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CAMOUFLAGE MISMATCH IN SEASONAL COAT COLOR DUE TO DECREASED  
SNOW DURATION: WILL SNOWSHOE HARES KEEP UP WITH CLIMATE CHANGE?

By

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B.S., Charles University, Prague, Czech Republic, 2009

Thesis

presented in partial fulfillment of the requirements

for the degree of

Master of Science  
in Wildlife Biology

The University of Montana  
Missoula, MT

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**Title:** Camouflage mismatch in seasonal coat color due to decreased snow duration: Will snowshoe hares keep up with climate change?

Chairperson: Dr. L. Scott Mills

### ABSTRACT

As wild species face anthropogenic stressors, they will either adapt, shift their geographic range, or decline, perhaps towards extinction. The relative scope of these responses has not been well studied, especially for climate change where geographic range shifts and population declines have been widely discussed but the potential for adaptation mostly ignored. Adaptation to anthropogenic stressors can occur through phenotypic plasticity and/or evolution. My thesis first establishes, based on field studies of wild snowshoe hares, a novel and high-profile stressor directly linked to climate change. The stressor arises from a decrease in snow duration due to climate change, which causes seasonal coat color molt of individual hares to become mismatched with their background. The immediate adaptive solution to this form of camouflage mismatch is phenotypic plasticity, either in phenology of seasonal color molts or in behaviors that reduce mismatch or its consequences. Based on nearly 200 snowshoe hares across a wide range of snow conditions and two study sites in Montana, USA that differed in elevation and climate, I found minimal plasticity in response to mismatch between coat color and background. I found that molt phenology varied between study sites, likely due to differences in photoperiod and climate, but was largely fixed within study sites where seasonal changes in phenology were limited across years of very different snow duration. Hares exhibited some plasticity in the rate of the spring molt in response to immediate snow conditions but temperature or snow cover were not strong modifiers of the white-to-brown molt phenology. I also found no evidence that individual hares modify their behavior in response to color mismatch. Hiding and fleeing behaviors and immediate microsite preference of hares were more affected by variables related to season, site, and concealment, than by color mismatch. Although hares do not appear to be responding to camouflage mismatch with behavioral plasticity, adaptation could also occur through evolutionary changes facilitated by natural selection. We found that the raw material for natural selection to act on does exist in our populations in the form of individual variation in coat color phenology and consequently in color mismatch. We also found high fitness costs of coat color mismatch, with hares suffering 3 to 7% lower weekly survival rates when mismatched against their background. Coupling these fitness costs to local estimates of increased seasonal color mismatch as snow duration decreases in the future, we predict that annual hare survival will decline up to 12% by mid- and 24% by late century. Such changes in survival are sufficient to cause increasing hare populations to decline strongly towards extinction, with annual population geometric growth rate decreasing by 11% (24%) by mid (late) century. We conclude that plasticity in molt phenology and behaviors in snowshoe hares is insufficient for adaptation to camouflage mismatch, and that potential adaptive responses to future climate change will have to be facilitated by natural selection. These results form the basis for future work to evaluate whether evolution by natural selection can operate fast enough to prevent decline of this species.

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## CHAPTER 1: INTRODUCTION

The warming of the climate system and its effects on organisms are unequivocal. Global mean air temperatures have risen by about 0.74°C over the last 100 years and the warming is expected to accelerate in the future (Solomon et al. 2007). In temperate regions the rises in air temperatures is reducing duration of snow cover, with later onset of snow in the fall and earlier loss of snow in the spring (Brown and Mote 2009, Pederson et al. 2011, Kapnick and Hall 2012). The decreased duration of snowpack represents a new, potentially severe stressor for at least eleven animal species undergoing seasonal coat color molts.

In ecosystems with seasonal snow cover, color molting from brown to white presumably provides background matching, a form of crypsis that minimizes color contrast between the animals and their surroundings. Snowshoe hares (*Lepus americanus*), a key prey species of boreal forests, undergo seasonal coat color molts to avoid predator detection. The mistiming between ground snow cover presence and photoperiod-induced color molts results in camouflage mismatch during spring and fall. White animals on non-snowy background (or vice versa) are extremely conspicuous and would appear to be easier to detect by a visually hunting predator.

Seasonally molting species, including snowshoe hares, may successfully respond to camouflage mismatch by individual phenotypic plasticity or evolution. Phenotypic plasticity, the range of phenotypes expressed by a genotype in different environmental conditions, is the most immediate adaptive solution to the rapid pace of climate change (Gienapp et al. 2008). In some cases, plasticity in circannual behavior and other traits has explained most of the observed change in phenology (Przybylo et al. 2000, Valtonen et al. 2011) and has been shown to maintain or increase fitness (Berteaux et al. 2004, Charmantier et al. 2008, Ozgul et al. 2010). The obvious adaptive solution to decreased snow cover would be to adjust the phenology of the color molts to the changed snow conditions.

Another form of phenotypic plasticity in response to color mismatch or its potential costs would be individual adjustments in certain anti-predatory behaviors. Ptarmigans (*Lagopus lagopus* and *L. mutus*), a widely distributed color molting species, modify their behaviors in response to color mismatch (Steen et al. 1992, Montgomerie et al. 2001). Snowshoe hares rely strongly on their crypsis to avoid predation; they sit completely still with minimal attempts at hiding or concealment and do not flee until immediate danger arises. Intuitively, this strategy is maladaptive when selection of a microsite results in mismatch between coat color and background. One possible behavioral modification that could reduce camouflage mismatch is selection of microsites that match the hares' coat color. Alternatively, mismatched hares might achieve effective camouflage by selecting sites associated with cover provided by dense understory, trees, or rocks. Finally, because hares rely on both crypsis and flight, mismatched hares may increase the distance at which they flee when approached by a predator, thus minimizing the potential consequences of camouflage mismatch.

Separate from or in combination with phenotypic plasticity, color molting species may adapt to camouflage mismatch through natural selection. Adaptive changes on the genetic level have successfully facilitated adaptation to recent climate change (Nussey et al. 2005, Bradshaw and Holzapfel 2008). Evolution of a trait proceeds fastest when populations are under strong selection and when the trait is variable and heritable. For hares, the selective cost of mismatch is unknown but expected to be strong, as previous research on mice demonstrated high fitness costs and strong selection against contrasting coloration (Dice 1947, Kaufman 1974, Linnen et al. 2009, Vignieri et al. 2010). Further, considerable variation in the seasonal coat color in hares at the individual and population level suggests the potential for natural selection. Both the timing and rate of the molts varies between individuals (Grange 1932, Aldous 1937, Severaid 1945). At the population level, snowshoe hares (and indeed other species with seasonal coat color change [Hall 1951, Hewson 1958, Hansen and Bear 1963]) show geographic variation in seasonal coat color, indicating local adaptation

to regions with less predictable winter snow. Snowshoe hares on the Pacific coast (coastal Washington and Oregon, U.S. and southern British Columbia, Canada), maritime areas without continuous winter snow cover, retain brown coat color all year (Dalquest 1942, Nagorsen 1983). Finally, the heritable component of molt phenology is not well established, but limited captive studies indicate a strong genetic component of molt initiation (Severaid 1945).

In my Master's thesis I describe color mismatch between snowshoe hares' coat color and their surroundings, and provide an evaluation of hares' adaptive potential to this novel climate change induced stressor. This thesis consists of an appendix and two main chapters. The appendix, published in 2013, identifies color mismatch in hares as a new form of seasonal mistiming induced by climate change, provides an evaluation of phenotypic plasticity in the phenology of the color molts, and projects future frequencies of color mismatch under different climate change scenarios. The paper depends strongly on data collected during my M.S. research and is the first description of the seasonal coat color change phenomenon. The reason this paper is not a main chapter of my thesis is that my advisor (L.S. Mills) is the primary author, because he began work on this topic before I became his student.

In Chapter 2, I extend the exploration of phenotypic plasticity in coat color molt phenology to an independent replicate study site and conduct additional analysis of modifiers of molt phenology. I then examine for the first time how snowshoe hares' anti-predatory behaviors may be modified in response to color mismatch. Collectively, this chapter evaluates the adaptive potential of snowshoe hares to minimize color mismatch and its consequences through phenotypic plasticity.

Finally, to complete the evaluation of hares' adaptive potential, in Chapter 3, I quantify the fitness costs of color mismatch. I first describe the current levels of individual variation in coat color molt phenology and consequently in the degree of color contrast over time between individuals and their surroundings. I then test a series of hypotheses to quantify the fitness costs of

color contrast using innovative approaches to model and accommodate for the weekly varying individual color contrast variable. Lastly, I simulate future survival rates under downscaled snow cover reduction scenarios using the estimated fitness cost of color contrast and projected frequencies of color contrast resulting from future reductions in snow cover duration.

Overall, this research enhances our knowledge on how an ecologically important species is affected by a novel stressor and enables us to predict how it will respond. The focus is on adaptive potential of snowshoe hares to a newly identified phenological mismatch induced by climate change, but the methods and implications are much more general. At least eleven other color molting species (including arctic fox [*Vulpes lagopus*] and several species of weasels [*Mustelidae spp.*]), collectively distributed across the temperate and arctic regions of the planet, are likely experiencing camouflage mismatch. The research methods and results described here can be directly applied to, or motivate research on, any other color molting species. At a broader level, this work addresses the question of how much a species can adapt in place to climate change and what mechanisms can facilitate its adaptive response. Finally, due to the high visual appeal of this research, it lends itself to fostering awareness and enhancing public knowledge of potential impacts and responses of wildlife to climate change.

The following thesis chapters are formatted for publication in peer-reviewed scientific journals. As all of the work contained in this thesis reflects the efforts of many important collaborators (see Acknowledgements section above), I use the collective “we” throughout the thesis.



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## CHAPTER 2

**Title:** Snowshoe hares display limited phenotypic plasticity to mismatch in seasonal camouflage.

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**Summary:** As duration of snow cover decreases due to climate change, species undergoing seasonal colour moults can become colour mismatched with their background. The immediate adaptive solution to this mismatch is phenotypic plasticity, either in phenology of seasonal colour moults or in behaviours that reduce mismatch or its consequences. We observed nearly 200 snowshoe hares across a wide range of snow conditions and two study sites in Montana, USA, and found minimal plasticity in response to mismatch between coat colour and background. We found that moult phenology varied between study sites, likely due to differences in photoperiod and climate, but was largely fixed within study sites with only minimal plasticity to snow conditions during the spring white-to-brown moult. We also found no evidence that hares modify their behaviour in response to colour mismatch. Hiding and fleeing behaviours and resting spot preference of hares were more affected by variables related to season, site, and concealment by vegetation, than by colour mismatch. We conclude that plasticity in moult phenology and behaviours in snowshoe hares is insufficient for adaptation to camouflage mismatch, suggesting that any future adaptation to climate change will require natural selection on moult phenology or behaviour.

**Key words:** crypsis, concealment, flight initiation distance

**Draft manuscript for Proceedings of the Royal Society B- Biological Sciences**

**INTRODUCTION**

Phenological shifts in plant and animal populations have been linked widely to climate change [1, 2]. Pressing questions of interest include how these phenological shifts link mechanistically to climate variables and whether the observed shifts are adaptive. Although evolution by natural selection is a possible means of adaptation, the most immediate adaptive solution to the rapid pace of climate change is phenotypic plasticity [3], the range of phenotypes expressed by a genotype in different environmental conditions. In some cases, plasticity in circannual behaviour and other traits has explained most of the observed change in phenology [4, 5] and has been shown to maintain or increase fitness [6]. For instance, plasticity in phenology of egg laying in a population of great tits (*Parus major*) in the United Kingdom was adaptive in minimizing phenological mismatch with food sources, thereby maintaining population growth [7].

Snowshoe hares (*Lepus americanus*), and at least nine other mammal species globally, undergo seasonal moults to a white or brown coat to match the presence or absence of snow. Background matching is a crypsis strategy that reduces risk of detection by predators [8, 9]. In recent decades, persistence of snow cover in the Northern Hemisphere has decreased due to increased air temperatures and more precipitation falling as rain instead of snow [10-12]. In a recent study of the mistiming between presence of ground snow cover and seasonal colour moults in snowshoe hares, strong background mismatch was documented during spring and fall, and predicted to greatly increase in the future [13]. White animals on non-snowy backgrounds are extremely conspicuous and would appear to be easier to detect by a predator that hunts visually. Both individual behaviours

and population dynamics of hares are overwhelmingly shaped by predation, which can comprise 85-100% of mortality [14].

Snowshoe hares might be able to minimize fitness costs of seasonal mismatch in camouflage through plasticity in the phenology of coat colour moults. Timing of moult in fall and spring is presumably initiated by photoperiod, but temperature and possibly presence of snow may affect the rate of the change [15-17]. Mills et al. [13] showed average timing of the fall and spring moult in snowshoe hares in Montana to be fixed across years with disparate snow cover, with some plasticity in the rate of spring moult, once the white-to-brown transition had been initiated.

Separate from or in combination with phenological shifts, hares might be able to modify their behaviour to minimize the mismatch of coat colour or its potential costs. Snowshoe hares rely strongly on their crypsis to avoid predation, with minimal attempts at hiding in vegetation (here referred to as concealment). In contrast to other lagomorphs in the region that stay brown during the winter (i.e., Mountain cottontails [*Sylvilagus nuttallii*] or pikas [*Ochotona princeps*]), snowshoe hares do not build burrows for escape underground. Rather, during the day, hares sit completely still at a resting spot and do not flee until immediate danger arises. Intuitively, this strategy is maladaptive when selection of a resting spot results in mismatch between coat colour and background. Steen et al. [18] observed that willow ptarmigans (*Lagopus lagopus*) moulting from white to brown plumage during snow melt fed in areas that matched their coloration, even though areas selected for optimal crypsis often offered less nutritious food. Similarly, hares could be resting during the day at spots where background colour is similar to their coat colour, and thus reduces colour contrast. Whether hares are able to recognize their coat colour and choose resting spots that match it is not known. Alternatively, mismatched hares might achieve effective camouflage by selecting resting spots associated with cover provided by dense understory, trees, or rocks, as suggested by [19]. Finally,

because hares rely on both crypsis and flight, mismatched hares may increase the distance at which they flee when approached by a predator [20]. Crypsis in prey species decreases the risk perceived by an animal and thus consequently can decrease flight initiation distance (FID) [21, 22]. For example, round-tailed horned lizards (*Phrynosoma modestum*), whose colouring resembles small stones, displayed shorter FIDs on rocky substrates than on uniform sand, likely as a response to higher crypsis among rocks [23]. Similarly, hares mismatched to their background might perceive higher predation risk and flee sooner (longer FID).

Here we provide an evaluation of the adaptive potential of snowshoe hares to minimize negative effects of colour mismatch through phenotypic plasticity in moult phenology and behaviour. Mills et al. [13] found little plasticity in seasonal coat colour change at a single study site (Seeley Lake, MT). Here we extend that investigation to a second site which differed considerably in climate and photoperiod, and compare moult phenologies at both sites. Next, we analyse at both sites variables influencing moult phenology, and explore reaction norms in moult phenology. Lastly, we examine, whether anti-predatory behaviours are being modified in response to colour mismatch and consequently evaluate whether behavioural plasticity may ameliorate negative effects of colour mismatch.

## **MATERIALS AND METHODS**

### ***Study Area***

We conducted our research at two sites in western Montana, USA separated by approximately 330 km: the Seeley Lake study site (used in [13]) in the Lolo National Forest (Morrel Creek drainage) and the Gardiner study site in the Gallatin National Forest (Bear Creek drainage). The Gardiner study site is about twice as high in elevation (2400 to 2700 m ASL) as the Seeley Lake

study site (1300 to 1450 m ASL). This elevation difference leads to cooler temperature and longer duration of snow cover in the Gardiner study site; snowpack persists at the Gardiner site from late October until May [24], compared to December to April at the Seeley Lake site [13]. The Seeley Lake site (Lat.= 47.23°, Long.= -113.43°) is 240 km further north than the Gardiner site (Lat.= 45.08°, Long.= -110.57°).

Both sites are temperate boreal coniferous forest on U.S. Forest Service lands with little to no permanent human habitation, and logging being the primary land use. Common predators of hares in the sites include Canada lynx (*Lynx canadensis*), bobcat (*L. rufus*), coyote (*Canis latrans*), red fox (*Vulpes vulpes*), American marten (*Martes americana*), great horned owl (*Bubo virginianus*), and northern goshawk (*Accipiter gentilis*).

### ***Capture and Handling***

We captured hares at each study site throughout the year in live traps (Tomahawk Live Trap Company, Tomahawk, WI), then ear-tagged, weighed and sexed each individual; hares weighing over 900 g (=199 individuals) were fitted with VHF radiocollars (weight  $\leq$  40 g, Wildlife Materials, Murphysboro, IL, USA; [25, 26]). All handling procedures were approved by the University of Montana Animal Care and Use Committee (Protocol No. 021-10SMWB-051110).

### ***Moult Phenology***

At the Gardiner site, we applied the methods used by Mills et al. [13] at the Seeley Lake site, of visually locating hares weekly using radiotelemetry to quantify coat colour phenology and colour contrast between hares and their background. We monitored 51 hares (32 different hares in 2011, and 31 in 2012) at the Gardiner study site and 148 hares (43 different hares in 2010, 63 in 2011, and 58 in 2012) at the Seeley Lake study site. The percentage of white coat colour (% whiteness) and the

percentage of ground snow cover within 1- and 10-m radii circles centred at each hare's resting spot (% snow cover) were visually estimated in 20% increments with a standardized protocol of observation and photographs to control for light conditions and distance. All final percentages were visually estimated by a single observer using primarily the photographs, and secondarily the field visual estimates when the quality of the photograph was insufficient, did not show the whole hare's body, or the photograph was absent. We classified animals that just initiated or nearly completed the moult as 5% or 95% white. We measured colour contrast as the difference between per cent whiteness of the hare and the per cent snow cover. It is not known at which scale crypsis may be perceived by either prey or predators; thus we measured colour contrast within the 1- and 10-m radii circles. We chose these radii because we felt that they were reasonable approximations of the finest and coarsest scales at which crypsis could be effective (i.e., crypsis would be completely ineffective at <1 m, and completely effective at >10 m). A positive contrast indicated a white hare on a non-snowy background, whereas a negative value indicated a brown hare on a snowy background. We considered a hare mismatched when the absolute difference (here referred to as contrast) between its coat colour and background was at least 60% [see 13 for consideration of other thresholds], as at this threshold hares began to clearly stand out against their surroundings.

### ***Anti-predatory Behaviours***

We evaluated behaviour of each located hare at both sites. For hares stationary at a resting spot we visually estimated concealment as the percentage of the hare's body concealed by vegetation at four levels (1= 0- 25% of body concealed to 4= 75- 100% concealed), from the direction from which the hare was initially sighted and from a low angle (approx. 1 m above ground, mimicking the view of common mammalian carnivores). To estimate FID, observers approached a hare at a consistent walking pace (approximately 0.5 m/s) until the hare fled or the observer was within 3 m



of the hare. We used a digital laser rangefinder (Leupold, Beaverton, OR, USA) to estimate FID to the nearest meter. We used a minimum approach distance of 3 m to minimize disturbance to the hare; hares that did not flush at the 3-m distance were recorded as “no flush” and were not disturbed further. The maximum distance at which we were able to estimate distance reliably in the forest was 20 m.

Finally, we tested whether hares randomly chose spots to rest with respect to minimizing colour contrast or snow presence in their immediate vicinity. We estimated percentage of snow cover (20% increments) at eight, non-overlapping subsections of the 10-m radius circle around each hare by photographing the ground from where the hare rested at each cardinal and inter-cardinal direction to create eight ‘pie slices’. Snow cover and colour contrast at these eight ‘available’ spots were compared to that in the 1-m radius immediately surrounding the hare’s resting spot; we excluded from analysis resting spots where all subsections and the resting spot were entirely snow-covered or snow-free, as these cases provided no information on whether the chosen resting spot differed from the surroundings. Our final sample sizes for this analysis yielded a total of 251 observations from 77 individual hares.

### ***Statistical Analysis***

#### *Moult phenology*

We used a mixed effects change point analysis to estimate the population mean initiation and completion dates of coat colour change phenology in the Gardiner site (as previously done for the Seeley Lake site [13]), and to test for the effects of snow, temperature, and sex on moult phenology at both sites. We assessed temperature as the rate of seasonal cooling in the fall and warming in the

spring; we calculated degree days for each day as the cumulative sum of mean temperature below 0°C in the fall (September–December) and above 0°C in the spring (March–June).

We were able to document individual moult phenology over >1 fall or spring moult for none of the hares at the Seeley Lake site and only seven individuals in the Gardiner site due to the high mortality rates typical of snowshoe hares [25, 27] and due to incomplete detection. We plotted coat colour observations over time of those seven individuals for visual assessment of the reaction norm (range of phenotypes produced by a particular genotype in different environmental conditions) in the moult phenology.

### *Concealment*

To test whether concealment behaviour increased with colour contrast we fitted linear mixed effects models in software R version 2.15.2 (R Development Core Team, 2012) using the package lme4 [28]. We included the identity of individual hares as a random effect to control for variation among individuals. We included the fixed effects of coat colour (per cent whiteness), snow cover around hares (at 1 and 10-m radius), coat colour contrast (at 1 and 10-m radius; ranging from -100 to 100), coat colour mismatch (at 1 and 10-m radius), site, sex and season. Coat colour mismatch was a categorical variable distinguishing between positive (white hare on brown background: contrast  $\geq 60$ ), negative (brown hare on white background: contrast  $\leq -60$ ) and no mismatch ( $-60 < \text{contrast} < 60$ ). Further, to examine whether the two different types of contrast and mismatch (positive and negative) had equivalent effects, we established an absolute contrast covariate (ranging from 0 to 100) and a binary categorical covariate for absolute mismatch (mismatch: contrast  $\leq -60$  and contrast  $\geq 60$  versus no mismatch:  $-60 < \text{contrast} < 60$ ). In addition to linear terms, we used quadratic terms to allow for the possibility of a curvilinear response of concealment to contrast. We differentiated seasons separately for the two sites based on local climate (Seeley Lake: winter [Dec-

Mar], spring [Apr- May], summer [Jun- Aug], fall [Sep- Nov]; Gardiner: winter [Nov- Apr], spring [May- Jun], summer [Jul- Aug], fall [Sep- Oct]).

Because hare whiteness and snow cover at both the 1- and 10-m radius around hares were highly correlated for most of the year ( $r \geq 0.8$ ), we considered each separately in model construction. Whiteness and contrast as well as snow cover and contrast were not highly correlated ( $r \leq 0.1$  and  $r \geq -0.5$ , respectively) and so were both present in some models. To test for habituation in concealment behaviour to human observers we ran a univariate linear mixed model, with concealment as a function of number of location attempts per hare (including unsuccessful sightings) and individual hares coded as random effects to control for variation among individuals.

We selected a set of best models (within  $2 \Delta AIC_c$ ) fitted with maximum likelihood using  $AIC_c$  criterion [29]. The precision of model parameters was based on a sample (100,000 iterations) from the posterior distribution of the fixed effects parameters using a Markov Chain Monte Carlo approach (function `mcmcsmamp`) to determine if the 95% highest posterior density (HPD) intervals included zero.

#### *Flight initiation distance*

We used Cox proportional hazards regression [30] to test whether FID increased with colour mismatch. Our data were a form of time-to-event data, with flight the event of interest and observations with no flight response at the maximum approaching distance of 3 m classified as right-censored data. We fitted the models using the package `survival` [31] in R. We included the same covariates and potential correlations among them as in the previous analysis: whiteness, snow cover around hares, colour contrast (regular and absolute), colour mismatch (regular and absolute), site, sex, season, and concealment. We also tested for potential habituation in FID behaviour as in

the previous analysis. The proportional hazard assumption was tested using score test and scatterplots of scaled Schoenfeld residuals. We selected a set of best models (within  $2 \Delta AIC_c$ ) fitted with maximum likelihood using  $AIC_c$  criterion.

### *Resting spots*

To test whether hares chose resting spots randomly with respect to colour contrast and snow cover, we fitted separate mixed effects models with fixed effects of colour contrast and snow cover. The models were fitted with binomial error distribution and a logit link function in R using the package lme4 [28]. The binomial dependent variable coded as one for the immediate resting spot (1-m) and zero for the eight other available ‘pie slices’ within the 10-m radius of the hare. The identity of individual hares and the date of when each hare was located were included as random effects to control for variation among individuals and to specify a nested design of the nine spots available to a hare at each location. We compared importance of the tested predictors using the statistical significance of the fixed effects slopes and the models’  $AIC_c$ .

## **RESULTS**

### *Phenology*

The colour moult phenology analysis at the Gardiner site in two years that differed strongly in amount of snowpack indicated that drivers of this circannual trait, and plasticity across different snow years, were similar to our previous findings at the Seeley Lake study site [13]. The fall moult for hares in the Gardiner site was fixed across 2011 and 2012 both for initiation date and rate of change (overlapping confidence intervals among initiation and completion dates; Figure 1). For the spring moult, we detected plasticity in the rate of the white-to-brown moult. The completion date

of the spring moult occurred 19 days later in 2011, consistent with the month longer snow duration in that year (Figure 1).

Analysis of the spring initiation date in the Gardiner site was compromised by a small sample size in spring 2012. Specifically, only three radiocollared hares were alive between May 4<sup>th</sup> and May 30<sup>th</sup>, as 16 out of 19 hares were depredated in April and early May, and new hares were not collared until early June (see the electronic supplementary material S1). Thus, the model likely underestimated the initiation date of the spring 2012 moult, leading to the 95% credible intervals of initiation dates between the two years being separated by 1 day in timing (Figure 1).

The limited sample size in spring 2012 also restricted our analysis of the effects of snow cover, temperature, and sex on the rate of the spring moult in the Gardiner site by biasing model results. Thus, we combined the Gardiner site data and the Seeley Lake site data from springs 2010-2012 to test for the effects of the covariates on the spring moult rate using a larger sample size. Snow cover was negatively related to the rate of change, but the magnitude of the effect was small. A change from 100% to 0% snow shifted the average completion date of the spring moult by only 3 days ( $\beta_{\text{snow}} = 0.054$ ,  $SD = 0.015$ ). Temperature also had an effect on the rate of the moult, but the coat colour phenology model with temperature (degree days) as a covariate predicted that the span from 0°C to 23.1°C (the highest daily average temperature during the spring moult period) explained only a 1-day modification of the completion date of the spring moult ( $\beta_{\text{temp}} = 0.15$ ,  $SD = 0.016$ ). Lastly, when testing for the effects of sex on spring moult rate at the two sites, the sex-skewed spring data from the Gardiner site in 2012 positively biased the estimate. In spring 2012, five out of the seven hares observed to change to 5 or 0% white were females, which indicated that females completed the spring moult 14 days earlier than males. By contrast, omitting the Gardiner spring 2012 data resulted in a minimal influence of sex on the rate of the spring moult, with females completing the spring moult on average 2 days earlier than males ( $\beta_{\text{sex}} = -4.43$ ,  $SD = 5.27$ ).

We observed a large difference in the timing of the coat colour moult phenology between our two study sites. For each year, hares at the Gardiner site initiated fall moults by about two weeks earlier in the fall and by a month later in the spring, corresponding to cooler temperatures and longer lasting snowpack in the Gardiner site. However, the duration of the colour moults was very similar across sites with fall and spring moults lasting on average 39.9 days (SD= 3.22) and 41.9 days (SD= 7.00), respectively.

Finally, our limited data for the seven individuals that were observed over multiple seasons at the Gardiner site also indicated no plasticity in the fall but some in the spring rate of moult. According to the plots, reaction norms of the six hares that we observed over two disparate falls displayed similar phenologies, differing by only 0- 10 days between the two falls (Figure 2a). In contrast, the one hare which was observed over two springs had moult phenologies that differed between springs by 15-20 days, comparable to the range of plasticity observed across all six individuals in the fall moult (Figure 2b).

### ***Concealment***

Contrary to our predictions, hares did not conceal themselves more with increasing colour contrast; rather, the level of concealment was mostly affected by season and site. First, we detected habituation to human observers, as concealment began to significantly decrease with number of location attempts when hares were located more than 9 times. Therefore, we truncated the dataset to include only the first 9 observations per hare which yielded a total of 731 observations from 139 radiocollared individuals at the two sites. Each individual was observed an average of 4.6 occasions (SD= 2.5).

The best model included season, site, and quadratic form of colour contrast at 1 m (see the electronic supplementary material S2 for the set of best models tested). The other three best models

included one additional term each: snow at 10 m, whiteness, and snow at 1 m (in order) that had positive effects on concealment, but their 95% highest posterior density (HPD) intervals included zero. The significant quadratic relationship of contrast on concealment was in the opposite direction than expected, with highest concealment at medium levels of positive colour contrast and reduced concealment at high negative and high positive contrasts ( $\beta_{\text{Contrast}} = 0.0051$ ,  $\text{SD} = 0.0021$ ;  $\beta_{\text{Contrast}}^2 = -0.000085$ ,  $\text{SD} = 0.000026$ ) (see the electronic supplementary materials S3 and S4). Concealment varied seasonally, and hares were on average concealed by 25% more in the summer and 8% more in the fall than in the winter, but not significantly different in the spring than in the winter. Concealment was significantly different at the two sites; hares at the Seeley Lake site were on average 11% more concealed than at the Gardiner site.

### ***Flight Initiation Distance***

Hares did not flee at farther distances with increasing mismatch as we predicted, but rather their concealment level, season, and site variables played important roles in predicting their FID. We detected habituation to human observers, as FID began to significantly decrease with number of location attempts when hares were located more than 5 times. Therefore, we truncated the dataset to include only the first five observations per hare which yielded a total of 284 observations from 91 radiocollared individuals. Each individual was located on average 2.9 occasions ( $\text{SD} = 1.4$ ).

Our set of best models included concealment, site, season, sex, and either contrast or mismatch (see the electronic supplementary material S5 for the set of best models tested). The model results can be interpreted as the increase in probability of flight initiation throughout the distance within which we measured the FID response ( $=20$  m). Our first, second, and sixth best model included mismatch at 10 m. Hares matched with their background were 5.6 times more likely to flee than brown hares on snowy background (hazard ratio<sub>NegativeMismatch</sub> = 5.62,  $\text{SE} = 1.72$ ), but there

was no difference for white hares on brown background (hazard ratio<sub>PositiveMismatch</sub> = 1.62, SE= 1.39; see the electronic supplementary material S6 for a list of coefficients from the best model). A similar trend was observed in the fourth and fifth best model that included absolute mismatch at 10 m scale, where matched hares were about 2 times (4<sup>th</sup> best model: hazard ratio<sub>AbsMismatch</sub> = 2.02, SE= 1.33; 5th best model: hazard ratio<sub>AbsMismatch</sub> = 1.87, SE= 1.33) more likely to flee than mismatched hares. The third best model included a linear relationship with colour contrast at 1 m. Hares were 0.77% more likely to flee with each 1% decrement in colour contrast (hazard ratio<sub>Contrast</sub> = 1.01, SE= 1.00).

Concealment significantly decreased flight distance; with each 25% increment in body concealed hares were 26% less likely to flee. There was a significant difference in FID at the two sites; hares at the Gardiner site were 89% more likely to flee than hares at the Seeley Lake site. Season appeared in all best models but only summer was significantly different from winter; hares were 21% more likely to flee in summer than in winter. Sex was present in all best models as it improved model fit but was not significant in any of them. Similarly, snow at 1 m around hares and whiteness were present in three models of the best models set but their effects were not significant in any. According to the score tests and scatterplots of scaled Schoenfeld residuals, there was no evidence of non-proportional hazards in any of the terms in the best models.

### ***Resting Spots***

Hares were not more likely to rest at spots within their immediate vicinity where colour contrast was reduced but instead preferred spots with relatively little snow. Colour contrast was an important predictor of presence but hares were located at spots that resulted in higher colour contrast relative to the available spots within 10-m radius of the hares ( $\beta = 0.0076$ ,  $SD = 0.0022$ ). Further, we found strong evidence that hares were more likely to be found at spots with less snow



cover. The probability that a hare would be found at a spot with no snow cover was 3.92 times higher than at a spot with complete (100%) snow cover ( $\beta = -0.016$ ,  $SD = 0.0019$ , Figure 3). The model which included snow cover received more support than the model including colour contrast ( $\Delta AIC_c = 63$ ) or the null model ( $\Delta AIC_c = 72$ ).

## DISCUSSION

Across a wide range of snow conditions and two study sites, snowshoe hares demonstrated little plasticity for modifying coat colour phenology or behaviours to track seasonal snowpack. The fixed initiation dates of coat colour moults are consistent with a photoperiod modulator of timing, as occurs for other circannual processes [32-34]. We observed no plasticity in the rate of the fall brown-to-white moult on both the population (Figure 1) and individual level (Figure 2). Consistent with the findings of [13], we found plasticity in the rate of the spring white-to-brown moult with mean completion dates shifted by 19 days across two years of different snowpack. Additionally, we observed plasticity in the individual rate of moult in the spring. The one hare which was observed over two springs at the Gardiner site displayed different moult phenology each year, with a difference in spring moult rates nearly as large as observed across all of the six individuals over multiple fall moults (Figure 2).

The mechanisms for a fixed fall moult phenology and only limited plasticity in the spring rate are unclear. One explanation for plasticity in the spring moult could be an elevated predation rate in the spring (Zimova et al., In Prep), placing higher selection pressure to adjust the rate of the spring moult as a means of optimizing camouflage against immediate snow conditions. Further, hares might simply be able to trace the change in the snow conditions better in the spring than in the fall. Over three years and two study sites, we observed four substantial snow fluctuations ( $> 30\%$  and in the opposite direction of the seasonal change) in the weekly average snow cover around

hares in the falls and only one such fluctuation in the springs. Thus, the spring change in the snow conditions might be more predictable compared to fall snow change, where early snowfalls are often followed by full melt-out before continuous winter snow cover builds up.

We did not detect any strong variables influencing the rate of the spring white-to-brown moult. Despite the more consistent snow change in the spring, our change point analysis indicated that snow cover explained only about a 3-day shift in the average spring completion date. Temperature also was not a strong regulator of the spring moult rate as it only explained a 1-day shift in the completion date. Finally, the rate of moult in the spring was not significantly influenced by sex, with females completing the spring moult on average two days earlier than males. The faster colour moult for females is consistent with previous observations [13, 35, 36].

The spring and fall moults across the different study sites were similar in duration, each lasting about 40 days. Despite this similarity in moult length and limited coat colour plasticity within sites, natural selection appears to have aligned the moult phenology to correspond to average local climate at each site. Although the Gardiner site is slightly south of the Seeley Lake site, and therefore has a similar or slightly longer photoperiod, the higher elevation of the Gardiner site leads to considerably longer lasting snowpack. As might be expected with the longer snowpack, hares in the higher elevation Gardiner site obtained their white coats sooner in the fall and retained them longer in the spring. Elevational and latitudinal gradients have been shown to affect the timing of the moults in several leporid species. Watson [15] showed that mountain hares (*L. timidus*) occupying high elevations became white earlier, turned dark later, and became whiter in winter than those at low elevations. Similarly, latitudinal differences were observed in museum specimens [37], where snowshoe hares from northern latitudes moulted from brown to white earlier in the fall and retained the white coat longer.

We found that hares did not modify their hiding behaviour in a manner that reduced colour contrast at either the 1- or 10-m radius scale. If our assessment of the range at which predators visually perceive hares is correct, then hares mismatched to their surroundings within a radius of up to 10 m (an area of 314 m<sup>2</sup>) are more vulnerable to detection. The relationship between concealment and colour contrast suggested that hares most concealed themselves when their coats were about 40% whiter than their immediate (1-m radius) background (40% contrast) and least when brown hares were on snowy backgrounds (-100% contrast; see the electronic supplementary material S3). Because the effect size was small this relationship may represent weak biological importance. Overall, concealment levels of hares seemed to be most affected by season and site, which may be good proxies for available hiding cover. Hares were more concealed in the summer and fall when leafy vegetation in the understory provided more horizontal cover than in the winter and spring when leafy vegetation was either absent or covered by snow.

Second, we did not find evidence for hares responding to colour contrast at either the 1- or 10-m radius scale by fleeing at a farther distance from a potential threat. FID of positively mismatched hares (white hares on brown background) was no different than for matched hares; negatively mismatched hares (brown hares on snowy background) consistently had the shortest FID. On the contrary, concealment had a strong effect on FID; hares that were most concealed stayed still longest. Shorter FIDs with high concealment likely represented decreased perceptions of risk, as has been reported, for example, for pygmy rabbits (*Brachylagus idahoensis*; [22]). Seasonally, hares fled at longer distances in the summer than in the winter, consistent with our field observations that hares seemed to be more active in the summer (see also [38] who observed lowest activity for hares in winter). Longer flight distance in summer is also consistent with the general expectation that prey flees at farther distances when in better body condition [21]. Indeed, our personal field observations of hares during winter are that they generally appear calmer when approached, flee less even if they

are fully exposed, and often have their eyes closed, perhaps a strategy to save energy during winter periods of food limitation. Additionally, hares might perceive less predation risk in winter as their low foot loading provides a likely escape advantage from potential carnivores on snow [39].

Lastly, we found no evidence of hares preferring resting spots with colour background that would reduce colour contrast. On the contrary, hares were more likely to be found at spots within their immediate surroundings that increased their colour contrast with the background within 10-m radius. This is likely result of their overall preference to rest at spots with little snow cover. We noticed this behaviour during field observations; when snow cover was heterogeneous on the landscape, hares were located at non-snowy spots such as under logs or in tree wells. Thermoregulation may therefore be playing an important role in resting spot choice.

Finally, we note several caveats and assumptions. First, our choices of 1- and 10-m radius of snow cover around hares might not represent the spatial scale of perceived colour contrast for hares and/or their predators. We did not consider larger areas than 10-m radius for estimating colour contrast based on the assumption that visual detection of hares by predators at such scales was unlikely in these relatively dense forests. Second, because little is known about the drivers of the circannual rhythm of the moult, our measurements of moult regulators (e.g. snow cover, cumulative sum of temperature degree days) may not capture the correct regulators of colour moult phenology in the wild. Likewise, hares may be pursuing behavioural strategies to reduce colour contrast that we did not measure. Hares and many of their predators are primarily crepuscular and nocturnal, and thus hares could be deploying anti-predatory strategies that minimize colour contrast during the main periods of activity. For example, hares could be foraging during the night preferentially at areas that match their coat colour or they could be modifying their FID in response to colour contrast during those times of the day. Finally, our use of human observers as a proxy for predators assumes that FID response to humans is the same as to hares' natural terrestrial predators.

Nevertheless, across multiple years, two study sites, a wide range of snow conditions, and nearly 200 hares monitored in the wild, we find no evidence that hares perceive coat colour mismatch and act to shift concealment or flight behaviours or immediate microsite choice. We also confirm that moult initiation dates are fixed across years of different snowpacks, even as the moult phenology is locally shaped within regions by a combination of photoperiod and climate. Given the prospect for substantially decreased snowpack duration in the future due to climate change [13, 40], it seems that the most likely avenue for reducing camouflage mismatch or its potential predation consequences in local populations is evolutionary shifts in moult phenologies or anti-predatory behaviours.

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[www.snowshoeharechronicles.com/publications/](http://www.snowshoeharechronicles.com/publications/).

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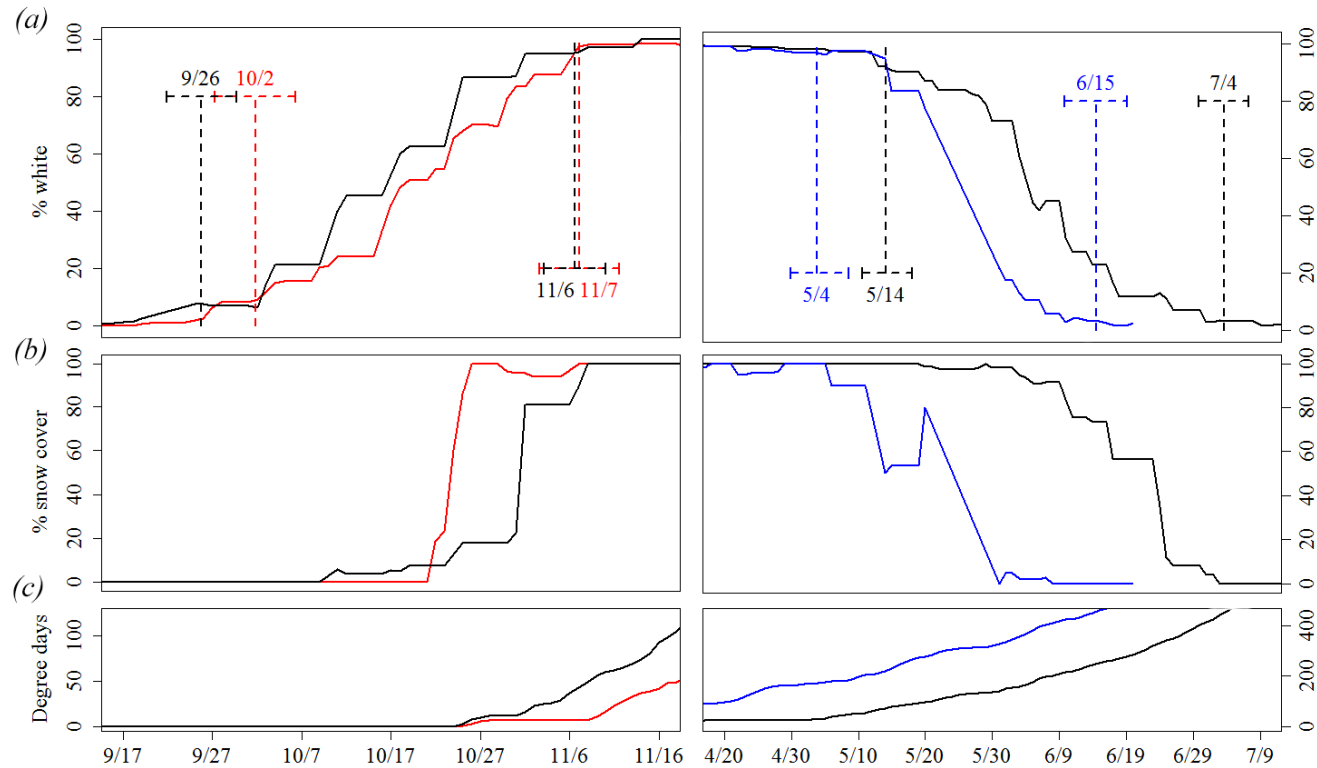
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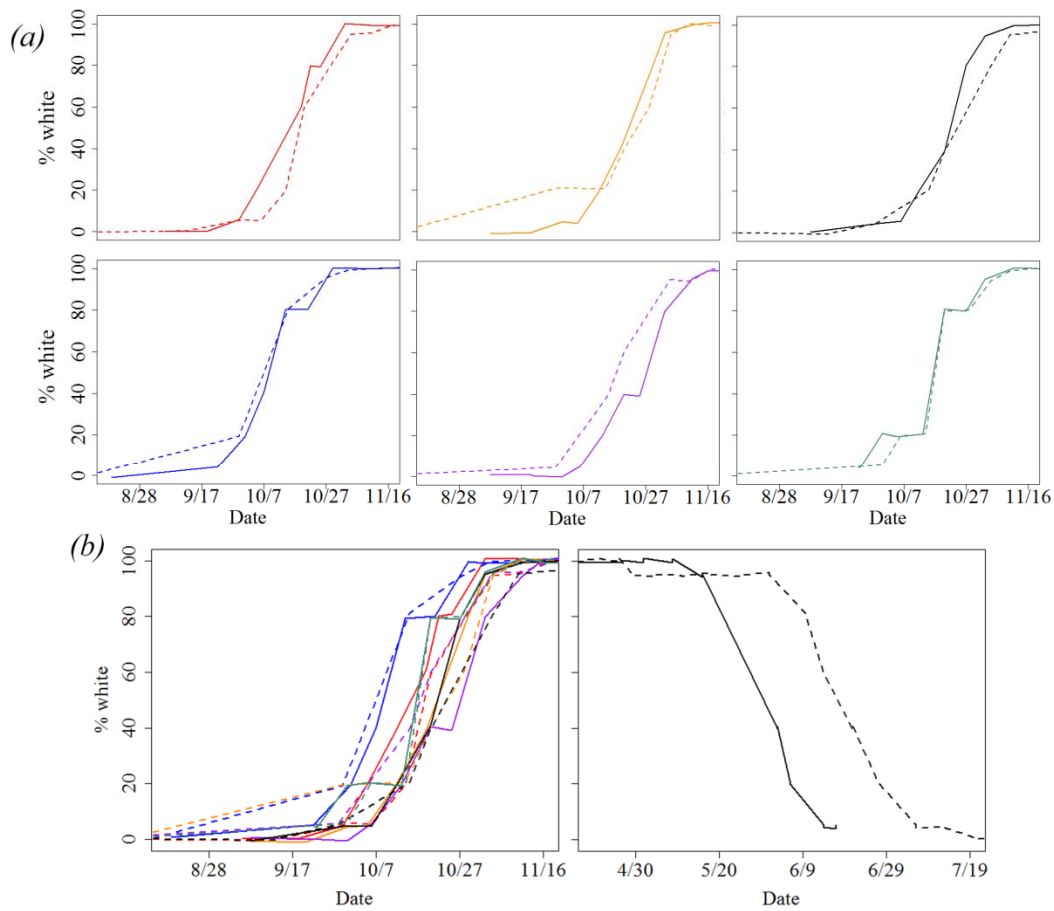
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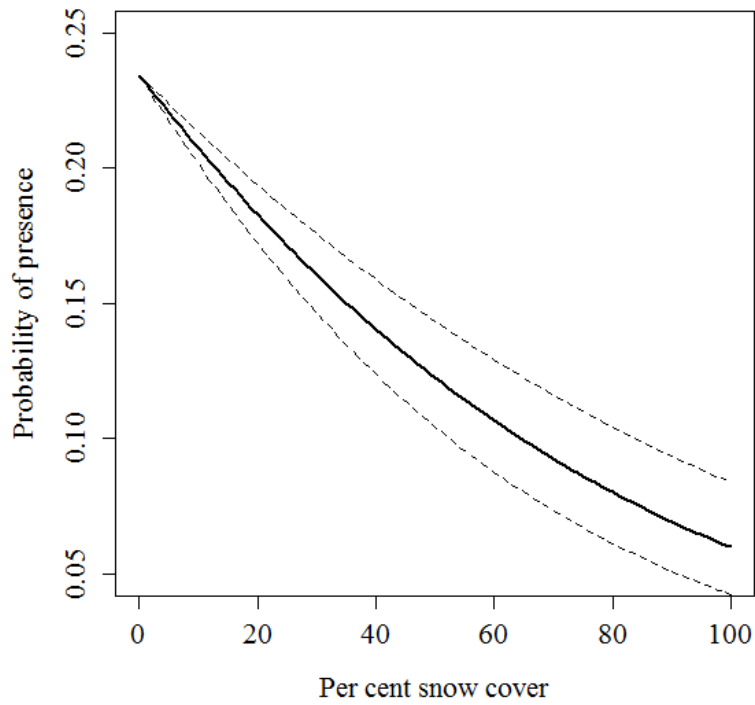
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**Figure 1.** Coat colour phenology, snow cover, and degree days at the Gardiner study site, MT (9/17/2010 – 7/9/2012), with fall seasons on the left and spring seasons on the right. (a) Weekly average of observed coat colour of 51 hares (2010 [red], 2011 [black], and 2012 [blue]). 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 colour moult for each season each year. (b) Weekly average of observed snow cover in a 10-m radius around each hare. (c) Degree days as a measure of cooling trend in the fall and warming trend in the spring.

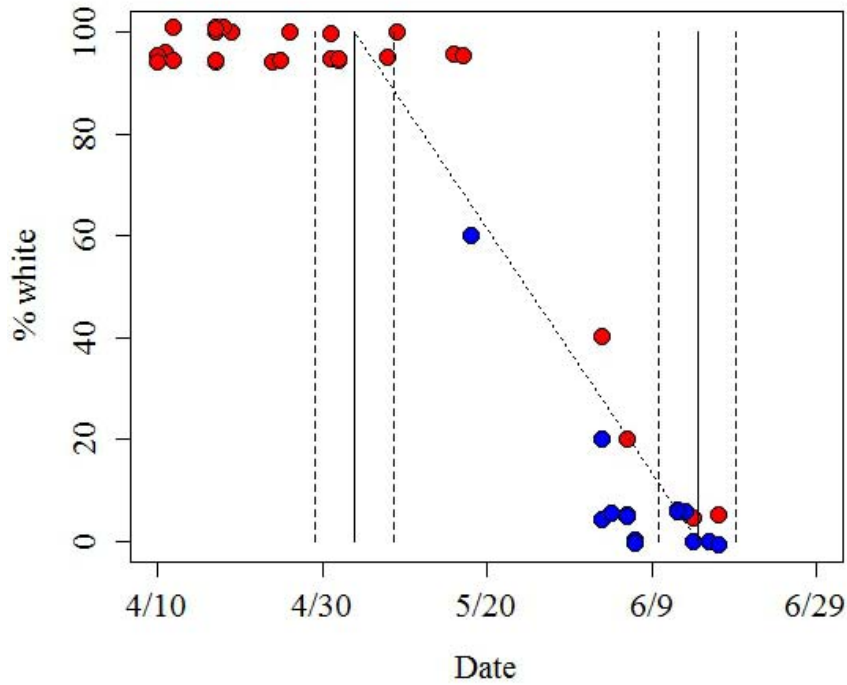


**Figure 2.** Spring moult phenology reaction norms of hares at the Gardiner study site, MT (9/17/2010 – 7/9/2012). (a) Fall coat colour moult phenologies of six individual hares observed over two falls. (b) Fall (left) moult reaction norms of the individuals shown in panel (a) combined, and spring (right) moult reaction norm of one hare observed over two springs. Each coloured line represents reaction norms of a different individual in year 2011 (dashed line) and either 2010 or 2012 (full lines).



**Figure 3.** Probability of presence of a hare at a resting site with percentage of snow cover at the Gardiner and Seeley Lake study sites, MT (9/17/2009 – 7/9/2012). Dashed lines show 95% confidence intervals.

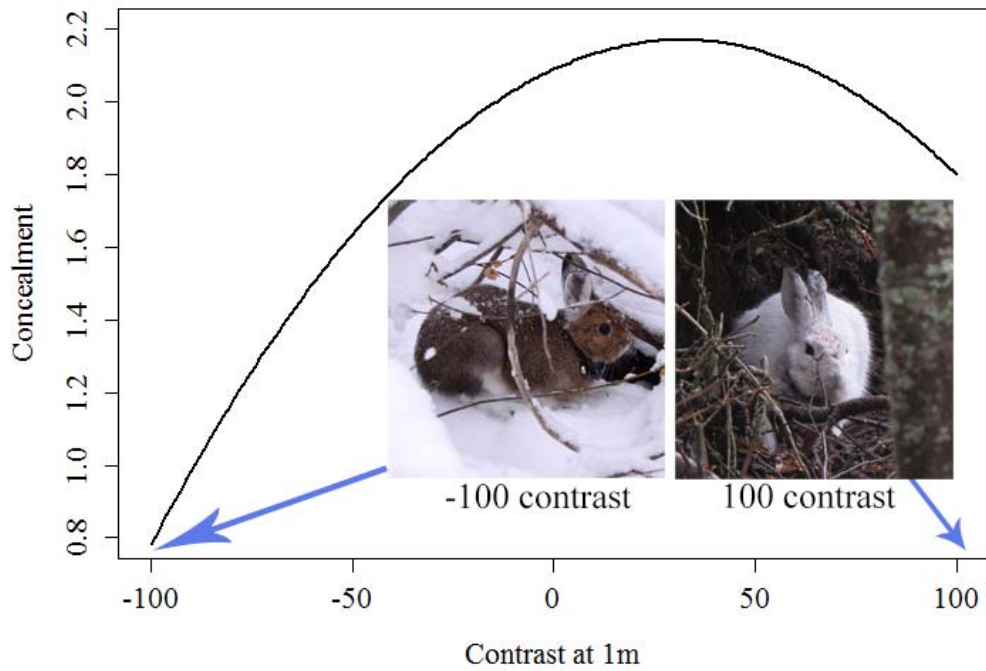
**ELECTRONIC SUPPLEMENTAL MATERIAL:**



**S1. Spring 2012 phenology data from Gardiner study site.** Dots represent coat colour observations of hares radiocollared during the previous seasons (red dots) and in May and June 2012 (blue dots). Vertical black full lines show estimated mean initiation and completion dates with 95% credible intervals (dashed black lines) based on the change point analysis. Dotted black line shows estimated slope of the change.

**S2. Set of best models tested to explain variation in concealment (Conc) for hares at the Gardiner and Seeley Lake sites, MT (9/17/2009 – 7/9/2012).**  $AIC_cWt$  stands for  $AIC_c$  weight, and LL for log likelihood.

#	Model	K	$AIC_c$	$\Delta AIC_c$	$AIC_cWt$	LL
1	Conc ~ Season + Site + Contrast1m + Contrast1m <sup>2</sup>	9	2122.85	0.00	0.35	-1052.30
2	Conc ~ Season + Site + Contrast 1m + Contrast 1m <sup>2</sup> + Snow10m	10	2124.70	1.86	0.14	-1052.19
3	Conc ~ Season + Site + Contrast 1m + Contrast 1m <sup>2</sup> + Whiteness	10	2124.77	1.93	0.13	-1052.23
4	Conc ~ Season + Site + Contrast 1m + Contrast 1m <sup>2</sup> + Snow1m	10	2124.77	1.93	0.13	-1052.23



**S3. Effect of colour contrast within 1-m radius on hares' concealment at the Gardiner and Seeley Lake study sites, MT (9/17/2009 – 7/9/2012).** Relationship is based on coefficients from the best model according to AIC (see the electronic supplementary material S4).

**S4. Effects of season, site and colour contrast at 1 m (Contrast1m) on concealment (Conc) according to the best model.** 95% HPD are the 95% highest posterior density intervals for the coefficients. Variables with statistically significant effects are identified by two asterisks (\*\*).

<b>Conc ~ Season + Site +</b>			
<b>Contrast1m + Contrast1m<sup>2</sup></b>	<b>Coefficient</b>	<b>SD</b>	<b>95% HDP</b>
Season (spring)	-0.13	0.15	(-0.46, 0.099)
Season (summer)**	1.00	0.26	(0.45, 1.47)
Season (fall)**	0.33	0.11	(0.11, 0.54)
Site (Seeley Lake)**	0.43	0.12	(0.23, 0.65)
Contrast1m**	0.0051	0.0021	(0.0012, 0.0092)
			(-0.00014, -
Contrast1m <sup>2</sup> **	-0.000085	0.000026	0.000036)



**S5. The best models tested to explain variation in FID for hares at the Gardiner and Seeley**

**Lake sites, MT.** Conc is concealment.  $AIC_c$ Wt stands for  $AIC_c$  weight, and LL for log likelihood.

#	Model	K	$AIC_c$	$\Delta AIC_c$	$AIC_c$ Wt	LL
1	FID ~ Conc + Sex + Site + Season + Mismatch10m	8	1577.35	0.00	0.15	- 780.42
2	FID ~ Conc + Sex + Site + Season + Mismatch10m + Snow1m	9	1577.63	0.27	0.13	- 779.48
3	FID ~ Conc + Sex + Site + Season + Contrast1m	7	1577.99	0.64	0.11	- 781.79
4	FID ~ Conc + Sex+ Site + Season + AbsMismatch10m	7	1578.62	1.27	0.080	- 782.11
5	FID ~ Conc + Sex+ Site + Season + AbsMismatch10m + Snow1m	8	1578.69	1.34	0.080	- 781.08
6	FID ~ Conc + Sex + Site + Season + Mismatch10m + Whiteness	9	1579.28	1.93	0.060	- 780.31

**S6. Effects of concealment (Conc), sex, site, season, and colour mismatch at 10-m radius (Mismatch10m) around hares on flight initiation distance (FID) according to the best model.** Variables with statistically significant effects are identified by two asterisks (\*\*).

<b>Model: FID ~ Conc + Sex + Site + Season + Mismatch10m</b>	<b>Hazard Ratio</b>	<b>P-value</b>	<b>95% CI</b>
Conc**	1.26	0.00059	(1.10, 1.44)
Sex (female)	1.06	0.73	(0.77,1.45)
Site (Seeley Lake)**	1.89	0.0054	(1.21, 2.97)
Season (spring)	0.88	0.64	(0.53, 1.47)
Season (summer)**	0.21	0.00054	(0.086, 0.51)
Season (fall)	1.17	0.54	(0.71, 1.95)
Mismatch10m (positive)	1.62	0.14	(0.85, 3.07)
Mismatch10m (negative)**	5.62	0.0014	(1.95, 16.18)

## CHAPTER 3

**Title:** High fitness costs of seasonal camouflage mismatch in snowshoe hares suggest future population declines

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**Abstract:** Reduction in snow duration represents a direct potential stressor for species undergoing seasonal color molts. Over 3 widely disparate snow years in 2 study regions, we found high fitness consequences of color mismatch for wild snowshoe hares, with weekly individual survival rates reduced by 3-7%. In the absence of adaptive changes in the molt phenology, by midcentury these fitness costs coupled to decreasing duration of snow season are projected to decrease annual survival by 12% by mid-century and 24% by late-century. Such changes in survival are sufficient to cause increasing hare populations to decline strongly towards extinction, with annual population geometric growth rate decreasing by 11% (24%) by mid (late) century. While we establish color mismatch as a powerful case for joint attribution of biological consequence to anthropogenic climate change, we also find high individual variation in the trait that might enable microevolutionary response to future seasonal mismatch.

**One Sentence Summary:** Climate change-induced seasonal camouflage mismatch is projected to decrease annual survival and population growth rates by about a quarter by the end of the century.

**Draft manuscript for Science**

## MAIN TEXT

Duration of seasonal snow cover on earth is rapidly decreasing as a result of anthropogenic greenhouse gas emissions, with later onset of snow in the fall and earlier loss of snow in the spring (1, 2). For at least 10 mammal species occupying ecosystems with seasonal snow cover, color molting from brown to white presumably provides background matching, a form of camouflage that minimizes color contrast between the animals and their surroundings to avoid predator detection. Photoperiod-induced change of seasonal coat color, and subsequent mismatch in the face of decreasing snowpack, could be expected to have strong fitness consequences for individuals and populations as white prey species become increasingly exposed to brown snowless backgrounds in the future (3).

Individual and population fitness costs have rarely been quantified for any climate-induced phenologic mismatch (4-6) and may be especially severe for snowshoe hares (*Lepus americanus*), where predation comprises 85- 100% of mortality (7) and shapes both population dynamics and behaviors (8, 9). Further, we previously found minimal plasticity in molt phenology to track seasonal snowpack or in anti-predatory behaviors to minimize camouflage mismatch (10) for 2 snowshoe hare populations, implying a 4-8 fold increase in color mismatch by the end of the century as snow cover decreases under various climate scenarios (3). Because seasonal coat color mismatch occurs at local spatial scales and is not confounded by interactions with other anthropogenic stressors or by organism mobility or life cycle complexities, this trait lacks the controversial aspects of joint attribution (11-14); in this case the trait serves as a strong test of whether a clear anthropogenic climate change stressor (decreased snow duration) results in detection of a biologically critical impact (increased mortality) in a wild population.

Here, we quantify individual and population consequences of color mismatch using weekly observations on 186 radiocollared hares over 3 years at 2 sites separated by >300 km in the US

Northern Rockies. First, we describe the individual variation in the coat color molt phenology and consequent color contrast between hares and their surroundings. Second, we quantify the survival costs of increased color contrast using several different hypotheses. Next, we project future survival and population growth rates, given the estimated fitness costs of color contrast and future snow cover reductions under a scenario without future plasticity or microevolution to reduce mismatch or its consequences. Lastly, we discuss the potential of microevolutionary response to rescue hares from the dire climate change consequences.

### ***Individual variation***

Within-population individual variation in seasonal color molt phenology, and resulting mismatch with the background, was considerable (15-17). On average, for 7 weeks out of a year we found >50% differences in percent white of coat color among individuals sampled in one week. Anecdotally, in the field it was not uncommon on the same day and site to observe hares with the full range of coat colors, ranging from just initiating the molt to almost completely color changed. When combined with mean snow cover at each site, the individual variation in coat color phenology resulted in individual variation in color contrast [difference between % white of an individual and % coverage of snow cover (18)], with maximum weekly difference in color contrast among individuals exceeding 50% for on average 4 weeks out of a year.

### ***Survival cost of mismatch***

To assess the mortality consequences of increased color contrast, we tested a series of *a priori* hierarchical known fate survival models (table S1). First, we predicted that hares with higher color contrast each week will have lower survival. This prediction was highly supported, providing strong evidence for decreased survival for individuals in weeks when they were highly contrasted with background color. According to this model, annual and weekly survival probability at the two sites

was 0.10 (SD= 0.026) and 0.96 (SD= 0.0050), respectively, and the effect size of color contrast on survival was -0.95 [95% CRI= (-1.82, -0.035)] on the logit scale (Fig. 2, Table 1). Such effects indicate that during weeks when hares are color mismatched (color contrast >60%) weekly survival probability proportionally decreases by 3.27- 6.53%.

Second, we tested whether hares that have higher lifetime propensity to be color contrasted with their background (= higher average color contrast during each hare's monitoring period) have lower survival. Interestingly, an individual's color contrast propensity had no effect on hares' survival, likely because most of the time hares were not mismatched with their background and thus contrast propensity index was similarly very low for all hares (Table1).

Next, we predicted lower survival during weeks of high population color contrast (= average weekly color contrast of all individuals at each site) than during weeks when hares match their background. We found some support for negative effect of population color contrast on weekly survival (Table 1, fig. S2). This population contrast has lower explanatory power than weekly individual color contrast, probably because of the large individual variation in color contrast, with some hares almost 100% contrasted to their surroundings while others match perfectly on the same week (Fig. 1). Further, population color contrast exceeded 60% for only 1 week out of a year on average.

Lastly, we tested whether hares' survival was higher during years with snow conditions most similar to the recent past. Coat color molt phenology of hares is locally shaped by latitude and elevation and corresponding snow conditions (17, 19). Thus, we predicted higher survival in years closest to historic mean snow phenology. Specifically, we predicted that hares would have the highest survival in 2012 as the snow conditions were most similar to the climatic mean of recent past (1970- 1999) in terms of both snow cover duration and snow water equivalent (SWE) (3). However, the amount of color contrast did not vary between years with widely varying snowpacks ( $P_{2011} =$

0.066,  $P_{2012} = 0.11$ ), and we did not find differences in survival across years (Table 1) (18). We suggest that the high level of individual variation in the molt phenology maintains constant annual survival even in years when snow conditions vary considerably from the climactic mean. If natural selection directionally selects for individuals having shorter periods with white coats, thereby decreasing population-level variation in the trait, then the loss of among-year buffering may make populations more vulnerable to extreme weather events with long snow seasons.

Next, we further explored the effects of color contrast in relation to other covariates possibly affected or complemented by color contrast. We first tested for effects of 4 seasons (winter, spring, summer, fall) and month, because hare survival has been shown to vary over the year, with lowest survival during the spring and fall periods of color contrast occurrence (9). We found weekly survival to be fairly high and stable during the winter, dropping sharply in April and May, and steadily increasing over the summer before peaking in the fall (fig. S3). When we included individual weekly color contrast in the univariate model with month, color contrast had a strongly negative effect on survival and improved model by providing additional explanatory power to the temporal variation in survival (Table 1). Although seasonal changes in predation pressure and food types likely contribute to the spring survival decrease, coat color contrast evidently plays a substantial role as well. First, the two months associated with lowest survival in spring are those with highest color contrast. Also, the strong individual fitness costs associated with hares of changing color contrasts monitored through these same months support contrast *per se* as a driver of decreased spring survival. Next, the univariate model with 4 seasons provided some evidence that color contrast negatively affects hare survival, despite the peak in hare survival in the fall during which hares also experience color contrast. The basis of the increased survival in the fall remains unclear, but apparently other biological mechanisms, including top-down (e.g. predation) and bottom-up (e.g. foraging) dynamics, overwhelm the signal of color contrast.

Lastly, based on findings that males retain the white coat longer than females (3, 15, 16), which in turn might produce fitness differences between the sexes, we tested for an additive effect of sex and weekly individual color contrast on hares' survival. We did not find evidence for males having lower survival, but again, individual weekly color contrast was strongly negative in the model (Table 1).

### ***Future survival and population growth rate projections***

Because this phenologic mismatch lacks the confounding alternative anthropogenic factors that often cloud the connection between a climate forcing and biological effect, a pressing question relevant to policymaking is how increased anthropogenic climate forcing in the future would affect snowshoe hares in the future, assuming coat color phenology remains as it is currently. Without adaptive shifts in the molt phenology or its phenotypic plasticity, projected consequences for hare populations will be considerable. Using our field-estimated effect size of color contrast on survival (18), we find a steep survival decrease as current coat color phenology confronts additional weeks of color contrast in the future (Fig. 3). We have shown previously that hares will confront decreased snowpack duration that will increase their mismatch (color contrast >60%) by up to 4 additional weeks by mid-century and up to 9 additional weeks by the end of the century (3). With this many more weeks of mismatch, we project that annual survival would proportionately decrease by 12% by mid-century and by 24% by late century (Fig. 3).

A related way to envision the consequences of increased mortality due to mismatch is at the population level, where  $\lambda$  represents both the annual geometric growth rate and the population mean fitness (20-22). Again, assuming current molt phenology unchanged into the future, we can extend our measured costs of mismatch on weekly survival rate to projected future changes in  $\lambda$ . We decremented spring and fall survival rates based on the cost of mismatch for the predicted increase in number of weeks of mismatch (3) and projected them through a matrix population model along



with other previously field-estimated vital rates for an adjacent snowshoe hare population (18). The population growth rate for that baseline hare population went from strongly increasing ( $\lambda=1.14$ ) to nearly stationary by mid-century (an 11 % decrease in annual growth rate). By late century this population would be catastrophically declining, experiencing a 24% decrease to  $\lambda=0.87$ . Thus, despite the fact that the demographic cost of mismatch is only relevant for a few weeks per year, its severe mortality consequences and the expected longer duration of mismatch in the future imply serious effects that would cause healthy, growing populations to decline towards extinction.

### ***Potential role of natural selection***

Importantly, future population dynamics consequences could be ameliorated if natural selection acts to minimize color mismatch either through shifting molt phenology or increasing its plasticity. Documented strong selection on coat color leading to cryptic background matching (23) and recurrent evolution of seasonal camouflage in seasonally variable environments suggest high potential for microevolutionary change in response to color mismatch. Further, selection on body color has been recently demonstrated in tawny owls (*Strix aluco*), probably in response to altered snow conditions by climate change, although the fitness advantages of the color morphs are unclear (24).

The color contrast regression coefficient from the univariate survival model with individual contrast can also be interpreted as a directional selection coefficient on the trait (25). The negative value of -0.95 (Table 1) of color contrast on survival indicates strong selection for decreased color contrast in hares and its magnitude is particularly striking when compared to other selection coefficients documented in natural populations with a median strength of absolute value of 0.16 (26, 27). Further, if the observed phenotypic variation between individuals is a result of heritable genetic variation, natural selection for reduced mismatch could occur. Whether and how much of the variation in molt phenology is heritable remains unknown, but limited captive studies indicate a

strong genetic component of the molt phenology (16). Further, snowshoe hares (and other species with seasonal molts) show geographic variation in the occurrence and timing of seasonal coat color molts, indicating local adaptation to regions with less predictable winter snow (28, 29).

In short, in the emerging framework for identifying vulnerability to evaluate conservation responses to climate change (30) we can now state with high certainty that snowshoe hares (and likely other seasonal coat color changing species) will have substantial exposure to decreased snowpack as an anthropogenic stressor, and that sensitivity to this exposure is high in the form of decreased survival, population mean fitness, and population growth rate. Although we find ample material on which natural selection could act to ameliorate fitness consequences of coat color mismatch, a deep understanding of the genomic basis of seasonal coat color change is required to determine adaptive capacity, or the potential for evolutionary rescue, in the face of rapid anthropogenic climate change.

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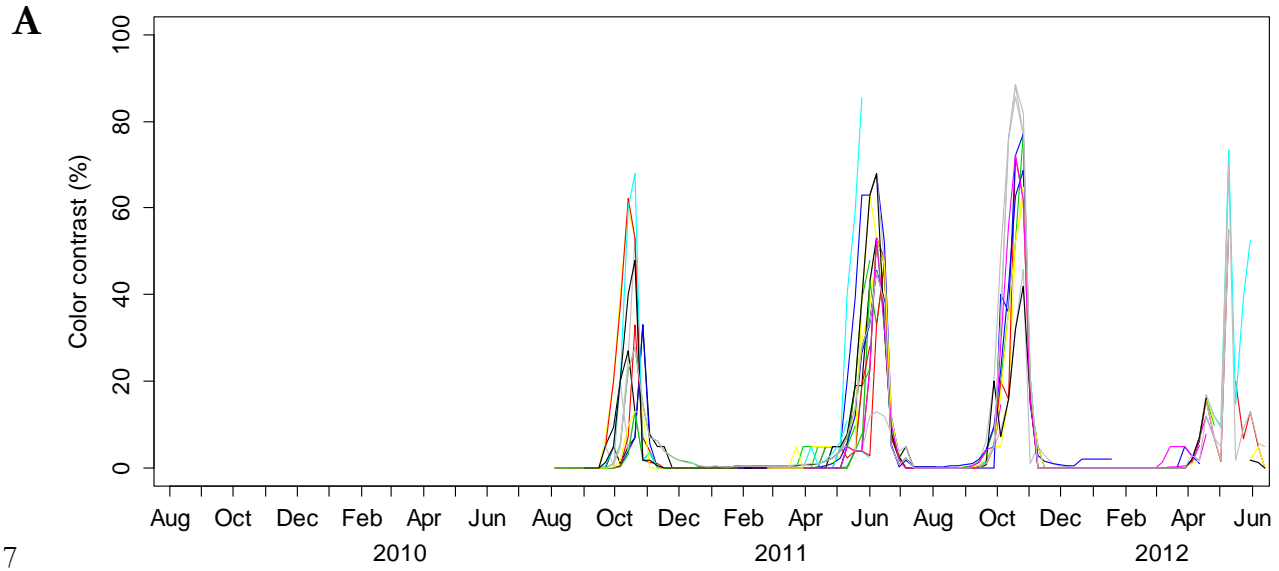
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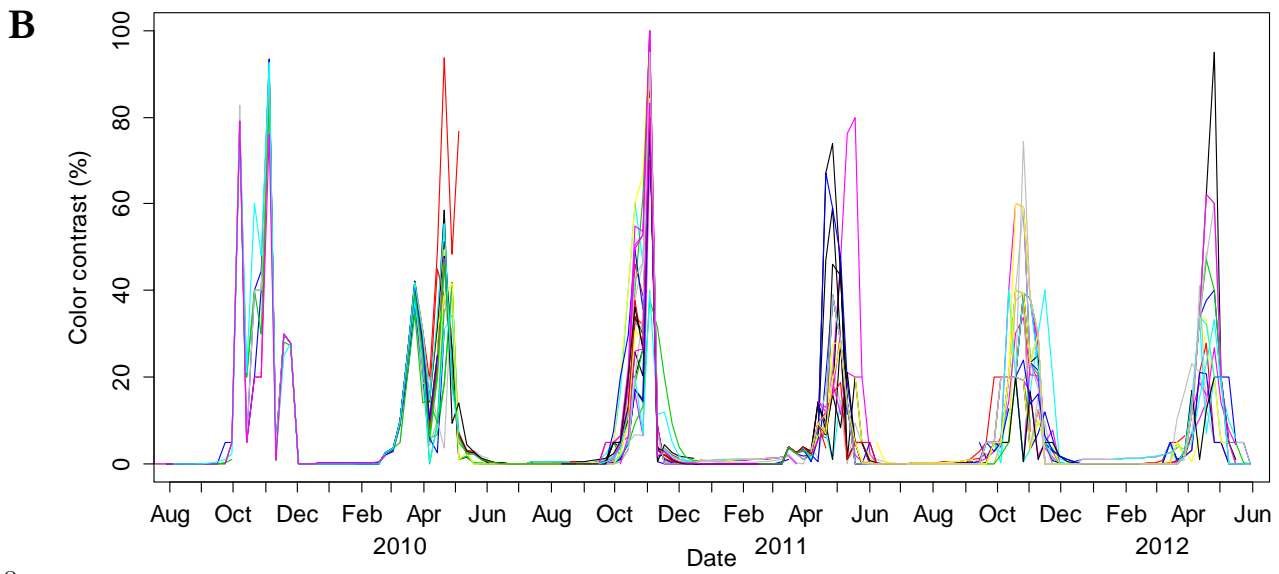
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1 **Table 1.** Results from 11 *a priori* models used to assess the survival costs of seasonal color contrast. Models are ordered by  $\Delta$  DIC (DIC=  
2 Deviance Information Criterion; an estimate of expected predictive error analogous to frequentist  $\Delta$  AIC). Covariate coefficients are the  
3 regression coefficients from the model reported on the logit scale. When only one coefficient is reported for a multivariate model, it is for  
4 the color contrast covariate. 95% CRI are the 95% credible intervals analogous to frequentist confidence intervals. Bolded model  
5 represents the selection coefficient of color contrast on survival.

#	Survival model	$\Delta$ DIC	DIC	Covariate coefficient	95% CRI
11	S = Month + Individual contrast	0.0	943.6	-1.21	(-2.22, -0.12)
10	S = Month	2.6	946.2	-	-
				0.68 Season <sub>Summer</sub>	(0.11, 1.30) Season <sub>Summer</sub>
6	S = Season	18.9	962.5	1.14 Season <sub>Fall</sub>	(0.60, 1.69) Season <sub>Fall</sub>
				0.84 Season <sub>Winter</sub>	(0.39, 1.29) Season <sub>Winter</sub>
7	S = Season + Individual contrast	19.0	962.6	-1.00	(-2.07, 0.14)
9	S = Constant	24.5	968.1	-	-
2	S = Individual contrast	25.4	969.0	-0.95	(-1.82, -0.035)
3	S = Population contrast	25.5	969.1	-0.70	(-1.65, +0.37)
4	S = Individual contrast propensity	28.5	972.1	0.93	(-3.58, 5.64)
1	S = Site	30.5	974.1	0.004	(-0.54, 0.52)
				0.13 Year <sub>2011</sub>	(-0.65, 0.84) Year <sub>2011</sub>
5	S = Year	35.5	979.1	-0.32 Year <sub>2012</sub>	(-1.09, 0.38) Year <sub>2012</sub>
				0.15 Sex <sub>Male</sub>	(-0.23, 0.54) Sex <sub>Male</sub>
8	S = Sex + Individual contrast	278.5	1222.1	-0.95 Contrast	(-1.80, -0.02) Contrast



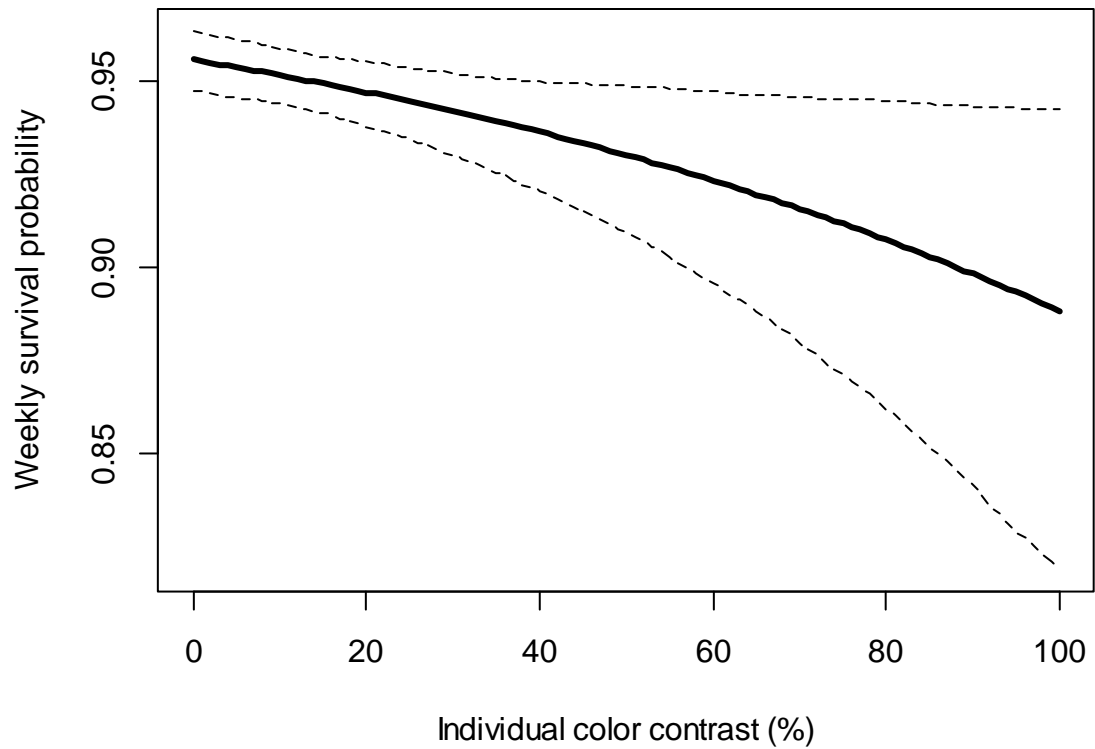
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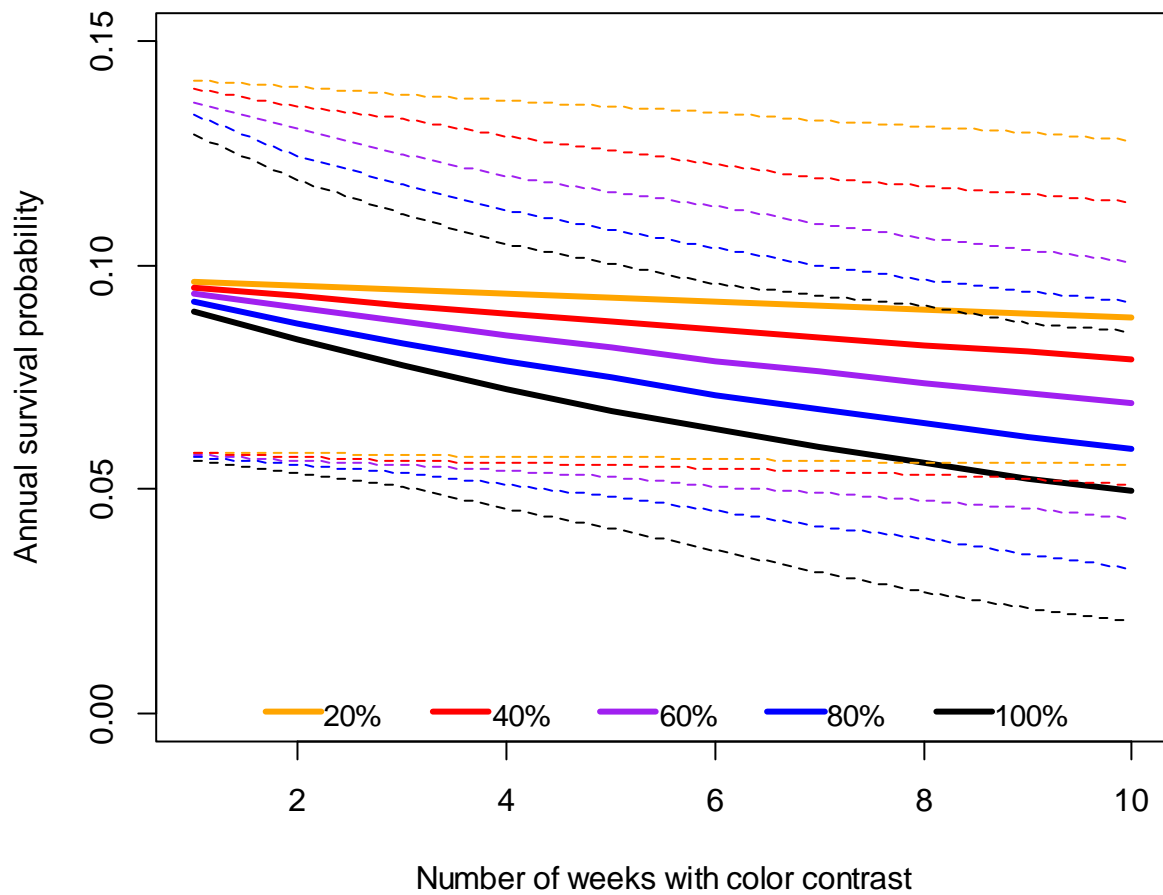
9 **Fig. 1.** Mean estimated individual color contrast of radiocollared snowshoe hares from August 2010

10 to July 2012 at Gardiner, MT (**A**) and from August 2009 to June 2012 at Seeley Lake, MT (**B**).



11  
 12 **Fig. 2.** Effects of individual color contrast on weekly snowshoe hare survival probability as  
 13 estimated by a univariate model including individual contrast (Table 1). Dashed lines indicate 95%  
 14 credible intervals. The effect size was extrapolated across the entire range of color contrast.





15  
 16 **Fig. 3.** Simulated snowshoe hare annual survival probability under different color contrast  
 17 scenarios. Full lines represent mean annual survival and dashed lines 95% credible intervals.  
 18 Different colors indicate different degrees of weekly individual color contrast.

19 **SUPPLEMENTARY MATERIALS:**

20 Materials and Methods

21 Figures S1-S3

22 Table S1

23 References (30-37)

24 **MATERIALS AND METHODS:**

25 ***Study Area***

26 We conducted our research in two areas in Western Montana, separated by about 330 km:  
27 Seeley Lake study site [used in (3)] in the Lolo National Forest (Morrel Creek drainage) and Gardiner  
28 study site in the Gallatin National Forest (Bear Creek drainage). The Gardiner study site is about  
29 twice as high in elevation (2400 to 2700 m ASL) as the Seeley Lake study site (1300 to 1450 m ASL).  
30 This elevational difference leads to cooler temperatures and longer duration of snow cover in the  
31 Gardiner study site; continuous snowpack persists at the Gardiner site from late October until May  
32 at the Gardiner site (31) and from December to April at the Seeley Lake site (3). The Seeley Lake  
33 site (Lat.= 47.23°, Long.= -113.43°) is 240 km further north than the Gardiner site (Lat.= 45.08°,  
34 Long.= -110.57°).

35 Both areas have little to no permanent human habitation, with moderate logging being the  
36 primary land use. The Seeley Lake study site is characterized by alternating 2.6 km<sup>2</sup> sections of clear  
37 cuts and mildly thinned to mature closed stands that create heterogeneous hare densities and  
38 population growth rates (9). Large portions of the Gardiner study site contain thinned forest stands  
39 resulting from extensive timber harvest during the 1940s and 1970s (31), with the rest of the site  
40 characterized by mature forest types.

41 Dominant tree species at both areas include Lodgepole pine (*Pinus contorta*), Douglas fir  
42 (*Pseudotsuga menziesii*), subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*), and in  
43 Gardiner also whitebark pine (*Pinus albicaulis*). The common hare predators at both sites include  
44 Canada lynx (*Lynx canadensis*), bobcat (*L. rufus*), coyote (*Canis latrans*), red fox (*Vulpes vulpes*),  
45 American marten (*Martes americana*), great horned owl (*Bubo virginianus*), northern goshawk (*Accipiter*  
46 *gentilis*), and red-tailed hawk (*Buteo jamaicensis*).

#### 47 ***Capture and handling***

48 Hares were captured continuously throughout the year in live traps (Tomahawk Live Trap  
49 Company, Tomahawk, WI), then eartagged, weighed and sexed. Hares weighing > 900 g were fitted  
50 with VHF radiocollars (Wildlife Materials, Murphysboro, IL) equipped with mortality sensors. The  
51 radiocollars weighing < 40 g were below the well-accepted radiocollar threshold of 5% of the  
52 animal's body weight (32). All handling procedures were approved by the University of Montana  
53 Animal Care and Use Committee (Protocol No. 021-10SMWB-051110).

#### 54 ***Survival and color contrast monitoring***

55 We monitored weekly survival status using radiotelemetry of a total of 186 radiocollared  
56 hares, including 136 in the Seeley Lake study site from July 4, 2009 to June 16, 2012 and 50 in the  
57 Gardiner study site from August 8, 2010 to June 16, 2012. When a mortality signal was detected, the  
58 individual was located to determine the cause of death. We confirmed 124 (67% of total) predation  
59 related mortalities. Mortalities within 10 days of capture or obviously not caused by predation (i.e.  
60 hare body found intact) were right censored (24 individuals). An additional 17 individuals were right  
61 censored due to radiocollar failure or permanent emigration out of the study area.

62 We attempted to visually locate all hares once a week using radiotelemetry to quantify coat  
63 color phenology and color contrast between hares and their surroundings at the two sites following

64 the methods of Mills et al. (3). The percentage of white coat colour (% hare whiteness) and the  
65 percentage of ground snow cover within 10-m radius circle centred at each hare's resting spot (%  
66 snow cover) were visually estimated in 20% increments with a standardized protocol of observation  
67 and photographs to control for light conditions and distance. Animals that just initiated or nearly  
68 completed the moult were classified as 5% or 95% white. All final percentages were visually  
69 estimated by a single observer using primarily the photographs, and secondarily the field visual  
70 estimates when the quality of the photograph was insufficient, did not show the whole hare's body,  
71 or the photograph was absent. We measured colour contrast as the difference between the percent  
72 of white coat colour and the percent of snow cover. We considered a hare mismatched when this  
73 difference was  $> |60|%$  [see (3) for consideration of other thresholds], as at this threshold hares  
74 began to clearly stand out against their surroundings.

75 We used t-tests to test whether the degree of variation in coat color varied between the 2  
76 populations of snowshoe hares and between the fall and spring seasons, assuming unequal variance  
77 between two samples. Linear univariate regression models with year as a covariate were used to test  
78 whether the variation in coat color and the amount of color contrast varied between the three years.  
79 We found that the degree of variation was equal between the populations ( $P= 0.48$ ), seasons ( $P=$   
80  $0.11$ ), and across the 3 years ( $P_{2011} = 0.32$ ,  $P_{2012} = 0.63$ ).

## 81 ***Statistical Analysis***

### 82 *Color contrast modeling*

83 Because we could not quantify coat color of each hare every week, we modeled missing  
84 observations of coat color using a logistic growth model and subsequently derived molt initiation,  
85 completion date and rate of molt for each hare. A fixed effect year was incorporated to allow for  
86 years to vary. Weekly individual color contrast was calculated as the absolute difference between the

87 individual's coat color and a weekly mean snow cover at each site. Weekly mean snow cover was  
88 calculated from all snow cover observations collected during that week in a 10-m radius circle  
89 around each observed hare at the respective site. Color contrast was defined on an absolute scale to  
90 allow estimation of mortality costs for both brown hares on white snowy backgrounds and white  
91 hares on brown backgrounds. We also calculated weekly population color contrast as the average of  
92 all individual color contrasts at each site each week. Lastly, we calculated color contrast propensity  
93 as a measure of an individual's tendency to be contrasted with its background by averaging all the  
94 modeled weekly color contrasts experienced by each animal.

### 95 *Survival analysis*

96 To quantify the effects of color contrast on hares' survival, we tested a series of *a priori*  
97 hierarchical known fate survival models (table S1). We first tested whether the mean survival of the  
98 two study populations (Seeley Lake and Gardiner) is equal by including study site as a categorical  
99 covariate. We found negligible differences in survival between the Seeley Lake and Gardiner  
100 populations (Table 1), allowing us to pool all 186 individuals together for the rest of the analyses.  
101 Next, we tested the hypothesis that color contrast negatively affects hares' survival using four  
102 different univariate models. First, we incorporated the model estimating weekly varying individual  
103 color contrast with its associated variance into the hierarchical survival model. Second, we included  
104 weekly varying population color contrast (= weekly mean of all hares within a site). Third, we  
105 included individual's color contrast propensity (= the mean individual's weekly color contrasts  
106 during each individual's monitoring period). Lastly, we included categorical variable year (2010,  
107 2011, and 2012) as a proxy for different snow conditions.

108 Next we tested a set of models including covariates that are potentially affected or  
109 complemented by color contrast (= month, season, and sex). Month was included as a random  
110 effect. Season was a categorical covariate differentiated separately for the two sites based on local

111 climate (Seeley Lake: winter [Dec- Mar], spring [Apr- May], summer [Jun- Aug], fall [Sep- Nov];  
112 Gardiner: winter [Nov- Apr], spring [May- Jun], summer [Jul- Aug], fall [Sep- Oct]). Lastly, we  
113 included weekly color contrast to each of these three models and determined using deviance  
114 information criterion (DIC; Bayesian equivalent to AIC) (33), whether color contrast provided  
115 additional explanatory power to the variation in survival.

116 All the hierarchical known fate survival models had linear predictors of the form:

$$117 \quad \text{logit}(\phi_{i,j}) = \beta_0 + \beta_{i,j} * x_{i,j} + \dots + \gamma_i \quad (1)$$

118 Where  $\phi$  is the expected monthly survival estimate given the covariate  $x$  and the estimated effects  
119  $\beta$  and  $\gamma_i$  is an individual level random effect. Error was assumed to be distributed according to a  
120 Bernoulli distribution. We included an individual level random effect to account for the repeated  
121 measures design and a lack of independence among individuals (34). Modeling at the individual level  
122 allowed us to account for staggered entry and right censoring of individuals. The model was fitted  
123 within a Bayesian framework which eased implementation of random effects and the simultaneous  
124 modeling of missing covariate values and derived parameters. We obtained posterior distributions  
125 along with their 95% credible intervals (CRI) using Markov chain Monte Carlo (MCMC) methods  
126 (35). Uniform priors were implemented on all parameters so that the inference was dominated by  
127 the information in the data. Convergence was assessed using the Gelman and Rubin potential scale  
128 reduction statistic  $\hat{R}$  (36) and visual inspection of the plotted chains and posteriors. The  $\hat{R}$  values  
129 were  $\leq 1.1$  for all parameters after running three parallel chains of length 100,000 and discarding the  
130 first 50,000 as burn-in. We thinned such that every 10th observation was retained for parameter  
131 estimation. All continuous variables were centered and scaled. All analyses were conducted in  
132 JAGS software (37), run from R 2.15.2 (R Development Core Team, 2012) via the R2jags package  
133 (38).

134 *Future survival simulations*

135 We simulated future annual survival rates under different color contrast scenarios. Survival  
136 estimates were calculated by sampling the posterior distributions of the estimated slope and  
137 intercept of color contrast from the survival model including weekly individual color contrast  
138 (model # 2, Table 1) in the following way:

$$139 \quad \text{logit}(\phi_t) = \beta_0 + \beta_1 * \text{weekly color contrast}_t \quad (2)$$

140 Annual survival rates were obtained by multiplying weekly survival estimates; for each future color  
141 contrast scenario we modified the number of weeks of the year with no color contrast and either 20,  
142 40, 60, 80, or 100% contrast. The resulting survival rates were then plotted along with their credible  
143 intervals. The credible intervals resulted from sampling the posterior distributions of the estimated  
144 parameters.

145 *Future population growth rate projections*

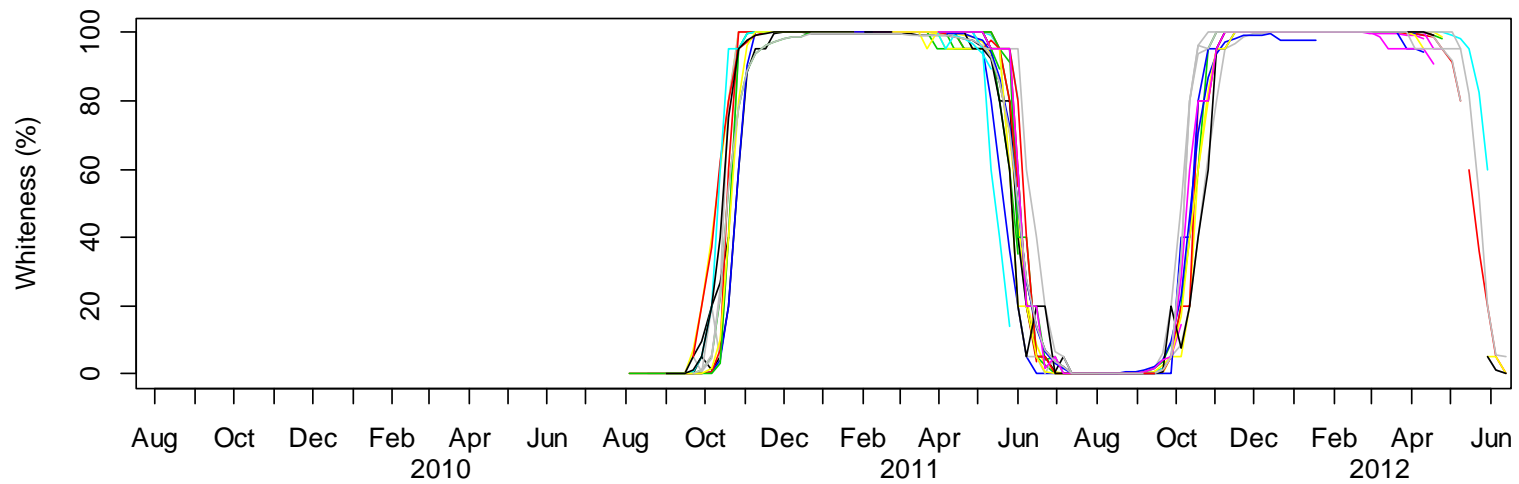
146 Next, we used the survival rates calculated in the previous section to estimate proportionate  
147 reduction in weekly survival due to mismatch by dividing weekly survival when color contrast is 0%  
148 by weekly survival rate when color contrast is 60%. This reduction value represents a decrement in  
149 weekly survival for each additional week in the future where absence of snow leads to color contrast  
150 of 60%, the lowest contrast at which we consider hares to appear mismatched. We note that this  
151 decrement is conservative, because for some weeks with no snow hares will reach color contrast  
152 >60%, and survival costs also occur when color contrast is <60%.

153 We predicted hares to experience more weeks of mismatch in the future, with 1.3 additional  
154 weeks of 60% color contrast in the fall and 2.4 weeks in the spring at mid-century and 2.6 additional  
155 weeks in the fall and 5.9 weeks in the spring by late century using the emission scenario 8.5 (3).  
156 Seasonal survival rates at mid-century and late-century were calculated for juveniles and adults by  
157 exponentiation of weekly survival rates under 0% and 60% contrast by their respective predicted

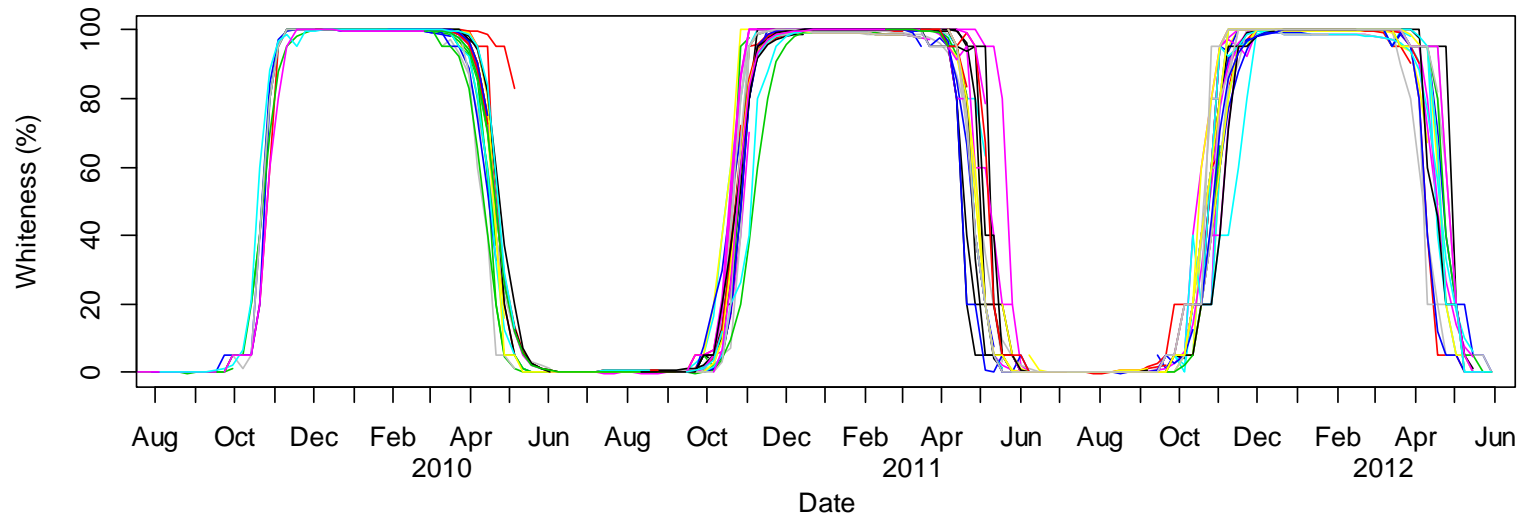
158 number of weeks at mid-century and late century. Baseline vital rates (stage-specific reproduction  
159 and seasonal survival) and an associated matrix population projection model were based on a hare  
160 population monitored 1999- 2002 within 20 km of the Seeley Lake population in the current study  
161 (9), with  $\lambda = 1.14$ . To calculate  $\lambda$  for the future time periods we projected the population matrix  
162 retaining these baseline vital rates, but replacing juvenile and adult spring and fall survival rates with  
163 the projected seasonal survival rates for mid- and late century.



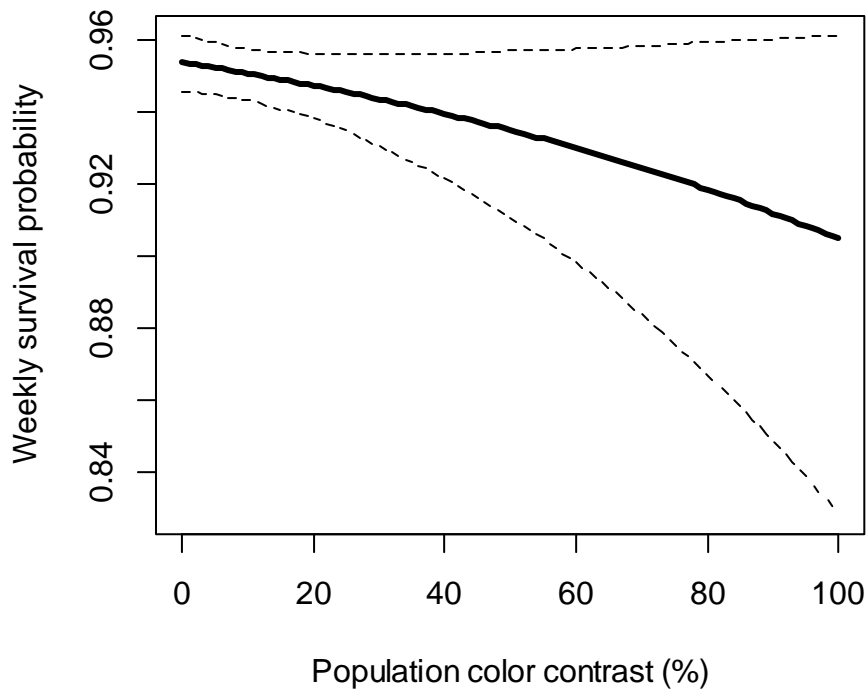
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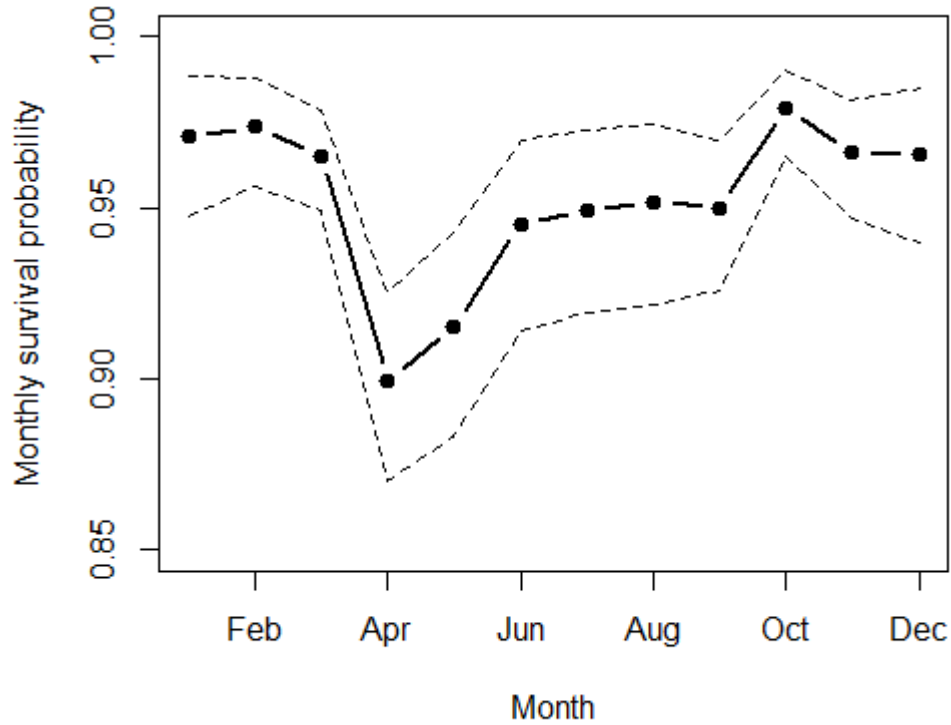
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166 **Fig. S1:** Individual molt phenology from August 2010 to July 2012 at the Gardiner, MT (top) and from August 2009 to June 2012 at the  
167 Seeley Lake, MT (bottom) study sites. Each colored line represents modeled phenology of a different individual.



**Fig. S2.** Effects of population color contrast on weekly survival probability as estimated by a univariate model including population contrast (Table 1). Dashed lines indicate 95% credible intervals. The effects size was extrapolated across the entire range of color contrast.



**Fig. S3.** Monthly survival averaged over 3 years at both sites as estimated by the model including month as a random effect. Dashed lines represent 95% credible intervals of the estimated survival probability.

**Table S1.** 11 *a priori* models testing specific predictions to assess the fitness costs of seasonal color contrast.

#	Survival model	Prediction
1	S = Site	Hares' survival will differ between the two populations.
2	S = Individual contrast	Hares' survival will be lower when individuals have higher color contrast.
3	S = Population contrast	Hares will have lower survival during weeks of high color contrast.
4	S = Individual contrast propensity	Hares with higher color contrast propensity will have lower survival.
5	S = Year	Hares will have lower survival when snow conditions differ from the climatic mean.
6	S = Season	Hares' survival will be lower during spring and fall.
7	S = Season + Individual contrast	Hares' survival will be lower during spring and fall and when individuals have higher color contrast.
8	S = Sex + Individual contrast	Hares' survival will be lower for males and when individuals have higher color contrast.
9	S = Constant	Hares' survival will be constant over time.
10	S = Month	Hares' survival will vary monthly.
11	S = Month + Individual contrast	Hares' survival will vary monthly, and will be higher when individuals have higher color contrast.

## APPENDIX A

**Title:** Camouflage mismatch in seasonal coat color due to decreased snow duration

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**Abstract:** 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 hare exposed to three years 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 days by mid-century and 40 - 69 days 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 3 – 8 fold. This novel and visually compelling climate-change induced stressor likely applies to >9 widely distributed mammals with seasonal coat color.

## INTRODUCTION

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 multi-trophic 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 9 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 non-snowy background. In the same way that cases of mismatch in animal camouflage are high profile (e.g. [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 U.S. 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 (2010-12) at our U.S. Northern 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 (see Methods and Materials). 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 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 three years (see 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 gender.

To quantify how these three years differed in snow cover and how they compared to the recent past and expected future, we developed ecologically relevant downscaled snow duration and temperature models applicable to our study area (Methods and Materials). 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 three years, we calculated a cumulative sum of degree days below 0<sup>0</sup>C in the fall (Sept- Dec) and above 0<sup>0</sup>C in the spring (Mar-Jun). 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 (RCP) 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-year time periods (“mid-century”=2030-2059; “late-century”=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 (Figure 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 (Figure 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 three years 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 years; Figs. 4a and S2), consistent with a photoperiod driver for this circannual trait (2). Also, the rate of coat color change (number of days between initiation and completion dates) in the fall was fixed (overlapping confidence intervals among completion dates; Fig. 4a), taking about 40 days 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 (non-overlapping confidence intervals among completion dates); in concert with the substantially longer snow season in 2011, hares completed the molt from white to brown 16 days later in 2011 compared to 2010 (Figs. 3a, 4, 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 main winter snowpack at our study site will persist for 29 (35) fewer days by the mid-century and 40 (69) fewer days by the late-century (Fig. 3a, 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 4-fold by the mid-century and by 8-fold by the late-century under the high emission scenario (Fig. 5, 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 years; for example molt from white to brown was slowest in spring 2011, which was both the coldest spring of the 3 years and had the longest lasting snowpack (Fig. 3, 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 days. 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 day modification of the completion date of molt from white to brown. In comparison to the 16 days 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. Additionally, the rate of molt in the spring was slightly influenced by sex, with females completing the spring molt on average 3 d earlier than males. Previous studies have similarly suggested faster color molt for females (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.

## **MATERIALS AND METHODS**

### ***Field Methods***

The study area (Morrell Creek) is located in the U.S. Northern Rockies near Seeley Lake, Montana at an elevation of about 1400 m (Lat.= 47.23°, Lon.= -113.43°). The area is temperate boreal coniferous forest comprised of 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 2 hares/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). 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 year. Of our 148 different animals monitored, only 7 survived for >1 fall or spring molt and only one survived for >1.5 years 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 (= 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 5 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 data sets). Slopes of the regression line prior to 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 (Figure S2).

Next we ran a series of change point regression models using spring data pooled across the 3 years to determine effect of each of the following covariates on the rate of the molt: snow (% snow cover within 10m radius around each individual hare on the date coat color was measured), temperature (sum of daily averages above  $0^{\circ}\text{C}$ ) and gender. 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 =  $(-100 - \beta_1 * \text{Covariate value})/\beta$ ], where  $\beta$  indicates the slope of the molt and  $\beta_1$  indicates the slope of a covariate. The range of values for the snow was 0 to 100% snow ( $\beta_1 = 0.093$ ,  $sd = 0.02$ ), for temperature from  $0^{\circ}\text{C}$  to  $15.4^{\circ}\text{C}$  (= highest daily maximum during spring) ( $\beta_1 = -0.354$ ,  $sd = 0.015$ ); and gender was binary (1= females, 0= males) ( $\beta_1 = -7.402$ ,  $sd = 6.678$ ).

### ***Future Coat Color Mismatch***

To estimate the increase in mismatch extent under future snow conditions we used average observed phenology of hares across the three years 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 defining mismatch (60% white hare on a snowless background) by also projecting number of days of mismatch using 40% and 80% thresholds (Table S3).

### ***Snow and Climate Modeling***

Daily SWE was modeled at the site from 1970-2012 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 detailed by (37). Model parameters were calibrated to 23.5 years (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 as described by (28). A total of 41 surrounding stations from 7 to 91 km from the site were



used to interpolate temperature while 38 stations from 7 to 89 km away were used for precipitation.

Compared to site observations, the annual modeled snow on date (first day of the snow season), was 2, 2, and 4 days too late in fall 2009, 2010, and 2011, respectively. The annual modeled snow off date (last day of the snow season), was 12 days too early in spring 2010, 1 day too late in spring 2011, and 4 days 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 24<sup>th</sup>, close to the modeled snow off date of April 22<sup>nd</sup>, but then new snowfall extended the season to May 4<sup>th</sup> 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 resolution 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-year 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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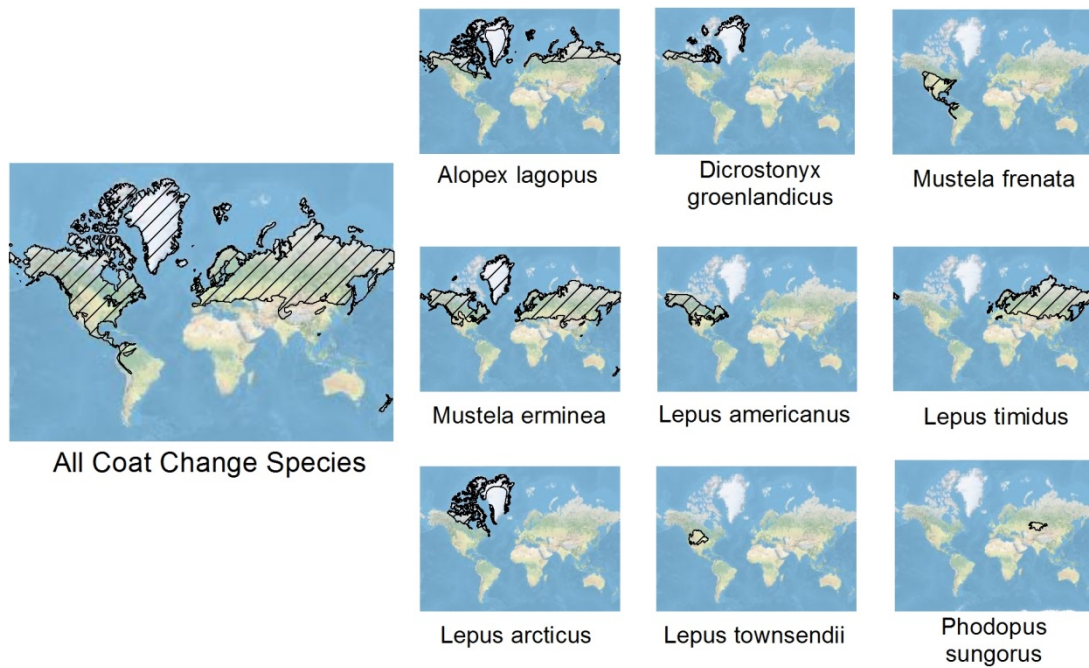


Figure 1 | Seasonally color changing species around the world. Geographical distributions of 9 mammal species with seasonal coat color changes from brown to white in at least some populations. Species include Arctic fox (*Alopex lagopus*), collared lemming (*Dicrostonyx groenlandicus*), long-tailed weasel (*Mustela frenata*), stoat (*M. erminea*), snowshoe hare (*Lepus americanus*), mountain hare (*L. timidus*), Arctic hare (*L. arcticus*), white-tailed jackrabbit (*L. townsendii*), and Siberian hamster (*Phodopus sungorus*). Additional species with seasonal coat color change (eg least weasel; *Mustela nivalis*) are not shown. Maps derived from IUCN redlist metadata (<http://www.iucnredlist.org/technical-documents/spatial-data#mammals>).

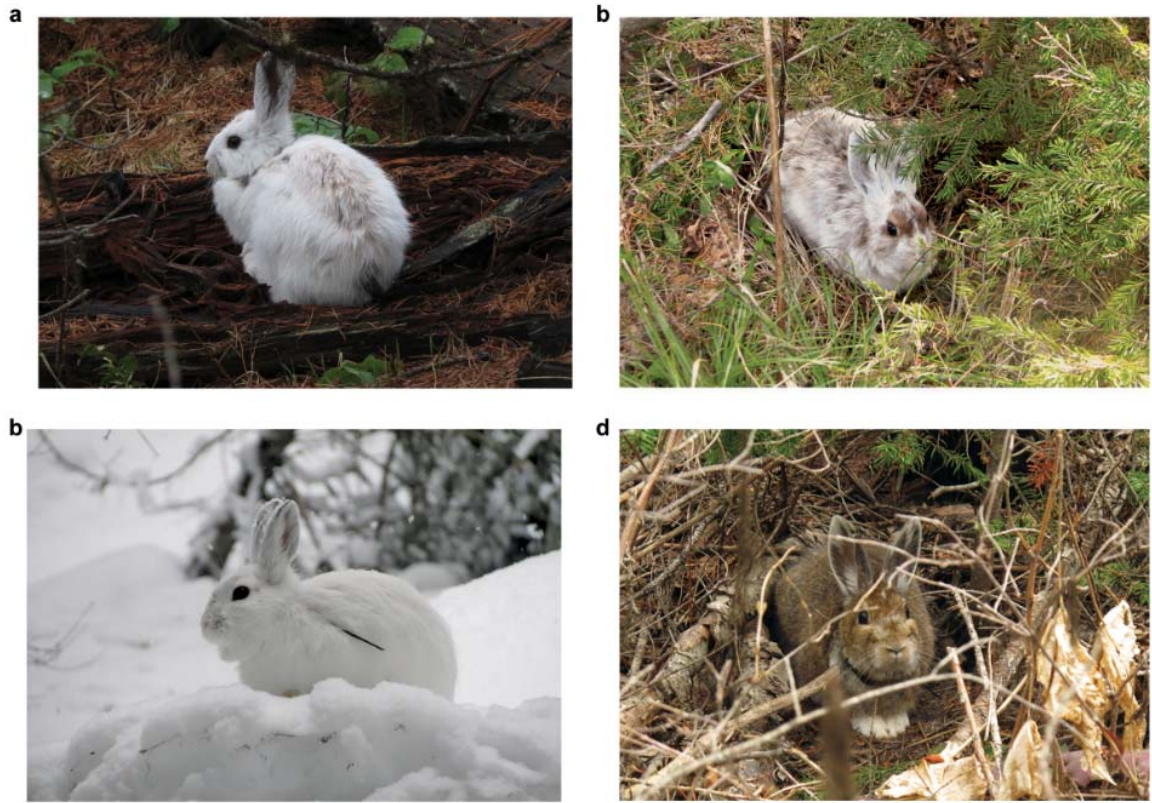


Figure 2 | Types of contrast between seasonal coat color and snow background. Radiocollared snowshoe hares from this study showing: a, 100% contrast (mismatch); b, 60% contrast (mismatch); c, 0% contrast (no mismatch); d, 0% contrast (no mismatch).



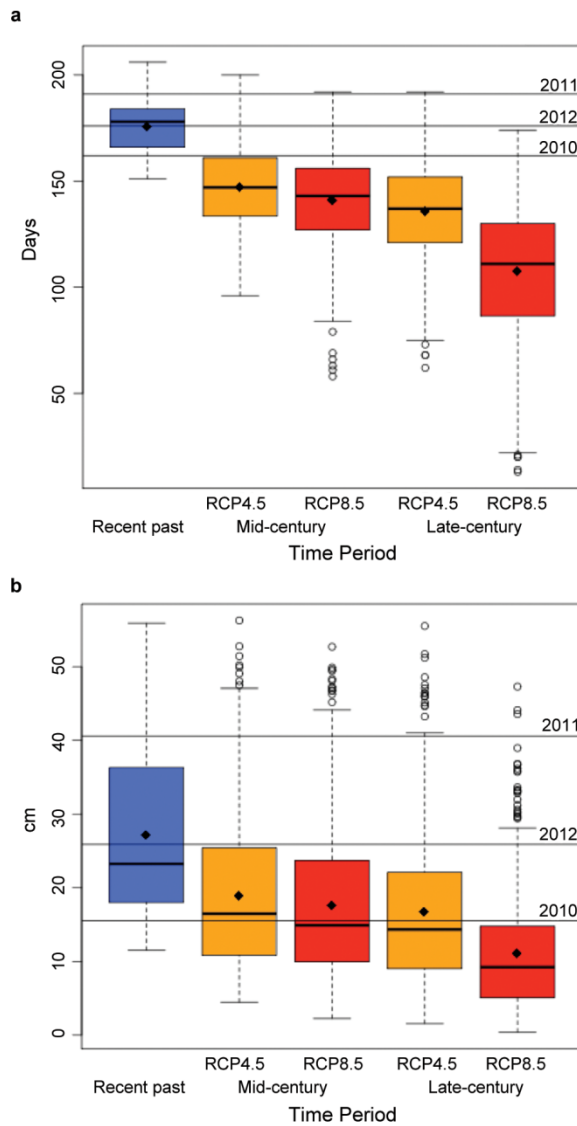


Figure 3 | Modeled baseline and future snow conditions. a, Length of the main snow season for the 3 observation years (black horizontal lines) and boxplots of snow season length for the recent past (1970-1999) baseline (blue shading) and future time periods (mid-century = 2030 – 2059; late-century = 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.

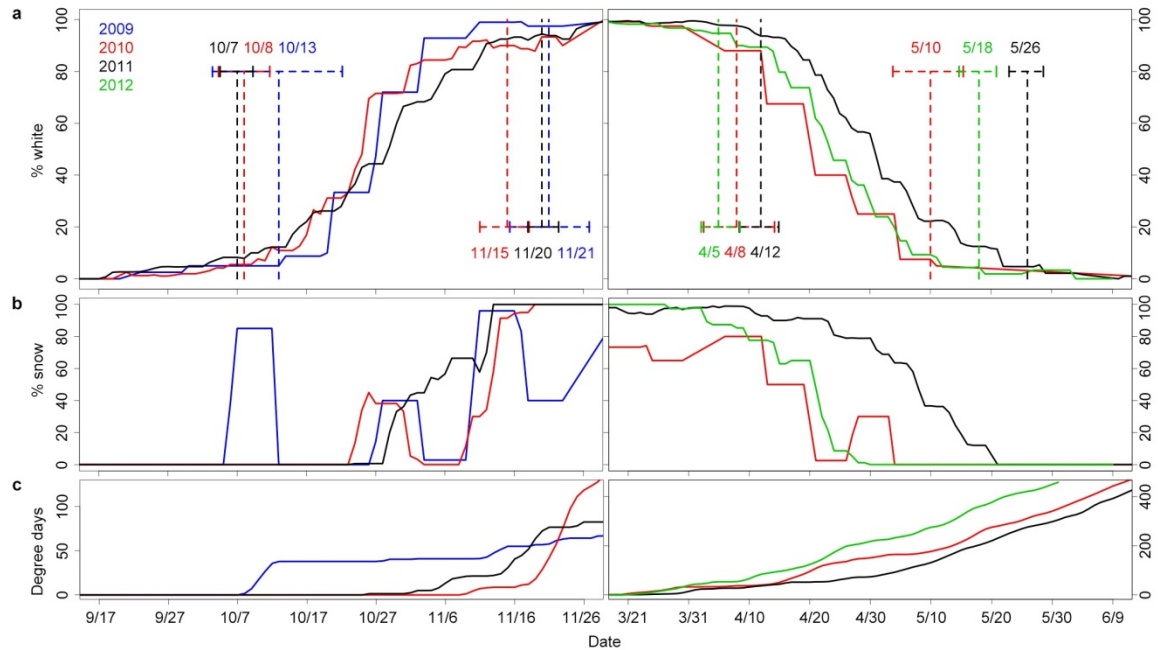


Figure 4 | Coat color phenology, snow cover, and degree days. a, Weekly average of observed coat color for a population of wild snowshoe hares in each of 3 years [2009 (blue), 2010 (red), 2011 (black) and 2012 (green)], with fall seasons on the left panel and springs on the right. Dotted lines show the 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 years (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 years.

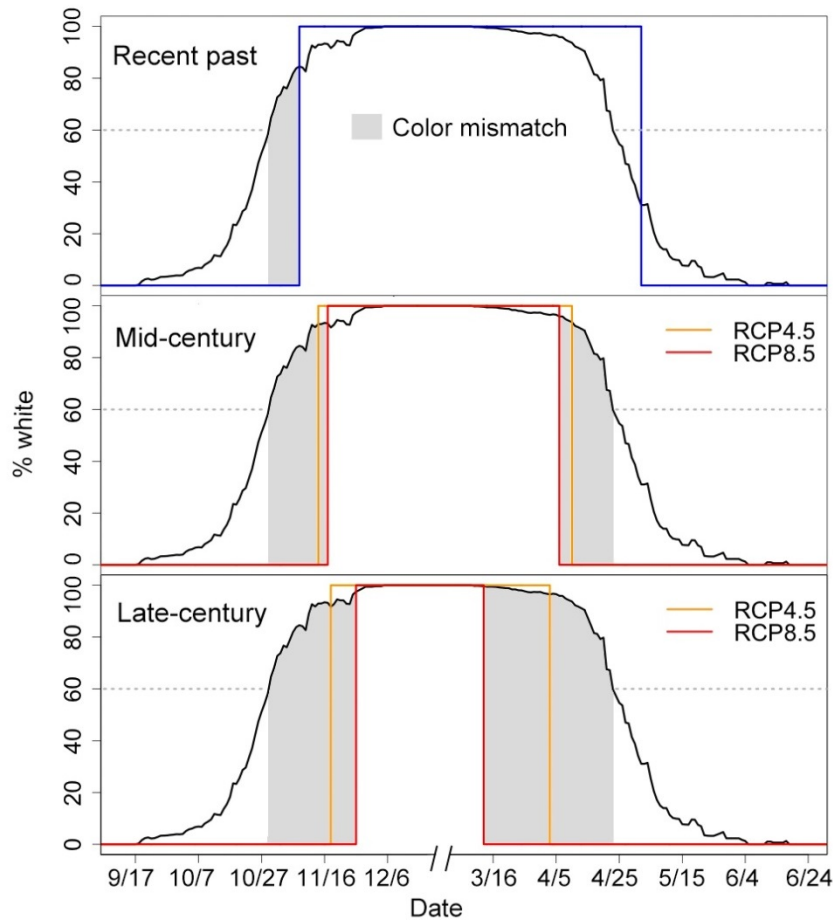


Figure 5 | Projections of increasing seasonal color mismatch in the future. The black line for all panels shows average phenology of hare seasonal color molt across the 3 years of the field study. The blue line shows mean modeled snow duration for the recent past (1970-1999). The orange and red lines 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 4-fold in the mid-century and 8-fold in the late-century.

SUPPLEMENTARY MATERIALS

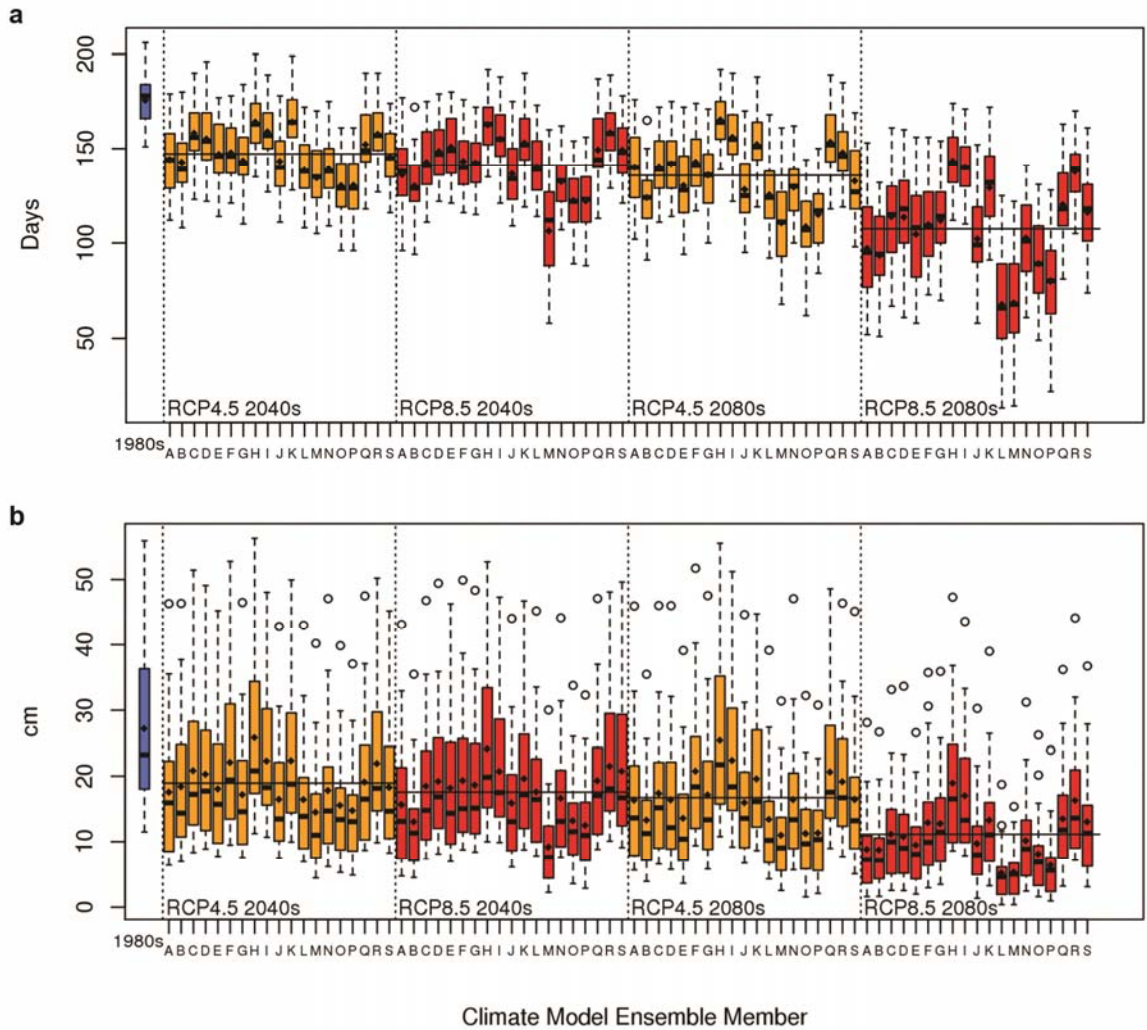


Figure S1. Modeled baseline and entire ensemble of future snow conditions. a, Boxplots of snow season duration for the 1980s baseline (blue shading) and for each climate model ensemble member in the future time periods and emissions scenarios (orange shading = RCP4.5, red shading = RCP8.5). Climate model ensemble members are identified in Table S1. Within each boxplot, bold horizontal lines are the median and diamonds are the mean. Horizontal lines in each time period/scenario are the overall ensemble mean. b, is the same as (a) except for annual maximum snow water equivalent.

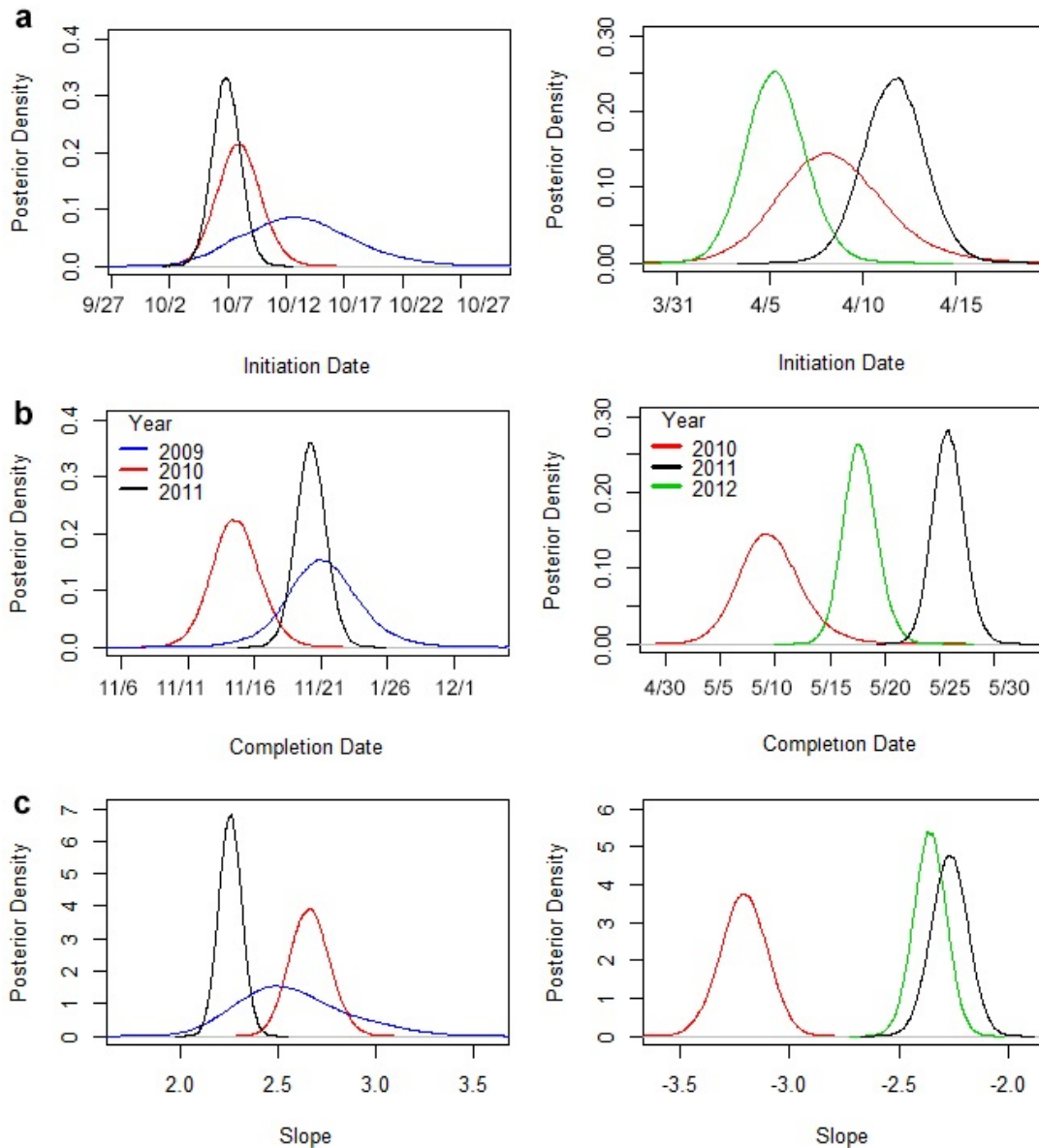


Figure S2. Posterior Bayesian probability distributions of the molt phenology parameters for different years resulting from the change point analysis. Posterior distributions of initiation dates (a), completion dates (b) and slopes (c) of spring (right side panels) and fall (left side panels) coat color molts color coded for years 2009 (blue), 2010 (red), 2011 (black) and 2012 (green line). The peaks in the distributions indicate the most probable means of the parameters and the overlap in the distributions represents the probability of the parameters being equal.

Table S1. Names of CMIP5 models used in the analysis.

<b>Modeling Center (or Group)</b>	<b>Model Name</b>	<b>Model Letter</b>
Beijing Climate Center, China Meteorological Administration	BCC-CSM1.1	A
Canadian Centre for Climate Modelling and Analysis	CanESM2	B
National Center for Atmospheric Research	CCSM4	C
Centre National de Recherches Météorologiques / Centre Européen de Recherche et Formation Avancées en Calcul Scientifique	CNRM-CM5	D
Commonwealth Scientific and Industrial Research Organization in collaboration with Queensland Climate Change Centre of Excellence	CSIRO-Mk3.6.0	E
LASG, Institute of Atmospheric Physics, Chinese Academy of Sciences and CESS, Tsinghua University	FGOALS-g2	F
NOAA Geophysical Fluid Dynamics Laboratory	GFDL-CM3 GFDL-ESM2M	G H
NASA Goddard Institute for Space Studies	GISS-E2-R	I
Met Office Hadley Centre	HadGEM2-ES	J
Institute for Numerical Mathematics	INM-CM4	K
Institut Pierre-Simon Laplace	IPSL-CM5A-LR IPSL-CM5A-MR	L M
Atmosphere and Ocean Research Institute (The University of Tokyo), National Institute for Environmental Studies, and Japan Agency for Marine- Earth Science and Technology	MIROC5	N
Japan Agency for Marine-Earth Science and Technology, Atmosphere and Ocean Research Institute (The University of Tokyo), and National Institute for Environmental Studies	MIROC-ESM- CHEM  MIROC-ESM	O  P
Max Planck Institute for Meteorology	MPI-ESM-LR	Q
Meteorological Research Institute	MRI-CGCM3	R
Norwegian Climate Centre	NorESM1-M	S

Table S2. Number of days of expected hare mismatch, where mismatch is defined as  $\geq 60\%$  difference between hare coat color (based on average phenology across the 3 years of field data) and the modeled snow presence/absence. Recent past = 1970-1999; mid-century = 2030-2059; late-century = 2070-2099. Emission scenarios: 4.5 = moderate-low; 8 = high.

	<b>Recent past</b>	<b>Mid Century 4.5</b>	<b>Mid Century 8.5</b>	<b>Late Century 4.5</b>	<b>Late Century 8.5</b>
	<b>60%</b>	<b>60%</b>	<b>60%</b>	<b>60%</b>	<b>60%</b>
# days of mismatch in fall	<b>9</b>	<b>15</b>	<b>18</b>	<b>19</b>	<b>27</b>
# days of mismatch in spring	<b>0</b>	<b>13</b>	<b>17</b>	<b>20</b>	<b>41</b>
# days total	<b>9</b>	<b>28</b>	<b>35</b>	<b>39</b>	<b>68</b>
<b>-fold to recent past</b>	<b>1</b>	<b>3</b>	<b>4</b>	<b>4</b>	<b>8</b>

Table S3. Number of days of expected hare mismatch, where mismatch is now defined as  $\geq 40\%$  and  $\geq 80\%$  difference between hare coat color (based on average phenology across the 3 years of field data) and the modeled snow presence/absence. Recent past = 1970-1999; mid-century = 2030-2059; late-century = 2070-2099. Emission scenarios: 4.5 = moderate-low; 8 = high.

	Recent past		Mid Century 4.5		Mid Century 8.5		Late Century 4.5		Late Century 8.5	
	40%	80%	40%	80%	40%	80%	40%	80%	40%	80%
# days of mismatch in fall	14	2	20	8	23	11	24	12	32	20
# days of mismatch in spring	0	0	20	9	24	13	27	16	48	37
# days total	14	2	40	17	47	24	51	28	80	57
<b>-fold to recent past</b>	<b>1</b>	<b>1</b>	<b>3</b>	<b>9</b>	<b>3</b>	<b>12</b>	<b>4</b>	<b>14</b>	<b>6</b>	<b>29</b>



Table S4. Snow model parameter values before and after calibration.

<b>Parameter</b>	<b>Initial Value</b>	<b>Calibrated Value</b>
Snowfall Temperature (°C): cutoff daily average temperature for precipitation as snow vs. rain	1.0°C	1.0°C (held constant <sup>23</sup> )
Snowmelt Base Temperature (°C): daily average temperature at which snowpack will melt	0.0°C	0.0°C (held constant <sup>23</sup> )
Snowpack Temperature Lag Factor: factor that controls influence of current daily average temperature on snowpack temperature compared to previous days	0.5	0.05
Minimum Melt Factor for Snow on 12/31 (mm/°C)	4.0 mm/°C	0.0 mm/°C
Maximum Melt Factor for Snow on 6/21 (mm/°C)	6.5 mm/°C	3.2 mm/°C