

AN EVALUATION OF THE COSTS AND RESPONSES OF COAT COLOUR MISMATCH
IN SNOWSHOE HARES

By

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ABSTRACT

Animals that change colour seasonally to match the presence and absence of snow are becoming increasingly mismatched with their environment in many parts of the world. We evaluated the direct and indirect impacts of coat colour mismatch in snowshoe hares in two contrasting geographies, and further investigated the mechanisms that may be driving these impacts. First, we examined the impact of coat colour mismatch on snowshoe hare mortality risk and foraging behaviour in southwestern Yukon. We found that white mismatched hares survived better than their matched counterparts, presumably due to energetic benefits related to winter white coats that allowed hares to spend less time foraging. Next, we experimentally manipulated coat colour mismatch and perceived predation risk in central-eastern Newfoundland. We found that mismatched hares in risky situations experience increased body mass loss, which they may compensate for by altering their forage selection and intake rate. Our results shine light on the mechanisms that govern coat colour mismatch impacts across populations in different geographies, and how animals may compensate for these impacts.

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List of Abbreviations and Symbols

CI = Confidence Interval

CPH = Cox's Proportional Hazards

HR = Hazard Ratio

ICC = Intraclass Correlation Coefficient

N = Nitrogen

TERG = Terrestrial Ecology Research Group

VIF = Variance Inflation Factor

VHF = Very High Frequency

Chapter 1 – General Introduction

1.1 Phenological mismatch

Phenology refers to the timing of life-history events, such as spawning or breeding date (Phillimore et al. 2010, Moyes et al. 2011), migration timing (Rubolini et al. 2010) and emergence from hibernation (Lane et al. 2019). Species use environmental cues such as temperature and photoperiod to adjust and time their phenology with the optimal time window during which the trait in question should be expressed to maximize fitness (McNamara et al. 2011, Visser and Gienapp 2019). Climate change is generating warmer temperatures and earlier springs in the Northern Hemisphere (Gauthier et al. 2015, Pulliainen et al. 2017), which is causing the mistiming of various life-history events with their optimal environments, i.e., phenological mismatch (Parmesan 2007, Thackeray et al. 2016, Visser and Gienapp 2019). While the original ‘match-mismatch hypothesis’ (Cushing 1969) related to the phenological mismatch between a resource and its consumer, the hypothesis has since been applied to numerous asynchronous trophic interactions (Kharouba et al. 2018).

The impacts of phenological mismatch are inconsistent across species and populations (Miller-Rushing et al. 2010), but phenological mismatch is associated with negative impacts on food availability (Lane et al. 2012), offspring condition (Nussey et al. 2005), and reproductive success (Post and Forchhammer 2008). Coat and plumage colour mismatch is a particular case of phenological mismatch increasingly studied in recent years and that is likely becoming more common with climate change (Imperio et al. 2013, Sultaire et al. 2016, Zimova et al. 2018). Congruity of coat or plumage colour with the environment in species that moult from white to brown, and vice versa, is important as these species rely on colour as crypsis for camouflage (Zimova et al. 2018).

1.2 Camouflage, seasonal colour change and mismatch

Crypsis achieved through visual camouflage has evolved in many different taxa and represents an important antipredator trait for prey species to avoid detection (Caro 2005, Duarte et al. 2017) and reduce predation risk (Stevens and Merilaita 2009). Background matching is a form of visual camouflage where animals resemble the general colour or pattern of the environment around them (Skelhorn and Rowe 2015). Some species achieve background matching through colour polymorphism, where they change colours to ensure camouflage with their current environment (Zimova et al. 2018). For example, many seasonally colour-changing species moult biannually in the autumn and spring to match the presence or absence of snow (Zimova et al. 2018). The environmental cue attributed to colour change in many species is photoperiod, and species moult from brown to white or vice-versa as days get shorter or longer (Funakoshi et al. 2017, Zimova et al. 2018).

While photoperiod is constant, snow season timing has become increasingly variable with climate change, preventing many colour-changing birds and mammals from appropriately expressing camouflage with their environment (Imperio et al. 2013, Pedersen et al. 2017, Kumar et al. 2020). Colour mismatch has been associated with increased mortality risk in some cases (Mills et al. 2013, Atmeh et al. 2018). Species negatively impacted by climate change may persist by altering their range to track change, or by adapting to the new conditions they face (Thomas 2010, Vander Wal et al. 2013). Phenotypic plasticity, the ability to adjust a phenotype to variable environments (Nussey et al., 2007), is considered the most rapid mechanism for adaptation (Visser 2008). In species affected by colour mismatch, phenotypic plasticity could allow species to ‘match’ their colour change to the optimal environment despite fluctuating or

shifting environmental conditions (Lof et al. 2012). While there is limited evidence of colour changing species being able to adjust their phenotype to adequately match their surroundings (Mills et al. 2013), behavioural plasticity may allow mismatched animals to reduce potential negative impacts (Zimova et al. 2014).

1.3 Behavioural plasticity

Animals often adjust their behaviour as a first response to changing environments (Wong and Candolin 2015). Indeed, species exhibit plasticity in various behavioural traits to mitigate the effects of climate change (Sih et al. 2011, Wolff et al. 2020). Species affected by colour mismatch may mitigate the impacts of poor camouflage by adjusting their behaviours to select areas that promote concealment (Steen et al. 1992), soiling their white plumage when their environment is brown (Montgomerie 2001), or selecting habitats with greater visual complexity (Rowe et al. 2021). Camouflage is only one antipredator trait that comprises a suite of defences prey may use to reduce their predation risk (Makin et al. 2017). Through behavioural plasticity, species may compensate for lost or imperfect camouflage by leveraging other anti-predator traits. For example, as prey balance foraging decisions and vigilance to meet their energetic demands in a dynamic landscape of risk (Winnie and Creel 2017, Gaynor et al. 2019), they may alter their foraging decisions to mitigate heightened risk with lost camouflage. This behavioural adjustment has been observed in jumping spiders (*Marpissa muscosa*), which respond to colour mismatch by reducing their foraging intensity, i.e., speed of foraging, or time spent foraging and at food patches (Steinhoff et al. 2020).

1.4 Snowshoe hare

The snowshoe hare (*Lepus americanus*) is a keystone species of the boreal forest, given its essential role as a food source for numerous predators and significant effect on the ecosystem (Humphries et al. 2017, Peers et al. 2020). Hares occur in a famous population cycle with their predators (Krebs et al. 2018, Oli et al. 2020), which was originally studied using fur trading records collected by the Hudson's Bay Company in the early 1900s (MacLulich 1937, Krebs et al. 2001). Since then, it has become clear that the intrinsic associations between the snowshoe hare and its predators, particularly Canada lynx (*Lynx canadensis*), are foundational for the ecological integrity of the boreal forest.

Snowshoe hares change colour biannually in the autumn and spring to match the presence and absence of snow. While the exact underpinnings of how seasonal coat colour moults occur are still to be determined, genes that are likely associated with seasonal colour change include *Agouti*, *Myo7a* and *Spns2* (Ferreira et al. 2017, Zimova et al. 2018). These genes essentially play a role in regulating the production of melanin by melanocytes to produce brown or white fur. The cue driving these physiological changes is likely photoperiod (Grange 1932, Nagorsen 1983). As with many other species in northern latitudes, snowshoe hares are experiencing increased colour mismatch with climate change induced reductions in snow cover (Mills et al. 2013, Zimova et al. 2016, 2018). Coat colour change to reduce conspicuousness to predators is an important adaptation to predation for snowshoe hares, considering that predation accounts for 85-100% of hare mortality (Hodges, 2000). Given its important role as a prey species, snowshoe hare behaviour and decisions are governed by the trade-off that exists between food acquisition and predation risk (Richmond et al. 2022). As such, the snowshoe hare is an ideal model to

empirically study the effects and drivers of coat colour mismatch. Indeed, recent studies have linked high mortality rates in snowshoe hares in the southern extent of their range to coat colour mismatch (Zimova et al., 2014; Wilson et al., 2018).

In the southern extent of snowshoe hare range in Montana (Fig. 1), hares showed a lack of phenotypic plasticity in coat colour change rates and initiation dates in the autumn, but some plasticity to the change rate in the spring (Mills et al., 2013; Zimova et al., 2014). Snowshoe hares in Montana did not adjust their hiding and fleeing behaviours or resting spot preference and microhabitat selection in response to colour mismatch (Zimova et al. 2014, Kumar et al. 2020). However, as with most prey species, the anti-predator behaviours of hares are heavily shaped by the trade-off between resource acquisition and predator avoidance (Hik 1995, Majchrzak et al. 2022). As such, hares may adjust foraging behaviours to cope with the potential impacts of coat colour mismatch. Behavioural plasticity in foraging may include adjusting forage selection, or reducing foraging time to attenuate predator exposure and ultimately reduce mismatch costs.

1.5 Thesis overview

In this thesis, I investigate how snowshoe hares are affected by and respond behaviourally to coat colour mismatch. In Chapter 2, I evaluate the influence of coat colour mismatch on free-ranging snowshoe hare survival in a northern population (Fig. 1), and investigate whether hares may alter their foraging time in response to mismatch. In Chapter 3, I experimentally manipulate coat colour mismatch in wild hares in a captive setting in Newfoundland (Fig. 1) to evaluate whether they modify their intake rate, or intraspecific selection for forage quality in response to mismatch and

heightened risk. Furthermore, in Chapter 3, I evaluate the impact of altered foraging decisions on body mass loss. To synthesize these ideas, in Chapter 4, I discuss the distinctions and similarities across findings and snowshoe hare populations studied in Chapters 2 and 3, and provide insight on remaining knowledge gaps and future research directions.

1.6 Terrestrial Ecology Research Group

The snowshoe hare grid where I carried out my field work for Chapter 3 exists as part of the study areas used by the Terrestrial Ecology Research Group (TERG). This research group gathers three Principal Investigators (Dr. Eric Vander Wal, Dr. Yolanda Wiersma, and Dr. Shawn Leroux), graduate students and undergraduate students. The students that participated in TERG during my Master's included Gabby Riefesel, Isabella Richmond, Juliana Balluffi-Fry, and Matteo Rizzuto. Members of TERG work together to broadly explore boreal forest ecological stoichiometry and expand our understanding of how carbon, nitrogen, and phosphorus move across the ecological system (Richmond et al. 2020, Heckford et al. 2021, Balluffi-Fry et al. 2022). The various nature of TERG research, along with the collaborative and inclusive spirit of the group, allowed me to reflect on my research questions at a broader scope. I was able to participate in research being led by other students in TERG, and as a result became a co-author on three articles during the duration of my Master's (Richmond et al. 2020, 2022, Balluffi-Fry et al. 2022). The experimental manipulations and food-choice trials I carried out in Chapter 3 draw upon the experimental framework established by Juliana Balluffi-Fry, who considered the browse preferences of snowshoe hares under varying energetic and nutritional demands (Balluffi-Fry et al. 2022). Isabella Richmond's evaluation of how stoichiometric traits vary through time was important

research that allowed me to confidently draw conclusions on the elemental composition of the browse I used for experimental trials. The elemental and stoichiometric traits of the browse I collected were initially determined by previous TERG members, such as Travis Heckford (Heckford et al. 2021). The collaboration opportunities I gained while participating in TERG were extremely beneficial to the development of ideas for my Master's.

1.7 Co-authorship statement

Chapter 2 was co-authored by Michael J.L Peers, Eric Vander Wal, Yasmine N. Majchrzak, Allyson K. Menzies, Emily K. Studd, Rudy Boonstra, Murray M. Humphries, Thomas S. Jung, Alice J. Kenney, Charles J. Krebs, and Stan Boutin. E.V.W., M.J.L.P., S.B. and I designed the study. M.J.L.P., Y.N.M., A.K.M., and E.K.S. led data collection. Primary logistic support was provided by S.B. with assistance by M.M.H., T.S.J., A.J.K., C.J.K., and R.B. I performed the analysis with assistance from M.J.L.P., and E.V.W. I drafted the manuscript and all authors reviewed and commented on previous versions.

Chapter 3 was co-authored by Juliana Balluffi-Fry, Isabella Croft Richmond, Michael J.L. Peers, and Eric Vander Wal. I led the study design, data analysis and writing for Chapter 3. All co-authors provided feedback on the drafted manuscript for this Chapter, as well as guidance with research and experimental design. J.B.F. shared her knowledge by teaching me how to trap and handle snowshoe hares. I.C.R, M.J.L.P, and I collected field data. E.V.W provided funding.

Chapter 2 has been accepted at Ecology, and Chapter 3 will be submitted for review at a journal that has yet to be determined.

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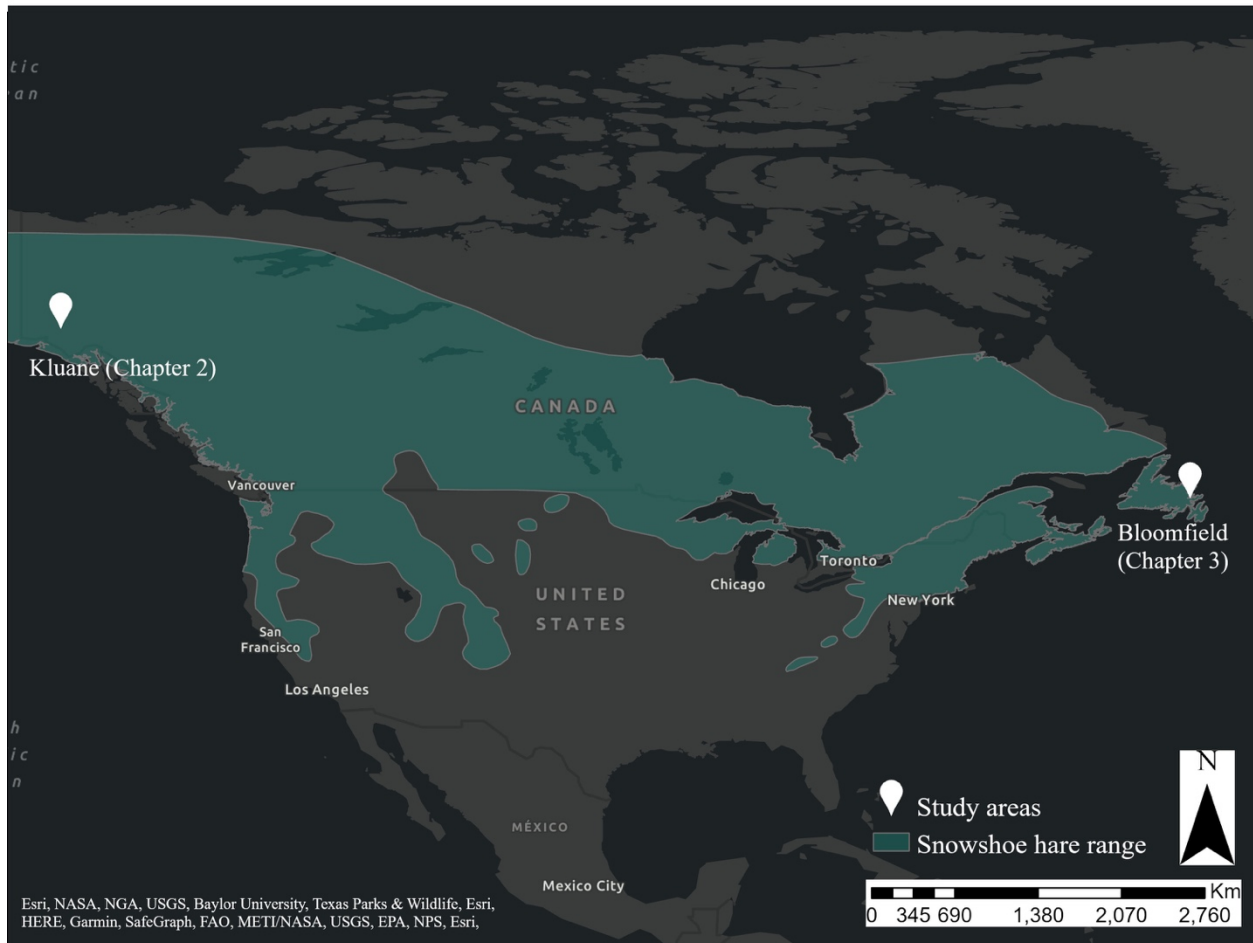


Fig 1-1. Snowshoe hare range and location of study sites for Chapter 2 and 3 manuscripts.

Snowshoe hare data from IUCN (International Union for Conservation of Nature), 2019.

Chapter 2 – Coat color mismatch improves survival of a keystone boreal herbivore: energetic advantages exceed lost camouflage[†]

[†]This Chapter has been accepted in Ecology and the publication process is underway.

2.1 Abstract

Climate warming is causing asynchronies between animal phenology and environments. Mismatched traits, like 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 minutes less per day than matched brown hares between 0 and -10 °C, thus lowering their predation risk and increasing survival. We found no effect of mismatch on spring mortality risk, where mismatch occurred at warmer temperatures, suggesting a potential temperature limit where the costs of conspicuousness outweigh energetic benefits.

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

2.2 Introduction

Phenological mismatch is one of the most documented pathways by which climate change negatively impacts species (Radchuk et al. 2019, Visser and Gienapp 2019). Earlier onset of spring and delayed onset of winter have the potential to cause incongruous timing of seasonal phenotypes (Møller et al. 2008, Lehikoinen 2011, Kudo and Ida 2013). 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 and Forchhammer 2008, Reed et al. 2013). However, the costs associated with phenological mismatches vary within species across populations (Heard et al. 2012, Doi et al. 2017). 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 (Phillimore et al. 2010, Gordo and Doi 2012, 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 (Zimova et al. 2016, Pedersen et al. 2017, Atmeh et al. 2018, Melin et al. 2020). 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; Zimova et al., 2016; Melin et al., 2020). 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 to 20 °C (Webster et al. 1969, Rogowitz 1990), or alter activity patterns, which taken together ultimately reduce daily energy requirements (Humphries et al. 2005, Fuglestad et al. 2006, Sheriff et al. 2009b). Accordingly, coat color transitions coincide with multi-trait change that differentiates long photoperiod, i.e., summer, from short photoperiod, i.e., winter, phenotypes (Lovegrove 2005, Boratyński et al. 2016). 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 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 and 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 (Zimova et al., 2014; Wilson et al., 2018). However, the thermal benefits of winter acclimatization in hares, including reducing their

resting metabolic rate by up to 20% (Sheriff et al. 2009a), may also affect susceptibility to predation and ultimately survival.

White winter-acclimatized snowshoe hares benefit from lower energetic demands compared to brown summer-acclimatized hares. Indeed, while temperatures below 0 °C increase energetic requirements for summer hares, white winter hares remain in their thermoneutral zone until temperatures below -10 °C (Sheriff et al. 2009a). 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 (McNamara and Houston 1987, Lima and Dill 1990). 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 (Sheriff et al. 2009b, Gigliotti et al. 2017). 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 reduces 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 *et al.* 2009a). 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 (Zimova *et al.* 2016, Wilson *et al.* 2018). 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 benefitted from reduced foraging time and thus increased survival relative to brown matched hares.

2.3 Methods

2.3.1. Study area

We studied snowshoe hares during two three month periods, for three autumns (September 1st to December 1st of 2015, 2016, and 2017) and four springs (March 1st to May 31st of 2015, 2016, 2017, and 2018) in southwestern Yukon, Canada (Lat: 60.9 ° N, Long: -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 and Krebs 2001). The daylight hours were shorter on average during the autumn, i.e., 10.07 ± 2.37 hours, than during the spring, i.e., 14.67 ± 2.43 hours. 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 (November 3rd) than in 2016 (October 16th) and 2017 (October 17th). Completion of snowmelt date, i.e., no more snow on ground, was similar across study years (May 6th, 2015, May 1st 2016, May 2nd 2017 and May 1st 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).

2.3.2. 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 minutes before sunset and checked either three hours 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 inter- and intra- observer ranking variability. We consider 10% bins as reasonably precise given that intra- and inter-observer intraclass correlation coefficients (ICC) for coat color assessment were high (ICC>0.9 in all cases, See Appendix A: Table A1). To monitor survival, we fit hares that we suspected were adults, i.e., those weighing > 1100g (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-2M, 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 to 3 days. To monitor behavior, we also fit 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 2 temperature loggers (ibutton, DS1922L, Maxim Integrated, Whitewater, USA) to obtain a single average daily temperature value for each trapping area.

2.3.3 Measuring coat color mismatch

Coat color mismatch was defined as the difference between hare percent white (10% bins) and the daily percent 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 greater than 50% difference between hare % white and snow cover (%). 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 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 to define mismatch (Appendix A: Tables A5, A6, A9, A10). 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 A, Tables A15 and A16).

2.3.4 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 and Oakes 1984) with the "coxph" function in the survival package in R (Therneau et al. 2021). The CPH model is a semi-parametric approach used to analyze binary response data, in our case: alive or dead (Sievert and Keith 1985). We attributed all recorded mortalities of monitored hares to predation, except in two cases, where cause of death was uncertain. We excluded mortality checks that exceeded seven days to limit the uncertainty in the timing of death events (Murray and 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 A: Table A2). Indeed, while snowshoe hare survival varies across their cycle (Majchrzak et al. 2022), we did not detect intra-seasonal survival differences within our autumn and spring seasons (Appendix A: Table A2), 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 $13.1 \pm \text{SD: } 10.8$ 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 $4.95 \pm \text{SD: } 3.70$ days between telemetry check and coat color assessment). We removed telemetry records where 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 A: Table A3).

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 and 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 Akaike Information Criterion for our model selection (Akaike 1974) and identified our top model based on AIC_c (Burnham and Anderson 2002) with the package `AICcmodavg` (Mazerolle 2019). We assessed multicollinearity in our top model using the variance inflation factor (VIF) and ensured no variables had VIF's greater than 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 and 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 and Bastille-Rousseau 2020) (Appendix A: Table A4). Using our top supported CPH model for both seasons, we also predicted 30-day survival between the periods of October 1st and October 30th for autumn, and May 1st and May 30th for spring (Appendix A: Fig. A1). We chose 30-day survival as this roughly corresponds to the average number of days mismatch occurred in both seasons.

2.3.5 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 (Sheriff et al. 2009a, Balluffi-

Fry et al. 2022), 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 second intervals at a 96% accuracy (Studd et al. 2019). We recorded foraging as the number of minutes spent foraging in a 24-hour 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 (SD) 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 A: Table A8). 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 $\leq 50\%$, 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 non-independence 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 A: Table A7).

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-squared calculated using the “r.squaredGLMM” function in the package MuMIn (Barton 2020), according to Nakagawa *et al.* 2017. We used Akaike Information Criterion (Akaike 1974) to rank our four competing models and identified our top model in each season based on AIC_c (Burnham and Anderson 2002). We completed all statistical analyses in R version 3.6.2 (2019) (R Core Team, 2019). We considered results where $P \leq 0.05$ as significant and reported all means with ± 1 standard error.

2.4 Results

2.4.1 Overview

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.

2.4.2 Effect of coat color mismatch on survival

We monitored 347 hares and recorded 41 deaths over four spring and 34 deaths over three autumns. Where 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 A: Table A11 & A12). However, the second highest ranking CPH model for spring, i.e., the model including only snow variables, was within 2 Δ AICc (AICc = 0.09) from our top spring CPH model (Appendix A: Table A11). Contrary to our prediction, matched hares had a significantly higher mortality risk than mismatched hares in the autumn (Hazard Ratio (HR) [mismatch]= 0.135; 95% Confidence Intervals (CI): 0.027, 0.679; z = -2.43; P =0.02; Fig 1a; Table 1). This translates 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 A: Fig. A1). In contrast, coat color mismatch was positively correlated with mortality risk for hares in the spring (Fig. 1b), but this effect was non-significant (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; Fig 1d) and mortality risk increased as snow cover increased (HR=1.046; 95% CI: 1.01, 1.08; Fig 1c).

2.4.3 Effect of coat color mismatch on foraging time

Across the periods when snow cover was $\leq 50\%$ during our study years, hares foraged on average 11.77 ± 0.038 hours per day in the spring and 12.52 ± 0.028 hours per day in the autumn. These foraging times represent $\sim 80\%$ 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 A: Table A13 and 14). 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 (Fig. 2a; Table 2). For instance, white mismatched hares foraged 17-77 minutes, i.e., 2-10 %, less per day than matched brown hares at temperatures between 0 and $-10\text{ }^{\circ}\text{C}$ (Fig. 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 non-significant ($t = -0.939$, $P = 0.348$).

2.5 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 insulation, and reducing their resting metabolic rate by 20% (Sheriff et al.

2009a). 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 (Fig. 1a), but that survival did not differ between matched and mismatched hares in the spring (Fig. 1b). Although this result contradicts previous studies that link coat color mismatch in snowshoe hares to reduced survival (Zimova et al. 2016, Wilson et al. 2018), it provides support for our *thermoregulation hypothesis*. Mismatched white hares spent significantly less time foraging than matched individuals during cold temperatures in the autumn (Fig. 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 (Fig 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 ($< -3^{\circ}\text{C}$) temperatures (Fig. 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 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 (Fig. 2). During the period when mismatch is possible in Montana, autumn temperatures can range from $\sim 3^{\circ}\text{C}$ to 17°C and spring temperatures can range from $\sim 4^{\circ}\text{C}$ to 20°C .

The seasonal differences in mismatch effects on survival and foraging time that we found highlight temperature as a unifying factor affecting the survival costs of coat color mismatch. Mismatch did not influence mortality risk in the spring (Fig. 1b) and matched and mismatched hares spent similar amounts of time foraging (Fig. 2b). Mismatched hares in the spring occurred at temperatures (-0.5°C to 11°C , Fig. 2b) that were above the lower critical temperature of both summer and winter-acclimatized hares (Sheriff et al. 2009a). In contrast, mismatched hares in the autumn experienced temperatures between -7°C and 4°C (Fig. 2a) which fall below the lower critical temperature for summer-acclimatized brown hares, but not winter-acclimatized white hares (Sheriff et al. 2009a). 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 (Fig. 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 (Fig. 1a). Only snow depth and snow cover significantly affected mortality risk in the spring (Table 1; Fig 1d; Fig 1c). 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 and Boutin 1991, Peers et al. 2020). The

increased risk that was associated increasing snow cover likely stems 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, like 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*), 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 ($> -3^{\circ}\text{C}$) at which the energetic benefits of white coats are lost, and survival costs driven by coat color mismatch could occur (Zimova et al. 2016, Wilson et al. 2018). However, elucidating the mechanisms through which phenological mismatches may be operating is essential to enable predictions on broad-scale changes in species distributions.

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Tables

Table 2-1. Hazard ratios (HR) and 95% confidence intervals generated for each variable of our top Cox’s Proportional Hazard’s 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)	<i>0.903</i> (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)

Notes: 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. Abbreviations are used for Hazard ratios (HR), Snow depth (SD), mismatch (mm) and snow cover (SC).

Table 2-2. Summary of variables included in top-ranking linear mixed-effects daily foraging time models for a) snow-free autumn and b) spring periods.

Model	Response: Daily foraging minutes		
	Coefficient (\pm SE)	t	P
a) Top model autumn from n=1505 daily foraging records from 66 hares			
Intercept	830.909 \pm 9.037	91.942	<0.001
Temperature	-2.306 \pm 0.505	-4.566	<0.001
mismatch	-17.385 \pm 6.170	-2.818	0.005
Year (2016)	-10.364 \pm 8.380	-1.237	0.217
Year (2017)	-101.607 \pm 12.188	-8.336	<0.001
Temperature \times mismatch	5.963 \pm 1.210	4.929	<0.001
b) Top model spring from n= 838 daily foraging records from 44 hares			
Intercept	858.868 \pm 22.800	37.669	<0.001
Temperature	-1.209 \pm 1.295	-0.933	0.351
Year (2016)	-16.582 \pm 19.380	-0.856	0.396
Year (2017)	-28.914 \pm 19.111	-1.513	0.137
Year (2018)	-93.029 \pm 21.089	-4.411	<0.001
Sex (F)	-34.832 \pm 17.000	-2.049	0.047

Notes: 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.

Figures

Fig. 2-1

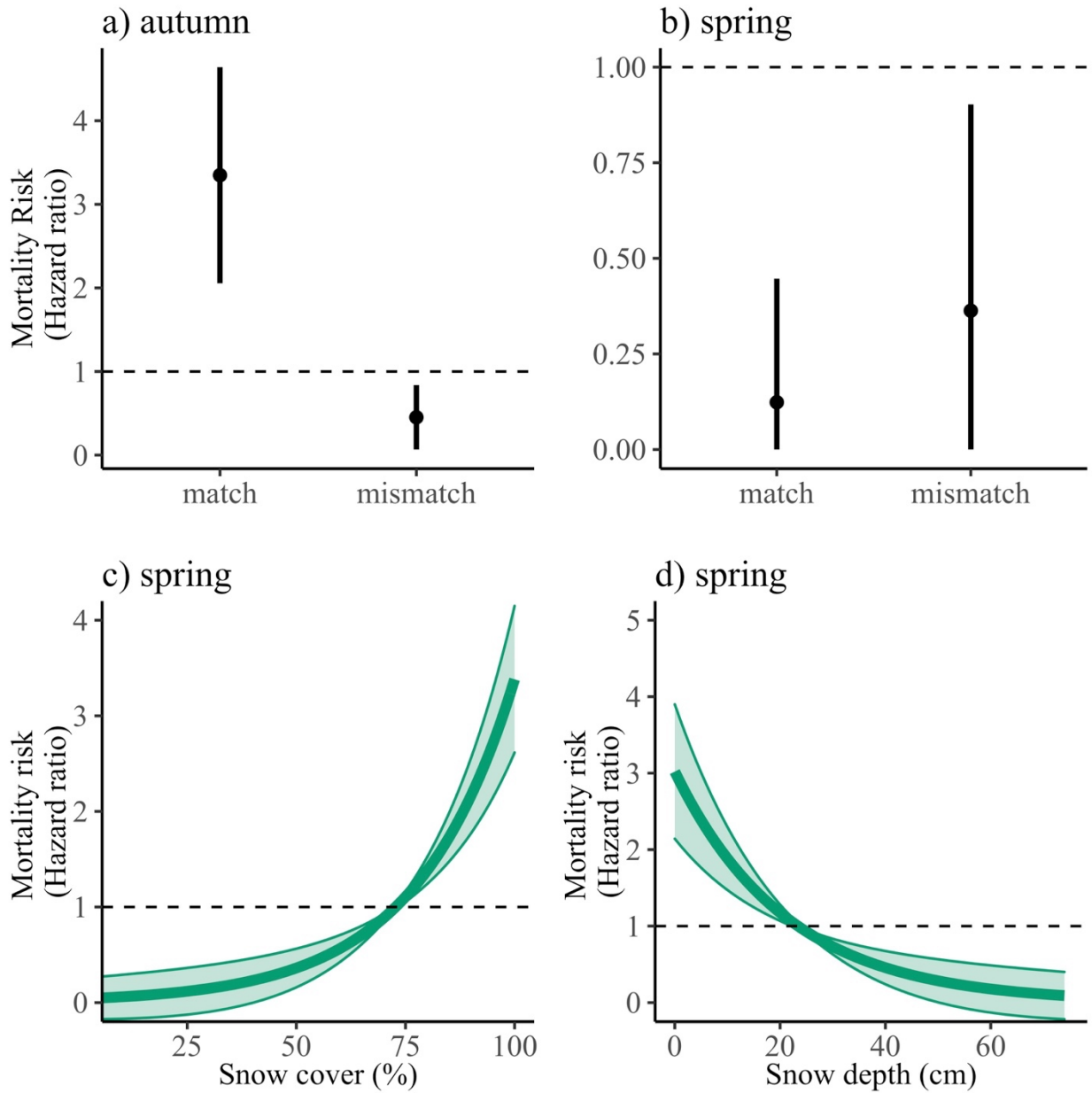
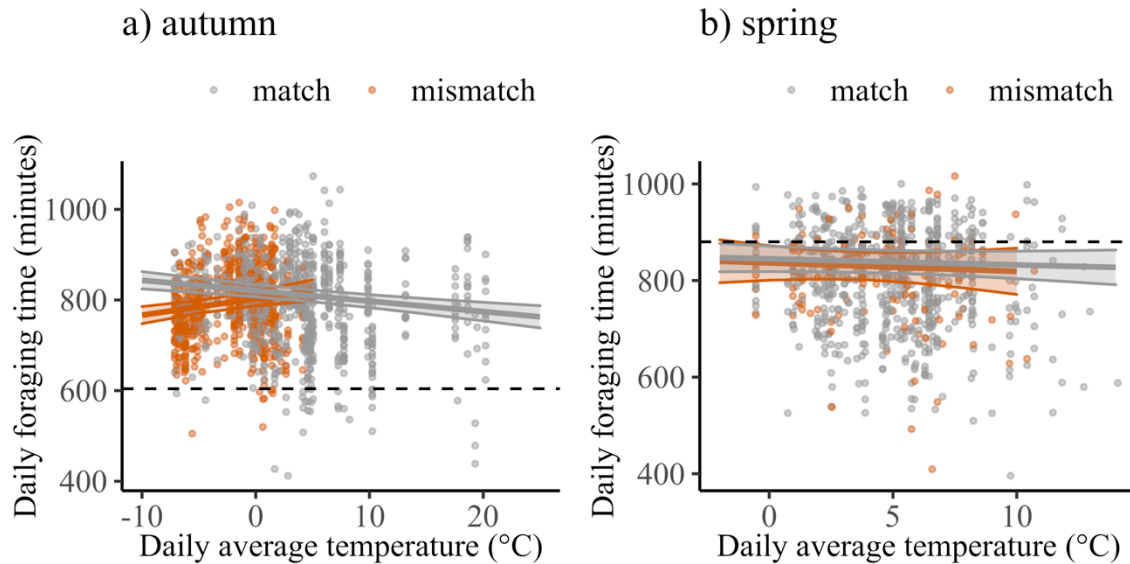


Fig 2-1. The modelled effect of coat color mismatch on snowshoe hare mortality risk, generated from our top supported CPH model for a) autumn and b) spring. Points represent predicted hazard ratios (HR) for matched and mismatched hares when snow depth and snow cover are held

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).

1 Fig. 2-2



2

3 Fig 2-2. Modelled effect of temperature on daily foraging time (minutes) for matched and

4 mismatched snowshoe hares in the snow-free period of a) autumn (marginal $R^2=0.12$,

5 conditional $R^2=0.32$) and b) spring (marginal $R^2=0.13$, conditional $R^2=0.28$) of 2016 (the year

6 with the most data). Data points show daily foraging records for individuals across all study

7 years and predicted foraging time of mismatched hares is restricted to temperatures where

8 mismatched hares occurred in our study. Predicted values for daily spring foraging time are for

9 males. Dashed line represents average number of nighttime minutes for both seasons.

10 Chapter 3 – Foraging decisions of snowshoe hares in response to experimentally induced coat

11 colour mismatch

12 3.1 Abstract

13

14 Animals may exhibit various strategies to mitigate the adverse effects of phenological mismatch.

15 In species experiencing coat colour mismatch, the effects of lost camouflage on predation risk

16 may be compensated for with other antipredator traits, such as altered foraging decisions, and

17 may further be dependent on the level of predation risk. We artificially simulated coat colour
18 mismatch in wild-caught snowshoe hares and measured their forage intake rate, intraspecific
19 selection for forage quality, i.e., % nitrogen of black spruce browse, and resulting body mass loss
20 across different risk levels, simulated by cover or lack thereof. We found that hares did not adjust
21 their intake rate in response to mismatch, but hares in our high-risk treatment, i.e., clear roof
22 enclosures, ate significantly more than hares in opaque roof enclosures. Mismatched brown hares
23 selected for more nitrogen-rich forage than their matched brown counterparts. White mismatched
24 hares lost 4.55% more body mass than their matched white counterparts, despite not significantly
25 reducing their intake rate. Hares in our high-risk treatment i.e., enclosure lacking cover, lost
26 1.29% more body mass than those in covered enclosures. We suggest that the increased selection
27 for nitrogen-rich forage observed in brown mismatched hares may occur to mitigate the body
28 mass loss consequences of mismatch. Similarly, the increased intake rate of hares in clear roof
29 enclosures relative to those in opaque roof enclosures may be a compensatory behavioural
30 response to increased body mass loss. Our results highlight the potential indirect effects of coat
31 colour mismatch on snowshoe hares, but also the corresponding behavioural mechanisms that
32 may partially mitigate these effects.

33

34 3.2 Introduction

35

36 Many prey traits have evolved to mitigate the risk of predation within and across ecological
37 contexts (Endler 1995). For example, background matching is an antipredator trait where animals
38 resemble the general colour or pattern of their environment (Caro 2005, Skelhorn and Rowe
39 2015, Duarte et al. 2017). In seasonal environments, some species achieve this camouflage
40 through colour polymorphism, where they change colour biannually in the autumn and spring to
41 match the presence or absence of snow (Zimova et al. 2018, Bernardi et al. 2021). The plumage
42 or coat moults that allow this seasonal colour change are often driven by driven by changes in
43 photoperiod (Zimova et al. 2014, Funakoshi et al. 2017). Climate change is causing increasingly
44 early springs and decreased snow duration (Brown and Mote 2009), which results in mistimed
45 coat and plumage colour change with snow cover in many bird and mammal species, e.g.,
46 mountain hare (*Lepus timidus*), snowshoe hare (*Lepus americanus*) and Alpine rock ptarmigan
47 (*Lagopus muta helvetica*) (Imperio et al. 2013, Pedersen et al. 2017, Zimova et al. 2018).
48 Mismatched coat or plumage colour is presumed to increase mortality risk in many species
49 (Imperio et al. 2013, Pedersen et al. 2017, Kumar et al. 2020). However, prey species exhibit
50 suites of antipredator traits that act in concert to reduce predation risk (Makin et al. 2017;
51 Kennah et al. In Review). Whether mismatched animals could potentially adjust other
52 antipredator traits to reduce any negative survival costs driven by lost camouflage remains
53 unknown.

54 Vigilance and foraging decisions are antipredator behaviours that animals can adjust to
55 balance the trade-off between food acquisition and predation risk (Winnie and Creel 2017). Prey
56 live in heterogeneous landscapes of risk and resources, and their decisions to allocate time to

57 foraging or vigilance behaviours intrinsically affect their nutritional intake, energetic expenditure
58 and susceptibility to predation (Hodges and Sinclair 2005, Gaynor et al. 2019, Richmond et al.
59 2022). Different foraging outcomes, such as reduced total intake or selection for high-quality
60 forage, may result from increased vigilance and may be used to achieve optimal energetic gains
61 under different risk scenarios (Verdolin 2006). Animals may adjust their intake rate by
62 modifying decisions such as how long to consume forage, how long to search for forage, and
63 how long to handle forage. These fine-scale foraging decisions that animals make to balance
64 energy gain under different risk scenarios are predicted under the Optimal Foraging Theory
65 (OFT) (Charnov 1976, Pyke et al. 1977). Similarly, according to the OFT, animals are expected
66 to choose an optimal diet to maximize energy gains under various risk scenarios. For example,
67 common voles (*Microtus arvalis*) decrease total food consumption with decreased feeding
68 duration when exposed to high perceived predation risk (Eccard et al. 2020), while elk (*Cervus*
69 *elaphus*) reduce intake of high-quality forage as they shift their habitat use when predators are
70 present (Hernández and Laundré 2005). Prey may become less selective and thus experience
71 reduced nutritional intake in high predation risk settings (Hawlana and Pérez-Mellado 2009,
72 Hawlana and Schmitz 2010). Such foraging strategies are influenced by perceived predation risk,
73 which varies across time and space, leading to dynamic responses by prey species altering the
74 trade-off between food acquisition and predation risk (Brown and Kotler 2004).

75 Animals that perceive heightened predation risk when their camouflage is reduced may
76 therefore adjust foraging decisions to favor protection from predation in different crypsis and
77 perceived risk situations. For instance, when camouflage mismatch was experimentally
78 simulated in jumping spiders (*Marpissa muscosa*), individuals reduced foraging intensity
79 (Steinhoff et al. 2020). Similarly, foxes reduce their intake rate on brighter moonlit nights, when

80 they may be more obvious to predators (Mukherjee et al. 2009). However, such altered foraging
81 strategies represent antipredator responses that may carry downstream costs, such as body mass
82 loss (Creel 2018). By examining how colour mismatch (i.e., lack of camouflage), influences
83 foraging decisions under varying levels of predation risk, we can gain a more comprehensive
84 understanding of how animals navigate complex landscapes of risk. If foraging time is reduced
85 and replaced by increased vigilance to compensate for camouflage loss, animals may mitigate the
86 negative costs of colour mismatch driven by climate change, although downstream effects of
87 behavioural adjustments such as body mass loss may occur.

88 The snowshoe hare (*Lepus americanus*) is a keystone species of the boreal forest that
89 supports multiple predators (Krebs et al. 2018). Snowshoe hares change their coat colour in the
90 autumn and spring to match the presence and absence of snow (Grange 1932). As climate change
91 decreases the duration of the snow seasons (Danco et al. 2016), hares are becoming increasingly
92 mismatched with their environment (Mills et al. 2013). Predation is a strong selective force in the
93 evolution of snowshoe hares (>80% mortality attributed to predation; Hodges 2000), and coat
94 colour mismatch has been linked to decreased survival in this species (Zimova et al. 2016).
95 However, hares can respond to high predation risk by adjusting their foraging and movement
96 behaviour (Hutchen and Hodges 2019, Shiratsuru et al. 2021). The trade-off between food
97 acquisition and vigilance to balance predation risk is critical for snowshoe hares as they are
98 income breeders; that is, they do not rely on stored reserves and can die after losing as little as
99 18% of their body weight (Pease et al. 1979, Kosterman et al. 2018). Therefore, the snowshoe
100 hare is an excellent species to investigate whether foraging decisions may be altered to
101 compensate for any negative coat colour mismatch effects.

102 We sought to answer how coat colour mismatch affects snowshoe hare foraging decisions
103 under different simulated perceived risk levels. We experimentally manipulated coat colour
104 mismatch in wild snowshoe hares at different autumn coat colour change progression levels by
105 placing them in enclosures that had a brown or white ground. Hares foraged during cafeteria
106 experiments in enclosures that further provided overhead cover, or lack thereof, as a proxy of
107 avian predation risk. We chose this proxy since hares are known to behaviourally adjust to the
108 perceived risk of open canopy and because the majority of known hare mortalities in our system
109 were assessed as avian (Hutchen and Hodges 2019, Richmond et al. 2022). We examined how
110 intake rate, intraspecific selection for nutritious, i.e., high % Nitrogen, forage, and weight loss
111 varied between matched and mismatched hares, and how perceived predation risk affected this
112 difference. We hypothesized that snowshoe hares would decrease forage consumption and
113 selection for nitrogen-rich forage when mismatched and exposed to perceived avian predation
114 risk to increase predator avoidance at the expense of nutritional intake. As such, we predicted
115 that mismatched hares in experimental enclosures lacking cover to simulate perceived avian
116 predation (riskiest treatment) would have (i) the lowest total intake rate and (ii) the lowest
117 intraspecific selection for nitrogen-rich forage. Consequently, we predicted that these modified
118 foraging decisions would result in mismatched hares exposed to perceived avian predation risk
119 experiencing (iii) the most body mass loss during experimental trials. Understanding whether
120 animals may – or may not – respond to colour mismatch is vital to predict their ability to persist
121 in the face of increased environmental stochasticity.

122

123 3.3 Methods

124

125 3.3.1 Study area and snowshoe hare trapping

126 Our study occurred from October to December of 2020, in the central-eastern region of
127 Newfoundland, Canada (Lat: 48.35 N, Long: -53.97 W). This region is a mature white spruce
128 plantation (*Picea glauca*) interspersed with black spruce (*Picea mariana*) and paper birch
129 (*Betula papyrifera*). The understory is characterized by lowbush blueberry (*Vaccinium*
130 *angustifolium*), sheep laurel (*Kalmia angustifolia*), and Labrador tea (*Rhododendron*
131 *groenlandicum*). Snowshoe hares at this study site experience avian predation by great horned
132 owls (*Bubo virginianus*) and goshawks (*Accipiter gentilis*), as well as terrestrial predation by
133 Canada lynx (*Lynx canadensis*) and coyotes (*Canis latrans*).

134 We live trapped snowshoe hares on a 500 m by 500 m trapping grid (Appendix B: Fig.
135 B1). The trapping grid contains 50 live traps (Tomahawk Live Trap Co. Tomahawk, WI, USA)
136 that are separated ~ 37-75 m along six transects. We set traps at sunset and baited them with
137 fresh apple slices, rabbit chow and alfalfa cubes. We checked traps and handled hares within 12
138 hours of baiting and setting, and installed eartags on captured individuals to identify them upon
139 subsequent recapture. We recorded the mass (to the nearest 0.02 kg), sex, right hind foot length
140 (cm), and age class of each individual captured, and identified 48 unique individuals during our
141 study.

142 3.3.2 Experimental setup

143 We held hares captive in experimental enclosures that allowed us to evaluate their foraging
144 decisions under different coat colour mismatch and perceived predation risk treatments. Our
145 eight enclosures were 100 cm wide, 90 cm high and 120 cm long. We installed enclosures at

146 least 10 m apart in areas lacking overhead cover, but with horizontal forest cover to obscure
147 neighbouring enclosures. We created an opportunity for cover with a hutch secured in each
148 enclosure (Fig. B2) and installed camera traps (Reconyx Hyperfire) facing the enclosures to
149 collect temperature ($^{\circ}\text{C}$) and photo data every 5 minutes during trials. We simulated perceived
150 avian predation risk by covering the roofs of four enclosures with transparent plexiglass sheets
151 (Fig. B2a-d), thus allowing overhead visibility while protecting hares from precipitation.
152 Conversely, we covered the roofs of four control enclosures with opaque tarps to simulate
153 perceived protection from avian predation risk (Fig. B2e-h). Indeed, prey have been shown to
154 display stronger behavioural adjustments to habitat characteristics, such as vegetative cover or
155 lack thereof, than cues of live predators (Verdolin 2006). More specifically, snowshoe hares are
156 known to behaviourally adjust to the perceived risk of open canopy (Hutchen and Hodges 2019).
157 We placed three iButtons (iButton ThermoChron) in one opaque roof enclosure and another three
158 iButtons in a transparent roof enclosure to ensure that roof type did not influence enclosure
159 temperature. Roof type did not influence temperatures experienced inside the enclosures (Fig.
160 B3). We experimentally simulated coat colour mismatch by placing hares at different levels of
161 coat colour change on white or brown enclosure floors (Fig. B2).

162 We selected hares weighing > 1300 g for experimental trials. We repeated experimental
163 trials for hares if they had recovered to within 5% of their original mass and a minimum of 10
164 days had elapsed since their previous trial. We did not allow hares to complete more than four
165 experimental trials during our field season. Hares were held captive for a maximum of 72 hours,
166 during which they underwent an adjustment period, two feeding trials and a recovery period
167 (detailed below). Snowshoe hare handling and experimental trials were approved by Memorial
168 University of Newfoundland's Animal Care and Use Committee (Protocol #18-02-EV).

169 3.3.3 Feeding trials

170 We evaluated how our different treatments influenced total browse consumed by snowshoe
171 hares, but also intraspecific selection for browse quality, since animals are known to adjust their
172 selection for forage quality with perceived predation risk (Edwards 1983, Hernández and
173 Laundré 2005, Barnier et al. 2014). We chose to test selection for quality using naturally
174 occurring quality variation within a single browse species. Indeed, intraspecific forage decisions
175 are likely prominent for herbivores in low plant diversity systems, such as the boreal forest
176 (Balluffi-Fry et al. 2022). Black spruce was used to test intraspecific foraging decisions because
177 it is widespread across our study site and constitutes the majority of hare diet in Newfoundland
178 after the senescence of deciduous plants, thus it represents a realistic diet item considering the
179 timing of our study (Dodds 1960, Rodgers and Sinclair 1997). We chose % nitrogen (N) content
180 as our proxy for black spruce quality, as it is known as a limiting item for herbivores (Fagan et
181 al. 2002, Boersma et al. 2008). Further, selection for black spruce with high N content has been
182 shown to mitigate snowshoe hare weight loss in our system (Balluffi-Fry et al. 2021; See
183 Appendix B for detailed spruce sampling method).

184 We offered 100 g piles of both high-quality and low-quality black spruce boughs to
185 snowshoe hares during 15-hour feeding trials that occurred between 18:00 and 9:00, to reflect the
186 hours during which hares are most active (Hodges 1999; See Appendix B for detailed spruce
187 sampling methods). Each pile was presented in a basket on either side of the enclosure (Fig B2),
188 and we randomly selected which side high and low quality forage was placed. We measured total
189 browse consumption by collecting the remaining spruce after feeding trials and subtracting its
190 mass from the total spruce offered, i.e., 200g. Finally, we assessed how feeding decisions
191 affected snowshoe hare body condition by measuring mass change during these 15- hour feeding

192 trials. Each hare underwent one to two feeding trials in the context of our 72-hour experimental
193 trials, which consisted of four distinct trial phases (Fig B4).

194 3.3.4 72- hour experimental trial phases

195 To begin, each hare was first randomly assigned to an enclosure with a clear or opaque roof, and
196 a brown or white floor. The first experimental trial phase was a 9-hour adjustment period (9:00
197 to 18:00, Day 1) during which we provided hares with water ad libitum, an apple slice, rabbit
198 chow ad libitum and ~ 200 g of mixed quality black spruce. The adjustment period was created
199 to ensure that all hares began their feeding trial after getting the opportunity to feed to satiation
200 and to allow hares to habituate to enclosures. The second phase (18:00 Day 1 to 9:00 Day 2) was
201 a 15-hour feeding trial, where hares received separated piles of 100 g of high quality and 100 g
202 of low-quality spruce and water ad libitum. For the third phase (9:00 Day 2 to 18:00 Day 3), the
203 recovery period, hares were transferred to a randomly selected new enclosure that provided them
204 with the opposite perceived predation risk treatment, i.e., clear or opaque enclosure roof, as their
205 first food choice trial but the same mismatch treatment, i.e., floor colour. This recovery period is
206 a necessary phase within the 72-hour experimental trials, as hares are known to lose weight
207 during single species feeding trials which could impact foraging decisions during the next
208 feeding trial, and survival post release (Pease et al. 1979, Rodgers and Sinclair 1997). During
209 this recovery period, hares were provided with rabbit chow and water ad libitum. The fourth and
210 last phase of the experimental trial (18:00 Day 3 to 9:00, Day 4) was a second 15-hour feeding
211 trial, identical to the first, but in the new enclosures which provided the opposite perceived
212 predation risk treatment.

213 To monitor mass change and ensure that hares remained within safe mass loss thresholds,
214 we weighed them after each phase of the experimental trial (Fig B4). Hares that did not meet our

215 requirements for safe mass loss during experimental phases were not held for the subsequent
216 steps of the trial and were immediately released at their capture site. Mass loss thresholds were
217 defined as: minimum mass maintenance during the adjustment phase, maximum mass loss of 8%
218 during feeding trial phase, and mass recovered to at least within 5% of initial mass at trapping
219 during recovery phase (Fig B4, Appendix B). Prior to release, we assessed coat colour of each
220 hare by visually ranking its white coat to the nearest 10%. Coat colour rankings were all
221 completed by the same observer, and intra-observer correlation in coat-colour rankings from
222 photos post-hoc was high (> 0.9 ; Table B1). Animal handling and experimental trial procedures
223 were approved by Memorial University's animal use ethics committee (AUP 20-02-EV).

224 3.3.5 Statistical analyses

225 We generated three linear mixed-effects models to evaluate how different mismatch and
226 perceived predation risk treatments affected foraging decisions and mass change. To test
227 prediction (i), we calculated total intake rate (g spruce/kg hare) as the difference between the
228 sum of high- and low-quality spruce offered and remaining at the end of the 15-hour feeding
229 trials (g), divided by individual hare mass prior to commencing feeding trials (kg). We calculated
230 intraspecific selection for quality as the difference between high-quality spruce intake rate (g
231 spruce/kg hare) and low-quality spruce intake rate (g spruce/kg hare) in order to test prediction
232 (ii). As such, in our intraspecific selection for quality model, positive effect sizes are associated
233 with selection for high-quality spruce, and negative effect sizes are associated with selection for
234 low-quality spruce. To test our final prediction (iii), weight change (%), was calculated as the
235 percentage mass difference between each snowshoe hare's weigh-in immediately before and
236 after the feeding trials.

237 All linear mixed-effects models included the same fixed explanatory variables: average
238 temperature during the feeding trial, mismatch, perceived predation risk, habituation, and
239 individual ID as a random factor. We calculated the average temperature (°C) during feeding
240 trials from a minimum of 13 hourly temperatures recorded by camera traps at each enclosure
241 during the 15-hour feeding trials. We chose to include temperature in our models, as snowshoe
242 hares are known to increase their intake rate as it gets colder (Sinclair et al. 1982, Balluffi-Fry et
243 al. 2022), which may subsequently affect weight change and intraspecific selection for quality.
244 Coat colour mismatch was defined as the difference between enclosure floor % white, i.e., 0%
245 for brown floors or 100% for white floors, and snowshoe hare coat % white. We first included
246 mismatch in our models as a binary variable, i.e., mismatched or not, where hares displaying an
247 absolute contrast of 60% or more with their enclosure floor were considered mismatched, as per
248 previous studies (Mills et al. 2013, Zimova et al. 2014) (Table B2). To increase the specificity of
249 the analysis, we then modelled the effect of different mismatch categories on foraging decisions
250 and mass change. Thus, our mismatch categories were white mismatch, i.e., white hare on brown
251 ground; brown mismatch, i.e., brown hare on white ground; white match, i.e., white hare on
252 white ground; and brown match, i.e., brown hare on brown ground. We included perceived
253 predation risk (i.e., roof type) as a binary variable. Habituation was included in our models, as
254 hares are known to increase forage consumption when they have previously been held captive for
255 another feeding trial within a same field season (Balluffi-Fry et al. 2022). As such, we
256 considered habituation as a fixed binary factor for whether or not hares had undergone at least
257 one feeding trial within our field season. We also included a random effect for individual ID to
258 control for non-independence of data within individuals. We assessed model fit using marginal
259 and conditional R-squared using the “r.squaredGLMM” function in the package MuMin

260 (Nakagawa et al. 2017, Barton 2020). We carried out statistical analyses in R version 4.0.4
261 (2021) (R Core Team, 2021). We considered $P \leq 0.05$ as our significance threshold and reported
262 all means with ± 1 standard error.

263 3.4 Results

264

265 3.4.1 Overview

266 We held 31 individuals captive for feeding trials, of which 23 met our criteria to complete full
267 72-hour experimental trials, whereas 8 individuals only completed a single feeding trial as they
268 exceeded mass loss criteria to be considered for a second trial. As a result, we completed 79 15-
269 hr feeding trials and 32 full 72-hour experimental trials. There were 12 individuals that were
270 recaptured throughout the field season and repeated one or more partial or full experimental
271 trials. The average daily temperature and precipitation during our study was $4.4 \pm 5.1^\circ\text{C}$ and 3.7
272 ± 6.1 mm, respectively. The hares we captured for trials ranged from 0% to 90% white (median
273 = 20% white).

274 3.4.2 Foraging decisions

275 Black spruce intake rate (prediction (i))

276 Hares consumed an average of 96.92 ± 37.71 g of black spruce during feeding trials, and total
277 consumption increased at colder temperatures; on average hares consumed 1.03 g/kg more for
278 each 1°C decrease in temperature ($P=0.018$) (Fig. 1). Contrary to our prediction, hares exposed
279 to perceived predation risk, i.e., in clear roof enclosures, consumed significantly more spruce
280 than those in opaque roof enclosures ($P=0.023$; Fig 1). For instance, when the temperature was
281 held at its mean (4.14°C), matched hares in clear roof enclosures consumed 8.51 g/kg more than
282 matched hares in opaque roof enclosures. There was no evidence that mismatch influenced black

283 spruce intake rate, regardless of mismatch type (Table 1). Individuals that had already completed
284 a feeding trial during our field season ate on average 13.56 g/kg more than those being held
285 captive for the first time ($P=0.008$) (Fig 1).

286 Intraspecific selection for nitrogen (prediction ii))

287 During feeding trials, hares consumed on average 50.57 ± 24.73 g of N-rich black spruce versus
288 47.07 ± 22.88 g of N-poor black spruce. Intraspecific selection for N-rich spruce was
289 significantly ($P = 0.02$) lower during subsequent recaptures, where hares that had previously
290 undergone experiments ate 10.44 g/kg less N-rich spruce than nitrogen-poor spruce (Fig. 2).
291 Mismatch only significantly affected black spruce nitrogen selection for brown hares, in that
292 mismatched brown hares ate on average 11.67 g/kg more N-rich spruce than matched brown
293 hares ($P = 0.02$) (Fig. 2; Table 1). Intraspecific selection for N was not affected by perceived
294 predation risk treatment ($P = 0.77$) or ambient temperature ($P = 0.16$).

295 Mass change (prediction iii))

296 On average, hares lost weight during feeding trials (i.e., $8.03 \pm 3.85\%$ of their body mass). In
297 contrast, individuals gained on average $4.24 \pm 3.64\%$, and $6.34 \pm 6.00\%$ body mass during the
298 adjustment and recovery periods, respectively. Mass loss was affected by temperature, and
299 snowshoe hares lost on average 0.24% more body mass with every 1 °C drop in temperature ($P =$
300 0.002; Fig. 3). White matched hares lost on average 4.55% less body mass than their white
301 mismatched counterparts ($P = 0.018$; Fig. 3). Similarly, white matched hares lost 4.09% less
302 body mass than brown mismatched hares ($P=0.005$) and 2.77% less body mass than brown
303 matched hares ($P = 0.04$) (Fig.3). Brown mismatched hares lost on average 1.32% more body
304 mass than their brown matched counterparts, although this effect was not significant ($P = 0.14$).
305 There were no significant differences in body mass loss between brown mismatched and white

306 mismatched hares; and between brown matched and white mismatched hares. Hares in clear roof
307 enclosures lost on average 1.29% more body mass than those in opaque roof enclosures ($P =$
308 0.04; Fig. 3).

309 3.5 Discussion

310

311 Antipredator traits function collectively to reduce an individual's risk of being killed by
312 predators (Garcia and Sih 2003, Kim and Velando 2015). Prey species that moult biannually to
313 match the presence and absence of snow are expected to become increasingly colour mismatched
314 under climate change, presumably resulting in heightened predation risk and thus increased
315 mortality (Zimova et al. 2016, Mills et al. 2018). We sought to determine whether the lack of
316 camouflage in snowshoe hares may be mitigated by changes in foraging decisions. Specifically,
317 we evaluated whether coat colour mismatched snowshoe hares alter their intake rate and
318 selection for forage N, and how these decisions correspondingly affect body mass loss. We
319 further assessed how these decisions and resulting body mass loss were influenced by elevated
320 risk. We found that:

- 321 1. Intake Rate: While we predicted that mismatched hares would have the lowest intake
322 rate, we did not find any adjustments to intake rate in response to mismatch (Table 1).
323 We predicted that hares in our elevated risk treatment, i.e., clear roof enclosures would
324 have the lowest intake rate, but found that they unexpectedly ate more, rather than less,
325 than hares in opaque roof enclosures (Fig. 1).
- 326 2. Selection for N: We predicted that mismatched hares would have the lowest intraspecific
327 selection for N-rich forage, but found that mismatched brown hares had a higher
328 preference for N-rich forage than matched brown hares (Fig. 2). Hares did not alter their

329 selection for N as a response to elevated risk, which does not support our initial
330 prediction that hares in clear roof enclosures would have the lowest intraspecific selection
331 for N-rich forage (Table 1).

332 3. Body Mass Loss: As predicted, mismatched hares lost more body mass than matched
333 hares and this effect was further amplified by heightened predation risk, as hares in clear
334 roof enclosures lost more body mass than those in opaque roof enclosures (Fig 3; Table
335 1).

336 Although mismatched hares in our elevated risk treatment did indeed lose more body mass as
337 expected, this effect was paired with foraging decisions we would not expect to minimize risk at
338 the expense of nutritional intake. For instance, hares increased intake rate in response to lack of
339 cover, and increased selection for N in response to brown mismatch, which presumably would
340 have resulted in nutritional intake being favoured over vigilance. Thus, we suggest that mismatch
341 generates indirect costs that are not fully compensated by modified foraging decisions.

342 The increased body mass loss that occurred in mismatched hares (Fig. 3) may be a
343 deleterious indirect effect of coat colour mismatch. Prey are known to respond to predation risk
344 through the “stress response”, whereby the hypothalamic-pituitary-adrenal axis is activated and
345 glucocorticoids are secreted to mobilize energy and face imminent threat (Boonstra et al. 1998,
346 Sheriff et al. 2011). When the stress response is activated, physiological responses including
347 increased body mass loss occur as a function of gluconeogenesis (Carlsen et al. 1999, Pérez-Tris
348 et al. 2004, Hodges et al. 2006). As such, we propose that hares may associate mismatch with
349 increased perceived predation risk, and that the resulting stress response could be a potential
350 driver for the heightened body mass loss we observed in mismatched hares (Fig. 3, Table B3).
351 As such, coat colour mismatch may have indirect costs on individual snowshoe hares beyond the

352 heightened mortality risk previously documented (Zimova et al. 2016, Wilson et al. 2018).
353 Similar to mismatch, we propose that hares in our elevated risk treatment, i.e., clear roof
354 enclosures, elicited this stress response which also exacerbated body mass loss (Fig. 3), despite
355 the increased intake rate of hares in this treatment (Fig. 1). Indeed, hares experience exacerbated
356 body mass loss with heightened predation risk (Majchrzak et al. 2022) and lack of cover has
357 been associated with higher stress levels in some species (Kordosky et al. 2021). However, our
358 results suggest that the increased intake rate of hares in clear roof enclosures did not compensate
359 for potential exacerbated body mass loss due to simulated heightened predation risk.

360 Protein is limiting for herbivores in the boreal forest (Hodges and Sinclair 2003), and
361 when snowshoe hares do not consume enough protein, they lose body mass (Sinclair et al. 1982,
362 Rodgers and Sinclair 1997). Hares may mitigate body mass loss by increasing their selection for
363 high N black spruce (Balluffi-Fry et al. 2022). We found that mismatched white hares lost 4.55%
364 more body mass than their matched white counterparts, and that mismatched brown hares lost
365 1.32% more body mass than matched brown hares, although the latter was not significant (Fig. 3;
366 Table 1). Intraspecific selection for N-rich black spruce was unexpectedly greater for brown
367 mismatched hares than for brown matched hares (Fig. 2). We suggest that brown mismatched
368 hares may increase their selection for N-rich black spruce to potentially mitigate the heightened
369 body mass loss that occurred with coat colour mismatch. Indeed, animals adjust their diet quality
370 selection to cope with dynamic metabolic and energetic needs (Mellado et al. 2005).

371 Compensatory responses to long-term predation risk have been shown to offset the
372 adverse effects that prey experience due to the physiological responses they mount to face short-
373 term predation risk (Thaler et al. 2012). These compensatory responses may be physiological or
374 behavioural in nature. For example, damselfly (*Enallagma cyathigerum*) larvae reduce energy

375 storage when exposed to predation risk (Van Dievel et al. 2016), while tobacco hornworm
376 caterpillars (*Manduca sexta*) demonstrate compensatory feeding by increasing their intake rate
377 after a certain level of predator exposure (Thaler et al. 2012). While we predicted that hares in
378 our elevated risk treatment, i.e., clear roof enclosure, would decrease their intake rate in contrast
379 with those in opaque roof enclosures, we found the opposite (Fig. 1). This increased intake rate
380 in response to lack of overhead cover contradicts previous findings (Kotler et al. 1991, Mohr et
381 al. 2003), although these studies did not assess the impacts of overhead cover on body mass loss.
382 We reconcile our result with our proposed interpretation of increased body mass loss as a
383 function of increased stress. Indeed, we suggest that hares may have increased their intake rate
384 (Fig. 1) to partially compensate for the heightened body mass loss they experienced in clear roof
385 enclosures (Fig. 3). A study that manipulated predation risk to assess the physiological responses
386 of snowshoe hares found expected physiological evidence of a stress response, but this stress
387 response was not associated with the expected downstream consequences on body condition
388 (Boudreau et al. 2019). Authors from this study propose compensatory behavioural or metabolic
389 responses as potential explanations for this result. Although we did not explicitly evaluate the
390 impacts of our experimental treatments on snowshoe hare stress response, we found increased
391 intake rate in snowshoe hares in our high-risk treatment. As such, we suggest that hares in our
392 study may have employed compensatory feeding through increased intake rate in an attempt to
393 mitigate the body mass loss impacts they experienced in high-risk enclosures.

394 Across all mismatch and heightened risk categories, white mismatched hares in clear roof
395 enclosures lost the most body mass (Table B3). Snowshoe hares undergo seasonal
396 acclimatization that includes changes in coat characteristics that ultimately result in winter white
397 hares having a lower metabolic rate than summer brown hares to facilitate winter survival

398 (Sheriff et al. 2009a, 2009b). As a function of these changes, daily foraging time is lower for
399 white mismatched hares than for brown hares when temperatures are below -3°C , presumably
400 due to reduced energetic demands (Kennah et al., In Review). In this study, we found that white
401 mismatched hares lost more weight than brown mismatched hares, implying that white coats did
402 not confer energetic benefits (Table B3). Our results may be explained by the relatively warm
403 temperatures experienced by mismatched hares during our feeding trials, i.e., on average 4.15°C ,
404 which were outside of the temperature range where energetic benefits were suggested in white
405 winter-acclimatized hares (Kennah et al. In Review). This supports the idea that coat colour
406 mismatch effects are temperature dependent, with potential indirect costs on body mass for
407 populations in the southern parts of their range.

408 Coat colour mismatch has the potential to negatively impact over 21 bird and mammal
409 species that change colour biannually, many of which are prey species that depend on
410 camouflage to reduce their predation risk (Mills et al. 2018, Zimova et al. 2018). We tested
411 whether coat colour mismatched snowshoe hares may be able to buffer these effects by altering
412 their foraging decisions. We found that brown mismatched hares selected for N-rich forage, and
413 that both brown and white mismatched hares lost more body mass than their matched
414 counterparts. Complementary to the direct impacts of coat colour mismatch on survival that have
415 been documented (Zimova et al. 2016, Atmeh et al. 2018; Kennah et al. In Press), our results
416 highlight indirect mismatch effects that may additively affect fitness. We found evidence for
417 altered foraging decisions, which only partially mitigate the consequences of increased risk and
418 mismatch on body mass loss. We found that white mismatched hares lost the most body mass, in
419 contrast with other mismatch categories. Our work adds to a growing body of literature that
420 expands our understanding of how animals are affected by a rapidly changing climate.

421 3.6 References

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607

608

609 Table

610

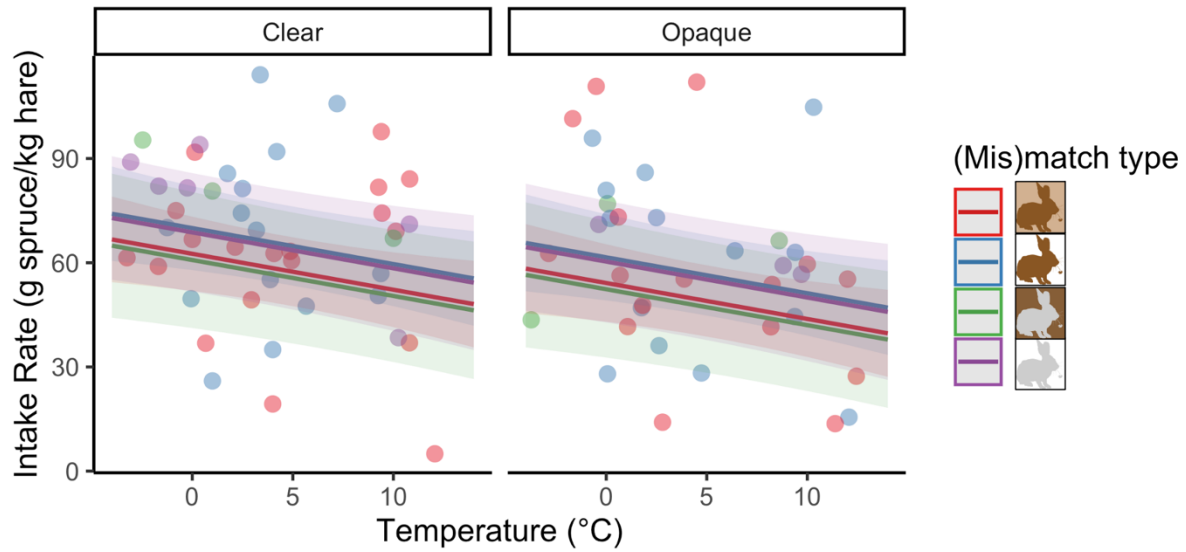
611 Table 3-1. Effects of variables included in linear mixed-effects models for black spruce intake
 612 rate (marginal $R^2= 0.15$, conditional $R^2=0.72$), selection of high-quality spruce (marginal $R^2=$
 613 0.13 , conditional $R^2=0.63$), and body mass change (marginal $R^2= 0.21$, conditional $R^2=0.57$). In
 614 the preference for high quality model, positive effect sizes are associated with selection for high-
 615 quality spruce, and negative effect sizes are associated with selection for low-quality spruce. In
 616 the body mass change model, positive effect sizes are associated with mass gain, whereas
 617 negative effect sizes are associated with mass loss. All models also include individual ID as a
 618 random effect. The reference variable for perceived predation risk, “roof”, is the clear roof and
 619 the reference for habituation is the first time hares were held captive. For mismatch variable: m =
 620 match; mm= mismatch.

Response variable	Fixed effects	Coefficient (\pm SE)	t	P
Intake Rate (g/kg hare)	Temperature ($^{\circ}$ C)	-1.03 \pm 0.42	-2.44	0.018
	Brown m vs brown mm	-7.40 \pm 5.27	-1.40	0.17
	Brown m vs white mm	1.80 \pm 9.00	0.20	0.84
	Brown m vs white m	-6.16 \pm 8.95	-0.69	0.49
	Brown mm vs white mm	9.19 \pm 9.24	1.00	0.32

	Brown mm vs white m	1.23± 9.24	0.13	0.89
	White mm vs white m	-7.96± 11.76	-0.68	0.50
	Roof	-8.41± 3.57	-2.36	0.023
	Habituation	13.56± 4.94	2.74	0.0081
Preference for high-quality	Temperature (°C)	0.55± 0.39	1.42	0.16
(g/kg hare)	Brown m vs brown mm	-11.67± 4.78	-2.44	0.018
	Brown m vs white mm	3.39± 8.09	0.42	0.68
	Brown m vs white m	-5.51± 7.71	-0.71	0.48
	Brown mm vs white mm	15.06± 8.28	1.82	0.074
	Brown mm vs white m	6.17± 8.02	0.77	0.44
	White mm vs white m	-8.89± 10.34	-0.86	0.39
	Roof	-0.97± 3.28	-0.30	0.77
	Habituation	-10.44± 4.44	-2.35	0.022
Mass change (%)	Temperature (°C)	0.24± 0.072	1.51	0.0015
	Brown m vs brown mm	1.32± 0.88	-2.44	0.14
	Brown m vs white mm	1.78± 1.50	1.18	0.24
	Brown m vs white m	-2.77± 1.37	-2.02	0.047
	Brown mm vs white mm	0.46± 1.54	0.30	0.77
	Brown mm vs white m	-4.09± 1.42	-2.89	0.0053
	White mm vs white m	-4.55± 1.88	-2.42	0.018
	Roof	1.29± 0.62	2.074	0.018
	Habituation	0.0084± 0.82	0.010	0.045

621 Figures

622

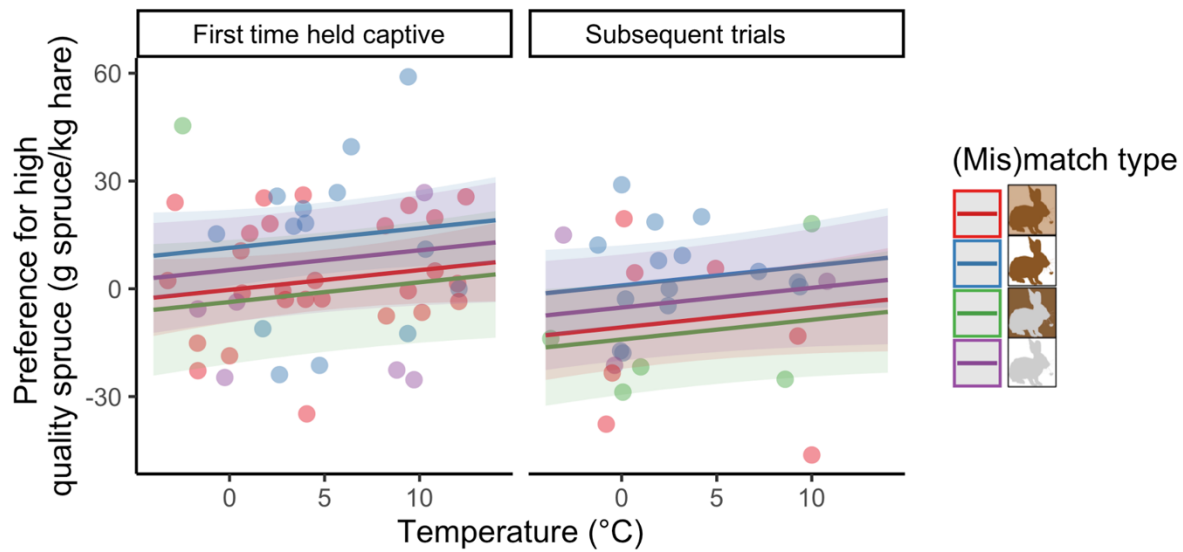


623

624 Fig 3-1. Effect of temperature on black spruce intake rate for experimentally matched or
625 mismatched snowshoe hares under perceived predation risk treatments, i.e., clear or opaque
626 enclosure roof. Effect is modelled for individuals during their first time held captive. Shaded areas
627 represent 95% confidence intervals.

628

629 Fig 3-2.

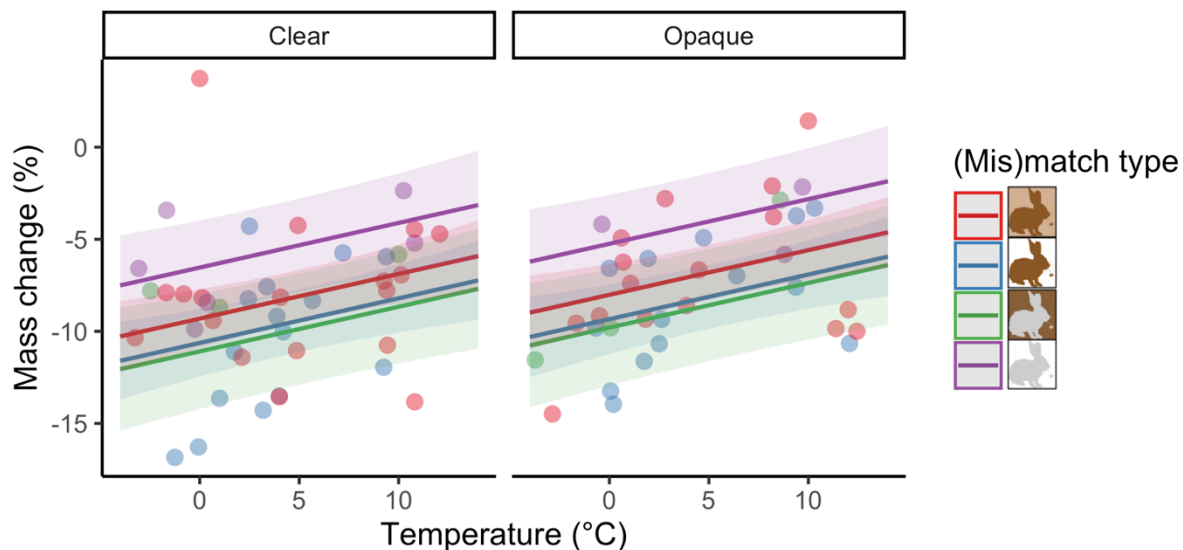


630

631 Fig 3-2. Effect of temperature on selection of N-rich black spruce, i.e., N-poor black spruce intake
 632 rate subtracted from N-rich black spruce intake rate, for experimentally matched or mismatched
 633 snowshoe hares. Effect is modelled for individuals in clear roof enclosures only. Shaded areas
 634 represent 95% confidence intervals.

635

636 Fig 3-3.



637

638

639

640 Fig 3-3. Effect of temperature on snowshoe hare mass change (%) under different mismatch and
641 perceived predation risk, i.e., clear or opaque roof, treatments. Effect is modelled for individuals
642 during their first time held captive. Shaded areas represent 95% confidence intervals.

643 Chapter 4 – Summary

644 4.1 Thesis Summary

645

646 Coat colour mismatch is affecting numerous species at northern latitudes (Pedersen et al. 2017,
647 Atmeh et al. 2018, Melin et al. 2020). Many of these species rely on camouflage to reduce
648 detection by predators (Caro 2005, Duarte et al. 2017). Considering that colour change is likely
649 under strong genetic control, and is mainly synchronized with photoperiod (Zimova et al. 2018),
650 the anticipated effects of climate change (Price et al. 2013) are likely to intensify the occurrence
651 of colour mismatch in some geographies. While research has begun to investigate how species
652 are affected by and respond to colour mismatch, further investigations are required as
653 temperatures warm and extreme weather events become more common (Easterling et al. 2000,
654 Price et al. 2013).

655 My thesis examined 1) how coat colour mismatch impacts snowshoe hares, and 2) which
656 mechanistic pathways may govern these impacts. As coat colour mismatch is presumed to hinder
657 the ability of prey to adequately reduce their predation risk (Mills et al. 2013, Zimova et al.
658 2018), I grounded my hypotheses and predictions in the fundamental balance that exists between
659 prey acquiring resources and avoiding predators (Lima And and Dill 1990). More specifically,
660 my hypotheses were structured as conditional statements underlying how foraging behaviour

661 may be affected or altered if predation risk is indeed impacted by colour mismatch. To
662 effectively tackle my questions under different lenses, I leveraged the insightful knowledge
663 kindly offered by researchers from two different research groups during my Master's. This
664 exposure to diverse ideas provided me with the opportunity to consider alternative hypotheses
665 while I examined these questions. The first research group was comprised of researchers
666 associated with the Kluane Boreal Forest Ecosystem Project (Krebs et al., 2001), hereafter the
667 Kluane Group. Researchers in the Kluane Group have diverse areas of focus, including but not
668 limited to boreal ecology, endothermic homeothermy, biologging technology, cycle dynamics
669 and predator-prey interactions (Menziés et al. 2020, Shiratsuru et al. 2021, Majchrzak et al.
670 2022). Engaging with the Kluane Group allowed me to study snowshoe hare behaviour with a
671 modern approach by using accelerometer data (Studd et al. 2019), and to thoroughly consider the
672 confounding factors that may influence snowshoe hare predation risk (Peers et al. 2020). The
673 second research group with which I collaborated was the Terrestrial Ecology Research Group,
674 hereafter TERG. Researchers in TERG are guided by broad questions related to boreal forest
675 ecological stoichiometry and how the movement of carbon, nitrogen and phosphorus intersects
676 with herbivory (Richmond et al. 2020, Balluffi-Fry et al. 2021, Heckford et al. 2021). Guidance
677 and input from TERG allowed me to consider how mismatched snowshoe hares may balance
678 foraging under the prism of intraspecific selection for nutrients with predation risk.

679 Chapter 2 considered remotely sensed data from wild snowshoe hares with naturally
680 occurring mismatch in the Yukon, while Chapter 3 considered data from experimentally
681 simulated mismatched wild hares in a captive setting in Newfoundland. We tested the
682 assumption that coat colour mismatch indeed increases mortality (Mills et al. 2013), and found
683 the opposite. Coat colour mismatch was associated with improved spring survival in snowshoe

684 hares in the Yukon (Chapter 2). We explained this result from an energetics perspective.
685 Mismatched white hares experience reduced metabolic and energetic demands at colder
686 temperatures, which subsequently lowered foraging rates that may have reduced predation risk
687 (Chapter 2). We also associated experimentally simulated mismatch with increased body mass
688 loss and found that mismatched brown hares select for higher quality black spruce, presumably
689 to mitigate coat colour mismatch impacts (Chapter 3).

690 While the energetic benefits of white mismatch on snowshoe hare survival documented in
691 Chapter 2 may seem to contradict the heightened body mass loss experienced by mismatched
692 hares in Chapter 3, I highlight the importance of temperature as a governing factor that enables
693 the integration of these seemingly contrasting results. Snowshoe hares in the Yukon experience
694 colder temperatures during their autumn coat colour change than hares in Newfoundland. My
695 second Chapter highlighted how energetic benefits of white mismatched coats are conditional on
696 temperature, where reduced foraging time and its corresponding impacts on increased survival
697 only occur at temperatures $< -3^{\circ}\text{C}$. The average temperature experienced by colour changing
698 snowshoe hares in my third Chapter was 4.15°C , and mismatched hares experienced heightened
699 body mass loss (Chapter 2). As such, my third Chapter provided further support that coat colour
700 mismatch generates more adverse effects at warmer temperatures. The heightened body mass
701 loss that we documented in white mismatched hares relative to their brown counterparts (Chapter
702 3) may also be associated with costs related to thermoregulation. Animals use physiological and
703 behavioural mechanisms to remain within their thermoneutral zone, and these mechanisms often
704 result in negative energy balances (Jennewein et al. 2020). The thermoneutral zone of snowshoe
705 hares with summer brown coats is -10°C to 0°C , while the thermoneutral zone of snowshoe hares
706 with winter white coats is -15°C to -10°C . Considering that mismatched winter white hares in

707 our study experienced temperatures of $3.84 \pm 5.84^{\circ}\text{C}$ on average during our study, i.e., outside of
708 their thermoneutral zone in all cases, thermoregulation costs may have contributed to the
709 exacerbated body mass loss we observed (Chapter 3).

710 Aside from climatic differences, other notable differences exist in the ecological contexts
711 experienced by snowshoe hares across their wide range (Fig.1). For example, snowshoe hares in
712 the Yukon primarily experience predation from terrestrial predators, e.g., Canada lynx (*Lynx*
713 *canadensis*) and coyotes (*Canis latrans*) (Peers et al. 2020), while snowshoe hares in
714 Newfoundland primarily experience predation from avian predators, e.g., goshawks (*Accipiter*
715 *gentilis*) and great horned owls (*Bubo virginianus*) (Richmond et al. 2022). The composition of
716 predator guilds, associated hunting modes, and sensory abilities of prevailing predators may be
717 important to consider while examining the influences of coat colour mismatch across snowshoe
718 hare range (Jordan and Ryan 2015). For example, avian predators such as goshawks rely
719 primarily on vision to detect prey (Kane et al. 2015), whereas terrestrial predators such as
720 coyotes may also rely on auditory and olfactory cues (Thibault and Ouellet 2005). Predator guild
721 composition may partially influence the varying effect of coat colour mismatch observed across
722 studies, but this requires further research. While the results of my Chapters highlight the
723 importance of temperature in governing the impacts of coat colour mismatch across snowshoe
724 hare range, understanding how phenological mismatch is experienced by populations across
725 broad geographies will require investigating other mechanistic pathways and driving factors.

726 4.2 Future Directions

727

728 Going forward, an important extension of my work would be to explicitly test the
729 proposed explanations for the results found in both of my chapters. While we suggest that white

730 mismatched hares may be experiencing survival advantages because of reduced foraging time, an
731 analysis of the influence of foraging time on predation risk could be used to support this idea
732 (Majchrzak et al. 2022). Moreover, as behavioural data classification advances to a finer scale,
733 understanding the proportion of time allocated to vigilance behaviours by matched and
734 mismatched hares may provide further insight into the impacts of coat colour mismatch. Aside
735 from reducing potential heightened predation risk by increasing vigilance and reducing foraging
736 time, mismatched hares may also select high visual complexity habitats (Rowe et al. 2021, but
737 see: Zimova et al. 2014). While we suggest that mismatched hares may have experienced
738 heightened body mass loss due to a stress response (Chapter 2), analyzing differences in cortisol
739 levels between matched and mismatched hares would be critical to support this idea and merits
740 further testing. We still lack genetic and physiological details on how seasonal coat colour
741 moults occur, and further studies could help clarify implicated pathways and physiological
742 changes (Zimova et al. 2018). Finally, evaluating the potential for phenotypic plasticity in coat
743 colour change rate in snowshoe hare populations across varied geographies may also provide
744 insight on the ability of hares to persist in the face of increased environmental stochasticity
745 (Mills et al. 2013).

746 4.3 Concluding remarks

747

748 My work highlighted the importance of examining phenological mismatch impacts at
749 broader geographic scales, while considering the continuous factors that vary across
750 biogeographic ranges as potential governing factors driving these impacts. Furthermore, my
751 work supports the notion that phenological mismatch is experienced differently across
752 populations that encounter different geographies and selective pressures (Phillimore et al. 2010,

753 Gordo and Doi 2012, Porkert et al. 2014). As climate change alters ecosystems at a rapid pace
754 (Loarie et al. 2009), understanding the mechanistic pathways behind phenological mismatches
755 will be crucial to anticipate their impacts across species and populations.

756

757 4.4 References

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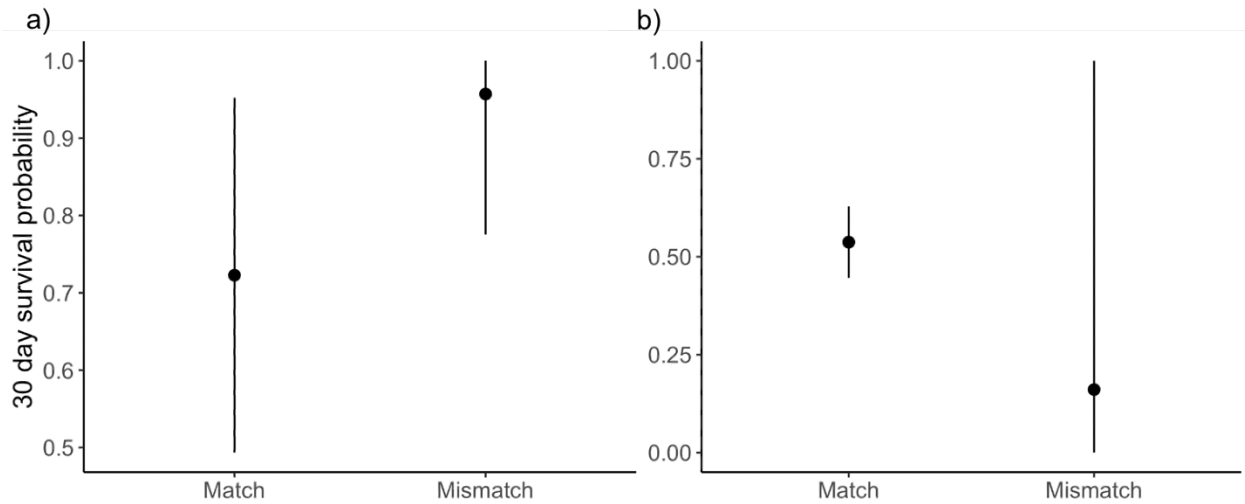
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848 Appendices

849 Appendix A. Chapter 2 Additional Results

850



851

852

853 Fig A1. Modelled effect of coat color mismatch on snowshoe hare 30-day survival probability,

854 generated from our top supported CPH model for a) autumn during October 1st to October 30th

855 and b) spring during May 1st to May 30th. Points represent survival probabilities for matched and

856 mismatched hares and error bars represent predicted standard errors. Snow depth and snow cover

857 are held at zero for a) autumn and are held at their mean for b) spring.

858

859

860 Table A1. Intraclass correlation coefficients (ICC) describing intra-observer repeatability and
861 inter-observer repeatability of measurements taken within and between three observers. Each
862 observer ranked coat colour three times to the nearest 5% for 50 hares (total of n=150 rankings
863 for each observer). Inter-rater repeatability was estimated using the average of the three
864 measurements for each observer.

	ICC	95% confidence intervals	F (df1, df2)	p-value
Observer 1	0.978	0.966, 0.987	137 (49,100)	< 0.001
Observer 2	0.957	0.933, 0.974	67.7 (49,100)	< 0.001
Observer 3	0.949	0.92, 0.969	56.9 (49,100)	< 0.001
Between observers	0.913	0.855, 0.947	32.6 (49,100)	< 0.001

865

866 Table A2. Effect of various predictors that may affect spring and autumn hazard ratio (HR). Each
 867 variable was tested in a univariate model during exploratory data analysis to evaluate its effect
 868 on HR.

Variable	Levels	Season	HR	z	P
Sex	Reference=Male				
	Female	Autumn	1.465	1.04	0.298
		Spring	0.929	-0.23	0.818
Trapping area	Reference=TA-1				
	TA-2	Autumn	0.702	-0.914	0.361
		Spring	0.556	-1.632	0.103
	TA-3	Autumn	0.415	-1.867	0.062
		Spring	0.675	-0.930	0.352
Year	Reference= 2015				
	2016	Autumn	0.519	-1.670	0.095
		Spring	0.532	-1.381	0.167
	2017	Autumn	1.091	0.179	0.858
		Spring	1.247	0.539	0.590
	2018	Spring	0.830	-0.366	0.714

869

870 Table A3. Hazard ratios (HR) and 95% confidence intervals generated for each variable of top
 871 CPH models when only survival records occurring within 8 days of known coat colour
 872 assessment are considered. Values that are bolded represent significant effects and italicized
 873 values represent P values < 0.1. HR>1 indicates increased risk of dying and HR<1 indicates
 874 reduced risk of dying.

Variable	Spring top model: HR~SD+SC+mm	Autumn top model: HR~SD+SC+mm
Snow depth (SD)	0.960 (0.914, 1.010)	<i>0.831</i> (0.685, 1.009)
Mismatch (mm;factor)	3.004 (0.335, 26.962)	0.128 (0.023, 0.707)
Snow cover (SC)	1.064 (1.016, 1.114)	1.113(0.073, 16.966)

875

876 Table A4. Hazard ratios (HR) and 95% confidence intervals generated for each variable of top
 877 CPH models when missing individuals are treated as deaths. Values that are bolded represent
 878 significant effects. HR>1 indicates increased risk of dying and HR<1 indicates reduced risk of
 879 dying.

Variable	Spring top model: HR~SD+SC+mm	Autumn top model: HR~SD+SC+mm
Snow depth (SD)	0.960 (0.926, 0.996)	0.890 (0.798, 0.992)
Mismatch (mm;factor)	2.284 (0.608, 8.580)	0.134 (0.027, 0.675)
Snow cover (SC)	1.035 (1.009, 1.062)	0.810 (0.074, 8.893)

880

881 Table A5. Hazard ratios (HR) and 95% confidence intervals generated for each variable of top
 882 autumn CPH model when mismatch is defined as hares at least 40% whiter than their
 883 environment (environmental whiteness measured by snow cover). Values that are bolded
 884 represent significant effects and italicized values represent P values < 0.1. HR>1 indicates
 885 increased risk of dying and HR<1 indicates reduced risk of dying.

Variable	Spring top model: HR~SD+SC+mm	Autumn top model: HR~SD+SC+mm
Snow depth (SD)	<i>0.953</i> (0.915, 0.993)	<i>0.904</i> (0.809, 1.010)
Mismatch (mm:factor)	<i>6.780</i> (2.390, 19.240)	<i>0.285</i> (0.073, 1.107)
Snow cover (SC)	<i>1.056</i> (1.025, 1.087)	<i>1.376</i> (0.138, 13.734)

886

887 Table A6. Hazard ratios (HR) and 95% confidence intervals generated for each variable of top
 888 autumn CPH model when mismatch is defined as hares at least 60% whiter than their
 889 environment (environmental whiteness measured by snow cover). Values that are bolded
 890 represent significant effects and italicized values represent P values < 0.1. HR>1 indicates
 891 increased risk of dying and HR<1 indicates reduced risk of dying.

Variable	Spring top model: HR~SD+SC+mm	Autumn top model: HR~SD+SC+mm
Snow depth (SD)	0.953 (0.915, 0.993)	<i>0.903</i> (0.809, 1.009)
Mismatch (mm:factor)	3.640 (0.770, 17.207)	0.111 (0.019, 0.657)
Snow cover (SC)	1.044 (1.014, 1.075)	0.776 (0.077, 7.814)

892

893 Table A7. Effect of sex on spring and autumn daily foraging minutes when tested in a linear
 894 mixed-effects model including sex (fixed), and individual ID as a random factor.

Variable	Levels	Season	Coefficient (± SE)	t	P
Sex	Reference=Male				
	Female	Autumn	-22.09	-1.56	0.124
		Spring	-45.25	-2.632	<0.001

895

896 Table A8. Summary of top-ranking autumn and spring linear mixed-effects daily foraging time
 897 models during snow-free seasons when the maximum number of days elapsed between coat
 898 colour assessment and corresponding foraging records is eight days.

Response: Daily foraging minutes

Model	Coefficient (\pm SE)	t	P
Top autumn model from n=1382 daily foraging records from 65 hares			
Intercept	834.122 \pm 9.176	90.905	<0.001
Temperature	-2.285 \pm 0.516	-4.428	<0.001
mismatch	-17.899 \pm 6.183	-2.895	0.004
Year (2016)	-10.799 \pm 8.495	-1.271	0.204
Year (2017)	-110.748 \pm 13.181	-8.402	<0.001
Temperature \times mismatch	6.257 \pm 1.221	5.125	<0.001
Top spring model from n= 791 daily foraging records from 43 hares			
Intercept	857.642 \pm 22.946	37.377	<0.001
Temperature	-1.542 \pm 1.297	-1.189	0.235
Year (2016)	-13.325 \pm 19.571	-0.681	0.499
Year (2017)	-26.519 \pm 19.286	-1.375	0.175
Year (2018)	-89.545 \pm 21.118	-4.240	<0.001
Sex (F)	-30.925 \pm 17.247	-1.793	0.080

899

900 Table A9. Summary of top-ranking autumn and spring linear mixed-effects daily foraging time
 901 models during snow-free seasons when mismatch is defined as hares at least 40% whiter than
 902 their environment (environmental whiteness measured by snow cover.

Response: Daily foraging minutes

Model	Coefficient (\pm SE)	t	P
Top autumn model from n=1505 daily foraging records from 66 hares			
Intercept	831.650 \pm 8.981	92.603	<0.001
Temperature	-2.405 \pm 0.533	-4.511	<0.001
mismatch	-17.968 \pm 5.812	-3.091	0.002
Year (2016)	-9.604 \pm 8.046	-1.194	0.233
Year (2017)	-103.287 \pm 12.173	-8.485	<0.001
Temperature \times mismatch	5.549 \pm 1.071	5.181	<0.001
Top spring model from n=838 daily foraging records from 44 hares			
Intercept	858.868 \pm 22.800	37.669	<0.001
Temperature	-1.209 \pm 1.295	-0.933	0.351
Year (2016)	-16.582 \pm 19.380	-0.856	0.396
Year (2017)	-28.914 \pm 19.111	-1.513	0.137
Year (2018)	-93.029 \pm 21.089	-4.411	<0.001
Sex(F)	-34.832 \pm 17.000	-2.049	0.047

903

904 Table A10. Summary of top-ranking autumn and spring linear mixed-effects daily foraging time
 905 models during snow-free seasons when mismatch is defined as hares at least 60% whiter than
 906 their environment (environmental whiteness measured by snow cover.

Response: Daily foraging minutes

Model	Coefficient (\pm SE)	t	P
Top autumn model from n=1505 daily foraging records from 66 hares			
Intercept	828.614 \pm 8.917	92.926	<0.001
Temperature	-2.183 \pm 0.494	-4.420	<0.001
mismatch	-15.691 \pm 6.419	-2.445	0.015
Year (2016)	-9.339 \pm 8.408	-1.111	0.267
Year (2017)	-100.086 \pm 12.148	-8.239	<0.001
Temperature \times mismatch	6.065 \pm 1.260	4.813	<0.001
Top spring model from n= 838 daily foraging records from 44 hares			
Intercept	858.868 \pm 22.800	37.669	<0.001
Temperature	-1.209 \pm 1.295	-0.933	0.351
Year (2016)	-16.582 \pm 19.380	-0.856	0.396
Year (2017)	-28.914 \pm 19.111	-1.513	0.137
Year (2018)	-93.029 \pm 21.089	-4.411	<0.001
Sex (F)	-34.832 \pm 17.000	-2.049	0.047

907

908 Table A11. Selection of CPH models predicting spring snowshoe hare hazard ratio (HR) (risk of
 909 dying) generated from n= 41 deaths from a total of 229 hares recorded over 4 spring seasons
 910 (2015-2018), considering number of parameters (k) and ranked from most to least support by
 911 Δ AIC, Akaike model weights (w) and Log Likelihood (LL).

Model	k	Δ AIC _c	w	LL
HR~Snow depth+Snow cover +mismatch	3	0.00	0.50	-191.12
HR~Snow depth+Snow cover	2	0.09	0.48	-192.17
HR~1 (null)	0	5.72	0.03	-196.98

912

913 Table A12. Selection of CPH models predicting autumn snowshoe hare hazard ratio (HR) (risk
 914 of dying) generated from n= 34 deaths from a total of 218 hares recorded over 3 autumn seasons
 915 (2015-2018), considering number of parameters (k) and ranked from most to least support by
 916 Δ AIC, Akaike model weights (w) and Log Likelihood (LL).

Model	k	Δ AIC _c	w	LL
HR~Snow depth+Snow cover+mismatch	3	0.00	0.89	-157.78
HR~1 (null)	0	5.43	0.06	-161.50
HR~Snow depth+Snow cover	2	5.59	0.05	-163.58

917

918 Table A13. Selection of mixed linear models predicting daily foraging minutes for snowshoe
 919 hares in snow-free autumn seasons generated from N=1505 daily foraging records from 66 hares
 920 over 3 years (2015-2017). Considering number of parameters (k) and ranked from most to least
 921 support by ΔAIC_c , Akaike model weights (w) and Log likelihood (LL). . Marginal R^2 (Mar R^2)
 922 and conditional R^2 (Cond R^2) are included to show each model's fit. Response variable for all
 923 models is daily foraging time in minutes (Forage_T). Fixed effect predictors include:
 924 temperature (temp), mismatch (mm) and year (yr), and individual ID (ID) is included as a
 925 random factor .

Model	k	ΔAIC_c	w	LL	Mar. R^2	Con. R^2
Forage_T~temp*mm+yr+ID	8	0.00	1	-8659.89	0.12	0.32
Forage_T~temp+mm+yr+ID	7	22.08	0	-8671.95	0.10	0.31
Forage_T~temp+yr+ID	6	47.99	0	-8685.91	0.09	0.29
Forage_T~1+ID	3	103.65	0	-8716.76	0	0.32

926

927 Table A14. Selection of mixed linear models predicting daily foraging minutes for snowshoe
 928 hares in snow-free spring seasons generated from N= 838 daily foraging records from 44 hares
 929 over 4 years (2015-2018). Considering number of parameters (k) and ranked from most to least
 930 support by ΔAIC , Akaike model weights (w) and Log likelihood (LL). Marginal R^2 (Mar R^2) and
 931 conditional R^2 (Con R^2) are included to show each model's fit. Response variable for all models
 932 is daily foraging time in minutes (Forage_T). Fixed effect predictors include: temperature
 933 (temp), mismatch (mm) and year(yr), and individual ID (ID) is included as a random factor .

Model	k	ΔAIC_c	w	LL	Mar. R^2	Con. R^2
Forage_T~temp+yr+sex+(1 ID)	8	0.00	0.57	-4947.70	0.12	0.28
Forage_T~temp+mm+yr+sex+(1 ID)	9	1.16	0.32	-4947.26	0.13	0.28
Forage_T~temp*mm+yr+sex+(1 ID)	10	3.19	0.13	-4947.25	0.13	0.28
Forage_T~1+(1 ID)	3	20.26	0	-4962.90	0	0.28

934

935 Table A15. Selection of CPH models contrasting mismatch as a continuous or binary variable
 936 and predicting spring snowshoe hare hazard ratio (HR) (risk of dying) generated from n= 41
 937 deaths from a total of 229 hares recorded over 4 spring seasons (2015-2018), considering number
 938 of parameters (k) and ranked from most to least support by ΔAIC_c , Akaike model weights (w) and
 939 Log Likelihood (LL).

Model	k	ΔAIC_c	w	LL
HR~Snow depth+Snow cover +mismatch (binary)	3	0.00	0.41	-191.12
HR~Snow depth+Snow cover	2	0.09	0.39	-192.17
HR~Snow depth+ Snow cover+mismatch (continuous)	3	1.75	0.17	-192.00
HR~ 1 (null)	0	5.72	0.02	-196.98

940

Table A16. Selection of CPH models contrasting mismatch as a continuous or binary variable and predicting autumn snowshoe hare hazard ratio (HR) (risk of dying) generated from n= 34 deaths from a total of 218 hares recorded over 3 autumn seasons (2015-2018), considering number of parameters (k) and ranked from most to least support by ΔAIC_c , Akaike model weights (w) and Log Likelihood (LL).

Model	k	ΔAIC_c	w	LL
HR~Snow depth+Snow cover +mismatch (binary)	3	0.00	0.82	-156.72
HR~ Snow depth+Snow cover +mismatch (continuous)	3	3.31	0.16	-158.38
HR~1 (null)	0	7.72	0.02	-163.58
HR~ Snow depth + Snow cover	2	9.44	0.01	-162.44

Appendix B. Chapter 3 Supplementary information, additional results and figures.

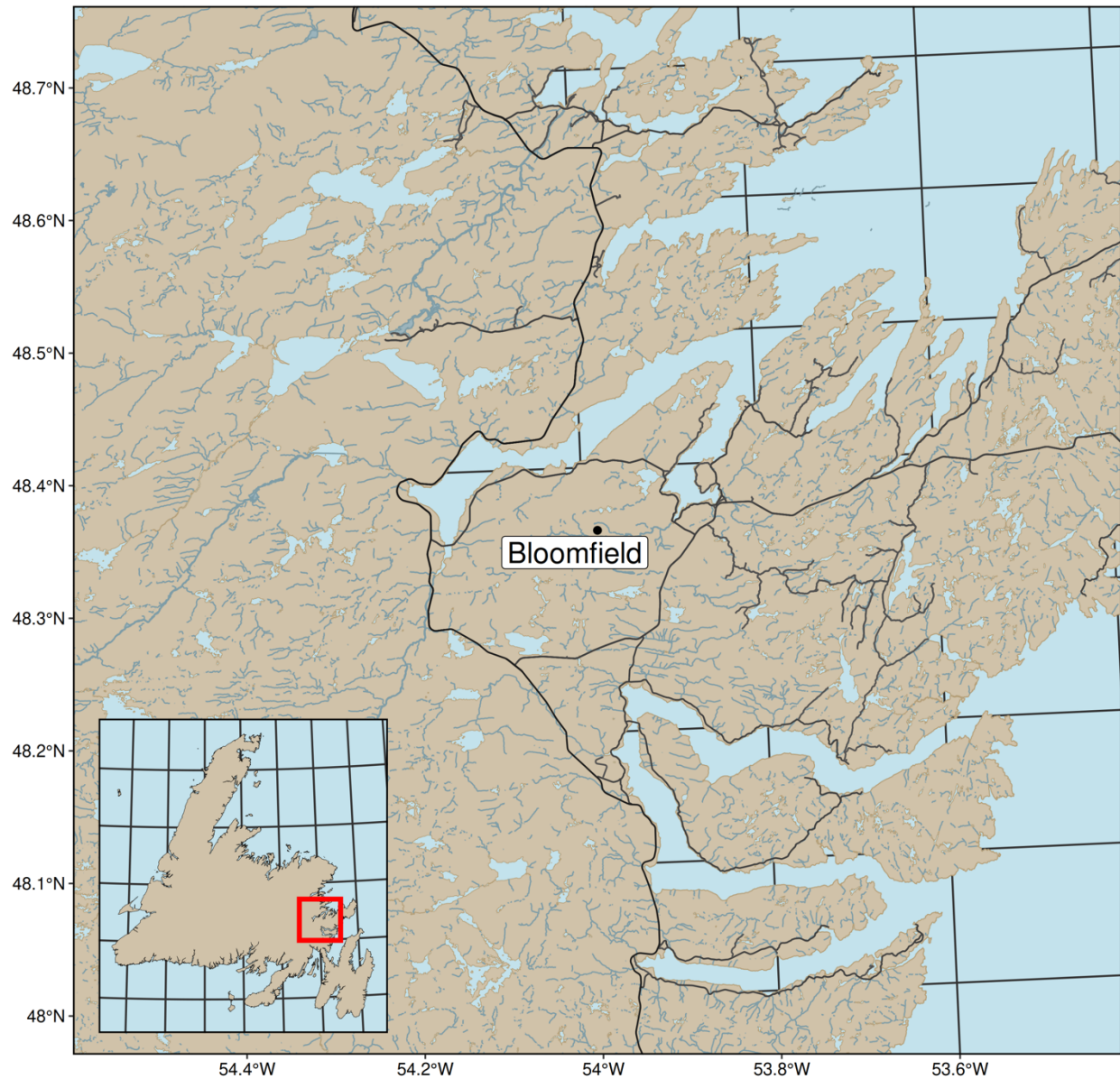


Fig B-1. Map showing our study site in Bloomfield, NL, created by Alec L. Robitaille, Isabella C. and Juliana Balluffi-Fry, with roads from Open Street Map (Robitaille et al. 2021).



2020-11-27 12:40:00 PM T 8°C



PC900 PROFESSIONAL



2020-10-10 1:40:00 PM T 12°C



2020-11-27 10:45:00 AM T 3°C



PC900 PROFESSIONAL
2020-11-28 10:40:00 AM T 12°C



PC900 PROFESSIONAL



PC900 PROFESSIONAL

Fig B-2. Experimental enclosures showing various mismatch and perceived predation risk treatments: a) mismatched brown hare with perceived predation risk; b) matched white hare with perceived predation risk; c) mismatched changing hare with perceived predation risk; d) matched brown hare with perceived predation risk; e) mismatched brown hare with perceived protection from predation risk; f) matched brown hare with perceived protection from predation risk; g) mismatched white hare with perceived protection from predation risk; h) matched white hare with perceived protection from predation risk.

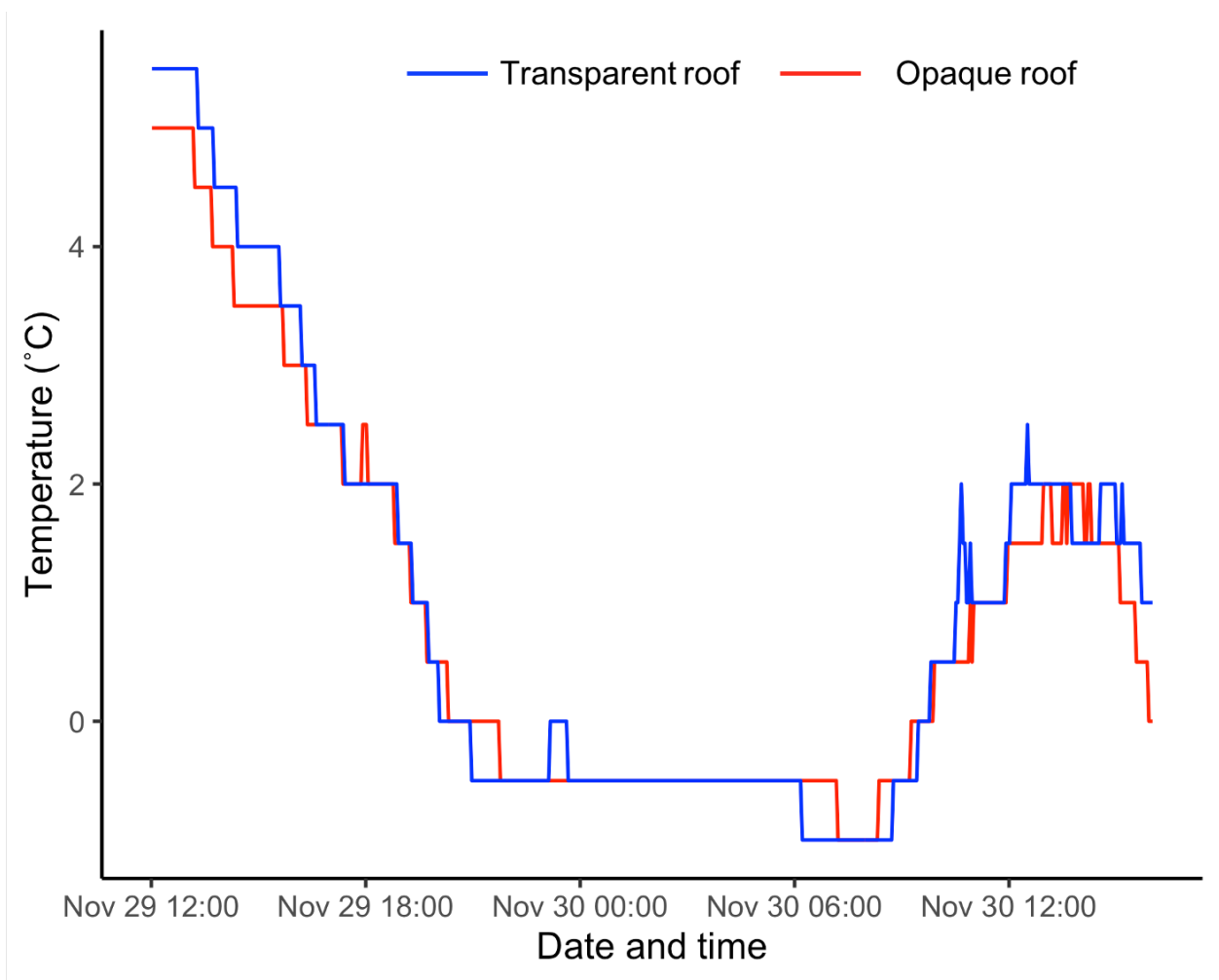


Fig B-3. Temperature profile comparing clear, i.e., perceived predation risk treatment, enclosure and opaque, i.e., perceived protection from predation risk treatment, roof enclosures

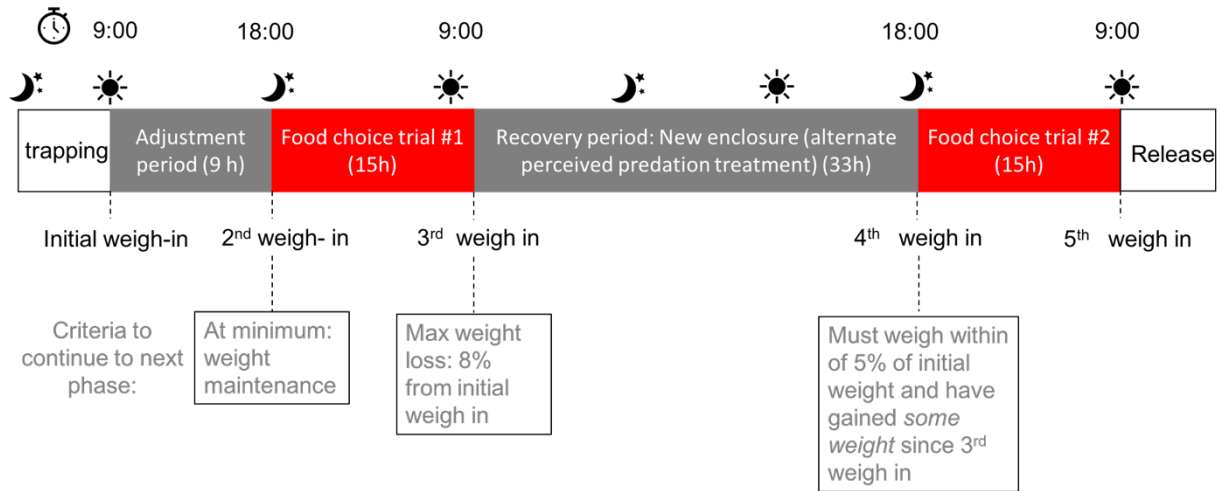


Fig B-4. Timeline outlining the phases included in our 72- hour experimental trials. Weight change threshold criteria used to determine whether hares qualified to continue onto each phase are indicated.

Table B-1. Intraclass correlation coefficients (ICC) describing intra-observer repeatability for our single consistent observer. The observer ranked coat colour twice to the nearest 5% for 31 hares (total of n=62 rankings).

	ICC	95% confidence intervals	F (df1, df2)	p-value
Observer 1	0.927	0.872, 0.958	26.2 (46,47)	< 0.001

Table B-2. Effects of variables included in linear mixed-effects models for black spruce intake rate, selection of high-quality spruce and body mass change when mismatch is considered as a binary variable. In the preference for high quality model, positive effect sizes are associated with selection for high-quality spruce, and negative effect sizes are associated with selection for low-quality spruce. In the body mass change model, positive effect sizes are associated with mass gain, whereas negative effect sizes are associated with mass loss. All models also include individual ID as a random effect. The reference level for predation risk, “roof”, variable is the clear roof, the reference for habituation is the first time hares were held captive, and the reference level for mismatch is matched.

Response variable	Fixed effects	Coefficient (\pm SE)	t	P
Intake Rate (g/kg hare)	Temperature ($^{\circ}$ C)	-1.11 \pm 0.42	-2.62	0.11
	Mismatch	4.76 \pm 4.74	1.00	0.32
	Roof	-8.51 \pm 3.59	-2.37	0.02
	Habituation	12.80 \pm 4.67	2.74	0.008
Preference for high-quality (g/kg hare)	Temperature ($^{\circ}$ C)	0.44 \pm 0.40	1.09	0.28
	Mismatch	8.77 \pm 4.41	1.99	0.05
	Roof	-1.30 \pm 3.48	-0.38	0.71
	Habituation	-12.30 \pm 4.40	-2.80	0.007
Mass change (%)	Temperature ($^{\circ}$ C)	0.23 \pm 0.07	3.09	0.003

Mismatch	-1.87±0.79	-2.35	0.02
Roof	1.23±0.63	1.95	0.06
Habituation	0.20±0.80	0.26	0.80

Table B-3. Predicted average body mass loss (%) and 95% Confidence Intervals during a single feeding trial across simulated risk levels, i.e., match or mismatch and clear or opaque top enclosure, when temperature is held constant at its mean and hares are in their first experimental trial (non-habituated). Letters show mismatch category pairs that are associated by a significant difference. 95% Confidence Intervals are presented in brackets for each predicted body mass loss value.

Simulated match/mismatch type	Enclosure roof	
	Clear	Opaque
White match ^{a,b,c}	5.53 (3.01, 8.04)	4.24 (1.63, 6.84)
Brown match ^a	8.30 (6.87, 9.73)	7.01 (5.51, 8.50)
Brown mismatch ^b	9.62 (7.93, 11.32)	8.33 (6.60, 10.07)
White mismatch ^c	10.08 (7.05, 13.1)	8.79 (5.75, 11.83)

Spruce sampling and intraspecific quality assessment

Sampling location

The black spruce used to test intraspecific selection for forage quality under our different experimental treatments was collected from a similar snowshoe hare trapping grid, “Unicorn”. The Unicorn grid is 32 km away from ours, just north of Terra Nova National Park. This grid was chosen for spruce harvesting because its vegetative composition is similar to our grid and

because black spruce trees at our trapping location had already been extensively clipped for previous feeding trial experiments. Spruce tree elemental composition data at this location was also available (Heckford et al. 2021).

Sampling to establish stoichiometric distribution maps

Black spruce was collected from 50 sample locations at the Unicorn grid along six trapping transect lines between July and August of both 2016 and 2017 (see Heckford et al. 2021). At each sampling location, the terminal ends, i.e., new growth, of black spruce branches on juvenile trees, i.e., <2 m in height, were collected. Sampling was completed within an 11.3 m radius plot around each sampling location, in four intercardinal directions, i.e. NE, NW, SE, SW, moving clockwise until 20 g was collected in total. The new growth of black spruce branches is representative of what is typically consumed by snowshoe hares. Samples were stored at -20°C until processing. Elemental analysis of these samples was conducted at the Agriculture and Food Lab at the University of Guelph, where percent nitrogen (N) was assessed using an Elementar Vario Macro Cube. Stoichiometric distribution models were used to extrapolate N composition values across the entire Unicorn grid (Heckford et al. 2021).

Spruce harvested for feeding trials

We collected black spruce from seven locations that had previously been sampled for elemental composition. We determined sampling locations from the N “hot spots” and “cold spots” from previously established stoichiometric distribution maps. N content (%) at high-quality sampling locations was on average 0.93 and N content (%) at low-quality sampling locations was on average 0.87. We collected black spruce boughs up to 30 cm in length and up to 0.5 cm in

diameter at the closest tree to the sampling point in each of the NW, NE, SE, SW directions (trees <15 m away from the sampling point). We strived to collect 25% of our harvest at each of the trees identified around the sampling point. Spruce boughs were collected only from mature trees (>2 m), as they are more palatable to hares and are less likely to cause significant weight loss during feeding trials than boughs from juvenile trees (Rodgers and Sinclair 1997). We only collected boughs with healthy needles, and from branches < 1.5 m from ground height, to harvest what would be accessible by a snowshoe hare from the summer to winter months, when snow allows access to higher branches. Although the individual trees that were sampled to inform the stoichiometric distribution map at this grid were juveniles, mature trees have shown similar stoichiometric trends as juveniles (Balluffi-Fry et al. 2022). We assume that the % N in the spruce at the time we harvested it was still representative of what it was determined to be at the time of sampling (Heckford et al. 2021), based on recent evidence of a lack of interannual differences in %N (Richmond et al. 2020). We stored harvested spruce outdoors to keep it fresh, and boughs were used for feeding trials within six days of collection. Before preparing black spruce for feeding trials, we thoroughly mixed high-quality spruce boughs to ensure a homogeneous distribution of the boughs sampled at each of the four trees of the sampling point and did the same for the low-quality spruce. Boughs were reduced to 10 cm twigs to fit in feeding baskets.