

Corrections

INNER WORKINGS

Correction for “Whole-climate experiments for peatlands,” by Stephen Ornes, which appeared in issue 23, June 4, 2013, of *Proc Natl Acad Sci USA* (110:9188; first published June 4, 2013; 10.1073/pnas.1307957110).

The author notes that on page 9188, right column, second full paragraph, lines 4–8, “Heaters both above and below ground—extending down 3 meters (9.8 feet)—will warm the air and soil of some enclosures up to 9 °C, or about 42 °F, above ambient.” should instead appear as “Heaters both above and below ground—extending down 3 meters (9.8 feet)—will warm the air and soil of some enclosures up to 9 °C, or about 16.2 °F, above ambient.”

www.pnas.org/cgi/doi/10.1073/pnas.1311224110

ECOLOGY

Correction for “Camouflage mismatch in seasonal coat color due to decreased snow duration,” by L. Scott Mills, Marketa Zimova, Jared Oyler, Steven Running, John T. Abatzoglou, and Paul M. Lukacs, which appeared in issue 18, April 30, 2013, of *Proc Natl Acad Sci USA* (110:7360–7365; first published April 15, 2013; 10.1073/pnas.1222724110).

The authors note that, due to a data entry error, on page 7362, right column, third full paragraph, lines 31–35 “Interestingly, the rate of molt in the spring was substantially influenced by sex, with females completing the spring molt on average 11 d earlier than males. The faster color molt for females is consistent with previous observations (32, 33)” should instead appear as “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).”

Also, on page 7363, right column, first full paragraph, line 13 “($\beta_1 = -25.640$, $sd = 10.263$)” should instead appear as “($\beta_1 = -7.402$, $sd = 6.678$).”

These errors do not affect the conclusions of the article.

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NEUROSCIENCE

Correction for “Regulator of G protein signaling is a crucial modulator of antidepressant drug action in depression and neuropathic pain models,” by Maria Stratinaki, Artemis Varidaki, Vasiliki Mitsi, Subroto Ghose, Jane Magida, Caroline Dias, Scott J. Russo, Vincent Vialou, Barbara J. Caldarone, Carol A. Tamminga, Eric J. Nestler, and Venetia Zachariou, which appeared in issue 20, May 14, 2013, of *Proc Natl Acad Sci USA* (110:8254–8259; first published April 29, 2013; 10.1073/pnas.1214696110).

The authors note that the title appeared incorrectly. The title should instead appear as “Regulator of G protein signaling 4 is a crucial modulator of antidepressant drug action in depression and neuropathic pain models.” The online version has been corrected.

www.pnas.org/cgi/doi/10.1073/pnas.1311399110

PSYCHOLOGICAL AND COGNITIVE SCIENCES

Correction for “Testosterone administration impairs cognitive empathy in women depending on second-to-fourth digit ratio,” by Jack van Honk, Dennis J. Schutter, Peter A. Bos, Anne-Wil Kruijt, Eef G. Lentjes, and Simon Baron-Cohen, which appeared in issue 8, February 22, 2011, of *Proc Natl Acad Sci USA* (108:3448–3452; first published February 7, 2011; 10.1073/pnas.1011891108).

The authors note that Figure 1 and its legend appeared incorrectly. The corrected figure and its legend appear below.

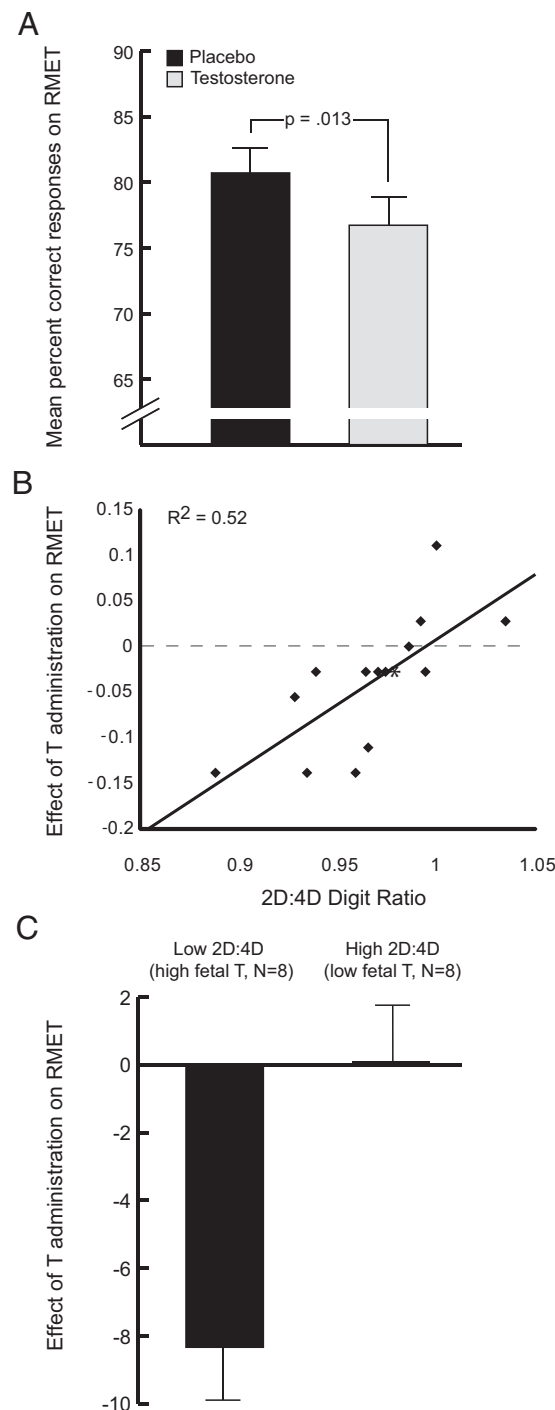


Fig. 1. (A) Effect of testosterone administration on cognitive empathy in young women: mean and SEM of the percentage correct responses on the RMET after administration of testosterone and placebo ($P = 0.013$, one-tailed). Testosterone administration impairs the ability to accurately infer motives, intentions, thoughts, and emotions from the eye region of the face of others. (B) Fetal testosterone exposure (inferred from 2D:4D ratio) predicts the effect of testosterone administration on cognitive empathy: scatter plot shows the interaction between the 2D:4D ratio fetal testosterone marker and the effect of testosterone (T) administration on cognitive empathy ($P < 0.001$). The group effect of testosterone administration on cognitive empathy varies strongly according to individual 2D:4D ratios. The asterisk defines two identical data points. (C) Effect of testosterone (T) administration on cognitive empathy in subjects with high and low fetal testosterone exposure (inferred 2D:4D ratio): Mean and SEM of the effect of testosterone administration on cognitive empathy in subjects with relatively low and high 2D:4D ratios, based on median split. Substantial effects of testosterone on cognitive empathy are observed in subjects with high fetal testosterone exposure ($P = 0.006$, one-tailed), and no effects are seen in subjects with low fetal testosterone exposure ($P = 1$).]

Camouflage mismatch in seasonal coat color due to decreased snow duration

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

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

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

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

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

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

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

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

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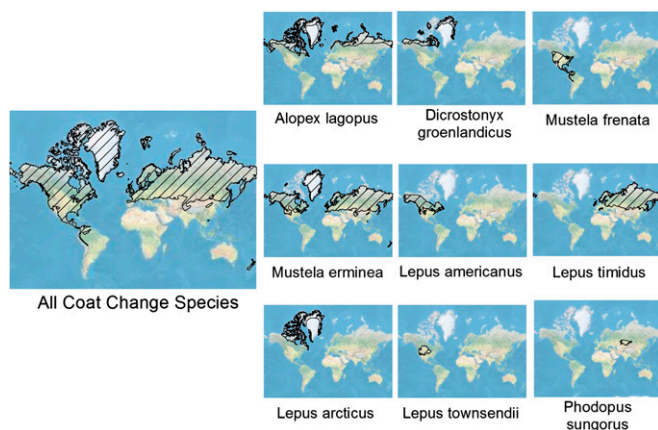
The authors declare no conflict of interest.

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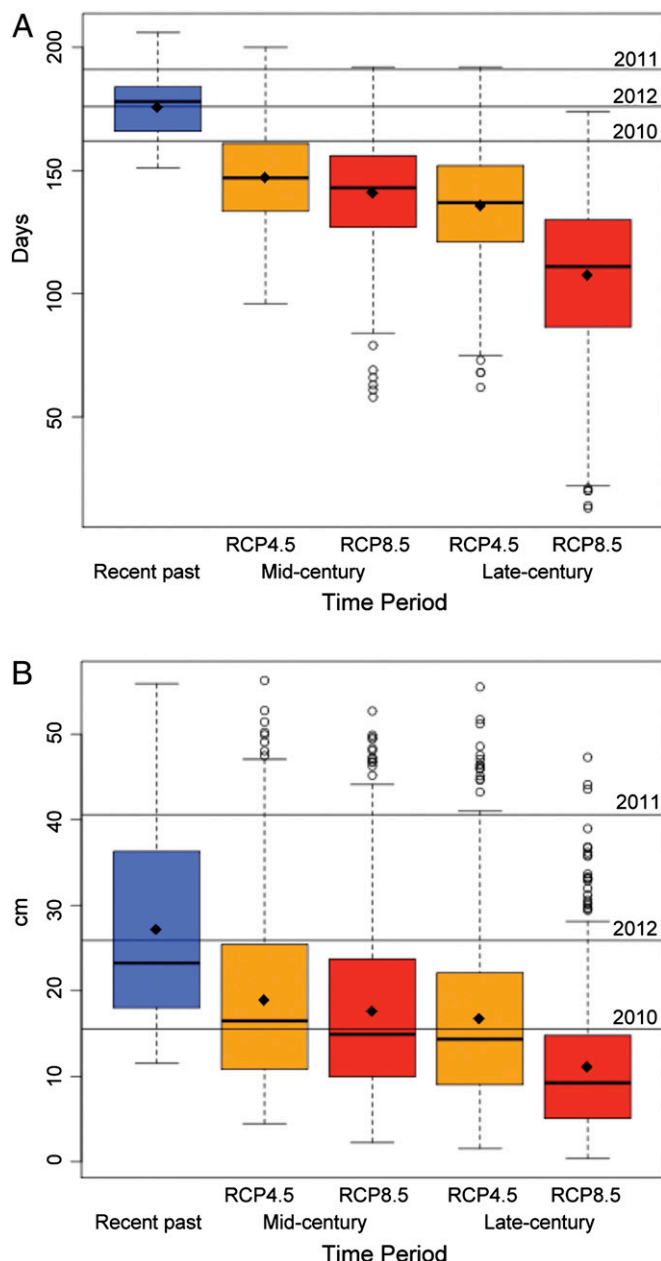


Fig. 3. Modeled baseline and future snow conditions. (A) Length of the main snow season for the three observation years (black horizontal lines) and boxplots of snow season length for the recent past (1970–1999) baseline (blue shading) and future time periods (mid-century, 2030–2059; late-century, 2070–2099)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

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

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

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

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

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

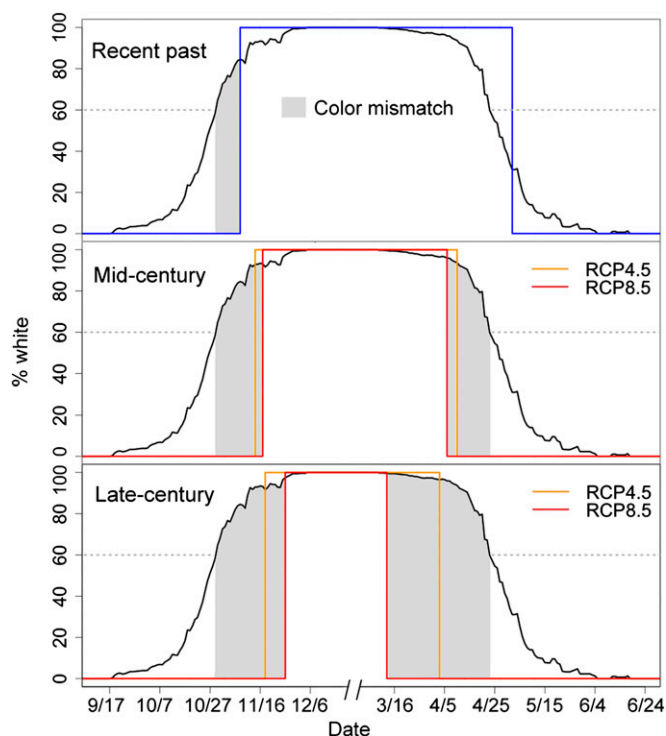


Fig. 5. Projections of increasing seasonal color mismatch in the future. The black line for all panels shows average phenology of hare seasonal color molt across the 3 y of the field study. The blue line shows mean modeled snow duration for the recent past (1970–1999). The orange and red lines show the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

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

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

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

Climate projections from 19 CMIP5 models were summarized by projected change in average monthly minimum temperature, maximum temperature, and precipitation in the mid-century (2030–2059) and late-century (2070–2099) relative to the recent past (1970–1999) using inverse distance weighting from the native 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-y future time period, climate model, and RCP combination to test the degree to which future snow conditions could change at the site.

ACKNOWLEDGMENTS. Michael Sweet prepared Fig. 1. We appreciate reviews from Paulo Alves, Doug Emlen, Jeff Good, Kevin McKelvey and Karen Hodges. We acknowledge the World Climate Research Programme's Working Group on Coupled Modelling, which is responsible for CMIP, and we thank the climate modeling groups (listed in Table S1) for producing and making available their model output. For CMIP, the US Department of Energy's Program for Climate Model Diagnosis and Intercomparison provides coordinating support and led development of software infrastructure in partnership with the Global Organization for Earth System Science Portals. Funding came from National Science Foundation Division of Environmental Biology Grant 0841884, the US Geological Survey National Climate Change and Wildlife Science Center, and the Bureau of Land Management (to L.S.M.); and National Aeronautics and Space Administration Grant NNX11AO47G (to S.R.) and Fieldwork was facilitated by the US Forest Service Seeley Lake Ranger District.

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Supporting Information

Mills et al. 10.1073/pnas.1222724110

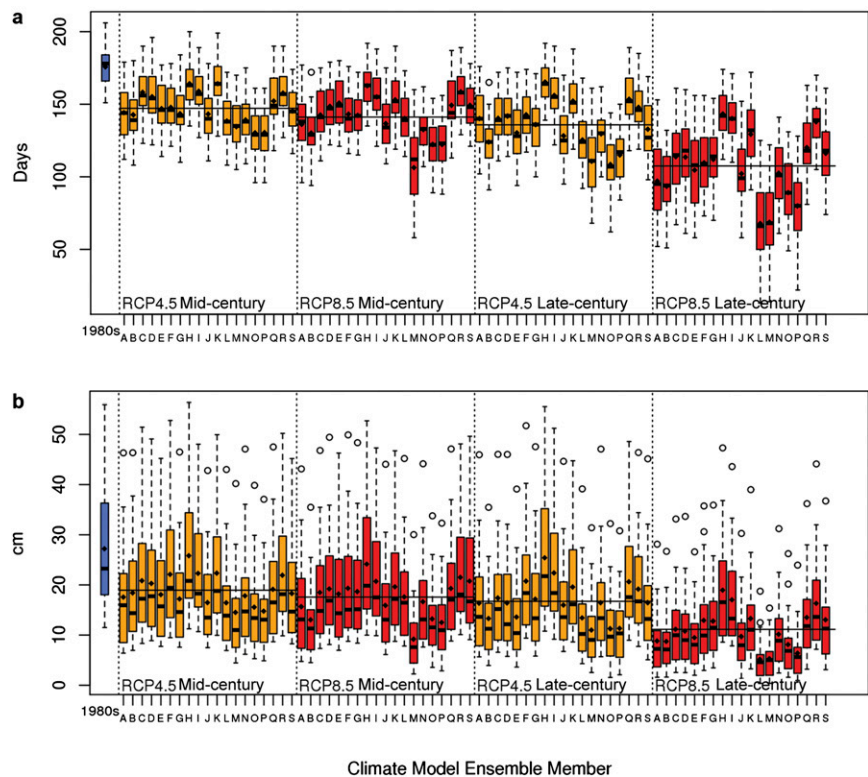


Fig. S1. Modeled baseline and entire ensemble of future snow conditions. (A) Boxplots of snow season duration for the recent past (1970–1999) baseline (blue shading) and for each climate model ensemble member in the future time periods and emissions scenarios [orange shading, representative concentration pathways (RCP) 4.5; 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) The same, except that B describes annual maximum snow water equivalent.

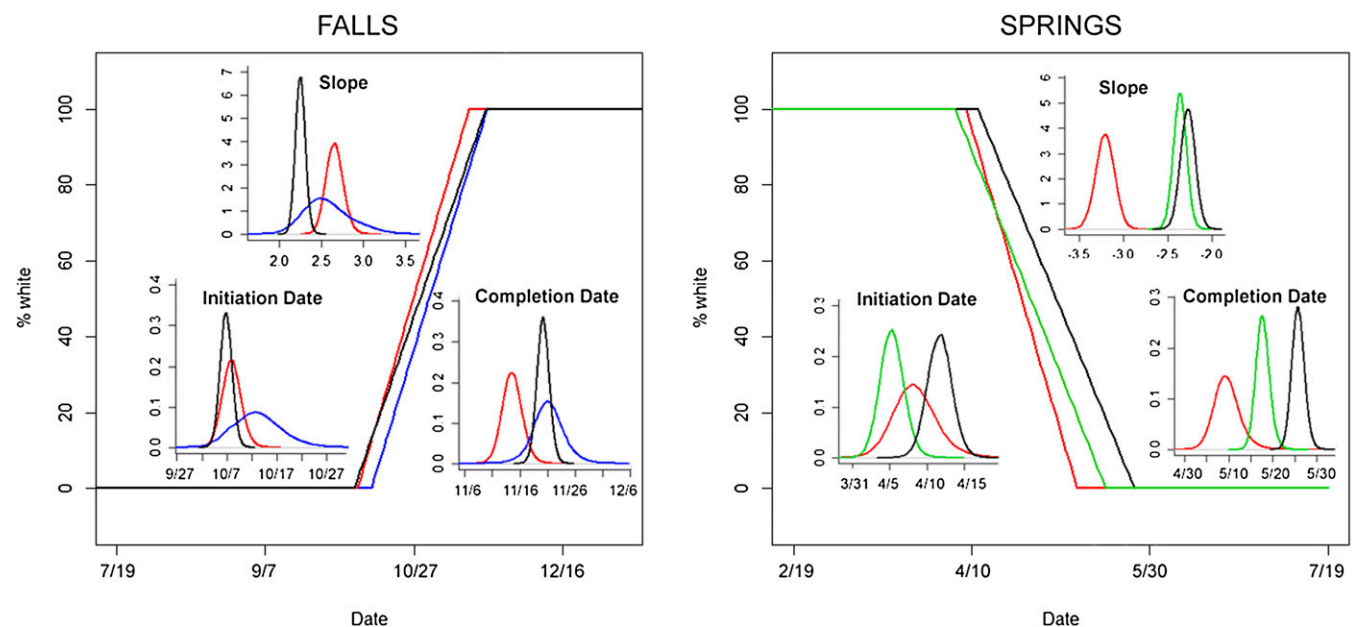


Fig. S2. Descriptors of reaction norm for seasonal coat color change of snowshoe hares over 3 y [fall 2009 (blue), spring and fall 2010 (red), spring and fall 2011 (black), and spring 2012 (green line)]. Main graph shows the population reaction norm, with hares 0% white in summer and 100% white in winter. In the fall, hares across the 3 y initiated at the same time and completed at the same time, with the rate of change (slope of line) also similar across years. In the spring, hares across the 3 y initiated at the same time but showed plasticity in completion date, leading to significantly different rates of change in molt rate. Statistical significance in the molt parameters can be inferred from the *Insets*, which give posterior probability distributions of the molt phenology parameters for different years for initiation dates, completion dates, and slopes for each season. The peaks in the distributions indicate the most probable means of the parameters, and the width accounts for uncertainty due to sample size and variance. The overlap in the distributions among years represents the probability of the parameters being equal. All distributions overlap, showing no plasticity, except for the plasticity exhibited in spring rate of change where the molt from white to brown in spring 2010 was significantly faster.

Table S1. Names of CMIP5 models used in the analysis

Modeling center (or group)	Model name	Model letter
Beijing Climate Center, China Meteorological Administration	BCC-CSM1.1	A
Canadian Centre for Climate Modeling and Analysis	CanESM2	B
National Center for Atmospheric Research	CCSM4	C
Centre National de Recherches Meteorologiques, Centre Europeen de Recherche et Formation Avancees 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
State Key Laboratory of Numerical Modeling for Atmospheric Sciences and Geophysical Fluid Dynamics, Institute of Atmospheric Physics, Chinese Academy of Sciences and Center for Earth System Science, Tsinghua University	FGOALS-g2	F
National Oceanic and Atmospheric Administration Geophysical Fluid Dynamics Laboratory	GFDL-CM3	G
	GFDL-ESM2M	H
National Aeronautics and Space Administration 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	L
	IPSL-CM5A-MR	M
	MIROC5	N
Atmosphere and Ocean Research Institute (The University of Tokyo), National Institute for Environmental Studies, and Japan Agency for Marine-Earth Science and Technology	MIROC-ESM-CHEM	O
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	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 a hare coat color (based on average phenology across the 3 y of field data) being $\geq 60\%$ different from modeled snow presence or absence

Description	Recent past 60%	Mid-century 4.5 60%	Mid-century 8.5 60%	Late-century 4.5 60%	Late-century 8.5 60%
No. of days of mismatch in fall	9	15	18	19	27
No. of days of mismatch in spring	0	13	17	20	41
No. of days total	9	28	35	39	68
Fold to recent past	1	3	4	4	8

Recent past, 1970–1999; mid-century, 2030–2059; late-century, 2070–2099. Emission scenarios: 4.5, moderate-low; 8.5, high.

Table S3. Sensitivity analysis of 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 y of field data) and the modeled snow presence or absence

Description	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%
No. of days of mismatch in fall	14	2	20	8	23	11	24	12	32	20
No. of days of mismatch in spring	0	0	20	9	24	13	27	16	48	37
No. of days total	14	2	40	17	47	24	51	28	80	57
Fold to recent past	1	1	3	9	3	12	4	14	6	29

Recent past, 1970–1999; mid-century, 2030–2059; late-century, 2070–2099. Emission scenarios: 4.5, moderate-low; 8.5, high.

Table S4. Snow model parameter values before and after calibration

Parameter	Initial value	Calibrated value
Snowfall temperature: cutoff daily average temperature for precipitation as snow vs. rain	1.0 °C	1.0 °C (held constant) (1)
Snowmelt base temperature: daily average temperature at which snowpack will melt	0.0 °C	0.0 °C (held constant) (1)
Snowpack temperature lag factor: factor that controls influence of current daily average temperature on snowpack temperature compared with previous days	0.5	0.05
Minimum melt factor for snow on December 31	4.0 mm/°C	0.0 mm/°C
Maximum melt factor for snow on June 21	6.5 mm/°C	3.2 mm/°C

1. Fontaine TA, Cruickshank TS, Arnold JG, Hotchkiss RH (2002) Development of a snowfall-snowmelt routine for mountainous terrain for the soil water assessment tool (SWAT). *J Hydrol (Amst)* 262(1-4):209–223.