

LETTER

High fitness costs of climate change-induced camouflage mismatch

Marketa Zimova,^{1*} L. Scott Mills,¹
and J. Joshua Nowak²

¹Fisheries, Wildlife and Conservation Biology Program, College of Natural Resources, North Carolina State University, Box 7617, David Clark Labs, Raleigh, NC 27695-7617, USA

²Wildlife Biology Program, University of Montana, Missoula, MT 59812, USA

*Correspondence: E-mail: mzimova@ncsu.edu

Abstract

Anthropogenic climate change has created myriad stressors that threaten to cause local extinctions if wild populations fail to adapt to novel conditions. We studied individual and population-level fitness costs of a climate change-induced stressor: camouflage mismatch in seasonally colour molting species confronting decreasing snow cover duration. Based on field measurements of radiocoloured snowshoe hares, we found strong selection on coat colour molt phenology, such that animals mismatched with the colour of their background experienced weekly survival decreases up to 7%. In the absence of adaptive response, we show that these mortality costs would result in strong population-level declines by the end of the century. However, natural selection acting on wide individual variation in molt phenology might enable evolutionary adaptation to camouflage mismatch. We conclude that evolutionary rescue will be critical for hares and other colour molting species to keep up with climate change.

Keywords

Camouflage, climate change, evolutionary adaptation, evolutionary rescue, fitness, molt phenology, natural selection, phenological mismatch, snow cover, snowshoe hare.

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INTRODUCTION

Organisms have always been subjected to biotic and abiotic changes in their environment that forced them to either move or adapt *in situ* to avoid extinction. These background ‘natural’ stressors are now being exacerbated by myriad new human-induced challenges occurring on a global scale and at rapid rates, often synergistically with each other. Because migrations to avoid those stressors are not always a viable option in contemporary landscapes, organisms increasingly rely on adaptation to ameliorate their effects. In the face of global environmental change, two urgent questions in ecology arise; first, what are the individual and population fitness consequences of anthropogenic stressors on wild populations, and second, what is the potential for local adaptation to the stressors through phenotypic plasticity and evolution?

Anthropogenic climate change poses a serious threat to persistence of wild species and is projected to occur at unprecedented rates in the 21st century (IPCC 2013). The most commonly discussed consequences of climate change involve phenological mismatches between locally adapted traits and novel environmental conditions (Root *et al.* 2003). Although phenological mismatches under climate change have been widely described (Parmesan 2007; Miller-Rushing *et al.* 2010; Thackeray *et al.* 2010), only a few studies have quantified actual demographic consequences of climate change: some populations successfully responded via phenotypic plasticity or evolution (Reale *et al.* 2003; Charmantier *et al.* 2008), while others experienced declines in vital rates due to inability to sufficiently track change (Both *et al.* 2006; Visser *et al.* 2006; Lane *et al.* 2012; Tafani *et al.* 2013). Further, progress in attributing phenological mismatches directly to climate change has been hampered by the fact that climate variables

change in complex ways across space and time, and often interact with other stressors that can confound the signal from climate change.

We focus on a direct climate change-induced phenological mismatch that arises from shortened duration of seasonal snow cover across temperate regions of the globe. With later onset of snow in the fall and earlier loss of snow in the spring, decreasing duration of snow cover is among the strongest and most globally consistent consequences of anthropogenic greenhouse gas emissions (Kapnick & Hall 2012; Diffenbaugh & Field 2013). This has potential to cause a mismatch in seasonal camouflage for at least 14 species undergoing colour molts from white to brown to minimize colour contrast when snow is seasonally present or absent (Mills *et al.* 2013). Because white animals appear extremely conspicuous against the snowless backgrounds, we predict that they face higher predation risk with fitness costs that could, in the absence of sufficient adaptive tracking, endanger population persistence.

Snowshoe hares (*Lepus americanus*) are an ideal organism to investigate consequences of camouflage mismatch because seasonal camouflage represents a critical adaptation for this strongly interacting prey species. We expect background matching to be under strong selection for hares, as 85–100% of mortality is predation related (Hodges 2000). To date, we have found limited plasticity in coat colour molt phenology of hares across multiple years, with some shifts in the spring molt phenology in relation to temperature or snow, but a fixed onset and rate of the fall molt (Mills *et al.* 2013; Zimova *et al.* 2014; Kumar 2015). Additionally, hares did not adjust their anti-predatory behaviours to reduce either the extent of camouflage mismatch (e.g. microsite selection) or vulnerability when mismatched (e.g. concealment via hiding, flight response) (Zimova *et al.* 2014). Based on locally downscaled

snow duration projections, the shortened duration of snow and the limited phenotypic plasticity exhibited by hares would be expected to yield 4–8 fold increase in the number of days of camouflage mismatch by the end of the century (from 9 to 39–68 days; Mills *et al.* 2013). The next key questions are whether this mismatch results in negative mortality consequences that could lead to population declines and local extirpation, and whether adaptive rescue may be possible.

Here, we quantify natural selection directly driven by anthropomorphic climate change in a wild population. We demonstrate high among-individual phenotypic variation in an ecologically important trait under selection and extend the survival costs to future population dynamics. Based on weekly observations of 186 radio collared snowshoe hares over three years at two sites, we first calculated survival costs of camouflage mismatch and found strong natural selection acting on seasonal molt phenology which was highly variable across individuals. Second, incorporating predicted future mismatch frequency due to decreased snow duration, we projected annual survival into the 21st century under two climate change scenarios. Lastly, we translated observed mortality costs of camouflage mismatch into population growth rate and demonstrated that selection against mismatch is capable of causing considerable population declines. We conclude that evolutionary rescue represents a critically important process to avert population declines due to future camouflage mismatch.

MATERIAL AND METHODS

Study area

We conducted our research in two areas in Western Montana, separated by about 330 km: Seeley Lake in the Lolo National Forest (Morrell Creek drainage, Lat. = 47.23°, Long. = –113.43°) and Gardiner in the Gallatin National Forest (Bear Creek drainage, Lat. = 45.08°, Long. = –110.57°). The Gardiner study site is about twice as high in elevation (2400–2700 m a.s.l.) as the Seeley Lake site (1300–1450 m a.s.l.), with associated cooler temperatures and longer duration of snow cover; continuous snowpack typically persists from late October until May at the Gardiner site (Zimmer *et al.* 2008) vs. December to April at the Seeley Lake site (Mills *et al.* 2013). The Seeley Lake site is 240 km south of the Gardiner site. Both areas consist of boreal coniferous forests with little to no permanent human habitation and moderate logging as the primary land use. Common predators for hares at both sites include the Canada lynx (*Lynx canadensis*), bobcat (*L. rufus*), coyote (*Canis latrans*), red fox (*Vulpes vulpes*), long-tailed weasel (*Mustela frenata*), American marten (*Martes americana*), great horned owl (*Bubo virginianus*), northern goshawk (*Accipiter gentilis*), and red-tailed hawk (*Buteo jamaicensis*).

Survival monitoring

We captured hares continuously throughout the year in live traps (Tomahawk Live Trap Company, Tomahawk, WI). Hares weighing > 900 g were fitted with VHF radiocollars

(Wildlife Materials, Murphysboro, IL) equipped with mortality sensors. The radiocollars weighed < 40 g, below the well-accepted radiocollar threshold of 5% of body weight (Wilson *et al.* 1996). All handling procedures were approved by the University of Montana Animal Care and Use Committee (Protocol No. 021-10SMWB-051110).

We monitored weekly survival status using radiotelemetry of a total of 186 radiocollared hares, including 136 in the Seeley Lake study site from 4 July 2009 to 16 June 2012 and 50 in the Gardiner study site from 8 August 2010 to 16 June 2012. When a mortality signal was detected, the individual was located to determine the cause of death. We confirmed 124 predator-related deaths (= 67% of all monitored hares). Next, 24 individuals were right censored as mortality was obviously not caused by predation (i.e. mortalities within 10 days of capture or when a hare body was found intact) and 17 individuals were right censored due to radiocollar failure or permanent emigration out of the study area. The remaining 21 individuals were alive at the time the study terminated. Weekly sample size of monitored individuals varied throughout the year with a median of 37 hares (SD = 15).

Molt and snow cover phenology monitoring

We attempted to visually locate all hares once a week using radiotelemetry to quantify coat colour molt phenology and snow cover around each hare following the methods described in (Mills *et al.* 2013; Zimova *et al.* 2014). The percentage of white coat colour (hare whiteness) was visually estimated in 20% increments with a standardized protocol of observations and photographs to control for light conditions and distance. Animals that just initiated or nearly completed the molt were classified as 5 or 95% white. 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 and did not show the whole hare's body, or the photograph was absent.

Similarly, using standardized protocols of observations and photographs, we estimated the percentage of ground snow cover within a 10-m radius circle centered at each hare's resting spot in 20% increments. Weekly mean snow cover for each site was averaged across all the snow cover observations collected at each site during that week.

Statistical analysis

Colour contrast modelling

Because we could not quantify coat colour of each hare every week, we used a nonlinear model for missing observations of coat colour. The model took the form as follows:

$$W_{ij} = \frac{100}{(1 + \exp(-\alpha_{0,i} + \alpha_{1,i} \times JD_j))} + \varepsilon,$$

where the value of whiteness (W_{ij}) for individual i in week j was a function of the maximum observable whiteness (100), and the effect of standardized Julian day (JD_j). The standardized Julian day was calculated by first subtracting the

day on which population mean whiteness was nearest 50% and then divided by the standard deviation of ($JD_{1,j}$). The α_i parameters were considered individual level random effects that controlled the shape of the curve. Individual level prior distributions of the α_i parameters were specified as $N(A, \sigma_\alpha)$ and the population level parameter A was specified as $N(0, 0.001)$, whereas dispersion parameter σ_α received $U(0, 50)$ prior. Finally, we assumed normal residual error ε about the mean with prior $N(0, \sigma)$. The prior distribution for σ assumed the same $U(0, 50)$ form as previous dispersion parameters.

Colour contrast was calculated as the absolute difference between the individual's estimated weekly coat colour and weekly mean snow cover at its respective study site. We referred to hares as being mismatched when contrast was $\geq |60\%$ (see Mills *et al.* 2013, for consideration of other thresholds), as at this threshold hares appear highly conspicuous against their surroundings. To allow for mismatch to affect survival for either a white hare against a brown background or vice versa, colour contrast was defined on an absolute scale.

Survival cost of camouflage mismatch

We used hierarchical known fate survival models to test whether survival was equal at the two sites and to calculate the fitness cost of camouflage mismatch on individual survival. The hierarchical known fate survival models had a linear predictor of the form:

$$\text{logit}(\phi_{ij}) = \beta_0 + \beta_1 \times x_{ij} + \gamma_i,$$

where ϕ_{ij} is the expected weekly survival estimate for individual i at time j given the mean overall survival β_0 , the level of the covariate x_{ij} and the effect of that covariate on survival β_1 , and γ_i is an individual level random effect.

We first tested whether the mean survival of the two study populations (Seeley Lake and Gardiner) was equal by including the study site as the sole categorical covariate in the model. Because we found negligible differences in survival between the two populations (see Results), we pooled all 186 individuals for the rest of the analysis. Next, to calculate the effects of colour contrast on individual survival, we combined the model estimating weekly varying individual colour contrast with the survival model. Combining the models had the advantage of propagating uncertainty in colour contrast, such that x_{ij} itself was a distribution estimated by the colour contrast model described above.

The models were fitted within a Bayesian framework which eased implementation of random effects and the simultaneous modelling of missing covariate values and derived parameters (e.g. annual survival). We included an individual level random effect to account for the repeated measures design and a lack of independence among individuals (Lebreton *et al.* 1992), and to minimize bias arising from individual heterogeneity (Cam *et al.* 2002). Modelling at the individual level allowed us to account for a staggered entry (i.e. animals entering the study at different times) and right censoring (i.e. animals leaving the study prior to its completion) of individuals. Error was assumed to be distributed according to a Bernoulli distribution.

We obtained posterior distributions along with their 95% credible intervals (CRI), using Markov Chain Monte Carlo (MCMC) methods (Gilks *et al.* 1996). Uniform priors $U(-10, 10)$ were placed on both β parameters, while the standard deviation of individual random effects received a $U(0, 50)$ prior. Convergence was assessed, using the Gelman and Rubin potential scale reduction statistic \hat{R} (Gelman & Rubin 1992) and visual inspection of the plotted chains and posteriors. The \hat{R} values were ≤ 1.1 for all parameters after running three parallel chains of length 200 000 and discarding the first 50 000 as burn-in. We thinned such that every 10th observation was retained for parameter estimation. Colour contrast data were scaled by dividing by 100 such that they took values from 0 to 1 except for the single estimate of the selection coefficient as specified below. The effect size of the colour contrast in Fig. 3 was extrapolated across the entire plausible range of colour contrast. All analyses were conducted in JAGS software (Plummer 2003), run from R 2.15.2 (R Development Core Team, 2012) via the R2jags package (Su & Yajima 2012).

Selection coefficient

We quantified a standardized linear selection coefficient of colour contrast on survival by rerunning the survival model with temporally standardized weekly colour contrast data. We standardized by subtracting the mean colour contrast of all individuals observed each week from each individual's colour contrast in the same week and then divided by the standard deviation of the population's colour contrast. Given the extreme amount of variability in the colour contrast within a year, we chose to standardize data on a weekly scale to best approximate the temporal scale of selection on this trait and thus considered the trait an individual level time-varying trait. The estimated slope quantified the deviation from the mean weekly survival that is due to the individual's colour contrast relative to the population's mean level of contrast – a standardized selection coefficient (Kingsolver & Smith 1995; Gimenez *et al.* 2008). We assumed that the form of selection against colour contrast would be directional; survival probability decreases linearly as hares become more contrasted against their background.

Annual survival rate projections

We projected annual survival rates into the 21st century under specific climate change scenarios. First, weekly survival estimates ϕ_j were calculated for colour contrast of 0 and 60% (the lowest degree of contrast when hares are considered mismatched) in the following way:

$$\text{logit}(\phi_j) = \beta_0 + \beta_1 \times \text{weekly colour contrast}_j,$$

where ϕ_j is the expected weekly survival estimate at week j given the mean overall survival β_0 , the degree of colour contrast during that week (0 or 60%) and the effect of colour contrast on survival β_1 as calculated by the survival model with weekly colour contrast. Next, annual survival estimates ϕ_{Annual} were calculated by multiplying weekly survival estimates for the predicted number of weeks out of the year (52 weeks total) hares are expected to experience colour contrast of either 0 or 60% under specific climate change scenarios:

$$\phi_{\text{Annual}} = \phi_{0\% \text{ contrast}}^{(c)} \times \phi_{60\% \text{ contrast}}^{(52-c)}.$$

The number of weeks of the year with 0% colour contrast (*c*) and 60% colour contrast was derived from the estimates of additional number of weeks of that colour contrast in the future (Table 1). We previously modelled future snow cover at our sites using a locally calibrated temperature index snow-fall-snowmelt model to estimate future daily snow water equivalent (SWE) at our sites (for complete description of the snow downscaling methods see Mills *et al.* 2013). The additional number of weeks was then calculated for two future time periods: mid-century (2030–2059) and late century (2070–2099). We considered two different climate change scenarios that were originally described by the Intergovernmental Panel on Climate Change (IPCC) Fifth Assessment Report (AR5). The scenarios include both the representative concentration pathway (RCP) 4.5 (medium-low emissions) scenario and the RCP8.5 (high emissions) scenario (Mills *et al.* 2013; Table 1).

Population growth rate projections

Survival cost due to camouflage mismatch is a direct index of fitness, but absolute fitness and consequences on population dynamics can be estimated by λ , representing both the annual geometric growth rate of the population and average individual fitness (Tuljapurkar *et al.* 2009). We used the measured survival costs of camouflage mismatch in a Lefkovich matrix population model to ask how population growth would be affected in the future for a snowshoe hare population whose complete demographic rates were intensively monitored 1999–2002 within 20 km of our Seeley Lake population (Griffin & Mills 2009). The asymptotic geometric population growth rate (λ) was 1.15 for this baseline population. To calculate λ for the future time periods, we projected the population matrix retaining these baseline vital rates, but modifying juvenile and adult spring and fall survival rates according to the cost of mismatch under decreased snow duration.

Specifically, we used the proportionate reduction in weekly survival due to camouflage mismatch measured in this study [(weekly survival when colour contrast is 60%)/(weekly sur-

vival when colour contrast is 0%)] as a decrement in weekly survival for each additional week in the future where absence of snow leads to colour contrast of $\geq 60\%$. As in the previous section, the number of additional weeks at the mid-century and late century leading to colour contrast $\geq 60\%$ was based on locally downscaled snow duration projections for spring and fall under the two emissions scenarios (Table 1; Mills *et al.* 2013).

We did not adjust reproductive rates (e.g. pre-weaning survival, litter size, number of litters), because weaning occurs before the fall molt and no obvious mechanism would connect camouflage mismatch to changes in reproductive rates. Further, reproductive rates are unlikely to confound the strong influence of post-weaning survival on population growth rate, because formal sensitivity analyses (Haydon *et al.* 1999) and other modelling of snowshoe hare population dynamics (Griffin & Mills 2009) show an overwhelming influence of post-weaning survival.

RESULTS

Individual variation in molt phenology and colour contrast

We found considerable phenotypic variation in seasonal colour molt phenology among individuals within populations (Fig. 1), translating to individual variation in colour contrast (Fig. 2). Different individuals within a population had $> 50\%$ differences in percent white of coat colour for an average of 7 weeks each year. Camouflage mismatch (colour contrast $\geq 60\%$) occurred infrequently for any particular individual, with each hare experiencing mismatch for < 1 week per year on average (Fig. 2).

Survival cost of camouflage mismatch and selection coefficient

The cost of being mismatched was high. According to the survival model including weekly colour contrast, the effect size of colour contrast on weekly survival was strongly negative [$\beta_{\text{Contrast}} = -0.95$, 95% CRI = $(-1.82, -0.035)$] on the logit scale (Fig. 3), such that a completely mismatched hare (100% contrast) had a 7% lower weekly survival than a hare at the same time and place that matched its background (0% contrast). When we rerun this model, using temporally standardized weekly colour contrast, it yielded a significantly negative standardized selection coefficient of -0.04 , 95% CRI = $(-0.061, -0.017)$. Finally, the univariate survival model with site as a covariate showed that the mean survival of the two study populations was equal [$\beta_{\text{Site}} = 0.004$, 95% CRI = $(-0.54, 0.52)$]. Plots of Markov chains revealed well mixed chains that appeared 'grassy' and free of trends. Density plots of all parameters were smooth and unimodal. In aggregate, the Gelman–Rubin statistics and graphical checks indicated convergence.

Annual survival rate projections

Projecting current costs of colour contrast of 60% into a future where climate change decreased snow duration and therefore increased the number of weeks with camouflage mis-

Table 1 Projected additional number of weeks of 60% colour contrast and projected annual survival. The current annual survival probability for our snowshoe hare population was 0.093. For each time period and future emissions scenario combination we show the additional number of weeks of contrast for the spring and fall seasons and total for the whole year (derived from locally downscaled prospective snow models; see Mills *et al.* 2013). The two future time periods are mid-century (2030–2059) and late century (2070–2099). The two climate change emissions scenarios are RCP4.5 (medium-low emissions) and RCP8.5 (high emissions)

	Mid-century RCP4.5	Late century RCP4.5	Mid-century RCP8.5	Late century RCP8.5
Additional no. weeks of 60% colour contrast				
Fall	0.9	1.4	1.3	2.6
Spring	1.9	2.9	2.4	5.9
Total	2.7	4.3	3.7	8.4
Annual survival probability	0.085	0.080	0.082	0.070

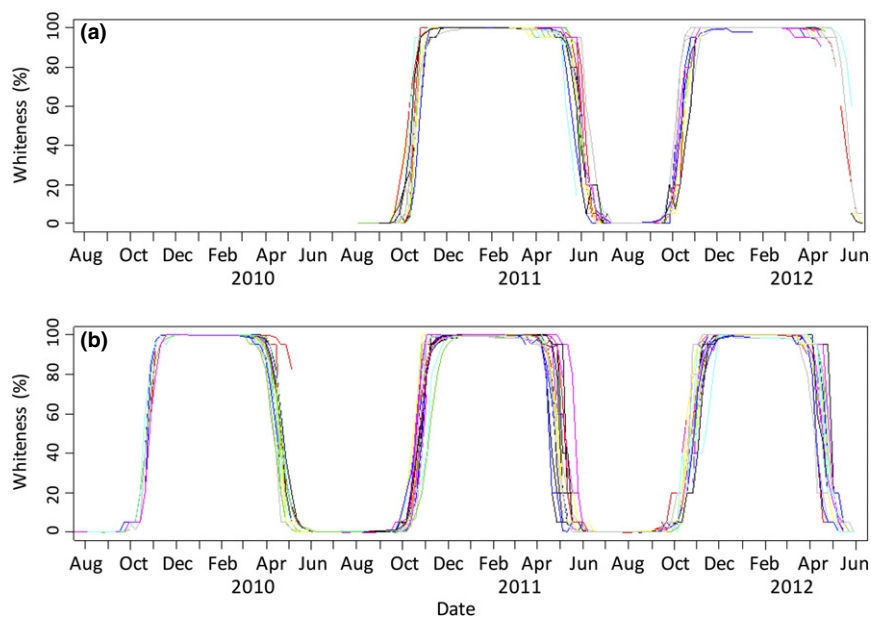


Figure 1 Individual coat colour molt phenology of radiocollared snowshoe hares. Continuous coloured lines represent modelled molt phenology of different individuals monitored from (a) August 2010 to July 2012 at Gardiner, MT ($n = 50$ individuals) and from (b) August 2009 to June 2012 at Seeley Lake, MT ($n = 136$ individuals).

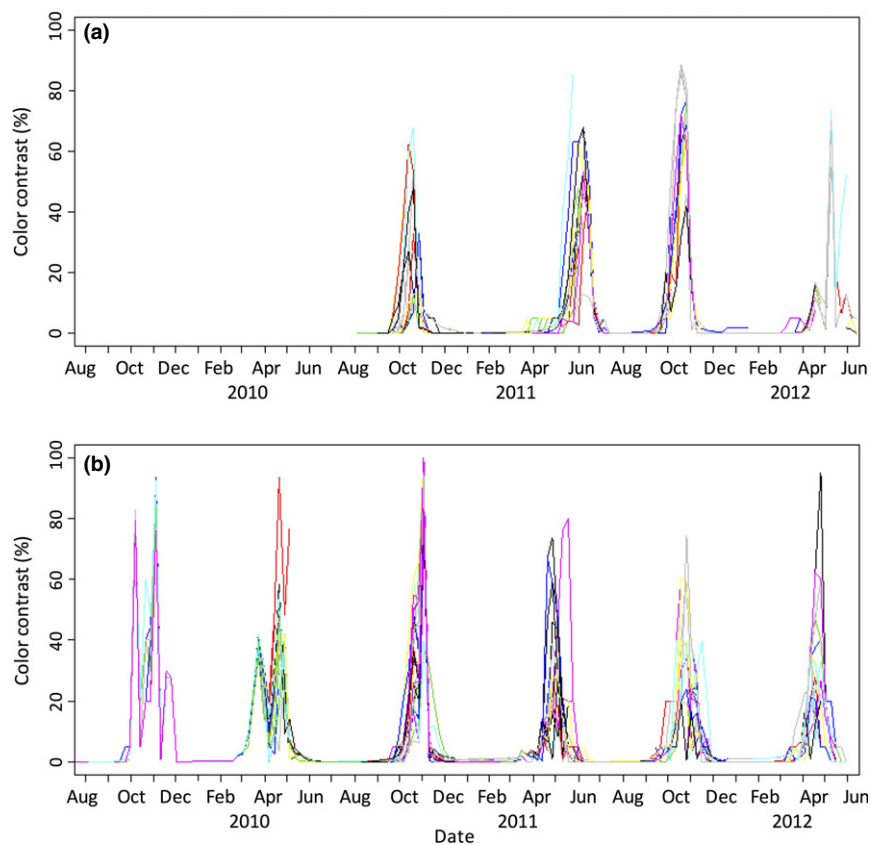


Figure 2 Individual colour contrast of radiocollared snowshoe hares. Continuous coloured lines represent modelled colour contrast phenology of different individuals monitored (a) from August 2010 to July 2012 at Gardiner, MT ($n = 50$ individuals) and (b) from August 2009 to June 2012 at Seeley Lake, MT ($n = 136$ individuals). Contrast $\geq 60\%$ signifies camouflage mismatch.

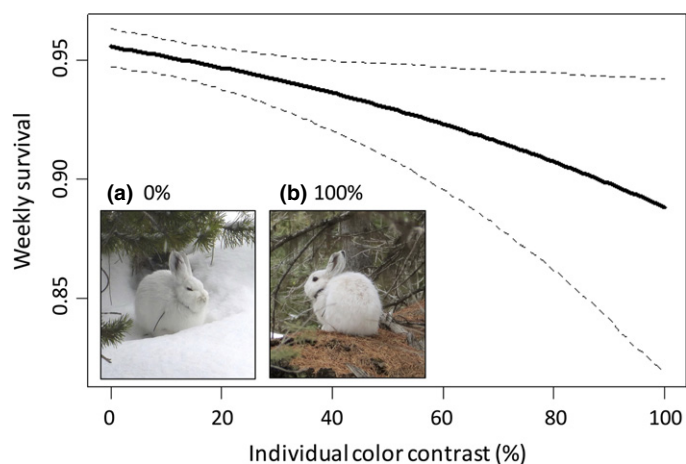


Figure 3 Effect of individual colour contrast on weekly snowshoe hare survival. Dashed lines indicate 95% credible intervals, while the solid line depicts mean survival at a given level of colour contrast between an individual hare and its background. Photographs depict radiocollared hares from our study showing (a) 0% and (b) 100% contrast.

match, led to steeply decreasing annual survival. For colour contrast of 60%, annual survival declined from 0.093 to 0.082 by mid-century and to 0.070 by the late century under the high emissions scenario (RCP8.5, Table 1). Similar consequences were predicted using the medium-low emissions scenario (RCP4.5, Table 1).

Population growth rate projections

The high measured costs of camouflage mismatch on survival translated into steep population declines when projected against the expected higher duration of mismatch in the future under climate change. The measured population growth rate ($\lambda = 1.15$) for an adjacent baseline hare population declined to nearly stationary ($\lambda = 1.02$) by the mid-century and to strongly decreasing ($\lambda = 0.88$) by the late century under the high emissions scenario (RCP8.5, Table 2). The population consequences of 60% colour contrast were milder for the medium-low emissions scenario (RCP4.5) with λ decreasing substantially but not dropping below replacement at mid- ($\lambda = 1.05$) and late century ($\lambda = 1.00$) (Table 2).

DISCUSSION

Here, we describe individual and population-level consequences of decreased snow cover duration on snowshoe hares as their seasonal molt phenology becomes maladaptive under the rapidly changing climate. This is among the first field-based studies that both demonstrates direct anthropogenic climate change induced selection on a highly variable trait in a wild population, and projects the potential demographic consequences of such selection under various climate change scenarios. Based on our results we conclude that, in the absence of evolutionary rescue, the high fitness costs of camouflage mismatch have the potential to drive population growth towards steep declines by the end of the century.

Table 2 Field-estimated (= baseline) and projected vital rates used to calculate population growth rate (λ) for the baseline population and for each future time period and emissions scenario combination. The vital rates for the baseline population were estimated during 1999–2002 from radiocollared hares in dense mature forest (Griffin & Mills 2009). The other columns modify weekly survival of adults (S_{Ad}) and juveniles (S_{Juv}) in spring and fall based on the cost of 60% colour contrast for the respective number of weeks of that given colour contrast under the medium-low (RCP4.5) and high (RCP8.5) emissions scenarios. The resulting λ values are included in the last row. F stands for fertility, f_1 , f_2 , f_3 are fecundity rates in each of three birth pulses and (S_{Lev}) is survival of leverets to weaning

	Baseline	Mid-century RCP4.5	Late century RCP4.5	Mid-century RCP8.5	Late century RCP8.5
S_{Ad} Spring	0.97	0.97	0.96	0.97	0.96
S_{Ad} Summer	0.99	0.99	0.99	0.99	0.99
S_{Ad} Fall	0.97	0.97	0.97	0.97	0.97
S_{Ad} Winter	0.99	0.99	0.99	0.99	0.99
S_{Juv} Spring	0.97	0.96	0.96	0.96	0.95
S_{Juv} Summer	0.99	0.99	0.99	0.99	0.99
S_{Juv} Fall	0.97	0.97	0.97	0.97	0.96
S_{Juv} Winter	0.99	0.99	0.99	0.99	0.99
S_{Lev}	0.56	0.56	0.56	0.56	0.56
f_1	1.40	1.40	1.40	1.40	1.40
f_2	1.87	1.87	1.87	1.87	1.87
f_3	0.89	0.89	0.89	0.89	0.89
F	0.81	0.74	0.70	0.57	0.62
λ	1.15	1.05	1.00	1.02	0.88

As we predicted, increased colour contrast leading to mismatch in camouflage had large negative consequences on individual fitness. During weeks when hares were mismatched against their background, weekly survival probability decreased from 0.96 for hares matching their background colour to 0.92 when colour contrast was 60% and to 0.89 when contrast was 100% (Fig. 3). Thus, as hares became colour mismatched (60–100%) their probability of survival during that particular week was 4–7% lower than that of hares in the same population that match their backgrounds. This is direct evidence of ongoing natural selection against molt phenology mistimed with snow cover duration, with a standardized selection coefficient of -0.04 (-0.061 , -0.017).

The important, yet rarely answered question is what would be the demographic consequences of strong selection caused by a particular stressor, given the anticipated frequency of the stressor in the future? We previously predicted that camouflage mismatch in our study region will increase by up to four additional weeks by mid-21st century and up to eight additional weeks by the end of this century under the high emissions scenario (RCP8.5, Table 1; Mills *et al.* 2013). Here, we estimate that under this scenario, annual survival would, in the absence of evolutionary shifts, decrease by 11% by mid-century and 23% by the late century (Table 1). Similar trends would be expected under the medium-low emissions scenario (RCP4.5; Table 1).

The substantial cost of camouflage mismatch on survival would be sufficient to decrease population growth rate (λ) in the future. Effects were especially strong under the high emissions scenario (RCP8.5) in which the projected population

growth rate for a baseline hare population with field-measured vital rates went from increasing ($\lambda = 1.15$) to nearly stationary ($\lambda = 1.02$) by the mid-century to strongly decreasing ($\lambda = 0.88$) by the late century (Table 2). Overall, the strong influence of camouflage mismatch on snowshoe hare survival rate would cause λ to proportionately decrease by 11% by the mid-century and by 24% by the late century under the high emissions scenario. Although the demographic cost of mismatch is only relevant for a few weeks per year, the severe fitness consequences and expected higher frequency in the future would cause growing populations to decline rapidly in the absence of evolutionary change in the molt phenology or phenotypic plasticity.

Importantly, our estimates of future fitness consequences (annual survival and absolute fitness or population growth rate) are conservative, because survival rate was only penalized by a cost of 60% colour contrast (the lowest contrast at which we consider hares to appear mismatched). Survival costs increased steeply with colour contrast severity (Fig. 3); therefore, for the weeks where hares reached colour contrast $\geq 60\%$, survival would be even lower than we modeled, causing even greater decreases than projected. Additionally, our estimates of fitness costs ignored survival costs observed when colour contrast was $< 60\%$ (Fig. 3).

A population declining strongly under environmental change can, however, undergo an evolutionary rescue (Gonzalez *et al.* 2012; Carlson *et al.* 2014), when evolution occurs sufficiently fast and allows population recovery before extinction ensues. Evolutionary rescue requires ample additive genetic variation in the trait under selection (Lynch & Lande 1993; Bürger & Lynch 1995). The substantial variation in molt phenology (and colour contrast) across individuals (Figs 1 and 2) implies a rich template for selection to adaptively track directional changes in snow conditions. Anecdotally, on some days during spring and fall over the years of our studies, we have observed hares exhibiting the full range of coat colours, from just initiating the molt to almost completely molted. How much of the observed variation in molt phenology reflects heritable genetic variation is currently unknown, but limited captive studies imply a strong genetic component for *Lepus* species (Severaid 1945; Bergengren 1969).

Further, the fate of a population in a changing environment and the likelihood of evolutionary rescue can be affected by phenotypic plasticity. Phenotypic plasticity can produce rapid adaptive response (Hendry *et al.* 2008) or may itself evolve in response to selection (Chevin & Lande 2010). For snowshoe hare colour molt phenology, field studies did not detect plasticity in the fall, but some adaptive plasticity was shown in spring molt onset and rate of change in response to snow cover and or temperature (Mills *et al.* 2013; Zimova *et al.* 2014; Kumar 2015). While the quantified standing plasticity seems unlikely to prevent increase in camouflage mismatch or its consequences in the future, it may evolve itself in response to selection against camouflage mismatch and accelerate adaptation.

Additional support for the potential of adaptive evolution to 'rescue' colour molting species from camouflage mismatch comes from the broad consensus for an adaptive basis of coat

colour. Camouflage in mammals is the most important evolutionary force explaining coloration (Stoner *et al.* 2003; Caro 2005; Stevens & Merilaita 2009) and rapid evolutionary change in cryptic coloration has been observed in the wild (Majerus 1998; Forsman *et al.* 2011). Seasonal camouflage in regions with winter snowpack has evolved independently across multiple taxa (including weasels, arctic foxes, ptarmigans, lemmings), and within colour molting species the timing of the molt across populations reflects local adaptation to snow duration (Zimova *et al.* 2014). Further, in some maritime populations with especially brief or erratic snow cover, the white molt has been lost and animals remain brown in winter (Dalquest 1942; Angerbjörn & Flux 1995). However, whether genetic shifts in molt phenology or in phenotypic plasticity may occur quickly enough to track rapidly decreasing snow cover duration under climate change remains unknown.

Because many of the species that undergo seasonal coat colour change are cyclic (including snowshoe hares), it is possible that this phenologic mismatch under selection may affect cyclic dynamics. Snow patterns have been proposed to potentially play a role in dampening cycles (Cornulier *et al.* 2013); colour contrast may be a useful covariate to include in analyses of cycles as a potential mechanism linking decreased snow cover duration to abundance and population growth.

The actual response of any species to global change will be influenced by simultaneous shifts in population dynamics of other species in other trophic levels (Zarnetske *et al.* 2012). Although those community-level effects have rarely been measured in any wild system, including ours, we show unequivocal consequences of a single powerful stressor operating in a wild population. Here, we demonstrate individual fitness costs of strong natural selection operating on a phenotypically variable trait. We show that if the intensive selection continues unchanged into the future and populations fail to respond through evolutionary change, the demographic consequences may be dire. To avert the negative population-level consequences of camouflage mismatch, the required conditions for evolutionary rescue to occur must be promoted by the maintenance of large population sizes with adequate gene flow and reduction in anthropogenic stressors including climate change (Bell & Collins 2008; Hoffmann & Sgrò 2011; Vander Wal *et al.* 2013).

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AUTHORSHIP

M.Z. and L.S.M. designed the research and collected the data; M.Z., L.S.M., and J.J.N. analysed the data and wrote the paper.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

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