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ARTICLE

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Coat color mismatch improves survival of a keystone boreal herbivore: Energetic advantages exceed lost camouflage

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Abstract

Climate warming is causing asynchronies between animal phenology and environments. Mismatched traits, such as coat color change mismatched with snow, can decrease survival. However, coat change does not serve a singular adaptive benefit of camouflage, and alternate coat change functions may confer advantages that supersede mismatch costs. We found that mismatch reduced, rather than increased, autumn mortality risk of snowshoe hares in Yukon by 86.5% when mismatch occurred. We suggest that the increased coat insulation and lower metabolic rates of winter-acclimatized hares confer energetic advantages to white mismatched hares that reduce their mortality risk. We found that white mismatched hares forage 17–77 min less per day than matched brown hares between 0°C and −10°C, thus lowering their predation risk and increasing survival. We found no effect of mismatch on spring mortality risk, during which mismatch occurred at warmer temperatures, suggesting a potential temperature limit at which the costs of conspicuousness outweigh energetic benefits.

KEYWORDS

accelerometer, camouflage, coat color, energetic expenditure, foraging, *Lepus americanus*, phenological mismatch, snowshoe hare, survival, thermoregulation

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INTRODUCTION

Phenological mismatch is one of the most documented pathways by which climate change negatively impacts species (Radchuk et al., 2019; Visser & Gienapp, 2019). Earlier onset of spring and delayed onset of winter have the potential to cause incongruous timing of seasonal phenotypes (Kudo & Ida, 2013; Lehikoinen, 2011; Møller et al., 2008). Mismatch occurs in the timing of numerous seasonal traits such as calving date with plant growth onset, and laying date with peak of key food sources, and has resulted in reduced reproductive success and recruitment (Post & Forchhammer, 2008; Reed et al., 2013). However, the costs associated with phenological mismatches vary within species across populations (Doi et al., 2017; Heard et al., 2012). Species are often adapted to broad ranges of ecological conditions, particularly those with large geographic distributions (Valladares et al., 2014). Local adaptations and variable selection pressures across environmental gradients alter the magnitude of phenological mismatch across populations (Gordo & Doi, 2012; Phillimore et al., 2010; Porkert et al., 2014). Such spatial variability in phenology across ecological conditions may also involve differences in the mechanistic pathways governing the demographic costs and benefits associated with phenological mismatch across species ranges.

An example of phenological mismatch that occurs in species across multiple taxa is coat and plumage color change mismatched with snow onset and melt (Atmeh et al., 2018; Melin et al., 2020; Pedersen et al., 2017; Zimova et al., 2016). At least 21 bird and mammal species in the Northern Hemisphere change color biannually and improved camouflage is considered the primary function of this change (Mills et al., 2018; Zimova et al., 2018). As snow cover duration is forecasted to decrease across the Northern Hemisphere (Danco et al., 2016), coat and plumage color mismatch is likely to increase. Mismatch may reduce survival due to decreased camouflage (Atmeh et al., 2018; Melin et al., 2020; Zimova et al., 2016). However, aside from color change, high-latitude species benefit from other winter acclimatization strategies meant to increase cold tolerance and endure periods of food shortage. For example, some mammals may increase hair length and density to increase their insulation by 12%–27% (Hart et al., 1965; Sealander, 1972), decrease their lower critical temperature by 17–20°C (Rogowitz, 1990; Webster et al., 1969), or alter activity patterns that, taken together, ultimately reduce daily energy requirements (Fuglesteg et al., 2006; Humphries et al., 2005; Sheriff, Speakman, et al., 2009). Accordingly, coat color transitions coincide with multitrait change that differentiates long photoperiod, i.e., summer, from short photoperiod, i.e., winter, phenotypes (Boratyński et al., 2016; Lovegrove, 2005). As such, the thermal and energetic benefits provided by a more insulative, white coat and associated metabolic and thermoregulatory adaptations may outweigh the negative costs of color mismatch in colder conditions.

The snowshoe hare (*Lepus americanus*) is a keystone species distributed across the boreal forests of North America (Krebs et al., 1995) that undergoes seasonal coat color change to match the seasonal accumulation and loss of snow (Ferreira et al., 2017). The initiation of coat color change in snowshoe hares is likely to be affected by photoperiod (Nagorsen, 1983) and, in the absence of evolutionary change, is predicted to become increasingly mismatched with anticipated reductions in snow cover duration (Brown & Mote, 2009; Mills et al., 2013). Coat color mismatch may impact snowshoe hare demography, as recent studies have reported high mortality rates in mismatched snowshoe hares at multiple locations in the southern extent of their range, presumably due to increased conspicuousness to predators (Wilson et al., 2018; Zimova et al., 2014). However, the thermal benefits of winter acclimatization in hares, including reducing their resting metabolic rate by up to 20% (Sheriff, Kuchel, et al., 2009), may also affect susceptibility to predation and ultimately survival.

White winter-acclimatized snowshoe hares benefit from lower energetic demands compared with brown summer-acclimatized hares. Indeed, whereas temperatures below 0°C increase energetic requirements for summer hares, white winter hares remain in their thermoneutral zone until temperatures below −10°C (Sheriff, Kuchel, et al., 2009). As such, lower energetic demands reduce foraging requirements for winter-acclimatized hares (Balluffi-Fry et al., 2022). Balancing the trade-off between obtaining sufficient food to meet energetic requirements and avoiding predators is a central assumption of prey behavior theory (Lima & Dill, 1990; McNamara & Houston, 1987). Therefore, white mismatched hares may benefit from lower energetic requirements, reduced foraging time, and thus reduced predator exposure. These benefits could compensate for the adverse effects of conspicuousness, particularly when seasonal temperatures remain low and the energetic demands for brown summer-acclimatized hares are elevated (Balluffi-Fry et al., 2022). Geographic variation in winter adaptations and acclimatization exists across the broad geographic range of the snowshoe hare (Gigliotti et al., 2017; Sheriff, Speakman, et al., 2009). As such, the effects of coat color mismatch may vary across populations according to the relative importance of the reduced camouflage cost relative to energy conservation benefits in different ecological contexts.

Here, we test two alternative hypotheses regarding the potential costs of coat color mismatch, while considering the seasonal acclimatization changes that co-occur with color change in snowshoe hares. The *thermoregulation hypothesis* posits that reduced foraging requirements with winter acclimatization reduce the costs of coat color mismatch in snowshoe hares. As such, under the *thermoregulation hypothesis*, we predict that mismatched white hares will spend less time foraging than matched brown individuals, particularly below the lower limit of the thermoneutral zone of summer brown hares (i.e., <0°C; Sheriff, Kuchel, et al., 2009). If this foraging difference and thus reduced time spent vulnerable to predation outweighs the costs of conspicuousness, we further predict no difference in survival between matched and mismatched individuals. Conversely, our *camouflage hypothesis* suggests that camouflage loss is the primary driver of predation risk during coat color change, regardless of foraging differences. Under the *camouflage hypothesis*, we predict that mismatched hares are more likely to be predated than camouflaged individuals, echoing results from previous studies in the southern extent of their range (Wilson et al., 2018; Zimova et al., 2016). To examine these contrasting hypotheses, we monitored the survival, coat color, and foraging time of individuals over the autumn and spring in southwest Yukon, Canada. We found that white mismatched snowshoe hares experiencing cold temperatures in snowless environments benefited from reduced foraging time and thus increased survival relative to brown matched hares.

METHODS

Study area

We studied snowshoe hares during two 3-month periods, for three autumns (1 September to 1 December of 2015, 2016, and 2017) and four springs (1 March to 31 May of 2015, 2016, 2017, and 2018) in southwestern Yukon, Canada (latitude: 60.9° N, longitude: −138.0° W). Snowshoe hares have been monitored for over 40 years in this region (Krebs et al., 2018). Our study area consists predominantly of white spruce (*Picea glauca*), trembling aspen (*Populus tremuloides*) and balsam poplar (*Populus balsamifera*). Gray willow (*Salix glauca*) and dwarf birch (*Betula glandulosa*) dominate the understory. The main predators of snowshoe hares in this region include Canada lynx (*Lynx canadensis*), coyotes (*Canis latrans*), goshawks (*Accipiter gentilis*), and great horned owls (*Bubo virginianus*) (Peers et al., 2020). Snowshoe hares went through the increase, peak, and early decline phase of their population cycle during our study period (Krebs et al., 2018). Snowshoe hares give birth to their first litters in this population during the spring season, in mid to late May (Stefan & Krebs, 2001). The daylight hours were shorter on average during the autumn, i.e., 10.07 ± 2.37 h, than during the spring, i.e., 14.67 ± 2.43 h. During our study years, the average temperature in the autumn was 3.10 ± 7.44°C, and the average temperature in the spring was −0.38 ± 7.25°C. The maximum snow depth recorded within autumn seasons was 35 cm and the maximum snow depth recorded within spring seasons was 75 cm. Permanent snow cover date, i.e., 100% snow cover without melting until the spring, was variable across our autumn seasons, occurring almost 3 weeks later in 2015 (3 November) than in 2016 (16 October) and 2017 (17 October). Completion of snowmelt date, i.e., no more snow on ground, was similar across study years (6 May 2015, 1 May 2016, 2 May 2017, and 1 May 2018). Although snow onset and melt have not been monitored consistently in our region to provide long-term trends, winter snow depths have been declining over the last three decades (Peers et al., 2020).

Field methods

The study area was divided into three 35-ha snowshoe hare trapping areas, located within ~8 km of each other (Peers et al., 2020). We captured snowshoe hares using Tomahawk live-traps (Tomahawk Live Trap Co. Tomahawk, WI, USA) baited with alfalfa and rabbit chow. Traps were set 30 min before sunset and checked either 3 h after sunset or at sunrise. We attached a numbered ear tag to each hare to identify individuals on subsequent recaptures, and we assessed coat color during each capture. To evaluate coat color, we examined hares from the front and sides and visually estimated their percentage white coat to the nearest 5%. We later binned coat color in 10% white categories for analyses to account for interobserver and intraobserver ranking variability. We consider 10% bins as reasonably precise given that intraobserver and interobserver intraclass correlation coefficients (ICC) for coat color assessment were high (ICC > 0.9 in all cases, see Appendix S1: Table S1). To monitor survival, we fitted hares that we suspected were adults, i.e., those weighing >1100 g ($n = 347$; 122 males and 225 females) with very high frequency (VHF) collars that were each equipped with a mortality sensor (Model SOM2380, Wildlife Materials Inc., USA, or Model MI-2 M, Holohil, Canada, both <27 ± 1 g). We collared more females than males because of an ongoing study targeting females that occurred in parallel to ours (Majchrzak et al., 2022). We performed mortality checks of VHF collared hares almost daily, i.e., 96.3% of checks occurred within 1–3 days. To monitor behavior, we also fitted a subset ($n = 102$) of VHF collared hares with an accelerometer (model Axy3, 4 g, Technosmart, Rome, Italy). Accelerometers measure force variation on three different axes and are increasingly being used to infer behavior in free-ranging animals (Mikkelsen et al., 2019; Studd et al., 2019). Fully equipped collars with both VHF and accelerometers had a total weight below 2.5% of each individual's body mass. Handling and collaring procedures were approved by the University of Alberta Animal Care and Use Committee (Protocol: AUP00001973).

We measured snow depth, snow cover, and temperature throughout our study period. We measured snow depth on >60% of days at three locations per trapping area, in relatively open forest, to the nearest 0.5 cm. Days with missing snow depth records were linearly interpolated using the "zoo" function in the *zoo* package in R (Zeileis et al., 2021). We measured snow cover by visually assessing daily landscape photographs from three camera traps installed on each trapping area. We calculated a combined average daily snow cover value to the nearest 10% in our study region. We converted % snow cover to a binary type variable above or below 60% snow cover (presence/absence) for the autumn seasons, as there were very few instances when snow cover estimates were between 0% and 100%. We measured temperature at least six times a day on each trapping area using a minimum of two temperature loggers (ibutton, DS1922L, Maxim Integrated, Whitewater, USA) to obtain a single average daily temperature value for each trapping area.

Measuring coat color mismatch

Coat color mismatch was defined as the difference between hare percentage white (10% bins) and the daily percentage snow cover (10% bins for both autumn and spring). For all analyses, we treated mismatch as a binary variable, as has been done previously (Mills et al., 2013; Zimova et al., 2014), defining mismatch as >50% difference between hare (percentage white) and snow cover (percentage). Accordingly, mismatched hares were white (>50% white) individuals in a snowless (<50% snow cover) environment. Considering that brown mismatched hares in a snowy environment were rare (1% of trapping records), we did not consider this type of mismatch in our analyses. Although the threshold for mismatch used in some previous studies is 60% contrast (Mills et al., 2013; Wilson et al., 2018), mismatch at this contrast threshold was rare in our study region, i.e., in 11% of trapping records, so we used 50% as our mismatch threshold to increase our sample size. We tested other thresholds to ensure that our results and conclusion were not dependent on our threshold choice, and found similar results when using 40% or 60% contrast with define mismatch (Appendix S1: Tables S5, S6, S9, and S10). Similarly, exploratory data analysis indicated that considering mismatch as a continuous variable performed worse than considering it as a binary variable in explaining variation in mortality risk (Appendix S1: Tables S15 and S16).

Effect of coat color mismatch on survival

To evaluate the effect of coat color mismatch on snowshoe hare survival, we generated Cox's proportional hazards (CPH) models (Cox & Oakes, 1984) with the "coxph" function in the survival package in R (Therneau et al., 2021). The CPH model is a semiparametric approach used to analyze binary response data, in our case: alive or dead (Sievert & Keith, 1985). We attributed all recorded mortalities of monitored hares to predation, except in two cases, for which cause of death was uncertain. We excluded mortality checks that exceeded 7 days to limit the uncertainty in the timing of death events (Murray & Bastille-Rousseau, 2020). We censored 15 individuals whose collars were removed before the end of the study period and six individuals with permanently missing VHF signals. We pooled data from different years, trapping areas, and sex, as exploratory analysis indicated that none of those variables had a significant effect on autumn or spring mortality risk (Appendix S1: Table S2). Indeed, whereas snowshoe hare survival varies across their cycle (Majchrzak et al., 2022), we did not detect intraseasonal survival differences within our autumn and spring seasons (Appendix S1: Table S2), although differences in winter survival, i.e., the season with the lowest survival, occurred across these study years (Peers et al., 2020). Considering that coat color was assessed only during capture opportunities (on average every 13.1 ± Standard Deviation: 10.8 days per individual), we assigned coat color for each record in our survival analysis as the nearest coat color assessment completed in the field (average difference of 4.95 ± Standard Deviation: 3.70 days between telemetry check and coat color assessment). We removed telemetry records in which a coat color assessment within 14 days did not exist, to ensure that coat color and derived mismatch values were an accurate representation of each individual at the time of the telemetry check. Results from models using survival records within 8 days of a coat color assessment were qualitatively similar to those we obtained with our chosen 14-day threshold (Appendix S1: Table S3).

We generated three competing CPH models for both autumn and spring. The first model included snow cover and snow depth, based on prior evidence of snow effects on hare survival (Meslow & Keith, 1971; Peers et al., 2020). Our second model included those same snow variables in addition to coat color mismatch, our variable of interest. The third model was the null (intercept-only) model. We used the Akaike information criterion (AIC) for our model selection (Akaike, 1974) and identified our top model based on corrected AIC (AIC_c) (Burnham & Anderson, 2002) using the package *AICcmodavg* (Mazerolle, 2019). We assessed multicollinearity in our top model using the variance inflation factor (VIF) and ensured no variables had VIFs > 2. The proportionality assumption of CPH models, which implies that the relative hazard (hazard ratio [HR]; i.e., risk of death) is assumed to be constant over time for different predictors (Joshua Chen & Liu, 2006), was checked with the "cox.zph" function in the *survival* package in R and was met for our top spring and autumn CPH model. Our results were not affected by informative censoring, as we found qualitatively similar results for both spring and autumn model coefficients when we treated censored individuals as deaths (Murray & Bastille-Rousseau, 2020) (Appendix S1: Table S4). Using our top supported CPH model for both seasons, we also predicted 30-day survival between the periods of 1 October and 30 October for autumn, and 1 May and 30 May for spring (Appendix S1: Figure S1). We chose 30-day survival as this roughly corresponded to the average number of days mismatch occurred in both seasons.

Effect of coat color mismatch on time spent foraging

To test our *thermoregulation hypothesis*, whereby white mismatched hares experience reduced energetic requirements leading to reduced foraging time (Balluffi-Fry et al., 2022; Sheriff, Kuchel, et al., 2009), we used linear mixed-effects models using the "lmer" function in the package *lme4* (Bates et al., 2015). Daily time spent foraging (minutes) was derived from tri-axial accelerometer data using behavioral classifications previously developed in this hare population (see Studd et al., 2019 for more information on classification methods). Daily time spent foraging was classified over 4-s intervals at a 96% accuracy (Studd et al., 2019). We recorded foraging as the number of minutes spent foraging in a 24-h period and thus had 1505 daily foraging records from 66 hares over the three autumns and 838 daily foraging records from 44 hares over the four springs. Similar to our survival analysis, we only kept foraging records that were within 14 days of a coat color assessment (average difference of 4.48 ± 3.51 [Standard Deviation] days). We reran our top foraging time models with data restricted to daily foraging records that were within 8 days of a coat color assessments instead, to ensure that our results were not affected by this 14-day threshold, and obtained qualitatively similar results (Appendix S1: Table S8). To eliminate the potential of seasonal changes in foraging impacting our results (Griffin et al., 2005), we restricted our data to only the autumn and spring periods when snow cover was ≤50%, i.e., mismatch was possible given our chosen threshold and therefore both matched and mismatched individuals occurred simultaneously.

We generated four linear mixed-effects models per season to test for differences in daily minutes spent foraging (our response for all models) between matched brown hares and mismatched white hares and their responses to changes in temperature. We included a random effect for individual ID in all models to control for nonindependence of data. We included sex as a fixed factor in all spring models only, as exploratory data analysis indicated that sex had a significant effect on time spent foraging for spring but not autumn (Appendix S1: Table S7). Furthermore, we included year as a fixed effect in each model to account for potential effects of yearly changes in predation risk on hare foraging behavior (Shiratsuru et al., 2021). Our first model included two fixed effects, temperature and year. Our second model included temperature, year, and coat color mismatch, and our third model included the same variables as the second in addition to an interaction between mismatch and temperature. Our fourth model was a null intercept-only model. We checked model fit using marginal and conditional R^2 calculated using the "r.squaredGLMM" function in the package *MuMIn* (Barton, 2020), according to Nakagawa et al., 2017. We used the AIC (Akaike, 1974) to rank our four competing models and identified our top model in each season based on AIC_c (Burnham & Anderson, 2002).We completed all statistical analyses in R version 3.6.2 (2019) (R Core Team, 2018). We considered results for which $p \leq 0.05$ as significant and reported all means with ±1 standard error.

RESULTS

When considering both seasons and all years together, the prevalence of coat color mismatched hares that contrasted with their snowless environment was low (14% of trapping records) in our population. Mismatch occurred more frequently in the autumn (19% of trapping records) than the spring (8% of trapping records). The autumn with the latest permanent snow cover arrival date, i.e., 2015, had the highest prevalence of mismatch

(33% of records). Prevalence of mismatch in the autumns of 2016 and 2017 were 10% and 13% of trapping records, respectively. Spring mismatch was consistent across years around ~10% (2015–9% of trapping records, 2016–10%, 2018–12%) with the exception of 2017, when only 1% of trapped hares were mismatched.

Effect of coat color mismatch on mortality

We monitored 347 hares and recorded 41 deaths over four spring and 34 deaths over three autumns. When deaths were assigned to specific predators, we attributed 6.9% to coyotes, 10.3% to great horned owls, 10.3% to goshawks, and 72.4% to lynx. The CPH model with the strongest support in both seasons included snow depth, snow cover, and mismatch (Table 1; Appendix S1: Tables S11 and S12). However, the second highest ranking CPH model for spring, i.e., the model including only snow variables, was within $2\Delta\text{AIC}_\text{c}$ ($\text{AIC}_\text{c} = 0.09$) from our top spring CPH model (Appendix S1: Table S11). Contrary to our prediction arising from our camouflage hypothesis, matched hares had a significantly higher mortality risk than mismatched hares in the autumn (HR [mismatch] = 0.135; 95% confidence intervals [CI]: 0.027, 0.679; $z = -2.43$; $p = 0.02$; Figure 1a; Table 1). This translated to a 30-day survival probability of 0.72 ± 0.23% for matched hares and 0.96 ± 0.18% survival probability for mismatched hares in the autumn when snow depth and snow cover are held constant at zero (Appendix S1: Figure S1). In contrast, coat color mismatch was positively correlated with mortality risk for hares in the spring (Figure 1b), but this effect was nonsignificant (Table 1; $z = 1.60$; $p = 0.11$). Models were qualitatively similar regardless of our classification of mismatch, except when considering mismatch as a minimum 40% contrast between coat color and snow cover; in this case mismatch significantly increased mortality risk in the spring (HR = 6.780; 95% CI: 2.390, 19.240; $z = 3.60$; $p < 0.001$). Snow depth ($z = -2.29$; $p = 0.02$) and snow cover ($z = 2.98$; $p = 0.003$) significantly affected mortality risk in the top spring model, but not in the top autumn model (Table 1). In spring, the risk of dying decreased as snow depth increased (HR = 0.95; 95% CI: 0.92, 0.993; Figure 1d) and mortality risk increased as snow cover increased (HR = 1.046; 95% CI: 1.01, 1.08; Figure 1c).

Effect of coat color mismatch on foraging time

Across the periods when snow cover was ≤50% during our study years, hares foraged on average 11.77 ± 0.038 h/day in the spring and 12.52 ± 0.028 h/day in the autumn. These foraging times represent ~80% of nighttime hours in the spring, and 125% of autumn nighttime hours. Coat color mismatch was an important predictor of daily foraging time in the autumn, but not the spring (Appendix S1: Tables S13 and S14). The top model for autumn foraging time included coat color mismatch, temperature, year, and the interaction between temperature and mismatch (Table 2). As autumn temperature decreased, mismatched hares decreased daily foraging time, whereas matched hares increased foraging time (Figure 2a; Table 2). For instance, white mismatched hares foraged 17–77 min, i.e., 2%–10%, less per day than matched brown hares at temperatures between 0°C and −10°C (Figure 2a). The top model for spring included temperature, year, and sex (Table 2), When coat color mismatch was included in our spring foraging models, its effect on daily foraging time was nonsignificant ($t = -0.939$, $p = 0.348$).

DISCUSSION

Phenotypes and climate change can vary widely within a species' distribution, as can phenological mismatch and its consequences on survival. Elucidating potential unifying mechanisms is crucial to reconcile varied responses to phenological mismatch. We evaluated the effect of coat color mismatch on snowshoe hare survival in a northern population and further tested two competing hypotheses that may explain this effect. Snowshoe hares acclimatize to winter by increasing their guard hair density by 148% and downy hair density by 128% thus increasing coat

TABLE 1 Hazard ratios (HR) and 95% confidence intervals generated for each variable of our top Cox's proportional hazards models.

Variable	Spring top model: HR ~ SD + SC + mm	Autumn top model: HR ~ SD + SC + mm
Snow depth (SD)	**0.953** (0.916, 0.993)	*0.903* (0.808, 1.009)
Mismatch (mm; factor)	2.940 (0.781, 11.062)	**0.135** (0.027, 0.679)
Snow cover (SC)	**1.046** (1.015, 1.077)	0.726 (0.065, 8.084)

Note: Values that are bolded represent significant effects and italicized values represent p-values <0.1. HR >1 indicates increased risk of dying and HR <1 indicates reduced risk of dying.

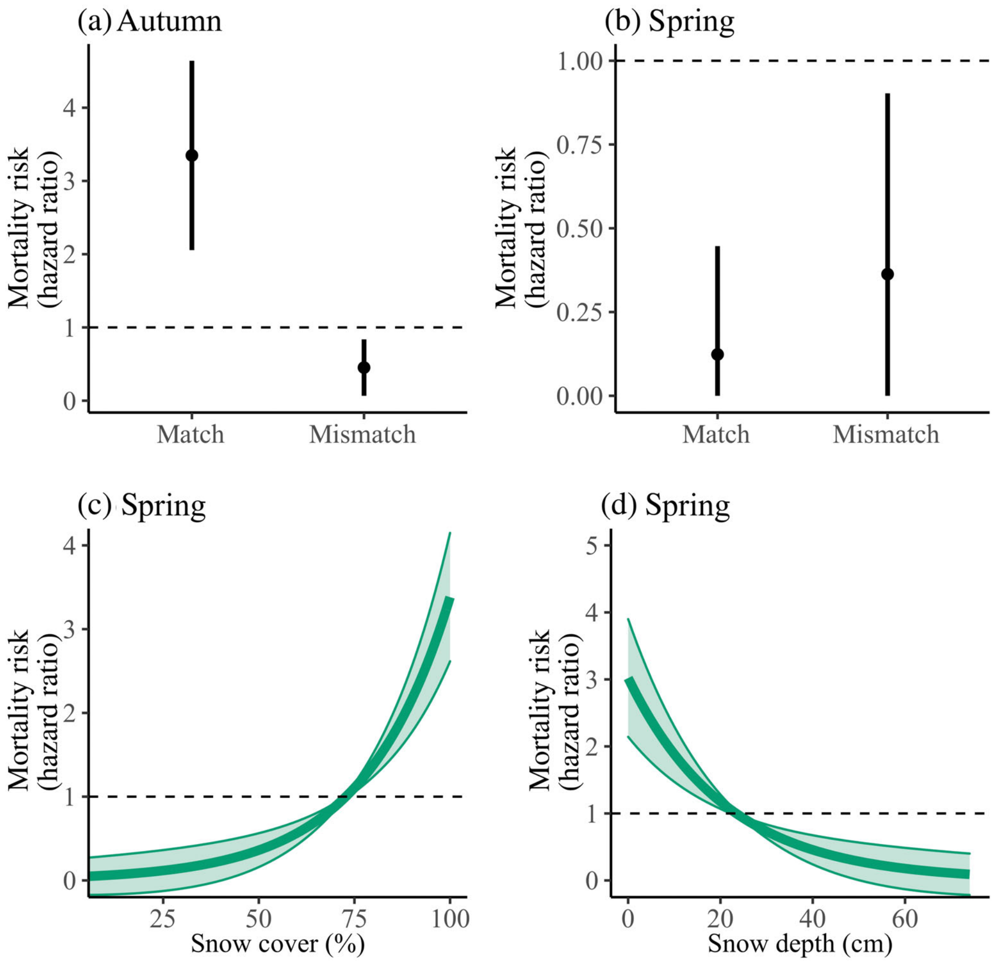

FIGURE 1 The modeled effect of coat color mismatch on snowshoe hare mortality risk, generated from our top supported CPH model for (a) autumn and (b) spring. Points represent predicted hazard ratios (HR) for matched and mismatched hares when snow depth and snow cover are held at zero. Shown below are the effects of (c) snow cover (snow depth held constant at its mean) and (d) snow depth (snow cover held constant at its mean) on matched snowshoe hare mortality risk. Error bars and shaded areas represent predicted standard errors, and the dashed lines represent baseline mortality risk (i.e., HR = 1).

insulation, and reducing their resting metabolic rate by 20% (Sheriff, Kuchel, et al., 2009). These changes ultimately reduce snowshoe hare foraging requirements (Balluffi-Fry et al., 2022). Under our “thermoregulation hypothesis,” we hypothesized that the reduced foraging requirements occurring as a function of winter acclimatization may reduce predation risk, which would reduce the costs of coat color mismatch. We contrasted this hypothesis with the “camouflage hypothesis,” which suggests that camouflage is the primary driver of predation risk during color change, and thus results in mismatched hares experiencing higher mortality than matched individuals. Surprisingly, we found that mismatched hares had higher survival than matched hares in the autumn (Figure 1a), but that survival did not differ between matched and mismatched hares in the spring (Figure 1b). Although this result contradicts previous studies that link coat color mismatch in snowshoe hares to reduced survival (Wilson et al., 2018; Zimova et al., 2016), it provides support for our “thermoregulation hypothesis.” Mismatched white hares spent significantly less time foraging than matched individuals during cold temperatures in the autumn (Figure 2a), presumably due to the thermal and energetic benefits of winter acclimatization. Indeed, reduced foraging time likely decreases exposure to predators and subsequently improves survival (Figure 1a). We reconcile our findings with those of previous studies by highlighting the differences in temperatures experienced by snowshoe hares across their range.

Matched hares foraged longer than mismatched white individuals in the autumn, and this difference was pronounced at lower (lower than −3°C) temperatures (Figure 1a). Given the wide range of ecological contexts, selection pressures, and local adaptations that exist across the distribution of snowshoe hares (Gigliotti et al., 2017), the cost–benefit ratio of lost camouflage versus energy

TABLE 2 Summary of variables included in top-ranking linear mixed-effects daily foraging time models for (a) snow-free autumn ($n = 1505$ daily foraging records from 66 hares) and (b) spring periods ($n = 838$ daily foraging records from 44 hares).

	Response: daily foraging (min)		
Model	**Coefficient (±SE)**	***t***	***p***
(a) Top model, autumn			
Intercept	830.909 ± 9.037	91.942	<0.001
Temperature	−2.306 ± 0.505	−4.566	<0.001
Mismatch	−17.385 ± 6.170	−2.818	0.005
Year (2016)	−10.364 ± 8.380	−1.237	0.217
Year (2017)	−101.607 ± 12.188	−8.336	<0.001
Temperature × mismatch	5.963 ± 1.210	4.929	<0.001
(b) Top model, spring			
Intercept	858.868 ± 22.800	37.669	<0.001
Temperature	−1.209 ± 1.295	−0.933	0.351
Year (2016)	−16.582 ± 19.380	−0.856	0.396
Year (2017)	−28.914 ± 19.111	−1.513	0.137
Year (2018)	−93.029 ± 21.089	−4.411	<0.001
Sex (F)	−34.832 ± 17.000	−2.049	0.047

Note: Daily foraging time was considered in minutes. Both autumn and spring models also include individual ID as a random effect and the spring model includes sex as a random effect.

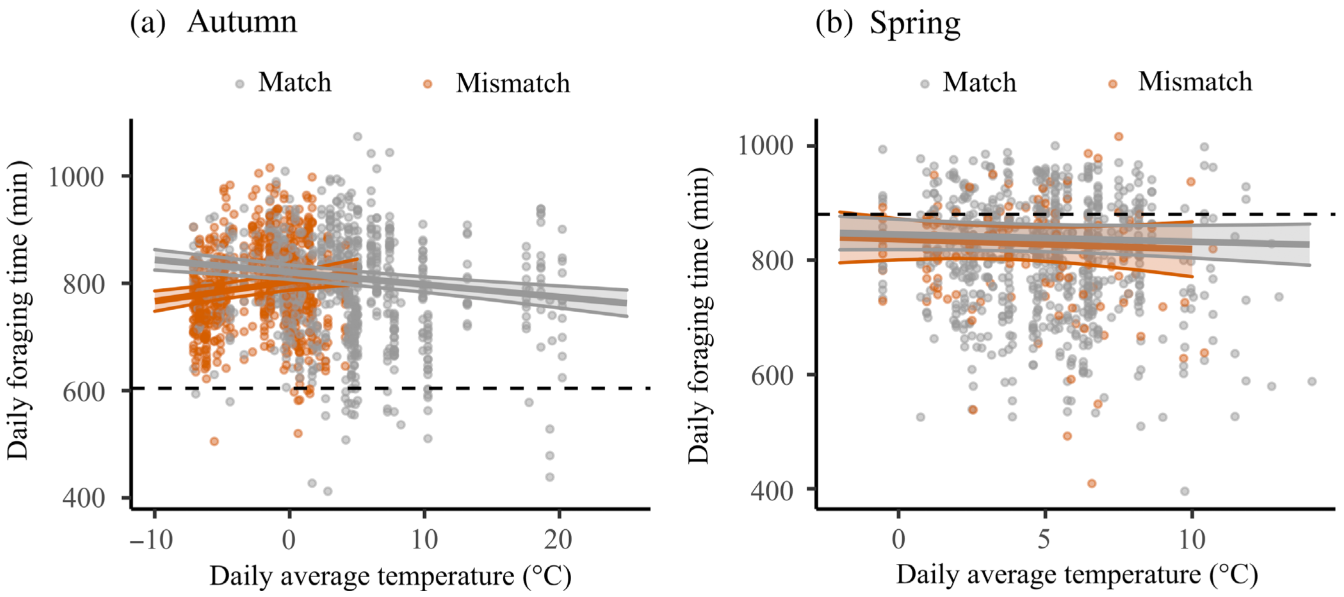

FIGURE 2 Modeled effect of temperature on daily foraging time (minutes) for matched and mismatched snowshoe hares in the snow-free period of (a) autumn (marginal $R^2 = 0.12$, conditional $R^2 = 0.32$) and (b) spring (marginal $R^2 = 0.13$, conditional $R^2 = 0.28$) of 2016 (the year with the most data). Data points show daily foraging records for individuals across all study years and predicted foraging time of mismatched hares is restricted to temperatures for which mismatched hares occurred in our study. Predicted values for daily spring foraging time are for males. Dashed line represents average number of nighttime minutes for both seasons.

conservation may vary across populations experiencing different temperatures. For example, northern populations experiencing cold temperatures benefit from the energetic advantages of winter coats despite mismatch during snow-free periods, whereas southerly populations experiencing warmer temperatures may not. Indeed, adverse survival effects associated with mismatch in southern snowshoe hare populations in Montana

(Zimova et al., 2016) and Wisconsin (Wilson et al., 2018) occur in regions that experience warmer temperatures than those in southwestern Yukon (Figure 2). During the period when mismatch is possible in Montana, autumn temperatures can range from ~3°C to 17°C and spring temperatures can range from ~4°C to 20°C.

The seasonal differences in mismatch effects on survival and foraging time that we found highlighted temperature as a unifying factor affecting the survival costs of coat color mismatch. Mismatch did not influence mortality risk in the spring (Figure 1b) and matched and mismatched hares spent similar amounts of time foraging (Figure 2b). Mismatched hares in the spring occurred at temperatures (−0.5°C to 11°C; Figure 2b) that were above the lower critical temperature of both summer-acclimatized and winter-acclimatized hares (Sheriff, Kuchel, et al., 2009). In contrast, mismatched hares in the autumn experienced temperatures between −7°C and 4°C (Figure 2a) which fell below the lower critical temperature for summer-acclimatized brown hares, but not winter-acclimatized white hares (Sheriff, Kuchel, et al., 2009). Animals must increase their energetic expenditure when they are exposed to temperatures outside of their thermoneutral zone (Kingma et al., 2012), which may represent a likely mechanism explaining the longer foraging time in matched brown hares in the autumn relative to mismatched white hares (Figure 2a). However, other ecological factors affecting mismatched hares in the autumn may also improve their survival, given the substantial impact on mortality risk we observed (Figure 1a). Only snow depth and snow cover significantly affected mortality risk in the spring (Table 1; Figure 1c,d). As snow depth increased, mortality risk decreased, which we attribute to the low foot-load of snowshoe hares, which allows them to outperform their predators in deeper snow (Murray & Boutin, 1991; Peers et al., 2020). The increased risk that was associated with increasing snow cover is likely to stem from the significant increase in risk experienced by hares at shallow snow depths (Peers et al., 2020).

Although camouflage is thought to be the primary adaptive benefit of coat color polymorphism, such as most traits, alternate benefits, e.g., thermal and physiological, exist (Caro, 2005; Duarte et al., 2017; Zimova et al., 2018). We found that these alternate benefits offset the costs of camouflage loss at cold temperatures. Our “thermoregulation” hypothesis, whereby the thermal and energetic benefits of winter acclimatization may influence coat color mismatch effects through reduced time spent foraging, has the potential to reconcile intraspecific variation among other snowshoe hare populations and merits testing in other color-changing species, i.e., arctic hares (*Lepus arcticus*) and mountain hares (*Lepus timidus*). Climate change-induced variation in temperature and precipitation regimes are likely to vary across species ranges (Loarie et al., 2009). Such variation in climate change effects will be particularly large for species with broad distributions, i.e., circumboreal color-changing species. Ultimately, as temperatures in the Northern Hemisphere are projected to warm (Danco et al., 2016), northern snowshoe hare populations are likely to reach the threshold (more than −3°C) at which the energetic benefits of white coats are lost, and survival costs driven by coat color mismatch could occur (Wilson et al., 2018; Zimova et al., 2016). However, elucidating the mechanisms through which phenological mismatches may be operating is essential to enable predictions on broad-scale changes in species distributions.

AUTHOR CONTRIBUTIONS

Joanie L. Kennah, Eric Vander Wal, Michael J. L. Peers and Stan Boutin designed the study. Michael J. L. Peers, Yasmine N. Majchrzak, Allyson K. Menzies, and Emily K. Studd led data collection. Primary logistic support was provided by Stan Boutin with assistance by Murray M. Humphries, Thomas S. Jung, Alice J. Kenney, Charles J. Krebs, and Rudy Boonstra. Joanie L. Kennah performed the analysis with assistance from Michael J. L. Peers, and Eric Vander Wal. Joanie L. Kennah drafted the manuscript and all authors reviewed and commented on previous versions.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data used to generate survival analyses (Kennah et al., 2022d) are available in Figshare at https://doi.org/10.6084/m9.figshare.20557296, and data used to generate foraging time analyses (Kennah et al., 2022a) are available in Figshare at https://doi.org/10.6084/m9.figshare.20699818, The code used to generate the survival analyses (Kennah et al., 2022c) is available in Figshare at https://doi.org/10.6084/m9.figshare.20800237, and the code used to generate the foraging time analyses (Kennah et al., 2022b) is available in Figshare at https://doi.org/10.6084/m9.figshare.20802355.

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REFERENCES

Akaike, H. 1974. "A New Look at the Statistical Model Identification." *IEEE Transactions on Automatic Control* 19: 716–23.

Atmeh, K., A. Andruszkiewicz, and K. Zub. 2018. "Climate Change Is Affecting Mortality of Weasels Due to Camouflage Mismatch." *Scientific Reports* 8: 1–7.

Balluffi-Fry, J., S. J. Leroux, Y. F. Wiersma, I. C. Richmond, T. R. Heckford, M. Rizzuto, J. L. Kennah, and E. Vander Wal. 2022. "Integrating Plant Stoichiometry and Feeding Experiments: State-Dependent Forage Choice and its Implications on Body Mass." *Oecologia* 198: 579–91.

Barton, K. 2020. "Multi-Model Inference." R Package Version 1.43.17. https://cran.r-project.org/web/packages/MuMIn/MuMIn.pdf.

Bates, D., M. Mächler, B. M. Bolker, and S. C. Walker. 2015. "Fitting Linear Mixed-Effects Models Using lme4." *Journal of Statistical Software* 67: 1–51.

Boratyński, J. S., M. Jefimow, and M. S. Wojciechowski. 2016. "Phenotypic Flexibility of Energetics in Acclimated Siberian Hamsters Has a Narrower Scope in Winter than in Summer." *Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology* 186: 387–402.

Brown, R. D., and P. W. Mote. 2009. "The Response of Northern Hemisphere Snow Cover to a Changing Climate." *Journal of Climate* 22: 2124–45.

Burnham, K. P., and D. R. Anderson. 2002. *Model Selection and Multimodel Inference*. New York, NY: Springer.

Caro, T. 2005. "The Adaptive Significance of Coloration in Mammals." *Bioscience* 55: 125–36.

Cox, D. R., and D. Oakes. 1984. *Analysis of Survival Data*. New York, NY: Chapman and Hall.

Danco, J. F., A. M. Deangelis, B. K. Raney, and A. J. Broccoli. 2016. "Effects of a Warming Climate on Daily Snowfall Events in the Northern Hemisphere." *Journal of Climate* 29: 6295–318.

Doi, H., O. Gordo, T. Mori, and M. T. Kubo. 2017. "A Macroecological Perspective for Phenological Research under Climate Change." *Ecological Research* 32: 633–41.

Duarte, R. C., A. A. V. Flores, and M. Stevens. 2017. "Camouflage through Colour Change: Mechanisms, Adaptive Value and Ecological Significance." *Philosophical Transactions of the Royal Society B* 372: 1–8.

Ferreira, M. S., P. C. Alves, C. M. Callahan, J. P. Marques, L. S. Mills, J. M. Good, and J. Melo-Ferreira. 2017. "The Transcriptional Landscape of Seasonal Coat Colour Moult in the Snowshoe Hare." *Molecular Ecology* 26: 4173–85.

Fuglesteg, B. N., Ø. E. Haga, L. P. Folkow, E. Fuglei, and A. S. Blix. 2006. "Seasonal Variations in Basal Metabolic Rate, Lower Critical Temperature and Responses to Temporary Starvation in the Arctic Fox (Alopex Lagopus) from Svalbard." *Polar Biology* 29: 308–19.

Gigliotti, L. C., D. R. Diefenbach, and M. J. Sheriff. 2017. "Geographic Variation in Winter Adaptations of Snowshoe Hares (Lepus Americanus)." *Canadian Journal of Zoology* 95: 539–45.

Gordo, O., and H. Doi. 2012. "Drivers of Population Variability in Phenological Responses to Climate Change in Japanese Birds." *Climate Research* 54: 95–112.

Griffin, P. C., S. C. Griffin, C. Waroquiers, and L. S. Mills. 2005. "Mortality by Moonlight: Predation Risk and the Snowshoe Hare." *Behavioral Ecology* 16: 938–44.

Hart, J. S., H. Pohl, and J. S. Tener. 1965. "Seasonal Acclimatization in Varying Hare (*Lepus americanus*)." *Canadian Journal of Zoology* 43: 731–44.

Heard, M. J., S. H. Riskin, and P. A. Flight. 2012. "Identifying Potential Evolutionary Consequences of Climate-Driven Phenological Shifts." *Evolutionary Ecology* 26: 465–73.

Humphries, M. M., S. Boutin, D. W. Thomas, J. D. Ryan, C. Selman, A. G. McAdam, D. Berteaux, and J. R. Speakman. 2005. "Expenditure Freeze: The Metabolic Response of Small Mammals to Cold Environments." *Ecology Letters* 8: 1326–33.

Joshua Chen, Y. H., and G. H. F. Liu. 2006. "A Note on the Estimate of Treatment Effect from a Cox Regression Model when the Proportionality Assumption Is Violated." *Communications in Statistics - Theory and Methods* 35: 521–6.

Kennah, J., M. J. L. Peers, E. V. Wal, Y. N. Majchrzak, A. Menzies, E. K. Studd, R. Boonstra, et al. 2022a. "Accelerometer Data for Analysis." Figshare. Dataset. https://doi.org/10.6084/m9.figshare.20699818.v1.

Kennah, J., M. J. L. Peers, E. V. Wal, Y. N. Majchrzak, A. Menzies, E. K. Studd, R. Boonstra, et al. 2022b. "Snowshoe Hare Foraging Analysis Code." Figshare. Software. https://doi.org/10.6084/m9.figshare.20802355.v1.

Kennah, J., M. J. L. Peers, E. V. Wal, Y. N. Majchrzak, A. Menzies, E. K. Studd, R. Boonstra, et al. 2022c. "Snowshoe Hare Mismatch Survival Analysis Code." Figshare. Software. https://doi.org/10.6084/m9.figshare.20800237.v1.

Kennah, J., M. J. L. Peers, E. V. Wal, Y. N. Majchrzak, A. Menzies, E. K. Studd, R. Boonstra, et al. 2022d. "Survival Data for Analysis." Figshare. Dataset. https://doi.org/10.6084/m9.figshare.20557296.v1.

Kingma, B., A. Frijns, and W. V. M. Lichtenbelt. 2012. "The Thermoneutral Zone: Implications for Metabolic Studies." *Frontiers in Bioscience - Elite* 4(5): 1975–85.

Krebs, C. J., R. Boonstra, and S. Boutin. 2018. "Using Experimentation to Understand the 10-Year Snowshoe Hare Cycle in the Boreal Forest of North America." *Journal of Animal Ecology* 87: 87–100.

Krebs, C. J., S. Boutin, R. Boonstra, A. R. E. Sinclair, J. N. M. Smith, M. R. T. Dale, K. Martin, and R. Turkington. 1995. "Impact of Food and Predation on the Snowshoe Hare Cycle." *Science* 269: 1112–5.

Kudo, G., and T. Y. Ida. 2013. "Early Onset of Spring Increases the Phenological Mismatch between Plants and Pollinators." *Ecology* 94: 2311–20.

Lehikoinen, A. 2011. "Advanced Autumn Migration of Sparrowhawk Has Increased the Predation Risk of Long-Distance Migrants in Finland." *PLoS One* 6: 1–4.

Lima, S. L., and L. M. Dill. 1990. "Behavioral Decisions Made under the Risk of Predation: A Review and Prospectus." *Canadian Journal of Zoology* 68: 619–40.

Loarie, S. R., P. B. Duffy, H. Hamilton, G. P. Asner, C. B. Field, and D. D. Ackerly. 2009. "The Velocity of Climate Change." *Nature* 462: 1052–5.

Lovegrove, B. G. 2005. "Seasonal Thermoregulatory Responses in Mammals." *Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology* 175: 231–47.

Majchrzak, Y. N., M. J. L. Peers, E. K. Studd, A. K. Menzies, P. D. Walker, S. Shiratsuru, L. K. McCaw, et al. 2022. "Balancing Food Acquisition and Predation Risk Drives Demographic Changes in Snowshoe Hare Population Cycles." *Ecology Letters* 25: 981–91.

Mazerolle, M. 2019. "Model selection and multimodel inference based on (Q)AIC(c) Version 2.2-2." https://cran.r-project.org/web/packages/AICcmodavg/AICcmodavg.pdf.

McNamara, J. M., and A. I. Houston. 1987. "Starvation and Predation as Factors Limiting Population Size." *Ecology* 68: 1515–9.

Melin, M., L. Mehtätalo, P. Helle, K. Ikonen, and T. Packalen. 2020. "Decline of the Boreal Willow Grouse (*Lagopus lagopus*) Has Been Accelerated by more Frequent Snow-Free Springs." *Scientific Reports* 10: 1–10.

Meslow, E. C., and L. B. Keith. 1971. "A Correlation Analysis of Weather Versus Snowshoe Hare Populatio Parameters." *The Journal of Wildlife Management* 35: 1–15.

Mikkelsen, L., M. Johnson, D. M. Wisniewska, A. van Neer, U. Siebert, P. T. Madsen, and J. Teilmann. 2019. "Long-Term Sound and Movement Recording Tags to Study Natural Behavior and Reaction to Ship Noise of Seals." *Ecology and Evolution* 9: 2588–601.

Mills, L. S., E. V. Bragina, A. V. Kumar, M. Zimova, D. J. R. Lafferty, J. Feltner, B. M. Davis, et al. 2018. "Winter Color Polymorphisms Identify Global Hot Spots for Evolutionary Rescue from Climate Change." *Science* 359: 1033–6.

Mills, L. S., M. Zimova, J. Oyler, S. Running, J. T. Abatzoglou, and P. M. Lukacs. 2013. "Camouflage Mismatch in Seasonal Coat Color Due to Decreased Snow Duration." *Proceedings of the National Academy of Sciences of the United States of America* 110: 7360–5.

Møller, A. P., D. Rubolini, and E. Lehikoinen. 2008. "Populations of Migratory Bird Species that Did Not Show a Phenological Response to Climate Change Are Declining." *Proceedings of the National Academy of Sciences of the United States of America* 105: 16195–200.

Murray, D. L., and G. Bastille-Rousseau. 2020. "Estimating Survival and Cause-Specific Mortality from Continuous Time Observations." In *Population Ecology in Practice*, edited by D. L. Murray and B. Sandercock, 448. Hoboken, NJ: Wiley-Blackwell.

Murray, D. L., and S. Boutin. 1991. "The Influence of Snow on Lynx and Coyote Movements: Does Morphology Affect Behavior?" *Oecologia* 88: 463–9.

Nagorsen, D. W. 1983. "Winter Pelage Colour in Snowshow Hares (Lepus Americanus) from the Pacific Northwest." *Canadian Journal of Zoology* 61: 2313–8.

Nakagawa, S., P. C. D. Johnson, and H. Schielzeth. 2017. "The Coefficient of Determination R2 and Intra-Class Correlation Coefficient from Generalized Linear Mixed-Effects Models Revisited and Expanded." *Journal of the Royal Society Interface* 14: 1–11.

Pedersen, S., M. Odden, and H. C. Pedersen. 2017. "Climate Change Induced Molting Mismatch? Mountain Hare Abundance Reduced by Duration of Snow Cover and Predator Abundance." *Ecosphere* 8: 1–8.

Peers, M. J. L., Y. N. Majchrzak, A. K. Menzies, E. K. Studd, G. Bastille-Rousseau, R. Boonstra, M. Humphries, et al. 2020. "Climate Change Increases Predation Risk for a Keystone Species of the Boreal Forest." *Nature Climate Change* 10: 1149–53.

Phillimore, A. B., J. D. Hadfield, O. R. Jones, and R. J. Smithers. 2010. "Differences in Spawning Date between Populations of Common Frog Reveal Local Adaptation." *Proceedings of the National Academy of Sciences of the United States of America* 107: 8292–7.

Porkert, J., S. Gashkov, J. Haikola, E. Huhta, M.-L. Kaisanlahti-Jokimäki, B. Kuranov, R. Latja, et al. 2014. "Variation and Long-Term Trends in the Timing of Breeding of Different Eurasian Populations of Common Redstart Phoenicurus Phoenicurus." *Journal of Ornithology* 155: 1045–57.

Post, E., and M. C. Forchhammer. 2008. "Climate Change Reduces Reproductive Success of an Arctic Herbivore through Trophic Mismatch." *Philosophical Transactions of the Royal Society B: Biological Sciences* 363: 2369–75.

Radchuk, V., T. Reed, C. Teplitsky, M. van de Pol, A. Charmantier, C. Hassall, P. Adamík, et al. 2019. "Adaptive Responses of Animals to Climate Change Are most Likely Insufficient." *Nature Communications* 10: 1–14.

Reed, T. E., V. Grtøan, S. Jenouvrier, B. E. Stæher, and M. E. Visser. 2013. "Population Growth in a Wild Bird Is Buffered against Phenological Mismatch." *Science* 340: 488–91.

R Core Team. 2018. *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing.

Rogowitz, G. L. 1990. "Seasonal Energetics of the White-Tailed Jackrabbit (*Lepus townsendii*)." *Journal of Mammalogy* 71: 277–85.

Sealander, J. A. 1972. "Circum-Annual Changes in Age, Pelage Characteristics and Adipose Tissue in the Northern Red-Backed Vole in Interior Alaska." *Acta Theriologica* 17: 1–24.

Sheriff, M. J., L. Kuchel, S. Boutin, and M. M. Humphries. 2009. "Seasonal Metabolic Acclimatization in a Northern Population of Free-Ranging Snowshoe Hares, Lepus Americanus." *Journal of Mammalogy* 90: 761–7.

Sheriff, M. J., J. R. Speakman, L. Kuchel, S. Boutin, and M. M. Humphries. 2009. "The Cold Shoulder: Free-Ranging Snowshoe Hares Maintain a Low Cost of Living in Cold Climates." *Canadian Journal of Zoology* 87: 956–64.

Shiratsuru, S., Y. N. Majchrzak, M. J. L. Peers, E. K. Studd, A. K. Menzies, R. Derbyshire, M. M. Humphries, C. J. Krebs, D. L. Murray, and S. Boutin. 2021. "Food Availability and Long-Term Predation Risk Interactively Affect Antipredator Response." *Ecology* 102: e03456.

Sievert, P. R., and L. B. Keith. 1985. "Survival of Snowshoe Hares at a Geographic Range Boundary." *The Journal of Wildlife Management* 49: 854–66.

Stefan, C. I., and C. J. Krebs. 2001. "Reproductive Changes in a Cyclic Population of Snowshoe Hares." *Canadian Journal of Zoology* 79: 2101–8.

Studd, E. K., M. R. Boudreau, Y. N. Majchrzak, A. K. Menzies, M. J. L. Peers, J. L. Seguin, S. G. Lavergne, et al. 2019. "Use of Acceleration and Acoustics to Classify Behavior, Generate Time Budgets, and Evaluate Responses to Moonlight in Free-Ranging Snowshoe Hares." *Frontiers in Ecology and Evolution* 7: 1–14.

Therneau, T. M., T. Lumley, A. Elizabeth, and C. Cynthia. 2021. "Survival Analysis." R package version 3.2-10. https://cran.r-project.org/web/packages/survival/survival.pdf.

Valladares, F., S. Matesanz, F. Guilhaumon, M. B. Araújo, L. Balaguer, M. Benito-Garzón, W. Cornwell, et al. 2014. "The Effects of Phenotypic Plasticity and Local Adaptation on Forecasts of Species Range Shifts under Climate Change." *Ecology Letters* 17: 1351–64.

Visser, M. E., and P. Gienapp. 2019. "Evolutionary and Demographic Consequences of Phenological Mismatches." *Nature Ecology and Evolution* 3: 879–85.

Webster, A. J., A. M. Hicks, and F. L. Hays. 1969. "Cold Climate and Cold Temperature Induced Changes in the Heat Production and Thermal Insulation of Sheep." *Canadian Journal of Physiology and Pharmacology* 47: 553–62.

Wilson, E. C., A. A. Shipley, B. Zuckerberg, M. Z. Peery, and J. N. Pauli. 2018. "An Experimental Translocation Identifies Habitat Features that Buffer Camouflage Mismatch in Snowshoe Hares." *Conservation Letters* 12: 1–8.

Zeileis, A., G. Grothendieck, J. A. Ryan, and F. Andrews. 2021. "Package 'Zoo'. S3 infrastructure for Regular and Irregular Time Series (Z's Ordered Observations)." R package version 1.8-9. https://cran.r-project.org/web/packages/zoo/zoo.pdf.

Zimova, M., K. Hackländer, J. M. Good, J. Melo-Ferreira, P. C. Alves, and L. S. Mills. 2018. "Function and Underlying Mechanisms of Seasonal Colour Moulting in Mammals and Birds: What Keeps them Changing in a Warming World?" *Biological Reviews* 93: 1478–98.

Zimova, M., L. S. Mills, P. M. Lukacs, and M. S. Mitchell. 2014. "Snowshoe Hares Display Limited Phenotypic Plasticity to Mismatch in Seasonal Camouflage." *Proceedings of the Royal Society B: Biological Sciences* 281: 1–9.

Zimova, M., L. S. Mills, and J. J. Nowak. 2016. "High Fitness Costs of Climate Change-Induced Camouflage Mismatch." *Ecology Letters* 19: 299–307.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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