(B)* is the same as *A* except for annual maximum snow water equivalent.

completion dates) in the fall was fixed (overlapping confidence intervals among completion dates; Fig. 4*A*), taking about 40 d each year for hares to transition from brown to white. In contrast to initiation dates and the fall rate of change, plasticity in the rate of color change was apparent in spring (nonoverlapping confidence intervals among completion dates); in concert with the substantially longer snow season in 2011, hares completed the molt from white to brown 16 d later in 2011 compared with 2010 (Figs. 3*A* and 4 and Fig. S2).

The fixed initiation dates of molt, with plasticity only in spring rate of molt from white to brown, would result in increased coat color mismatch as snow seasons shorten under future climate change. Our ensemble prospective snow modeling results indicate that, relative to the recent past, for a medium-low (high) emissions scenario, the duration of the main winter snowpack at our study site will be 29 d (35 d) shorter by the mid-century and 40 d (69 d) shorter by the late-century (Figs. 3*A* and 5). Consistent with previous observational and sensitivity analyses of North American snow cover (8, 29), this projected decrease in snowpack duration is dominated by changes in spring snow cover (Fig. 5).

Linking this decreased snow duration to our average observed hare phenology and conservative definition of mismatch ($\geq 60\%$ difference between hare coat color and snow cover) translates the reduced snow days into a measure of future mismatch between white hares and brown ground: without an evolved shift in initiation of the seasonal molt, coat color mismatch of white hares on brown snowless backgrounds will increase by as much as fourfold by the mid-century and by eightfold by the late-century under the high emission scenario (Fig. 5 and Table S2).

With the expected compromised camouflage due to lack of plasticity in molt initiation dates and only limited plasticity in spring rate of color molt, key unresolved questions include the environmental variables that underlie the plasticity in the rate of the white-to-brown coat color molt in spring, and more generally the potential to modify the circannual rhythm of seasonal coat color molt through genetic and epigenetic mechanisms (30). Environmental drivers of the reaction norm of coat color molt are unknown; however, other circannual processes synchronized by photoperiod may be affected by modifiers such as temperature and snow presence (31). Our simple indices describing temperature and snow presence in our natural hare populations appeared to rank consistently with rate of spring molts across the 3 y; for example, molt from white to brown was slowest in spring 2011, which was both the coldest spring of the 3 y and had the longest lasting snowpack (Figs. 3 and 4). In the statistical models, however, the biological effects across individuals and years for these putative modifiers were relatively small (*Materials and Methods*). For the coat color phenology model with percent snow as a covariate, a change from 100 to 0% snow shifted the average completion date of molt from white to brown by only 4 d. Similarly, the coat color phenology model with temperature (degree days) as a covariate predicted that the span from 0 °C to 15.4 °C (the highest daily average temperature during the spring molt period) explains only a 3-d modification of the completion date of molt from white to brown. In comparison with the 16-d difference between completion dates between springs 2010 and 2011, these indices appear to be minimally informative as drivers of the reaction norm in the rate of spring coat color molt. Interestingly, the rate of molt in the spring was substantially influenced by sex, with females completing the spring molt on average 11 d earlier than males. The faster color molt for females is consistent with previous observations (32, 33).

As a threshold trait with distinct initiation and rate components that determine crypsis, coat color mismatch is a more direct climate change-induced phenological stressor than the trophic-level asynchronies usually discussed. The compelling image of a white animal on a brown snowless background can be a poster child for both educational outreach and for profound scientific inquiry into fitness consequences, mechanisms of seasonal coat color change, and the potential for rapid local adaptation.

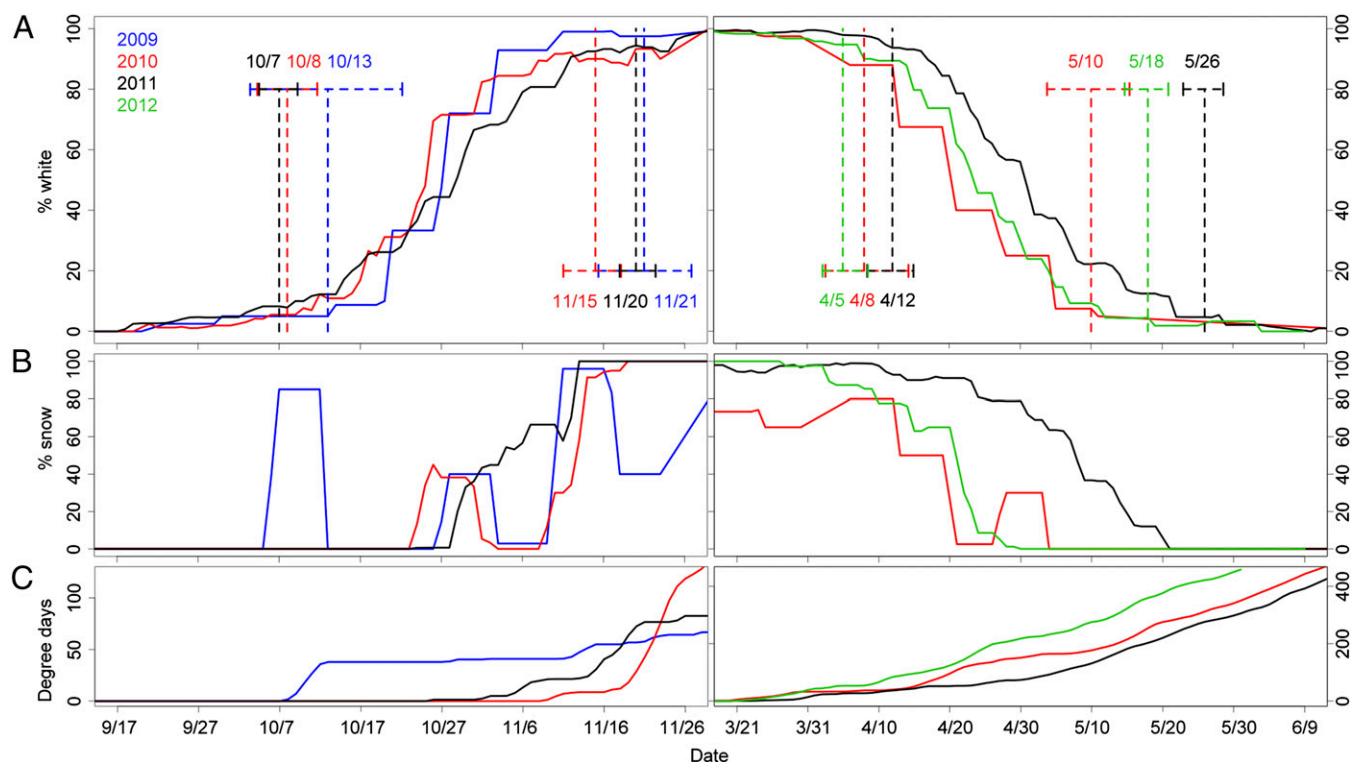


Fig. 4. Coat color phenology, snow cover and degree days. (A) Weekly average of observed coat color for a population of wild snowshoe hares in each of 3 y [2009 (blue), 2010 (red), 2011 (black), and 2012 (green)], with fall seasons on the *Left* and springs on the *Right*. Dotted lines show the results of Bayesian change point analyses, giving the 95% credible intervals for the mean dates of initiation and completion of the color molt for each season each year. (B) Weekly average of observed snow cover in a 10-m radius around each wild hare for each of the 3 y (fall on *Left* and spring on *Right*). (C) Degree days as a measure of cooling trend in the fall and warming trend in the spring at our study site for each of the 3 y.

Materials and Methods

Field Methods. The study area (Morrell Creek) is located in the US Northern Rockies near Seeley Lake, Montana at an elevation of about 1,400 m (latitude 47.23°, longitude -113.43°). The area is temperate boreal coniferous forest comprising an array of uncut and harvested stands mostly on US Forest Service lands that are largely unpopulated. Hare densities in this region vary but tend to be less than two hares per ha (34). Snowshoe hares were live-trapped using Tomahawk traps (Tomahawk Live Trap Company, Tomahawk, WI) and fitted with radiocollars (Wildlife Materials, Murphysboro, IL) (17). All handling procedures were in accordance with the University of Montana Institutional Animal Care and Use Committee animal use protocol (Protocol no. 021-10SMWB-051110). We monitored weekly 148 radiocollared hares over the study periods (43 different hares in 2010, 63 in 2011, and 58 different hares in 2012). As animals died, new individuals were radiocollared, year-round and throughout the study. Wild snowshoe hares generally have low annual survival rates (17, 35), limiting the expression of individual plasticity across >1 y. Of our 148 different animals monitored, only 7 survived for >1 fall or spring molt and only one survived for >1.5 y after collaring; because of incomplete detection and temporary emigration of radiocollared animals, we were not able to document consecutive spring or fall molts for any of these 7 hares.

Molt Phenology Analysis. We used a repeated-measures change point analysis to estimate the initiation date and rate of coat color change. Change point analyses are similar to standard linear mixed models such as ANOVA with the addition of a parameter estimating the timing of a change in pattern (i.e., molt initiation date). We considered individual hares to be the primary sampling unit (random effects) with repeated measures through time of coat color for each hare. Because hare mortality, temporary emigration, and incomplete detection punctuate individual hare phenologies, and new individuals must be staggered into the analysis as others die, we chose to fit the model with Bayesian methods to more cleanly handle the random effect of individual hares than could be done with maximum likelihood.

We fit the change point regression model with Markov chain Monte Carlo (MCMC) in WinBugs (36). Inference was made from five chains of 100,000

MCMC iterations after discarding 10,000 burn-in iterations. We used the Gelman-Rubin statistic to test for chain convergence, which was achieved ($R \leq 1.1$ for all datasets). Slopes of the regression line between initiation date and after completion date were fixed to zero (0% white in summer and 100% white in winter). To quantify phenology of coat color change across days for each year, we included in the model parameters for initiation date (change point in the fixed slope) and slope of the change, and ran models separately for each combination of observed season (fall and spring) and year (2009, 2010, 2011, and 2012). Completion date was derived from the regression line as the date it reaches the slope fixed at zero [fall completion date = $100/(\beta + \text{initiation date})$; spring completion date = $-100/(\beta + \text{initiation date})$]. Resulting means and credible intervals (the Bayesian analog of confidence intervals) (as shown in Fig. 4A) were used to test for statistically significant differences between years in initiation and completion dates and slopes of change. Further, the posterior probability distributions of the derived parameters confirmed the significant differences between years (Fig. S2).

Next, we ran a series of change point regression models using spring data pooled across the 3 y to determine the effect of each of the following covariates on the rate of the molt: snow (% snow cover within 10-m radius around each individual hare on the date coat color was measured), temperature (sum of daily averages above 0 °C), and sex. The effect size of these covariates on the rate of the molt (number of days between the initiation and completion date) was then derived from how the slope of the molt changed across the range of the covariate [molt rate = $(-100 - \beta_1 \times \text{covariate value})/\beta$], where β indicates the slope of the molt and β_1 indicates the slope of a covariate. The range of values for the snow was 0–100% snow ($\beta_1 = 0.093$, $sd = 0.02$) and for temperature was from 0 °C to 15.4 °C (i.e., highest daily maximum during spring) ($\beta_1 = -0.354$, $sd = 0.015$). Sex was binary (1, females; 0, males) ($\beta_1 = -25.640$, $sd = 10.263$).

Future Coat Color Mismatch. To estimate the increase in mismatch extent under future snow conditions, we used average observed phenology of hares across the 3 y of study to calculate the number of days during which hares would be mismatched during the recent past, and in the future (mid-century and late-century) (Table S2). We explored the sensitivity of our threshold

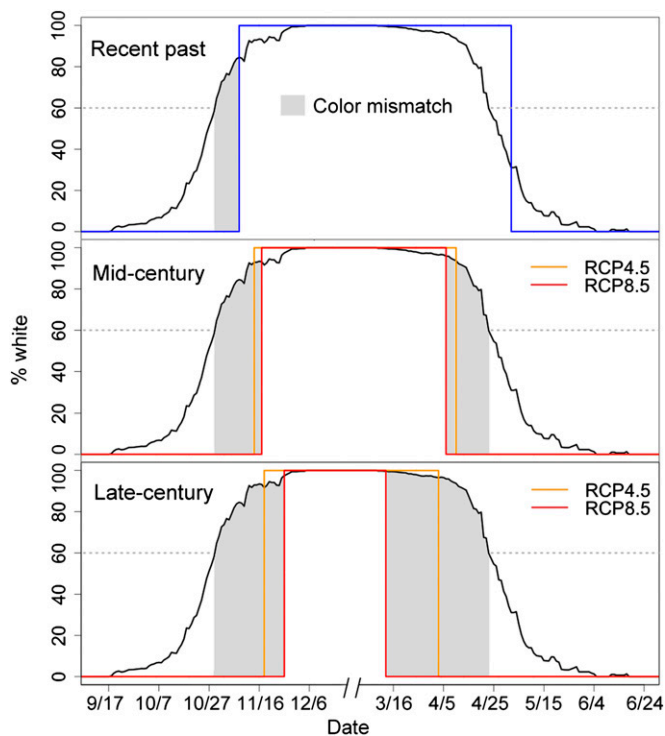


Fig. 5. Projections of increasing seasonal color mismatch in the future. The black line for all panels shows average phenology of hare seasonal color molt across the 3 y of the field study. The blue line shows mean modeled snow duration for the recent past (1970–1999). The orange and red lines show the future (mid-century and late-century) mean modeled snow duration for different emissions scenarios. The gray highlighted regions represent coat color mismatch, where white hares ($\geq 60\%$) would be expected on a snowless background. As the duration with snow on the ground decreases in the future, mismatch will increase by as much as fourfold in the mid-century and eightfold in the late-century.

defining mismatch (60% white hare on a snowless background) by also projecting number of days of mismatch using 40% and 80% thresholds (Table S3).

- Forrest J, Miller-Rushing AJ (2010) Toward a synthetic understanding of the role of phenology in ecology and evolution. *Phil Trans R Soc B Biol Sci* 365(1555): 3101–3112.
- Visser ME, Caro SP, van Oers K, Schaper SV, Helm B (2010) Phenology, seasonal timing and circannual rhythms: Towards a unified framework. *Phil Trans R Soc B Biol Sci* 65 (1555):3113–3127.
- Reale D, McAdam AG, Boutin S, Berteaux D (2003) Genetic and plastic responses of a northern mammal to climate change. *Phil Trans R Soc B Biol Sci* 270(1515): 591–596.
- Ozgul A, et al. (2010) Coupled dynamics of body mass and population growth in response to environmental change. *Nature* 466(7305):482–485.
- Lane JE, Kruuk LEB, Charmantier A, Murie JO, Dobson FS (2012) Delayed phenology and reduced fitness associated with climate change in a wild hibernator. *Nature* 489(7417): 554–557.
- Both C, Visser ME (2001) Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. *Nature* 411(6835):296–298.
- Martin TE, Maron JL (2012) Climate impacts on bird and plant communities from altered animal-plant interactions. *Nature C C* 2(3):195–200.
- Brown RD, Mote PW (2009) The response of Northern Hemisphere snow cover to a changing climate. *J Clim* 22(8):2124–2145.
- Pederson GT, et al. (2011) The unusual nature of recent snowpack declines in the North American cordillera. *Science* 333(6040):332–335.
- Lincoln GA, Clarke IJ, Hut RA, Hazlerigg DG (2006) Characterizing a mammalian circannual pacemaker. *Science* 314(5807):1941–1944.
- Cuthill IC, et al. (2005) Disruptive coloration and background pattern matching. *Nature* 434(7029):72–74.
- Caro T (2005) The adaptive significance of coloration in mammals. *Bioscience* 55(2):125–136.
- Traill LW, Lim MLM, Sodhi NS, Bradshaw CJA (2010) Mechanisms driving change: altered species interactions and ecosystem function through global warming. *J Anim Ecol* 79(5): 937–947.

Snow and Climate Modeling. Daily SWE was modeled at the site from 1970 to 2012 using a form of the soil water assessment tool (SWAT) temperature-index snowfall-snowmelt model (27) with modifications to the calculation of a snowmelt rate factor (37). Model parameters were calibrated to 23.5 y (1989–2012) of daily SWE observations from a nearby snow telemetry (SNOTEL) weather station 25 km to the west (Table S4). Interpolation of daily temperature and precipitation from surrounding weather stations was conducted via empirically modeling the effect of elevation on temperature and precipitation (28). A total of 41 surrounding stations from 7 to 91 km from the site were used to interpolate temperature whereas 38 stations from 7 to 89 km away were used for precipitation.

Compared with site observations, the annual modeled snow on date (first day of the snow season) was 2, 2, and 4 d too late in fall 2009, 2010, and 2011, respectively. The annual modeled snow off date (last day of the snow season) was 12 d too early in spring 2010, 1 d too late in spring 2011, and 4 d too early in spring 2012. The larger difference between the model and observations in spring 2010 was mainly due to a late spring snowfall. Observed snow cover was 2.5% on April 24th, close to the modeled snow off date of April 22nd, but then new snowfall extended the season to May fourth before snow cover reached 0% (Fig. 3B).

Climate projections from 19 CMIP5 models were summarized by projected change in average monthly minimum temperature, maximum temperature, and precipitation in the mid-century (2030–2059) and late-century (2070–2099) relative to the recent past (1970–1999) using inverse distance weighting from the native resolute of each climate model to the study area. Projected changes for both the representative concentration pathways RCP4.5 (moderate-low emissions scenario) and RCP8.5 (high emissions scenario) were applied to the daily interpolated historical temperature and precipitation values to statistically downscale the projections to the site. This type of downscaling removed possible climate model bias, but assumed that future weather would have the same variability as the recent past. The locally calibrated snow model was run for each 30-y future time period, climate model, and RCP combination to test the degree to which future snow conditions could change at the site.

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- Hodges KE (2000) In *Ecology and Conservation of Lynx in the United States*, eds Ruggiero L, et al. (Univ Press of Colorado, Boulder, CO), pp 163–206.
- Griffin PC, Griffin SC, Waroquiers C, Mills LS (2005) Mortality by moonlight: Predation risk and the snowshoe hare. *Behav Ecol* 16(5):938–944.
- Hodson J, Fortin D, Belanger L (2010) Fine-scale disturbances shape space-use patterns of a boreal forest herbivore. *J Mammal* 91(3):607–619.
- Griffin PC, Mills LS (2009) Sinks without borders: Snowshoe hare dynamics in a complex landscape. *Oikos* 118(10):1487–1498.
- Wirsing AJ, Steury TD, Murray DL (2002) A demographic analysis of a southern snowshoe hare population in a fragmented habitat: Evaluating the refugium model. *Can J Zool* 80(1):169–177.
- Stevens M, Merilaita S (2009) Animal camouflage: Current issues and new perspectives. *Phil Trans R Soc B Biol Sci* 364(1516):423–427.
- Litvaitis JA (1991) Habitat use by snowshoe hares, *Lepus americanus*, in relation to pelage color. *Can Field Nat* 105(2):275–277.
- Grange WB (1932) The pelages and color changes of the snowshoe hare, *Lepus americanus phaeonotus* Allen. *J Mammal* 13(2):99–116.
- Flux JEC (1970) Colour change of mountain hares (*Lepus timidus-scoticus*) in north-east Scotland. *J Zool* 162:345–358.
- Watson A (1963) The effect of climate on the colour changes of mountain hares in Scotland. *Proc Zool Soc Lond* 141(4):823–835.
- Charmantier A, et al. (2008) Adaptive phenotypic plasticity in response to climate change in a wild bird population. *Science* 320(5877):800–803.
- Montgomerie R, Lyon B, Holder K (2001) Dirty ptarmigan: Behavioral modification of conspicuous male plumage. *Behav Ecol* 12(4):429–438.
- Thomson JR, et al. (2010) Bayesian change point analysis of abundance trends for pelagic fishes in the upper San Francisco Estuary. *Ecol Appl* 20(5):1431–1448.
- Fontaine TA, Cruickshank TS, Arnold JG, Hotchkiss RH (2002) Development of a snowfall-snowmelt routine for mountainous terrain for the soil water assessment tool (SWAT). *J Hydrol (Amst)* 262(1–4):209–223.

28. Thornton PE, Running SW, White MA (1997) Generating surfaces of daily meteorological variables over large regions of complex terrain. *J Hydrol (Amst)* 190(3-4):214-251.
29. Choi G, Robinson DA, Kang S (2010) Changing Northern Hemisphere snow seasons. *J Clim* 23(19):5305-5310.
30. Franks SJ, Hoffmann AA (2012) Genetics of climate change adaptation. *Annu Rev Genet* 46:185-208.
31. Larkin JE, Freeman DA, Zucker I (2001) Low ambient temperature accelerates short-day responses in Siberian hamsters by altering responsiveness to melatonin. *J Biol Rhythms* 16(1):76-86.
32. Aldous CM (1937) Notes on the life history of the Snowshoe Hare. *J Mammal* 18(1):46-57.
33. Severaid JH (1945) Pelage changes in the snowshoe hare (*Lepus-americanus struthopus bangs*). *J Mammal* 26(1):41-63.
34. Mills LS, et al. (2005) Pellet count indices compared to mark-recapture estimates for evaluating snowshoe hare density. *J Wildl Manage* 69(3):1053-1062.
35. Krebs CJ, et al. (1995) Impact of food and predation on the snowshoe hare cycle. *Science* 269(5227):1112-1115.
36. Spiegelhalter DJ, Thomas A, Best NG, Gilks WR, Lunn D (2003) *WinBugs: Bayesian Inference Using Gibbs Sampling* (MRC Biostatistics Unit, Cambridge, UK).
37. Debele B, Srinivasan R, Gosain AK (2010) Comparison of process-based and temperature-index snowmelt modeling in SWAT. *Water Resour Manage* 24(6):1065-1088.