INFLUENCES ON THE BALANCE BETWEEN ENERGETICS AND RISK IN SNOWSHOE HARES

By

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ABSTRACT

Animals balance acquiring food for energy while minimizing their risk of predation, but climate or habitat features can tip the scales. I used snowshoe hare (*Lepus americanus*) to test how external variables influence foraging and survival. First, I used winter coat-colour mismatch to test the Camouflage Hypothesis. I predicted that white hares mismatched on a snowless winter background would be more vulnerable to predation than matched hares. Instead, mismatched hares had lower mortality risk than matched hares. Temperature and snow depth, not mismatch, influenced survival and foraging behaviour. Next, I tested the Risk Allocation Hypothesis with a novel risk simulation experiment in the context of spring environmental factors. Hares did not allocate risk based on simulated risk or weather conditions. Instead, hares were risk averse as a function of canopy cover. Taken together, my results demonstrate that multiple mechanisms likely impact the energetics-risk balance. Snow depth and canopy cover have direct implications on predation risk, while temperature impacts energetics; however, effects may not be detectable if conditions do not represent an energetic challenge. My work highlights the idiosyncrasies of place considering previous results across the hare range, and contributes to mismatch and behavioural frameworks for a seasonally coat-colour changing species.

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The lands I conducted field research on for this thesis, as well as the lands I lived and studied on during my time on the Island of Newfoundland, have been cared for, learned from, and held by diverse Indigenous Peoples since time immemorial. The Island of Newfoundland is the traditional, unceded territory of the Mi'kmaq and culturally extinct Beothuk peoples, and I recognize the Innu and Inuit as the traditional people of Labrador. Though I have only just begun to learn about their sacred relationships to the land that was ultimately stolen from them, we must work to honor traditional ways of knowing in our science and strive for true reconciliation.

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CO-AUTHORSHIP STATEMENT

Chapters 1 and 4 were written by me, Emily Monk. Chapter 2 of this thesis was co-authored with Michael Peers and Eric Vander Wal. Chapter 3 was co-authored with Michael Peers, Yasmine Majchrzak, and Eric Vander Wal. In both chapters 2 and 3 we use "we" to refer to all authors. I am the principal co-author and contributor to ideas, and lead the project designs, field data collection, data analyses, and writing for all chapters in this thesis. E. Vander Wal provided funding for the project and guidance on all stages of the thesis. M. Peers assisted with field data collection and provided guidance on all stages of this thesis. For Chapter 3, Y. Majchrzak provided guidance on the project design, field data collection, and interpretation of results. Chapters 2 and 3 will be reformatted and submitted to journals (targets unknown) upon thesis completion.

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CHAPTER 1. PROLOGUE

1.1 Driving Forces of Herbivore Behaviour

Species must balance consuming enough food to gain energy with minimizing the risks of predation while foraging (Brown and Kotler 2004). The balance of energy and risk can be shifted as energy requirements or predation risk changes, and there are complex costs that prevent animals from simply foraging more while avoiding predation (Lima and Dill 1990; Verdolin 2006). Predator avoidance can be costly, as anti-predator behaviours both use energy and represent time when the animal is not acquiring more energy via foraging. Foraging itself can be costly and represents a time of risk, as animals cannot always be vigilant or use anti-predator behaviours when finding or consuming food to meet energetic needs (Ferrari, Sih, and Chivers 2009). Though there are many other drivers of herbivore behaviour, the intersection of energy and risk represents a critical balancing act that drives fitness.

The balance between energy gain and predation risk is impacted by additional external factors, such as ambient temperature. Homeotherm species, or those who maintain a consistent body temperature via metabolic activity, endure the full range of extreme high and low temperatures in their environment. Energetic demands increase in homeotherms at extremely low or high temperatures to maintain a consistent body temperature (Sheriff et al. 2009). This increase in metabolic activity comes at the expense of additional energy input requirements, so animals alter behaviours or physiological processes to meet or mitigate thermal energetic demands. Animals may seek thermal refuge (Pauli et al. 2013) or alter their metabolism (Turbill and Stojanovski 2018) to avoid energetic demands, alter foraging to meet increased energetic demands (Camp et al. 2018; St. Juliana and Mitchell 2016), or shift the timing of metabolically demanding activities (Guiden and Orrock 2020). However, altering foraging or other behaviours can expose animals to greater predation risk, or alter an animal's ability to use anti-predator behaviours effectively (Lima and Dill 1990; Verdolin 2006; Turbill and Stojanovski 2018).

Despite the clear effects of temperature on energetic demands, as well as clear literature on how predation risk influences foraging behaviours, it remains unclear how climatic influences alter the balance between foraging and predation risk. Most studies to date have either explored climatic elements and foraging (Kotler, Brown, and Mitchell 1993; St. Juliana and Mitchell 2016; Camp et al. 2018), or foraging and predation risk (Abrams 1993; Brown and Kotler 2004; Majchrzak et al. 2022), but rarely have studies tied foraging and risk with climatic factors (Orrock and Danielson 2009; Falcy and Danielson 2013). Additionally, a single species will not experience the same balance between foraging and predation risk across its geographic range. Temperature ranges, local adaptations, and even predator regimes may vary across a geographic range, and thus the balance of foraging and risk will too. Individual studies rarely have the logistic ability to test a hypothesis in many locations across a species' range, and often fail to recognize factors that may vary expected or observed outcomes over a large area. This thesis seeks to illustrate key elements of the balance between foraging and predation risk in the context of climatic factors like temperature, as well as use climatic elements as context for this balance range-wide.

1.2 The Boreal Forest and Snowshoe Hares as a Model System

The boreal forest is among the largest biomes on earth, situated across Northern latitudes of multiple continents (Brandt et al. 2013). The coniferous forest of the boreal biome experiences great seasonality, with large differences in temperature between summer maximums and winter minimums. Given the vast land cover of the boreal forest, there are many regional differences in climate across the biome, though seasonal trends remain similar (Brandt 2009). Climate change has been readily documented in the boreal forest, with more rapid experienced and projected warming in Northern regions than the global average (Soja et al. 2007; IPCC 2022). Rapid warming in the boreal is already having wide ranging impacts on ecosystems (Soja et al. 2007), highlighting the importance of illustrating mechanistic effects of rising temperatures and other climatic pressures on animal behaviour.

Animals in the boreal must endure long cold winters and warm summers. Year-round inhabitants of the boreal forest have adaptations for winter that allow them to persist despite thermal challenges. Some heterotherm species, such as house mice and superb fairy-wrens, enter a state of torpor to avoid the metabolic challenges of extreme cold (Turbill and Stojanovski 2018; Romano et al. 2019). Homeotherms instead use a suite of other physical and behavioural adaptations to remain warm. Many species, such as mule deer and snowshoe hare, undergo a seasonal molt that provides an insulative winter coat (Marchand 2013b; Zimova et al. 2018), while some like beavers and voles create nests or dens that provide thermal refuge (Marchand 2013a). Though some species can lower their metabolic rate to lessen energetic demands, most adaptations allow species to balance the need for greater food consumption during thermal energetic stress with the dangers of cold exposure and potential predation risk.

Seasonal coat colour change is a specialized type of seasonal molt used by over 20 mammal and bird species in the boreal forest that remain active all year (Zimova et al. 2018). Seasonally colour changing animals molt from a dark summer coat to an insulative white winter coat; this molt provides both thermal and camouflage benefits (Zimova et al. 2018). A white animal on a snowy white background is less easily detected, and thus safer, than a dark-coloured animal on the same snowy background. Additionally, an insulative white winter coat can allow animals to endure lower temperatures before their metabolic demands increase to stay warm. Photoperiod dictates when seasonally colour-changing animals molt in autumn and spring, providing a consistent and unambiguous cue that an animal's background will also soon change (Farner 1961; Bradshaw and Holzapfel 2007; Zimova et al. 2018). This predictable change in day length stimulates a gene regulatory cascade which ultimately produces the phenotypic changes visible in seasonal molts (Ferreira et al. 2020). However, as the climate warms, the timing and persistence of snow cover is changing while photoperiod remains constant (Mote et al. 2018; IPCC 2022). Many seasonally colour changing species have and will become increasingly mismatched to the background, i.e. a white animal on a brown snowless background, as seasonal conditions are no longer consistent (Mills et al. 2013; Atmeh, Andruszkiewicz, and Zub 2018; Pedersen, Odden, and Pedersen 2017). Mismatch in seasonal coat colour is another external factor that may impact the balance of foraging and risk.

Snowshoe hares (*Lepus americanus*) are a keystone prey species of the boreal forest that undergo a seasonal molt from a summer brown coat to a more insulative winter white coat. This seasonal coat colour change allows hares to remain active throughout the winter. However, hares carry little body fat and do not have significant energy reserves, and thus must continue to forage even in thermally challenging conditions (Whittaker and Thomas 1983). Additionally, as high as 90% of mortality in hares is due to predation (Hodges et al. 2001; Krebs, Boonstra, and Boutin 2018). Hares are a critical prey species for lynx and other predators, especially in winter when most other small mammals are unavailable (Boutin et al. 1995; Krebs, Boonstra, and Boutin 2018). Thus, snowshoe hares can act as a model system to investigate the intersection of foraging and predation risk, through the lens of cold temperature energetics and seasonal camouflage.

1.3 Hare on the Island of Newfoundland

The fieldwork for this thesis took place in Butter Pot Provincial Park on the eastern Avalon Peninsula of the island of Newfoundland, located in the province of Newfoundland and Labrador, Canada. Work for this thesis was conducted on the unceded, traditional territory of the Beothuk and the Mi'kmaq. The ecology of the island has been fundamentally changed by introduced and invasive species, such as snowshoe hare. Snowshoe hares were introduced to the island of Newfoundland between 1864 and 1876 from Nova Scotia, headed by local magistrates as a food supplementation program. The introduced hares became established, increasing dramatically in numbers between 1896 and 1912 (Dodds 1960). Historical records indicate the population across much of the island then began cycling as seen in the hare’s native range, with lows recorded approximately every 10 years until a persistent low began in 1979 (Dodds 1960). Though a highly muted cycle may have occurred, the population did not substantially increase until approximately 1995, with a small peak occurring in 2000 (Joyce 2002). Since then, the population has fluctuated in a muted 10 year cycling pattern (Reynolds et al. 2017).

Snowshoe hares quickly became a culturally important species in Newfoundland after their introduction. Hunting and canning rabbits, as they are colloquially called, was often a critical food source for the winter months. As such, hunting was and is primarily for food, rather than for sport. Selling hunted hares has always been permitted in Newfoundland, and was historically an important component of many people’s incomes. Today, rabbit snaring and hunting remains popular and culturally important throughout the island.

1.4 The Newfoundland Climate

The Island of Newfoundland represents the Eastern extent of the North American boreal forest and the snowshoe hare range. The Atlantic climate of the island of Newfoundland is heavily influenced by the moisture feed from the Atlantic Ocean, prevailing winds blowing over the cold Labrador Current, and cold arctic air blowing down from the northwest (Abbasnezhadi, Rousseau, and Bohrn 2020). Summers are mild with high precipitation and frequent fog due to the warm gulf stream mixing with cool air from the Labrador Current (Environment Canada St. John's West 30 year climate normal: August daily maximum temperature = 20.2 °C; precipitation = 95.9 mm) (Environment Canada 2019b). Winters have very few days of extreme cold due to the buffering effect of the marine location, but have frequent storms and high precipitation (February daily minimum temperature = -9.0 °C; precipitation = 151.8 mm) (Environment Canada 2019b). On the Avalon Peninsula on the far Eastern extent of the island, winter precipitation falls as both rain and snow, with temperatures frequently just above 0 °C (February rainfall = 82.5 mm; snowfall = 67.5 cm) (Environment Canada 2019b). Newfoundland's climate has both similarities and key differences in temperature and precipitation to other regions of the boreal forest where snowshoe hares have been previously studied.

We compared 30-year climate normals, from 1981-2010, of our snowshoe hare study site in Newfoundland to frequently referenced study areas in the Yukon Territory in Canada, as well as Pennsylvania and Montana in the United States to provide context for the temperature and mismatch focus of this thesis (Figure 1.1). Climate normal data comes from the St. John's West weather station in Newfoundland (Environment Canada 2019b), Burwash Airport in the Yukon (Environment Canada 2019a), Tobyhanna Pocono Mountain Airport in Pennsylvania (Arguez et al. 2010b), and Seeley Lake in Montana (Arguez et al. 2010a). The temperature of our hare study site in Newfoundland is fairly moderate compared to hare study sites at the northern and southern extents of the hare range. Regions at the southern extent of the hare range, such as Montana, tend to experience much warmer maximum temperatures in the summer months, but are relatively similar in winter. In contrast, the Yukon Territory has similar maximum temperatures in summer months, but much colder minimum temperatures in the winter. Importantly, Newfoundland has the highest minimum winter temperatures of any of the three other regions compared. In warmer winter temperatures, hares in Newfoundland may not have to expend as much energy to maintain their body temperature compared to other regions, which may extend to foraging rates.

Precipitation varies dramatically across the hare range. Newfoundland receives significantly higher amounts of precipitation in winter, with higher amounts of snowfall, than in other regions. Though rainfall climate normals in addition to snowfall and precipitation were not available for all study sites, Newfoundland receives an average of 93.55 mm of rainfall each month between December and March (Environment Canada 2019b), while the Yukon receives an average of 0.08 mm over the same four month period (Environment Canada 2019a). The winter rain and relatively warm temperatures in Newfoundland can create periods of winter mismatch not commonly observed elsewhere in the hare range, which likely impacts predation risk. The unique climate of Newfoundland situates it as an ideal natural experiment to study the intersection of climate factors on foraging and predation risk.

1.5 Thesis Overview

The objective of this thesis is to investigate how climate variables influence the balance between foraging and predation risk for snowshoe hares in two ways. I use a combination of data collected from accelerometer data loggers and telemetry, as well an experiment conducted in a wild setting to empirically test my hypotheses. First, I tested how temperature may amplify the costs of foraging when hares are matched and mis-matched to their environment in winter, and whether these costs decrease survival. Second, I experimentally simulated differing risk to test the Risk Allocation Hypothesis with the context of climate factors. The combination of these studies allows a nuanced and mechanistic understanding of what drives foraging behaviour in snowshoe hares, and how climate-induced variations in energetics and predation risk may alter behavioural choices. My studies provide additional insight into the mechanisms behind winter mortality, and the consequences of climate change in the form of winter coat colour mismatch. Finally, the conclusions from my studies provide additional context for how hares balance energy and risk across their range.

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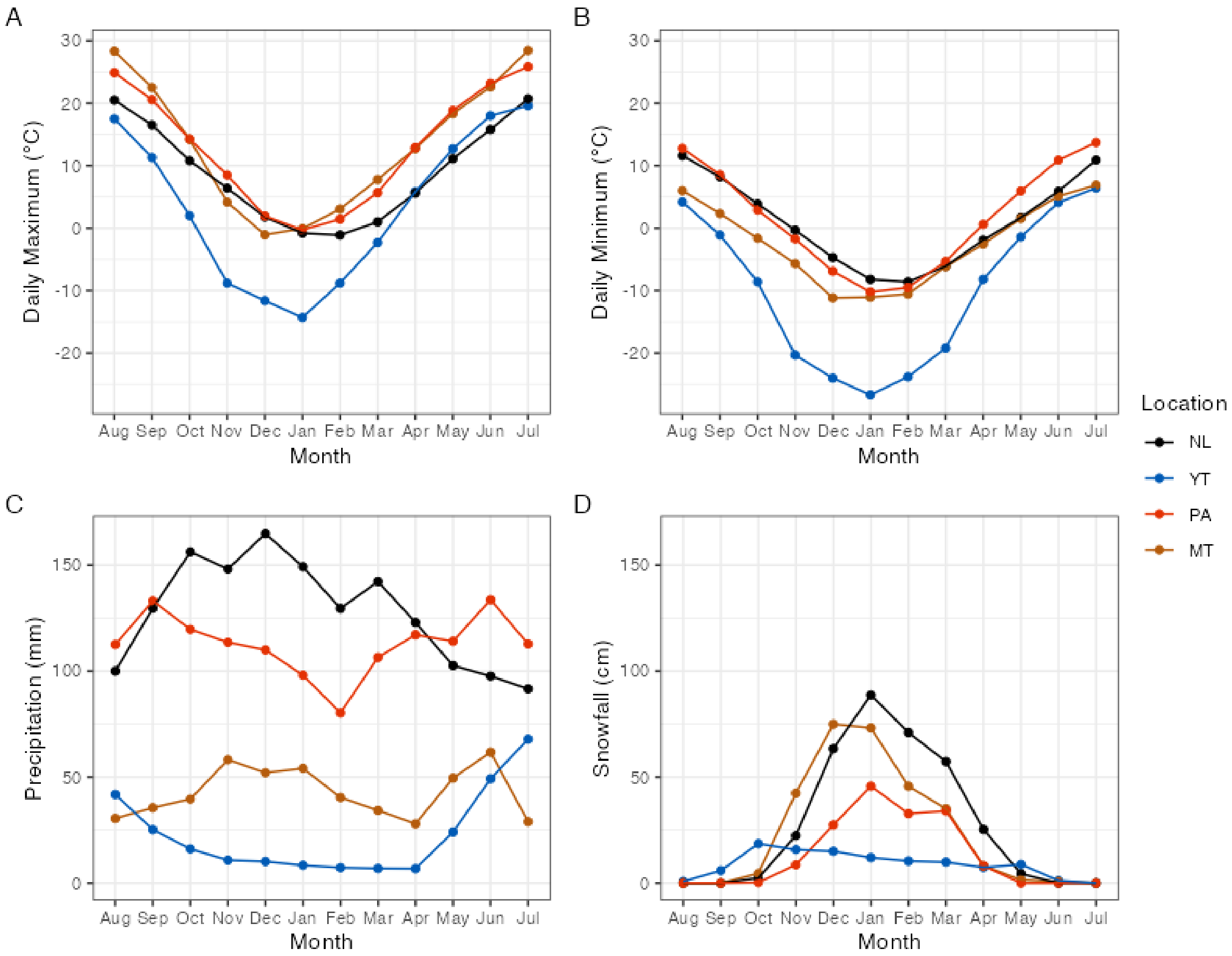

Figure 1.1 Comparison of the climate near four different snowshoe hare study sites, including where this study was conducted. Climate data is from 30-year climate normals from 1981-2010, from either Environment Canada (NL, YT) or NOAA (PA, MT). St. John's West climate station in Newfoundland, near our study site is shown in black, Burwash Airport in the Yukon in blue, Tobyhanna Pocono Mountain Airport in Pennsylvania in red, and Seeley Lake in Montana in tan. Daily maximum (A) and minimum (B) temperatures, as well as precipitation (C) and snowfall (D) for each month demonstrate the similarities and differences in some aspects of climate across the snowshoe hare range.

CHAPTER 2: FAILURE TO DETECT FORAGING AND MORTALITY COSTS TO WINTER COAT-COLOUR MISMATCH CONTINUES TO DEMONSTRATE A LACK OF EVIDENCE FOR A SINGULAR MECHANISM

2.1 Abstract

Species that molt to seasonally match the colour of their environment are becoming increasingly mismatched as climates warm, changing patterns in snowfall and its timing. Mismatch, i.e., a white animal on a snowless brown background, lowers survival in some animals and some contexts. Predation is implicated as the mechanism that lowers survival: more conspicuous animals are more likely to be depredated. Emerging evidence suggests, however, that contexts exist in which mismatch may not negatively affect survival. In such scenarios complementary adaptive benefits of winter pelage may outweigh the costs of mismatch. We examined winter survival and foraging behaviour of snowshoe hares (*Lepus americanus*) in eastern Newfoundland, Canada, where mild winters with rain creates a snowless natural mismatch experiment. Because hares in Newfoundland represent the southern extent of the species biogeographic range, we predicted that mismatch should negatively affect hare survival. We further predicted that mismatch-induced risk should decrease the time spent foraging, when mismatched in winter – an effect we presumed to be attributed to risk avoidance. Over two winters, we fit hares with VHF collars and accelerometers to quantify survival and foraging activity during periods of match and mismatch. Contrary to our predictions, we found that hares had lower mortality risk when mismatched to the background, and did not adjust foraging behaviour while mismatched. Winter survival depended most on temperature and snow depth, with lower survival in cold temperatures and shallower snow depth. Foraging also showed a

negative relationship with temperature and snow depth. Despite our expectations, coat-colour mismatch may not be consistently negative, even in southern portions of hare range. By testing for the consequences and costs of mismatch in different geographies, we hope to contribute to a more complete set of mechanisms to explain instances when mismatch has negative, equivocal, or even positive effects.

2.2 Introduction:

Warming and variable climate conditions continue to affect phenological events by creating mismatch between the timing of life history events and local environmental conditions (Miller-Rushing et al. 2010; Walker et al. 2019). Mismatch between life history and the environment is thought to predominantly affect fitness negatively (Post and Forchhammer 2008; Miller-Rushing et al. 2010; Visser and Gienapp 2019). However, the effect of phenological mismatch is not ubiquitous across all species and can be influenced by varying contexts, such as trophic interactions (Renner and Zohner 2018) and geography (Kennah et al. 2022). Importantly, mismatch can occur beyond a discrete phenological event, such as across a season if environmental conditions differ from seasonal adaptations. Thus, more tests for the costs and consequences of mismatch across contexts and geographies are needed. We capitalize on that need to test whether mismatch negatively affects survival and foraging at the southern extent of snowshoe hare range, where winters often experience snow-free periods.

Changing between brown summer pelage and white winter pelage is thought to improve camouflage, but also comprises other physiological adaptations that improve survival in seasonal environments (Zimova et al. 2018). Warming climates decrease snow cover (Mote et al. 2018; IPCC 2022), and seasonally pelage changing species are expected to become increasingly mismatched in their environment (Mills et al. 2013; Walker et al. 2019). Seasonal colour mismatch appears to often negatively impact survival, e.g., least weasels (Atmeh, Andruszkiewicz, and Zub 2018), mountain hare (Pedersen, Odden, and Pedersen 2017), snowshoe hare (Zimova, Mills, and Nowak 2016), rock ptarmigan (Imperio et al. 2013), and willow ptarmigan (Melin et al. 2020). The proposed mechanism is lost camouflage increasing vulnerability and predation rate (Zimova, Mills, and Nowak 2016; Atmeh, Andruszkiewicz, and

Zub 2018; Melin et al. 2020). Counter examples exist, however. For example, mismatched white snowshoe hares had higher survival than matched brown individuals during their autumn molt, with predation still implicated as the mechanism (Kennah et al. 2022). However, the increased insulation and favorable energetics of winter white pelage compared to brown summer pelage, i.e., thermal hypothesis, reduced the time spent foraging. Thus, despite being more conspicuous, it was proposed that animals were more vulnerable because they needed to move and feed more, consequently increasing the probability of being preyed upon (Kennah et al. 2022).

Notwithstanding areas with rare polymorphisms, mismatch frequently occurs around the autumn and spring molt. Indeed, the molt seasons have been the dominant focus of coat-colour mismatch (Mills et al. 2013; Kennah et al. 2022; Zimova et al. 2022). However, variable and warming climates will increasingly result in white animals on brown backgrounds throughout snow-free winter periods, beyond the phenological molt event. Even current studies looking at annual survival in response to coat-colour mismatch (Zimova, Mills, and Nowak 2016; Pedersen, Odden, and Pedersen 2017; Oli et al. 2023) are primarily testing and detecting effects during the molt seasons, i.e. one to two weeks of high contrast mismatch temporally near the molt (Zimova, Mills, and Nowak 2016; Wilson et al. 2019). The potential effects of winter mismatch have been addressed by one study using matched and mismatched animal decoys during winter (Atmeh, Andruszkiewicz, and Zub 2018). We submit that looking beyond phenological mismatch to winter mismatch in regions with relatively warm and snow free winter periods offers an opportunity to examine how climate change may impact winter survival in these species. Additionally, snow-free mismatch periods in winter, when all animals share the same cold advantaged winter pelage, control for the hypothesized thermal costs of being brown on white backgrounds in cold conditions (Kennah et al. 2022).

Snowshoe hares (*Lepus americanus*) exhibit seasonal coat colour change and are widely distributed through boreal and montane forests. Debate continues regarding which mechanisms link coat-colour mismatch to effects on survival and behavioural, and how climate change may impact hares across their range. The thermal and camouflage hypotheses for the implications of coat-colour mismatch require mismatch both affect risk-sensitive foraging. For example, temperature and its effect on energetics can impact the implications of mismatch (Kennah et al. 2022). Hares forage less in warmer temperatures (Kennah et al. 2022), as in other lagomorphs (Camp et al. 2018), which may reduce their exposure to risk. Additionally, prey species are predicted to reduce foraging proportional to predation risk (Lima and Dill 1990; Verdolin 2006). Hares show differing abilities across studies to alter behaviours in response to coat-colour mismatch. Hares appeared to have limited plasticity in resting site selection when matched versus mismatched (Kumar et al. 2020). However, hares were shown to alter foraging tactics in response to mismatch and perceived predation risk, but did not alter intake rate in response to experimentally manipulated mismatch (Kennah et al. 2023). In general contexts beyond coat-colour mismatch, hares are known to alter their spatial and foraging behaviour in response to both long-term (Majchrzak et al. 2022) and short-term changes in predation risk (Shiratsuru et al. 2021; Studd et al. 2022). Therefore, altering behaviour to minimize the effects of heightened predation risk while mismatched seems plausible, especially in warmer conditions, but remains unknown.

We monitored winter survival and foraging rates to disentangle the mechanisms behind coat-colour mismatch effects on foraging behaviours and survival in snowshoe hares at the south-eastern extreme of their biogeography. Winters in our southeastern Newfoundland study site remain near freezing throughout the winter with high amounts of both snow and rain. The

Atlantic climate has the potential to cause variable snow-free periods throughout the winter, potentially amplifying any effects typically observed during the autumn and spring. We tested the camouflage hypothesis, which posits that coat-colour mismatch to the environment increases predation risk. We therefore predicted that winter coat-colour mismatch would increase predation and mortality (P1). We further predicted that colder temperatures should amplify the risks to hares due to increased metabolic demands increasing risk of predation and mortality. (P2).

2.3 Methods:

2.3.1 Study site:

Hares lived in and adjacent to Butter Pot Provincial Park (47.3905 N, -53.0586 W) on the Avalon Peninsula of Newfoundland and Labrador, Canada. The Avalon Peninsula represents the eastern edge of snowshoe hare range, and is characterized by a mix of boreal forest, bogs, and barren areas. Primary predators in the region include coyotes (*Canis latrans*), northern goshawks (*Accipiter gentilis*), and red foxes (*Vulpes vulpes*); Canada lynx (*Lynx canadensis*), the main predator of hares elsewhere in their range, were not observed in the study area during our study, though they are present on the Island. The population was increasing during our study duration from 2022-2024 as part of a previously identified fluctuation pattern (Reynolds et al. 2017): hare density increased from 0.39 hare/hectare in autumn 2022 to 0.75 hare/hectare in autumn 2023. Winter temperatures in the study region are relatively mild compared to the continental interior boreal forest. Average daily temperatures during our study duration from December to April in 2022-2023 and 2023-2024 ranged from a minimum of -6.9° C in February 2023 to a maximum of 3.3° C in April 2024 (Environment Canada 2019). The region experiences a high amount of total precipitation, with a yearly average of 1582 mm based on a 30 year climate normal

(Environment Canada 2019). During our study the minimum monthly precipitation was 62.2 mm in January 2024, while the maximum was 169.4 mm in February 2024 (Environment Canada 2019). These warmer temperatures and higher precipitation results in winter rain that has the potential to create unpredictable snow free periods throughout the winter. These mid-winter snow free periods provide a natural mismatch experiment without the need for manual manipulation and allows for a longer duration of mismatch than previous studies. The Island of Newfoundland is projected to have increased precipitation but decreasing snow accumulation in climate projection models for the next 20-50 years (Abbasnezhadi, Rousseau, and Bohrn 2020). Winter mismatch in this region is likely to increase in the coming decades.

2.3.2 Field methods:

We monitored hares over two full winters, from October 2022 to April 2023, and from October 2023 to May 2024. Hares were studied in two 500m by 500m trapping areas within Butter Pot Provincial Park. The sites are approximately 2.5 km apart, and do not share individuals. We set up 50 Tomahawk live-traps (Tomahawk Live Trap Co. Tomahawk, WI, USA) approximately 75 m apart in a grid pattern in each study area (Joyce 2002). We baited traps with rabbit chow and a small slice of apple, and left traps open overnight from sunset to sunrise; hares were handled within approximately two hours of sunrise. We recorded mass and sex at each capture, and newly captured hares received a Monel #3 eartag (National Band and Tag Co., Newport, KY, USA) for identification in subsequent recaptures. During the molting season, we also visually assessed each hare's entire body for coat-colour whiteness to the nearest 10%. To indicate the beginning or end of a molt when a hare was minimally changed, we assigned 5% or 95% instead of a 10% increment.

A subset of hares (total n = 24; winter 1 n = 16, winter 2 n = 8) weighing > 1100 g received a very high frequency (VHF) collar with a mortality sensor (~31-36g) (Model MI-2 M, Holohil, Canada). We monitored hare survival once every 7-10 days throughout the winter season, as allowed by logistical constraints, using radio telemetry and located mortalities as soon as possible to reduce the potential for scavenging. We noted characteristics of the remaining carcass and searched for tracks, scat, or feathers to identify predator species when possible. Collars were retrieved from mortality sites and re-deployed.

We measured hare behaviour with accelerometer units deployed on a subset of the total VHF collared hares based on equipment availability (total n = 21; winter 1 n = 14, winter 2 n = 7) (Axy-5S; Technosmart, Rome, Italy). Accelerometers measure an animal's acceleration on three axes, allowing acceleration profiles to be built for different behavioural states (Studd et al. 2019). A sampling frequency of 1 Hz can identify behaviours like foraging or sprinting, allowing an overall activity budget to be produced for a long time period (e.g. many months). Previous work classified snowshoe hare accelerometer readings into behavioural categories using observations and acoustic recordings; we used a hierarchical tree model to identify not moving, foraging, hopping, and sprinting behavioural states (Studd et al. 2019). We used the algorithm produced by Studd et al. to classify hare behaviours; no difference was seen between acceleration profiles of snowshoe hares in the Yukon, where the algorithm was calibrated, and hares in Newfoundland in the present study. Accelerometer unites were also equipped with a temperature sensor, which we used to detect a precise mortality date when the measured temperature dropped below the hare's external body temperature. We used precise mortality dates from the accelerometers when available to improve on the 7-10 day telemetry monitoring window. Handling and collaring procedures were approved by Memorial University Animal Care, protocol 20-02-EV.

At each monitoring grid, we deployed two one-meter snow poles and camera traps (HyperFire 1, Reconyx, Holman, WI, USA) to measure local snow depth and cover. Each camera took one photo of the snow pole in the morning after sunrise and one photo in the afternoon before sunset. We manually assessed each photo to obtain snow depth to the nearest 2 cm and snow cover to the nearest 10% at each camera. Values from the 4 cameras were averaged to produce daily values for the study area. Coat-colour data from hare trapping was then combined with the snow data to assess daily mismatch data for each individual during the winter season. We considered snow presence in the environment when over 50% of the landscape had snow. Similarly, we considered hares winter-white if observed as 80% white or higher. Winter-white hares were thus considered mismatched if less than 50% of the landscape had snow present. To assess this 80% cutoff in the context of previous studies on snowshoe hare mismatch, we repeated all analyses using a 50% cutoff and assessed for differences to results (Appendix 1).

2.3.3 Analytical methods:

We analyzed all data using the R programming language (R Core Team 2024). We restricted all analyses to only the winter period when the majority of hares were white. We used the package Survival for survival analyses (Therneau and Grambsch 2000; Therneau 2024). We visualized winter survival with a Kaplan-Meier curve using the ggsurvfit package (Sjoberg et al. 2023), and overlaid snow cover data to visualize mismatch periods. We assessed the effect of mismatch and weather variables on mortality risk using a Cox's proportional hazards models (CPH) (Cox and Oakes 2018). We produced a suite of models with mismatch, temperature, and snow depth covariates, as well as an intercept only null model. Time intervals in our CPH models represented the time between each telemetry check, but we used exact mortality dates from accelerometer data when available. The values for temperature and snow depth in our models were represented as the average across the time intervals. For match and mismatch, we classified the time interval based on which category was more frequent during the interval. All models were checked for the proportional hazards assumption using Schoenfeld residuals. We then used a combination of Akaike information criterion (AIC), Bayesian information criterion (BIC), and concordance values to compare models. A combination of selection approaches allow us to view a more full image of how well a model predicts survival for our observations (concordance), and the goodness of fit and generalizability of a model under different penalization regimes (AIC and BIC). A strong model should show a similar pattern across multiple modes of inference. We considered a singular model as highest ranking if its AIC and BIC value was four units less than the next highest ranking model, and if it had a concordance value both greater than 0.5 to indicate improvement over chance and higher or at least similar in value to competing models. AIC and BIC model weights provide additional insight into the relative importance of variables under consideration; we used model weights as additional context if a singular high ranking model did not emerge (Symonds and Moussalli 2011). We used the highest-ranking model to calculate predicted risk, or hazard ratios.

For our behavioural analysis, we classified acceleration data for each individual into behavioural states using a previously developed classification algorithm (Studd et al. 2019). Foraging behaviour was isolated from this classification and converted into minutes spent foraging per day. We removed all days from the analysis when trapping occurred at the study site. We then built a suite of generalized linear mixed models, using the lmerTest package (Bates et al. 2015; Kuznetsova, Brockhoff, and Christensen 2017), to examine the impact of mismatch and weather variables on time spent foraging per day. All numeric variables were scaled prior to modeling. Both individual hare ID and month were included in all evaluated models as random effects. We tested the model conditions by assessing the residuals for normality and confirmed random effects to be normally distributed. We compared models using Akaike information criterion (AIC) and Bayesian information criterion (BIC). Different penalization methods in AIC and BIC provide multiple modes of inference into competing models. We ranked a model highest when its AIC and BIC values were at least four units less than the next highest ranking model. We gained additional insight into the explanatory ability of a given model using R squared values, but did not rank a model more highly due to a high R squared value since the metric does not penalize over fitting. Marginal R squared values assessed the variance explained by the fixed effects, while conditional R squared values assessed variance explained by the fixed and random effects. AIC, BIC, and both R squared values were calculated from the MuMln package (Bartoń 2023). We selected the top model from the model set and ran an ANOVA using Satterthwaite's method to obtain additional statistical outputs (Kuznetsova, Brockhoff, and Christensen 2017).

2.4 Results:

2.4.1 Winter mortality:

Over winter survival in our population was 0.50 (95% CI: 0.30, 0.70). Although we did not locate collars frequently enough to confirm all predator species, the majority of mortality events appeared to be predator caused. Four mortalities occurred at an unknown time due to collar failure and are censored from survival analyses. No mortality events occurred during times of mismatch (24.2% of total study period or 26 days, 29.1% of winter 1 or 30 days, 19.6% of winter 2 or 22 days), and all mortalities with a known date occurred during times of match with the snowy background (Figure 2.1). Using a 50% cutoff to consider a hare winter white did not change the results [Appendix 1].

We first tested the camouflage hypothesis by modeling winter survival with mismatch and other climatic variables. We did not find evidence for a single highest-ranking model. All seven evaluated models had AIC and BIC within four of the highest ranked model (Table 2.1). Concordance values do indicate some important differences across models however, with all values above 0.5 indicating greater concordance than random chance and some predictive ability (Table 2.1). The null model's concordance value of 0.5 indicates the null model has a predictive ability equal to chance. The model including both temperature and snow depth had the highest concordance value, indicating these two variables may be the biggest drivers of mortality across two winters. However, neither temperature (z = -1.23, p = 0.22) nor snow depth (z = -1.90, p = 0.058) were significant, nor the associated logrank, likelihood ratio, or wald tests (logrank = 5.32, df = 2, p = 0.07; likelihood = 5.72, df = 2, p = 0.06; wald = 4.2, df = 2, p = 0.1) when using an alpha value of 0.05. However, frequentist p-values for snow depth and the overall model are near the 0.05 alpha value, indicating this model is still likely biologically relevant. Predicted hazard ratios indicate low snow depths and low temperatures may increase mortality risk (Figure 2.2). It is important to note, however, that the lack of events while mismatched (n = 0) caused a violation of models containing the mismatch predictor due to singularity. The zero event group forced a division by zero, rendering the effect size as infinity and thus degenerate. However, the log-rank statistic is calculated without dividing by zero and can be used to compare groups.

2.4.2 Winter behaviour:

During the entire winter period, there was little difference in foraging times between mismatched and matched hares (Figure 2.3). Mismatched hares had a mean winter foraging time of 778.1 minutes (12.97 hours) per day (95% CI 768.8, 787.3), while matched hares averaged 785.1 minutes (13.09 hours) per day (95% CI 779.5, 790.8). Across both categories, daily foraging time was highly variable (min = 375.3 minutes or 6.26 hours, max = 1138.7 minutes or 18.98 hours).

Mismatch was not included as a predictor variable in our top model (Table 2.2). When included with snow depth, it was not within 4 ΔAIC (ΔAIC 20.5, ΔBIC 20.5). Our top model included both temperature and snow depth as fixed effects, and both variables had a significant effect on snowshoe hare foraging time over winter (Table 2.2). Our top model including mismatch and snow depth performs better than the null model in all metrics (ΔAIC 79.1, ΔBIC 68.7, Marginal $R^2 = 0.11$, Conditional $R^2 = 0.42$; Table 2.2). A one degree Celsius increase in temperature was associated with a 2.73 minute decrease in foraging time (standard error = 0.49 minutes, scaled mean squares = 19.82, t value = -5.55, F value = 30.78, denominator df = 1312.7, p-value = 3.5e-8) (Figure 2.4). Snow depth had a negative relationship with foraging time, where one additional centimeter of snow was associated with a decrease in foraging of 1.49 minutes (standard error = 0.16 minutes, scaled mean squares = 52.96, t value = –9.07, F value = 82.26, denominator df = 836.8, p-value = <2.2e-16) (Figure 2.4).

2.5 Discussion:

Animals mismatched to their environment often have lower survival than matched animals, as is consistent with the camouflage hypothesis. However, outcomes of mismatch are not always consistent, and rarely studied outside of the molting season. We examined the effect of winter mismatch on snowshoe hare survival and behaviour on the Island of Newfoundland. Our southeastern geography provided new insight into previously proposed mechanisms behind hare responses to climate change induced colour mismatch. Because our study took place at a southerly latitude similar to Zimova et al. (2016) and Wilson et al. (2019), we expected coat-colour mismatch to have negative fitness outcomes. We also predicted that low temperatures would build on and amplify existing mortality risk from mismatch, due to the increased energy requirements of colder temperatures (Kennah et al. 2022; Sheriff et al. 2009). We did not find evidence to support our hypothesis that mismatch increases predation risk. Contrary to our first prediction that mismatched hares would be preyed upon more than matched hares, we found that snowshoe hares had lower mortality risk when mismatched to their environment (i.e., white on a snowless background). Our second prediction, that cold temperatures will amplify mortality risk via differences in foraging time, is partially supported by our results. We failed to detect a relationship between coat-colour mismatch and winter foraging behaviour. Daily foraging time was instead influenced by environmental variables, and was therefore unlikely to amplify any risk from mismatch. Our results also highlight the importance of snow depth in addition to temperature for both survival and behaviour. Taken together, our results suggest that mechanisms such as energetics or snow-depth mediated predation risk, not lost camouflage due to mismatch, are likely driving hare survival and behaviour in our population. Despite the southern location of our study, we failed to find clear evidence that increased periods of overwinter mismatch associated with climate change were detrimental to snowshoe hares. Importantly, our results provide additional evidence that mechanisms beyond camouflage may impact hares in some parts of the range.

Despite the prevalence of mismatch in studies of coat colour changing species like snowshoe hare, neither the definition of mismatch nor the timing of studies relative to molting periods is consistent. The definition of mismatch used in our study excluded the duration of the molt, and only considered mismatch as periods with <50% of the landscape having snow cover since all hares were completely white (defined as >80% white, but see Appendix 1). Studies at both the northern and southern range extents included the duration of the molt, and vary in how much of the later autumn or winter and spring is included. Mismatch in previous hare studies has been defined as >50% or >60% difference between hare whiteness and percent snow cover (Zimova, Mills, and Nowak 2016; Wilson et al. 2019; Kennah et al. 2022). Despite this difference in definition and timing, hares in our population experience a relatively high proportion of the winter mismatched as a white animal against a snowless landscape (24% or 26 days). The majority of mismatch in our study occurred in early winter, after the autumn molt was completed, and there were very few days of mismatch in the late winter before the spring molt began (0 days in 2022-2023 and 5 days in 2023-2024). Studies at the southern and northern extents of the hare range have reported mismatch only during or directly surrounding autumn and spring molts, and have far fewer days of high contrast mismatch in the early winter. Additionally, when applying our study's definition to publicly available data, previous studies appear to only have one to two weeks of high contrast mismatch in a given year (Zimova, Mills, and Nowak 2016; Wilson et al. 2019; Kennah et al. 2022). These differences in definition may inflate the number of mismatch days present in other studies relative to ours, since the potential days to be mismatched are greater when including molt seasons. Despite having a greater quantity of mismatched days relative to other studies and excluding the molt, we failed to find evidence that periods of winter mismatch negatively affected hares, either through increased risk or changes in foraging rates. The overall trend is clear that hares across their range experience different pressures, and thus mechanistic impacts to winter survival, though some commonalities are present.

Foraging time can be considered as exposure to predation risk, and some animals alter time spent foraging to mitigate the risk of predation. Given that our camouflage hypothesis posits that mismatch increases predation risk, we predicted that hares would alter foraging behaviours while mismatched to mitigate the increased risk. However, mismatch failed to explain daily foraging time in our study. Hares in our study did not reduce their foraging time when mismatched, which is in line with previous studies that describe limited behavioural plasticity in response to mismatch, both in foraging uptake rate (Kennah et al. 2023), and in non-foraging resting site selection (Kumar et al. 2020). However, our prediction of a decrease in foraging when mismatched was based on the expectation that hares would experience higher risk during these periods. Instead, hares survived better when mismatched, likely due to increased risk associated with shallow snow (Peers et al. 2020). Several studies in hares suggest they can adjust their foraging rates under different levels of predation risks (Morris and Vijayan 2018; Shiratsuru et al. 2021; Majchrzak et al. 2022; Studd et al. 2022). Though our measure of mismatch mediated survival did not directly measure risk and may be stochastic, our lack of support for a mismatch mechanism indicates that hares did not experience obvious differences in risk conditions and thus would not differ in foraging behaviour.

Snow depth represents one unique physical challenge of winter, as deep and soft snow can impact animal mobility and access to forage. Though mismatch can never exist with a non-zero quantity of snow depth, we included snow depth in our analyses as a key variable that could impact winter survival and foraging behaviour. Our results, combined with previous studies, suggest snow depth is an important driver of winter mortality risk in snowshoe hares; snow depth and temperature were included as covariates in the top model for both survival and foraging. Snowshoe hares in the Yukon have previously been shown to be more vulnerable to predation in shallow snow, both during the winter (Peers et al. 2020), and the spring (Kennah et al. 2022). Importantly, these studies showed an increase in risk at similar snow depths (~25 cm in Kennah et al. 2022, and ~30 cm in Peers et al. 2020) to our current study (~23 cm). The effect of snow depth is thought to be driven by coyotes (Peers et al. 2020), which we think are likely the main predator is our system based on kill site investigations and camera observations. The effect of coyote predation is likely driven by increased hunting success of predators in shallow snow (Peers et al. 2020), but could be driven by behaviour as hares in our study foraged more at shallow snow depths. The effect of snow on foraging could be caused by a reduced access to food, as increasing snow depth has a small, but significant, effect on forage availability as herbivores gain access to higher reaches of trees (Nordengren, Hofgaard, and Ball 2003). However, the effect of snow depth on foraging rates in our study was relatively small. Snow depth may be indirectly acting on both hare survival and behaviour throughout the winter, but is likely to have regional differences based on predator regime and other local factors.

Though much of the previous mismatch work supports the camouflage hypothesis, one counter example proposes an energetics mechanism (Kennah et al. 2022). The proposed energetics hypothesis posits that the thermal advantages of a winter coat and decreased energetic needs were responsible for heightened survival of white mismatched hares. We investigated the potential energetics hypothesis in our study by examining the impacts of variable temperatures on all white hares. Temperature, in addition to snow depth, was also a predictor in our top survival and foraging models. Hares foraged more in cold temperatures, a pattern which has also been seen in previous work in lagomorphs (Camp et al. 2018). The increase in foraging at colder temperatures may be the mechanism driving the increased mortality risk in cold temperatures that we observed (Figure 2.2). Homeotherms such as hares must increase their caloric intake and increase their metabolism to stay warm when temperatures drop below their thermal neutral zone (Sheriff et al. 2009). Hares thus forage more to reduce mass loss in cold temperatures, likely increasing their risk (Kennah et al. 2023). In our study, hares experienced a tipping point in calculated mortality hazard when temperatures were below -1°C (Figure 2.2). The temperature of -1°C is significantly above the lower critical temperature observed for hares during winter in the Yukon Territory (Sheriff et al. 2009), but still may present a thermal challenge for either hares or predators in our system. Taken together, an energetics hypothesis as proposed by Kennah et al. (2022) may explain these temperature mediated, and not coat-colour, driven results, and should be considered with snow-depth mediated predation risk and adaptations to local environments.

Though coat-colour mismatch is frequently referenced as a negative symptom of the impacts of climate change, our results indicate climate-mediated mismatch may not always be the driver of winter survival and behaviour. Our research contributes to a growing body of evidence indicating that climate change will not have a uniform effects on species across their range. Our results demonstrate both similarities and key differences from other regions hare coat colour mismatch, winter survival, and foraging behaviour has been studied. In our region, environmental variables beyond mismatch drive winter survival and foraging behaviour. We found that snowshoe hares on the Island of Newfoundland had lower mortality while mismatched, but winter survival and foraging behaviour were best predicted by snow depth and temperature. Importantly, the consequences of mismatch are not consistent across the hare range, and may contribute to emerging evidence for local adaptations, where in ecological processes and their underlying mechanisms vary the costs of mismatch for hares. By drilling into complementary, rather than competing, mechanisms, we may build a more robust model of snowshoe hare survival and behaviour that withstands local differences in climatic pressures and adaptations. Unifying common mechanisms and key distinctions across the hare range may allow us to then predict responses of local adaptation to various regions (Houlahan et al. 2017).

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Table 2.1. Model comparison using multiple modes of inference of Cox's proportional hazard regression for snowshoe hare survival data across two winters, 2022-2023 and 2023-2024. Model predictors include mismatch (i.e. snow presence for a completely white hare), snow depth, and temperature. No singular top model emerged using a comparison of AIC and BIC values alone, but the model including both temperature and snow depth had the highest concordance value which is indicative of predictive ability.

Model Predictors	Log Likelihood	AIC	Δ AIC	AIC Weight	BIC	Δ BIC	BIC Weight	Concordance
Mismatch + Snow Depth	-30.06	64.12	0.00	0.29	65.09	0.00	0.26	0.48
Temperature + Snow Depth	-30.23	64.45	0.33	0.24	65.42	0.33	0.22	0.73
Snow Depth	-31.41	64.83	0.71	0.20	65.32	0.23	0.23	0.48
Mismatch	-32.10	66.21	2.09	0.10	66.69	1.60	0.12	0.54
Temperature	-32.30	66.60	2.48	0.08	67.09	2.00	0.10	0.62
Mismatch + Temperature	-31.37	66.74	2.62	0.08	67.71	2.62	0.07	0.62
Null (intercept only)	-33.08	66.17	2.05	0.09	66.17	1.08	0.13	0.50

Table 2.2. Model comparison of generalized linear models using multiple modes of inference for snowshoe hare foraging data across two winters, 2022-2023 and 2023-2024. Model predictors include mismatch (i.e. snow presence for a completely white hare), snow depth, and temperature. In addition to listed model predictors, we included individual hare ID and month as random effects in each model. The model including both snow depth and temperature is ranked highest when considering metrics from AIC and BIC values, and explains the most data via R^2 statistics.

Model Predictors	Log Likelihood	AIC	Δ AIC	AIC Weight	BIC	Δ BIC	BIC Weight	R^2 Marginal	R^2 Conditional
Snow Depth + Temperature	-1652.47	3316.95	0.00	1.0	3348.17	0.00	1.0	0.105	0.423
Mismatch + Snow Depth	-1662.70	3337.41	20.47	3.6E-05	3368.64	20.47	3.6E-05	0.078	0.380
Snow Depth	-1664.92	3339.83	22.89	1.1E-05	3365.86	17.68	0.0001	0.085	0.393
Snow Depth + Temperature + Mismatch	-1675.98	3363.96	47.02	6.2E-11	3395.19	47.02	6.2E-11	0.033	0.313
Temperature	-1687.86	3385.71	68.76	1.2E-15	3411.73	63.56	1.6E-14	0.012	0.299
Mismatch + Temperature	-1688.97	3389.94	73.00	1.4E-16	3421.17	73.00	1.4E-16	0.013	0.299
Mismatch	-1695.81	3401.63	84.68	4.1E-19	3427.65	79.48	5.5E-18	0.000	0.281
Null (intercept + random effects)	-1694.00	3396.00	79.06	6.8E-18	3416.83	68.65	1.2E-15	0.000	0.281

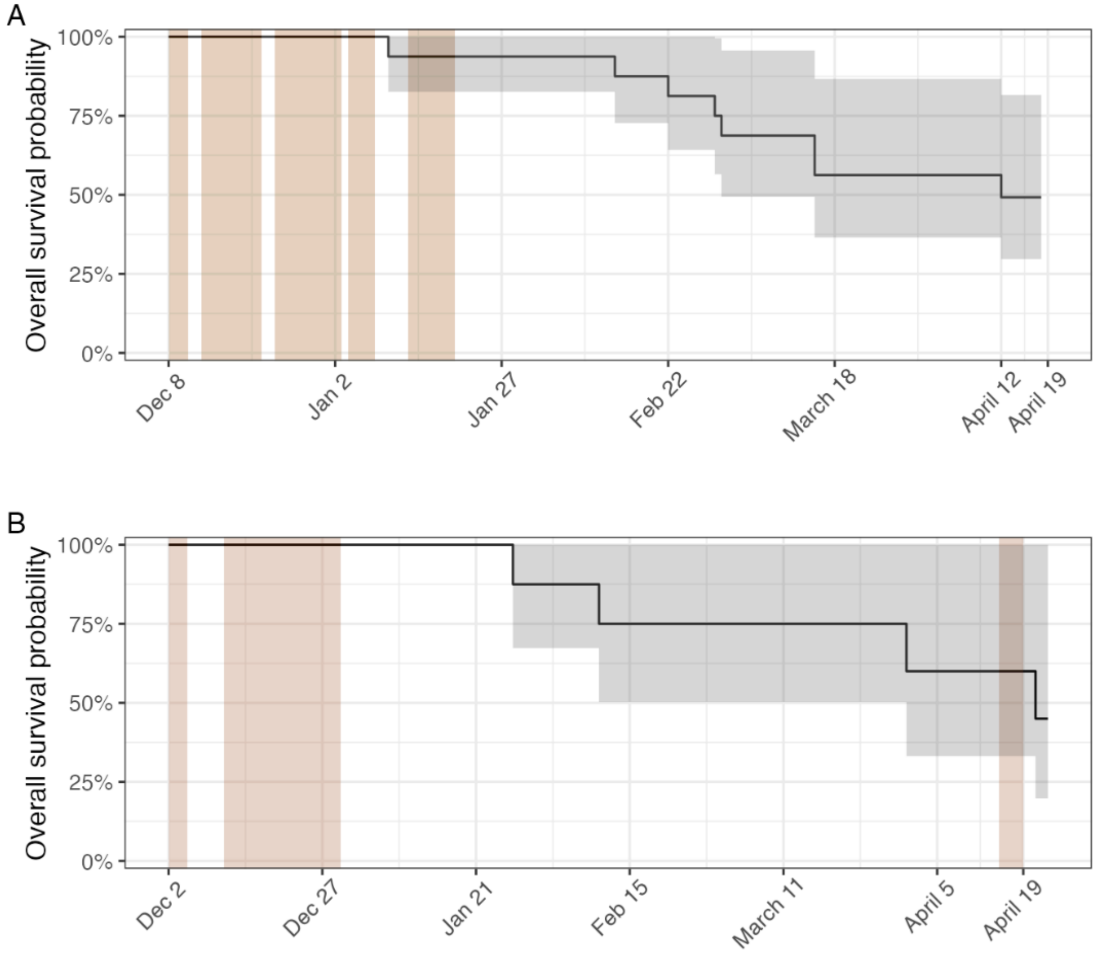

Figure 2.1. Kaplan-Meier survival plots showing overwinter mortality of collared snowshoe hares in Butter Pot Provincial Park in Newfoundland, Canada from A) December 8th 2022 through April 19th 2023 (n = 16) and B) December 2nd 2023 to April 19th 2024 (n = 8). The included date range represents the entire duration of the period when hares were in a winter white coat, as defined as being at least 80% white. Brown overlaid rectangles indicate periods of no snow when all hares were mismatched, while a white background indicates snow cover when hares were matched. The gray band represents the 95% confidence interval around the survival probability.

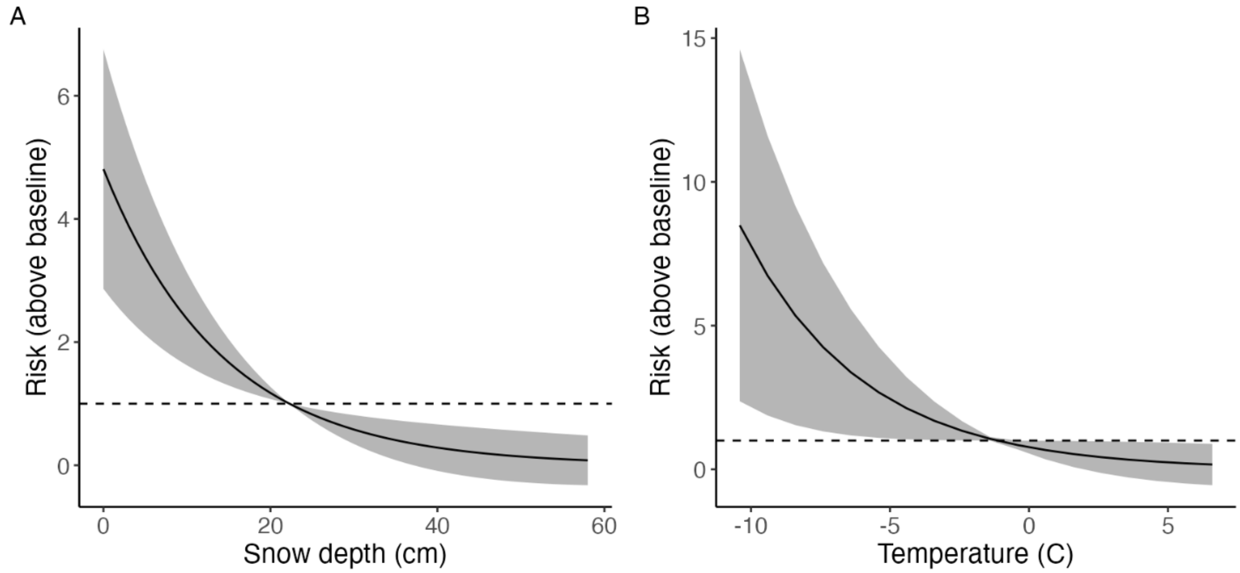

Figure 2.2. Predicted mortality risk (Hazard Ratio) of A) snow depth and B) temperature on snowshoe hares in winter in Butter Pot Provincial Park in Newfoundland, Canada. Dashed lines represent baseline mortality risk (i.e., Hazard Ratio = 1), while the gray shaded areas represent predicted standard errors. Predictions are based on the model including both snow depth and temperature as predictors, as it had the highest concordance value. We held the non-focal covariate from the model at zero for each prediction.

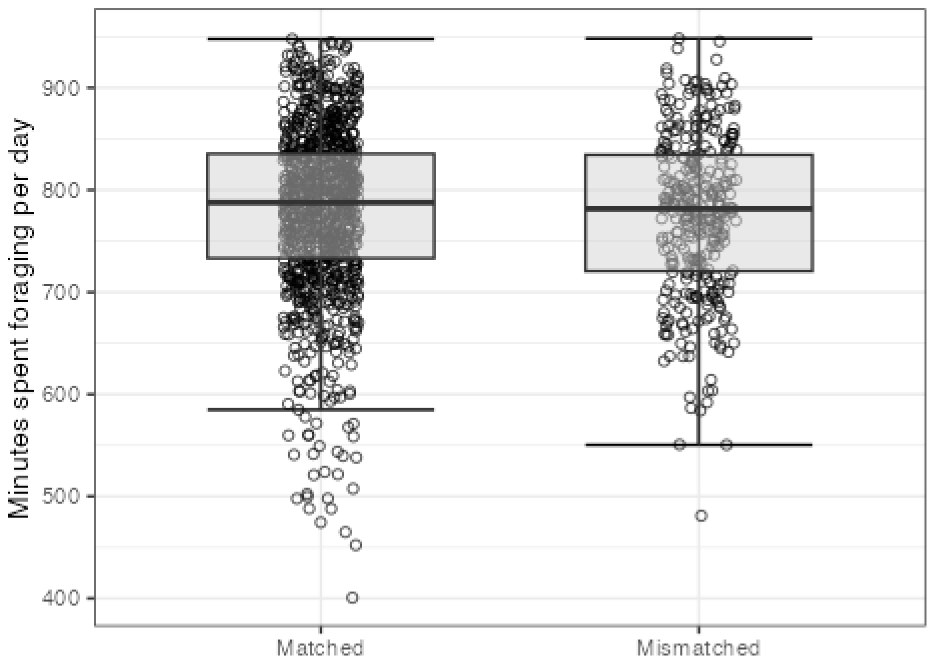

Figure 2.3. Minutes spent foraging per day by snowshoe hares (n = 21) in winter while matched or mismatched to the landscape. Open circles represent an individual’s daily average foraging in minutes. Horizontal lines within the box represent the median. The light gray box displays the upper 75th and lower 25th percentiles of the interquartile range, while whiskers represent the largest and smallest values within 1.5 times the interquartile ranges above or below the grey box.

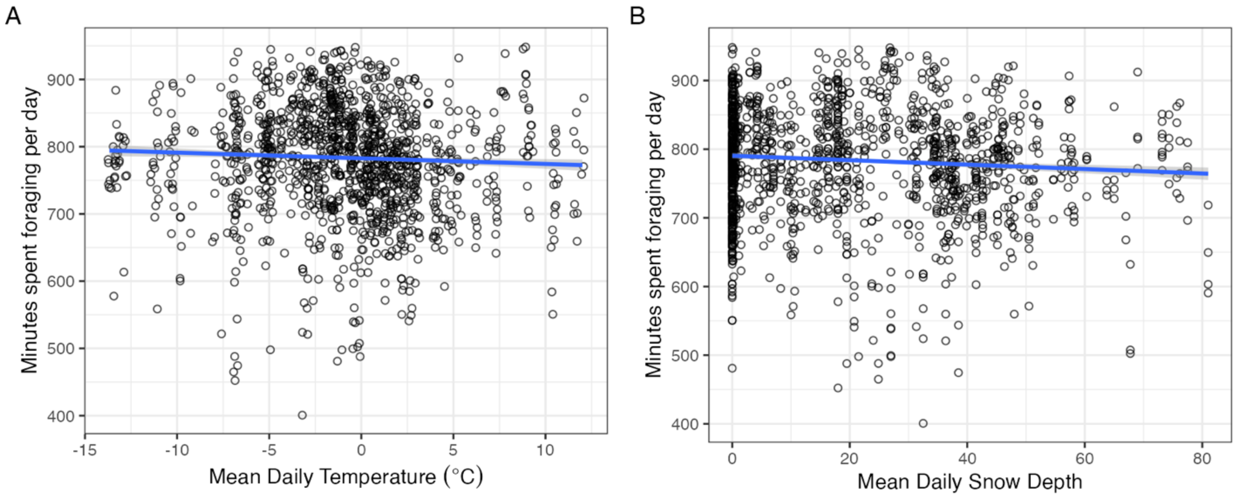

Figure 2.4. The relationship between A) mean daily temperature (°C) and B) snow depth (cm) and minutes spent foraging per day for snowshoe hares (n = 21) during the winter in Butter Pot Provincial Park in Newfoundland, Canada. The blue regression line represents the predicted values from a gaussian linear mixed model with snow depth and temperature as predictor variables, individual ID and month as random variables, and scaled seconds spent foraging per day as the response variable. The predicted fit was converted to minutes spent foraging. Open circles represent the minutes spent foraging in one day by one individual, corresponding to the A) mean temperature or B) mean snow depth that day.

CHAPTER 3: CAN WE DETECT RISK ALLOCATION THROUGH SMALL-SCALE EXPERIMENTAL MANIPULATIONS IN SNOWSHOE HARE? NOT REALLY.

3.1 Abstract:

Prey species balance the acquisition of energy to meet their metabolic demands against the risk of predation. Environmental variables such as habitat structures may influence risk. Risk allocation may also be amplified by climatic events that increase metabolic activity. We used a novel foraging experiment to study the Risk Allocation Hypothesis (RAH) in snowshoe hares (*Lepus americanus*). We tested how hares allocate risks while balancing energy intake and predation using electronic individually assigned feeders to measure give-up-densities of forage (GUDs) under different experimentally altered levels of risk. The RAH predicts that when foraging is more expensive, animals will take more risks to meet their energetic demands. We predicted that snowshoe hares would assume more risks and have a lower GUD when environmental conditions increased their energy needs, e.g., at low temperatures, in high precipitation, and in snow to maintain their energy balance. Contrary to our predictions, however, we found hares were risk averse as a function of the local-environment. We did not find an interactive effect with our simulated risk. Snowshoe hares appear to allocate risk based on local habitat structure, but not springtime weather fluctuations nor our experimental simulated risk conditions.

3.2 Introduction:

Arguably the most fundamental trade-off for an animal is balancing the benefits of foraging with the amplified risk of predation while foraging (Brown and Kotler 2004). Foraging typically increases movement, negatively affects vigilance, and exposes prey to more risk (Lima and Dill 1990). Predator avoidance, alternatively, typically involves minimal movements (Sih 1982) and heightened vigilance (Sirot and Pays 2011). Typically we assume that animals trade-off access to energy and avoidance of predators, via anti-predator adaptations or behavioural plasticity to mitigate risk (Lima and Dill 1990; Verdolin 2006). With greater energetic needs comes greater potential exposure to predation risk, and so animals have adaptations to minimize either side of the energy and risk balance. Though some species can minimize winter energy needs (Turbill and Stojanovski 2018), many adaptations minimize predation through behavioural changes. Some species forage socially to reduce vigilance requirements (Creel, Schuette, and Christianson 2014), while solitary species may reduce time spent or temporally shift foraging, tolerate lower quality forage, or seek “safer” habitat structures in response to heightened predation risk (Schmitz, Beckerman, and O’Brien 1997; Altendorf et al. 2001; Camp et al. 2017; Charalabidis et al. 2017). Climate and weather, such as temperature or snow presence, may also mediate or amplify behavioural responses to predation risk by altering the energy and risk balance, e.g., increased energetic demands at low temperatures (Orrock and Danielson 2009; Sheriff, Speakman, et al. 2009). The extent of effects climatic variables have on foraging behaviours may provide critical context for how animals balance energy intake and risk.

Behavioural changes made in response to predation risk can be understood through the Risk Allocation Hypothesis (RAH) (Ferrari, Sih, and Chivers 2009). The RAH states that animals will respond to temporal changes in predation risk by altering foraging effort and antipredator behaviours (Lima and Bednekoff 1999). Foraging responses can be measured in terms of a giving-up density (GUD), which is the threshold of food remaining in a patch when an animal stops foraging. A given GUD balances the costs of foraging and predation risk, and the opportunity cost of not foraging elsewhere, with the benefits gained from staying (Brown 1988). Foraging responses to predation risk have been widely studied using the RAH as a framework, with animals most often choosing to decrease the time spent foraging, which typically increases their GUD, as risk increases (Verdolin 2006; Catano et al. 2016). For example, large herbivorous reef fishes close to a risky decoy predator consumed less food and were smaller than fishes far from the decoy predator (Catano et al. 2016).

The RAH can also be applied to spatial differences in predation risk, as seemingly small changes in microhabitat can have large impacts on predation risk (Brown and Kotler 2004). Animals may choose to remain in areas with lower quality forage if risk increases with forage quality (Jones and Dornhaus 2011; Camp et al. 2017), or can become less choosy within a risky patch (Charalabidis et al. 2017). Elements of habitat complexity, such as canopy cover or ground level vegetation, can provide shelter or escape routes from predators. Habitat refuges can provide either increased or decreased foraging opportunity depending on habitat type and species involved. For example, some small mammals have a lower GUD in brush habitats than in high risk open habitats (Kotler, Brown, and Mitchell 1993; Orrock, Danielson, and Brinkerhoff 2004; Morris and Mukherjee 2007), while some ungulates and large herbivores have a lower GUD in open grasslands than in dense vegetation (Makin, Chamaillé-Jammes, and Shrader 2018). Changes in foraging behaviour can be a direct response to temporal and spatial predation to balance energy gain with risk and vigilance. The risk of predation in time and space, however, is not the only variable that changes in an herbivore's environment; behavioural responses may be modified by the influence of environmental and weather factors on energetic needs (Orrock and Danielson 2009).

Environmental and climatic variables likely mediate how, and to what extent, animals take risks or engage in antipredator behaviours. Extremes in climatic conditions such as low temperature, heavy snow, or high precipitation may introduce energetic constraints on the type of behavioural choices animals make, and thus may amplify costs to foraging and predator avoidance. The thermal neutral zone (TNZ) is the range of temperatures where an animal can maintain its body temperature without changing its metabolic rate. Animals may be obligated to forage more at low temperatures (Camp et al. 2018) as increased metabolic needs at temperatures below an animal's thermal neutral zone limit behavioural choices (Porter and Kearney 2009). However, when temperatures fall well below an animal's TNZ, the energy gained from foraging may be insufficient to replace the energy cost of foraging. For some small mammals in extremely low temperatures such as gerbilline rodents in Israel (Kotler, Brown, and Mitchell 1993), white footed mice in Iowa, USA (Orrock and Danielson 2009) and in Indiana, USA (St. Juliana and Mitchell 2016), and Alabama beach mice in Alabama, USA (Falcy and Danielson 2013), giving up density is negatively correlated with temperature; a negative correlation means patch use intensity decreases at temperatures significantly below the TNZ. For some small mammals, it appears energetically beneficial to forage more in warmer weather to avoid thermoregulatory costs in the coldest weather (Kotler, Brown, and Mitchell 1993; Orrock and Danielson 2009; St. Juliana and Mitchell 2016). Foraging less in extreme cold also fits the predictions of the RAH if cold temperatures represent periods of higher risk, as animals under the RAH exhibit more antipredator behaviours such as reduced movement in temporary high risk situations (Lima and Bednekoff 1999; Ferrari, Sih, and Chivers 2009). For some mammals small and large, changes in temperature represent an alteration in predator regime that impacts risk taking behaviours (Falcy and Danielson 2013; Vermeulen et al. 2024)). The presence of snow can also significantly impact both sides of the energy acquisition and predation trade-off. Snow can shift the accessible forage on a landscape as plants are physically covered, and is known to alter seed removal rates on some trees (Guiden and Orrock 2021). Snow depth can also directly affect predation risk, as predator success in varying snow depths varies by predator species (Peers et al. 2020). The effectiveness of one common antipredator adaptation, seasonal pelage colour camouflage, is also impacted by the presence or absence of snow (Zimova et al. 2018), and can impact both risk of predation (Zimova, Mills, and Nowak 2016) and nutrition (Kennah et al. 2023) in snowshoe hares. Similarly, precipitation can decrease GUD in small mammals, i.e., animals eat more in a patch in wet (Orrock, Danielson, and Brinkerhoff 2004) or humid (Kotler, Brown, and Mitchell 1993) weather.

Snowshoe hares (*Lepus americanus*) are a keystone species in the boreal forest and act as a critical year-round prey species for predators like coyotes, lynx, and goshawks. As high as 90% of hare mortality is attributed to predation (Hodges et al. 2001; Krebs, Boonstra, and Boutin 2018), and high predation risk alters hare behaviour and increases stress (Majchrzak, Peers, et al. 2022; Sheriff, Krebs, and Boonstra 2011). Snowshoe hares respond to predation risk by decreasing their foraging time when predation risk is high (Hik 1995; Shiratsuru et al. 2021; Majchrzak, Peers, et al. 2022; Shiratsuru and Pauli 2024). Hares under high predation risk also select for areas of high cover (Beaudoin et al. 2004; Gigliotti and Diefenbach 2018; but see Morris and Vijayan 2018) and certain habitat structures mediate predation during high risk periods (Wilson et al. 2019). However, the RAH is not always supported, indicating that predation risk is not the only factor to which hares are sensitive (Richmond et al. 2022). Climatic factors also influence hare behaviour, and thus should be expected to impact the balance between acquiring energy and predation risk. Hares reduce movement, which is closely associated with foraging, at extreme low or extreme high temperatures (Gigliotti, Diefenbach, and Sheriff 2017). Snow has a significant effect on predation risk for hares, where risk is influenced both by snow depth (Peers et al. 2020) and coat-colour mismatch (Mills et al. 2013; Zimova, Mills, and Nowak 2016; Kumar et al. 2020; but see Kennah et al. 2022; Monk Chapter 2, this thesis). Other environmental variables, such as wind speed (Studd et al. 2022) and moonlight (Gigliotti and Diefenbach 2018; Morris 2019; Studd et al. 2019), have been associated with changes in hare behaviour via elevated predation risk. The intersection of environmental climatic factors with the balance of energy and risk can help tease apart mechanisms behind how hares perceive and respond to changes in their environment.

We test the RAH and the trade-off between energy acquisition and predation risk under various environmental and weather conditions while experimentally manipulating risk in a wild population of snowshoe hares. We used microchip enabled feeders to measure behaviour via GUD. We placed each feeder under tables with switchable opaque or clear tops to manipulate environmental risk in each treatment beyond natural canopy cover variation. We predicted that a clear top table would be perceived as more risky than an opaque top table in a given location with constant canopy cover. Similarly, we predicted that areas of high canopy cover would have an interactive effect with opaque table tops to be less risky. The RAH submits that when foraging is temporarily more risky, animals will reduce risk taking behaviour. Animals will then forage more in low risk environments to meet their energetic demands (Lima and Bednekoff 1999). Using the RAH framework, we predicted that snowshoe hares would have a higher GUD, or consume less food from a feeder, at the higher risk (clear) table tops and under low canopy cover. We also predicted that additional climate variables would further mediate risk, and hares would forage less in low temperatures, high precipitation, and in snow.

3.3 Methods:

We conducted our experimental study in Butter Pot Provincial Park in eastern Newfoundland and Labrador, Canada. This region is a mix of boreal forest, barren areas, and bogs; forests are dominated by black spruce (*Picea mariana*) and balsam fir (*Abies balsamea*) with some tamarack (*Larix laricina*) and white birch (*Betula papyrifera*). The provincial park is home to coyotes (*Canis latrans*), northern goshawks (*Accipiter gentilis*), and red foxes (*Vulpes vulpes*); we did not detect Canada lynx (*Lynx canadensis*), the main predator of hares elsewhere in the boreal forest, on four motion activated trail cameras placed around the monitoring area (Hyperfire Reconyx, Inc, Holmen, Wisconsin, USA). Cameras were active both during and outside of this experimental study, from October through May 2022-2023 and 2023-2024. We began the experiment in late April 2023 before the snow melted, and ended in late May after spring green up began. The region receives a high number of days with precipitation, with a 30 year 1981-2010 climate normal average of 15.5 days with precipitation, totaling 105.3mm in May, when the majority of our study took place (Environment Canada 2019). The average 30 year climate normal temperature in May is 6.9°C (SD = 1.6), with a daily minimum of 2.5°C and a daily maximum of 11.3°C (Environment Canada 2019).

We captured snowshoe hares twice in April prior to the beginning of the experiment using Tomahawk live traps (Tomahawk Live Trap Co., Tomahawk, WI, USA). The first trap session established resident hares remaining from fall and early winter trap data (Monk Chapter 2, this thesis). Each hare received a unique ear tag for individual identification (Monel #3

National Band and Tag Co., Newport, KY, USA). Hares captured a second time in the same area of the trapping grid were outfitted with VHF radio telemetry collars with an attached pit tag (Model MI-2 M, Holohil, Canada). Pit tags allowed hares to access electronic selective feeders keyed for one individual (SureFeed Microchip Pet Feeder, Sure Petcare, Cambridge, UK) (Majchrzak, Peers, et al. 2022). Prior to the beginning of our experiment, hares (n=8) were habituated to using the electronic feeders with ad libitum access. During 7 habituation days, we slowly introduced the electronic sound and movement of the feeder lid to target hares. At each feeder, we placed motion activated camera traps (Hyperfire Reconyx, Inc, Holmen, Wisconsin, USA) to monitor successful use of feeders. We attached unique barcode patterns made of heat shrink to each collar's antenna to identify individual hares and ensure the correct hare was habituated to the correct feeder (Majchrzak, Menzies, et al. 2022). Following confirmation of successful feeder use by target hares, we began our experiment. Hares that did not successfully use the feeders, or feeders that broke in the habituation process, were not included in the experiment phase (n=3). Of the five hares that successfully used the feeders, two were female and three were male; all were adults.

We considered risk as the summation of vertical and lateral cover, and designed this experiment to investigate risk from vertical cover alone. We placed electronic feeders (n=5) under small wooden tables with changeable table tops made from wood or plexiglass to alter simulated vertical risk (Figure 3.1). A clear table top simulated a higher risk level, while a solid wood table top simulated a lower risk level. We sheltered feeders from precipitation using clear plastic bins placed on their sides, which did not inhibit feeder access (Figure 3.1). Each individual hare in the experiment (n=5) was exclusively assigned to one feeder under one table, but experienced switching table top types with each trial iteration. Previous GUD work and food patch experiments in small mammals has used nonedible substrate such as soil, sand, and pieces of plastic that provide diminishing returns as the ratio of nonedible substrate to remaining food increases (Brown 1988; Kotler, Brown, and Mitchell 1993; Orrock, Danielson, and Brinkerhoff 2004). To achieve a similar effect, we used natural LECA (lightweight expanded clay aggregate) gardening balls. We filled feeders with 150 g of undried commercial rabbit pellets mixed with 50 g of non-toxic clay balls (Figure 3.1). We use dried weights in all analyses; 150 g of undried rabbit chow is 139.8 g once completely dried. Each trial lasted two nights, with one table top type above a given feeder per trial (n = 59). After each trial we collected, dried, and weighed any remaining food in each feeder. There were no breaks between trials, and we swapped table top types at each feeder table and refilled the food in the afternoon between trial nights. Food not consumed from feeders in each trial time period represents the give up density (GUD) in this experiment, and is given by the dried weight of remaining food removed from the nonedible clay ball substrate. Trials when a hare did not eat any food (n = 14) were removed from our analysis, as there can be no measure of giving up if the hare does not visit the feeder. We also removed trials when a problem with the feeder or interference from other animals allowed non-target individuals to access food (n = 10). Finally, we removed one trial (n=1) because it did not have any matched observations with a different table top treatment.

We measured environmental and climatic variables in addition to the quantity of food eaten in a given trial. We measured canopy cover using the mobile densiometer application CanopyApp (University of New Hampshire). A photo of the canopy was taken from the center of the table at each feeder site, and then we applied a machine learning mask on each photo to determine the percentage of the image covered by the canopy. To ensure accuracy, we took and masked two photos at each site in the middle of the experiment and averaged the values. We estimated the amount of snow in a circle with a five meter radius around the feeder after each trial, at the same time remaining food was collected. Snow cover above 20% was considered as snow present in our analyses. Though higher snow cover cutoffs have been used in hare coat colour mismatch studies (Zimova, Mills, and Nowak 2016; Kennah et al. 2022) hares are likely still impacted by snow on the landscape at lower snow cover levels. Though hares do select for snow free resting sites (Kumar et al. 2020), patchy snow presence is often concentrated in shady and covered areas of the landscape where hares may rest. Camera traps at each feeder provided overnight temperatures for our analysis of minimum overnight temperature. Overnight temperatures were recorded from a minimum of three cameras each night between 6:30 PM and 6:30 AM. Motion activated cameras recorded images and temperatures when a hare was present, and three or more cameras prevented us from missing the true minimum if a single hare was not foraging at the time of the minimum. For precipitation, we used data from the St. John's West Environment Canada weather station, located 25 km away from our study site (Environment Canada 2019). We used the total amount of precipitation between 6:30pm on the first night of a given trial until 6:30 AM on the last day of the trial in our analysis.

We analyzed all data in the R programming language (R Core Team 2024). All models use the quantity of food remaining as GUD. To test our hypothesis that temperature, snow, and precipitation mediate risk taking while foraging, we used a model selection approach and built general linear candidate models using the package glmmTMB (Brooks et al. 2017). The candidate set included the treatment type (table top type) and/or environmental variables as predictors, and the amount of uneaten food eaten (GUD) as the response variable. We used interactive effects between predictor variables in most models where relevant to our specific predictions. We did not use hare ID as a random variable because many other variables are also unique to a feeder site, and thus are confounded with hare ID. All models used a gaussian distribution; we checked model assumptions in residuals using the DHARMa package (Hartig 2016). We then selected the top model using both Akaike information criterion (AIC) and Bayesian information criterion (BIC). Using both AIC and BIC allowed us to view a more full image of the goodness of fit and generalizability of a model under different penalization regimes. A strong candidate model must show a pattern of agreement between modes of inference. We considered a singular model as highest ranking if its AIC and BIC value was four units less than the next highest ranking model. We also used AIC and BIC weights to quantify the probabilities, or relative likelihood, of each model. Pseudo-R^2 values that replicate the multiple R^2 value, and do not penalize for the number of parameters, were then used to inform the results of the top models.

3.4 Results:

A total of 34 trials were successful and are included in our results, out of the 59 attempted. The maximum number of successful trials from an individual hare is 9, while the minimum is 4. The average amount of food eaten from feeders per successful trial was 115.1 grams (95% CI [106.7, 123.5]) out of a total of 139.8 grams, or 82.3%. The average GUD was 24.7 g (95% CI [16.3, 33.1]). The minimum GUD was 0 g, meaning that all food was consumed from a feeder, and the maximum GUD was 102.7 g, meaning that 37.1 g or 26.5% of available food was consumed.

Contrary to our predictions, the highest ranked model includes canopy cover as the sole predictor variable. Canopy cover accounts for 37% of variance in the data (Table 3.1). Using frequentist statistics, canopy cover had a significant effect on GUD (Residuals DF = 31, $z = 4.38$ $p < 0.001$). The direction of effect is also contrary to what we predicted using the RAH framework. The model with canopy cover indicated that with every one percent increase in canopy cover, the quantity of food left in a feeder increased by 1.37 grams (95% CI [0.75, 1.98]), i.e., hares ate less from feeders under greater canopy cover. (Figure 3.2).

From our candidate model set, no models had a ΔBIC within four units of the highest ranked univariate canopy cover model. However, six models had ΔAIC within four units of the highest ranked model (Table 3.1). The highest ranking model had AIC and BIC weights higher than any competing models. R^2 values of the top six ranked models are similar; slightly increased R^2 values are likely due to the additional predictors included in competing models compared to the single variable top model. Importantly, when predictors other than canopy cover were considered in univariate models, each ranked below the null model and may be considered uninformative parameters (Table 3.1). The similar R^2 values and likelihood of uninformative parameters provide evidence complementary to the AIC and BIC values to indicate that the highest ranking model including canopy cover alone best explains the data.

Our models failed to support our hypothesis and predictions that climatic variables mediate risk taking simulated by our experimental tables while foraging. The highest ranking model did not include table top treatment, temperature, snow cover, nor precipitation. As additional evidence that environmental variables did not influence foraging and risk taking decisions by hares, none of the environmental variables were statistically significant in their respective models using a frequentist approach with an alpha value of $p = 0.05$ (Figure 3.3). Snow and temperature can be considered independent based on a Pearson's correlation test ($r = -0.28$, $t = -1.67$, $df = 32$, p-value = 0.11).

3.5 Discussion:

The Risk Allocation Hypothesis posits that animals will respond to changes in predation risk by altering their behaviour. Additionally, animals trade off energy acquisition and predator avoidance in foraging and other behaviours. We used an experiment, inspired by Morris and Vijayan (2018) to test how snowshoe hare foraging behaviour is impacted by climatic and environmental variables known to impact the balance of energy acquisition and predation risk. Our experiment was designed to manipulate perceived risk based on a small built habitat feature, and held habitat risk constant while climatic variables impacting energy fluctuated. We predicted, in part, that higher canopy cover combined with an opaque table top would be less risky and associated with greater foraging than clear top tables. Though we did find risk aversion as a function of the environment, we did not find an interactive effect with our table treatment. Our study was likely limited by sample size and some unclear foraging responses resulting from the risk:reward ratio in our experimental set up. However, our intention to control for canopy cover revealed that snowshoe hares were foraging sensitive to risk; however, hares foraged more when risk was assumed to be higher, contrary to our predictions.

Habitat structure, such as canopy cover, is a frequent metric of behaviour and predation risk in studies of snowshoe hares and other species. While our study attempted to control for variance in canopy cover, our failure to detect behaviour changes from experimental table top treatments indicate hares might perceive habitat structures at different scales than our experimental tables. Though our predictions were specific to our table top treatment types, we expected a greater level of cover to be associated with more food consumed from feeders, or a lower GUD. Instead, hares in our study consumed more from the feeder under less dense canopy cover, with canopy cover as the sole predictor in our highest ranking model. A similar experimental study also failed to detect an effect of supplemental cover, and showed that hare responses to predation risk are more nuanced than the typical assumption that open habitats are more risky (Morris and Vijayan 2018). In contrast, greater hare abundance, measured by pellet counts or GPS, has been most often linked to high or non-open vegetation cover (Pietz and Tester 1983; Lewis et al. 2011; Ewacha, Roth, and Brook 2014; Gigliotti et al. 2018). Comparisons to previous canopy cover studies require careful attention to how words such as “moderate” or “high” are defined. Numerically, the lowest canopy cover value in our study is similar to the moderate value defined in Fuller and Harrison (2013); Fuller and Harrison (2013) found greater hare abundance under moderate canopy cover as compared to high canopy cover. . It is critical to consider, however, that a metric of hare abundance in a given area does not necessarily mean that is the area with the greatest foraging activity. Foraging selection can be considered a higher order selection than home range, and thus we cannot directly compare our results to studies considering the lower level selection processes of presence in a given place or home range (Johnson 1980). Foraging habitat selection, especially for our very high reward rabbit chow, may be decoupled with general abundance given that hares are not central place foragers.

The balance between energy acquisition and expenditure can provide critical context for why an animal may exhibit certain foraging or anti-predator behaviours, and was a key mechanism behind our predictions in this study. Our results failed to support our prediction that precipitation, snow presence, or minimum overnight temperature influenced the trade-off between energetics and predation risk. Studies in rodents both smaller and similar in body mass to snowshoe hares have also found no effect of precipitation on GUD (Ceradini and Chalfoun 2017; Flower et al. 2019), and indicate that wet weather may not represent an energetic challenge to smaller herbivores. When snow is patchy, as it was for much of our experiment, animals can make fine scale selections for microclimates to minimize unnecessary energy expenditure (Sarmento, Biel, and Berger 2019; Kumar et al. 2020). Hares may have been able to mediate energetic impacts from patchy snow with behavioural changes not captured in our foraging study, given that hares were mid-molt and not well matched to either a snowy or snowless background. With regards to temperature, the lowest nightly temperature recorded in our experiment was -2 °C, and minimum temperatures ranged in value by less than 10 °C over the experiment duration. The lower critical temperatures for hares in a summer brown coat has been reported as 0 °C to -10 °C, where oxygen consumption increases (Sheriff, Kuchel, et al. 2009). Our minimum temperature of -2 °C is near the edge of the thermal neutral zone for hares, and likely did not represent a sufficiently large thermal challenge. It is important to note, however, that many previous studies on GUD and thermal neutral zones were done on *Peromyscus* species e.g. (Orrock and Danielson 2009; St. Juliana and Mitchell 2016), which have different adaptations to winter than hares such as nest building. Sympatric species can deal with thermal challenges, behaviourally and physiologically, in both similar and quite different ways, limiting broad scale cross species comparisons among homeotherms (Menzies et al. 2020). Despite potential species level differences in cold temperature or wet weather foraging, our results indicate that temperatures near or above the lower critical temperature recorded for hares, precipitation, or snow presence are unlikely to alter behavioural responses.

A significant proportion of previous GUD studies in mammals have been conducted on small rodents due to the relative ease of using many small feeder trays over a given area (Kotler, Brown, and Mitchell 1993; Orrock, Danielson, and Brinkerhoff 2004; Morris and Mukherjee 2007; St. Juliana and Mitchell 2016). In contrast, comparably few GUD studies have been conducted on larger mammals, and many fail to meet assumptions of GUD studies (Wuensch, Pratt, and Ward 2023). Our a priori predictions were thus primarily based on feeding trials and risk assessments in small mammals, though the energetic demands of snowshoe hare differ. We sought to avoid making comparisons with central place foragers, as animals with centralized behaviours will respond differently to risk than species that do not return to a centralized place, or those who occupy a niche "safe" habitat (i.e. ibex sheltering on cliffs; (Iribarren and Kotler 2012). Despite snowshoe hares being moderately small, our results share similarities to those from larger bodied mammals like ungulates rather than studies with small rodents. Snowshoe hares remain exposed on the landscape year-round like many moderate and larger bodied mammals that are depredated, and lack safe refuges or physical barriers like snowpack above the subnivean. Constant exposure to unpredictable weather and risk, and a larger body size than small rodents, likely create different energetic demands that contribute to a difference in GUD outcomes. Hares in our study displayed lower GUD while in lower canopy cover sites, which contrasts much of the small mammal GUD work (Kotler, Brown, and Mitchell 1993; Morris and Mukherjee 2007; Orrock, Danielson, and Brinkerhoff 2004). Many ungulates have lower GUD while in open areas, though open canopy areas are often in contrast with a forest or forest edge and are not a direct equivalent of our lowest cover sites (Altendorf et al. 2001; Stears and Shrader 2015; Makin, Chamaillé-Jammes, and Shrader 2018). However, this trend is not consistent for all larger bodied mammals (Esparza-Carlos, Íñiguez-Dávalos, and Laundré 2018), and ungulates change risk taking behaviour with changes to food availability (Stears and Shrader 2015). Importantly, the cues animals use to determine the risk from a particular habitat appears to shift with each species and associated energetic demands.

Our experimental study used a novel method to assess the Risk Allocation Hypothesis via foraging changes to environmental and climatic conditions. Though our study provides insight into how hares allocate risks and respond to climatic conditions, we had a limited sample size. A larger than anticipated number of electronic feeders either broke, or animals did not become habituated to them, and thus we could not include those animal-feeder pairs in the experiment (n = 3). Future studies would benefit from an increased sample size to rule out individual personalities or stochastic results. Additionally, we may have underestimated the risk to reward ratio provided by supplying very high nutrition food with easy to sift through clay balls. For example, some trials did not provide sufficient information because hares consumed all provided food (n = 6, or 10.2% of attempted trials), and thus an accurate measure of giving up was not achieved. Animals may have also consumed more food than anticipated, as risk allocation can be more pronounced and foraging greater in environments where conditions fluctuate rapidly (Higginson et al. 2012). Our failure to detect risk allocation with regard to climatic variables may be in part due to highly stable and unanticipated weather conditions, which may not have provided an adequate range of energetic challenge to see results in our small sample size. Finally, we did not analyze all elements of habitat structure and risk, such as horizontal cover and predator regime. Terrestrial predators are more limited in Eastern Newfoundland than in much of the continental hare range, so we focused on vertical cover. Despite our choice in study design, horizontal cover density is known to be positively associated with hare selection and use (Berg et al. 2012; Ewacha, Roth, and Brook 2014; Holbrook et al. 2017; Gigliotti et al. 2018), and dense understory is associated with higher overwinter survival (Litvaitis, Sherburne, and Bissonette 1985). Sight distances can explain some habitat preferences in ungulates (Stears and Shrader 2015), and provide information about predation risk not captured by vertical canopy cover. Though this was not a study on predation, previous work has shown that predictability in predation risk has measurable consequences on growth and foraging, and that behavioural response studies alone can lead to an incomplete image of predator-prey dynamics (Trussell, Matassa, and Luttbeg 2011). Despite the limitations on our study, our novel experimental study contributes to the growing body of work relating to snowshoe hare risk allocation and foraging behaviour.

Our experimental study provides additional context for how hares balance energy and risk. Our results suggests that snowshoe hares display risk aversion as a function of the environment, but not with the experimental control and climatic variables we predicted. Our small built table structures with switchable tops did not garner a risk allocation response, and our results indicate that hares perceived other elements of habitat structure when making foraging selections. Though we recommend further study on the high level selection processes of foraging under habitat mediated risk, our study indicates that hares may not experience risks in the same way small mammals do. Though we failed to detect an effect of springtime minimum overnight temperature, snow presence, and precipitation on risk allocation, greater variance in climatic variables may shift the balance between energy acquisition and risk.

3.6 References:

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Table 3.1. Model comparison of generalized linear models using multiple modes of inference for GUD (amount of food remaining after two trial nights) from electronic feeders as the response variable. Model predictors include experiment treatment, canopy cover, precipitation, snow cover, and temperature. We used interactive effects between predictor variables in most models where relevant to our specific predictions. The model including canopy cover alone is selected as our top model when considering all modes of inference. Importantly, univariate models for predictors other than canopy cover rank below the null model and may be uninformative parameters.

Predictors	Log Likelihood	AIC	Δ AIC	AIC Weight	BIC	Δ BIC	BIC Weight	Pseudo R^2
Canopy Cover	-149.33	304.67	0.00	0.41	309.25	0.00	0.77	0.37
Canopy Cover * Precipitation	-148.04	306.09	1.42	0.20	313.72	4.47	0.082	0.41
Canopy Cover * Snow Cover	-148.73	307.46	2.79	0.10	315.09	5.84	0.041	0.39
Treatment + Snow Cover + Canopy Cover	-148.75	307.49	2.82	0.10	315.12	5.87	0.041	0.39
Canopy Cover * Temperature	-148.97	307.94	3.27	0.080	315.57	6.33	0.033	0.38
Treatment * Canopy Cover	-149.26	308.51	3.84	0.060	316.14	6.90	0.024	0.37
Treatment + Snow Cover + Canopy Cover + Temperature	-148.70	309.39	4.73	0.039	318.55	9.31	0.0073	0.39
Null (intercept only)	-156.94	317.88	13.21	< 0.001	320.93	11.69	0.0022	0.00
Precipitation	-156.79	319.58	14.92	< 0.001	324.16	14.92	< 0.001	0.009
Temperature	-156.91	319.81	15.14	< 0.001	324.39	15.14	< 0.001	0.002
Treatment	-156.92	319.84	15.17	< 0.001	324.42	15.17	< 0.001	0.001
Treatment * Snow	-156.94	319.88	15.21	< 0.001	324.46	15.21	< 0.001	< 0.001
Snow Cover	-155.64	321.27	16.61	< 0.001	328.91	19.66	< 0.001	0.076
Precipitation * Treatment	-156.41	322.83	18.16	< 0.001	330.46	21.21	< 0.001	0.031

Precipitation * Temperature	-156.63	323.26	18.59	3.8E-05	330.89	21.64	< 0.001	0.019
Treatment * Snow Cover	-156.86	323.72	19.05	3.0E-05	331.35	22.11	< 0.001	0.005
Treatment * Temperature	-156.87	323.74	19.07	3.0E-05	331.37	22.12	< 0.001	0.004

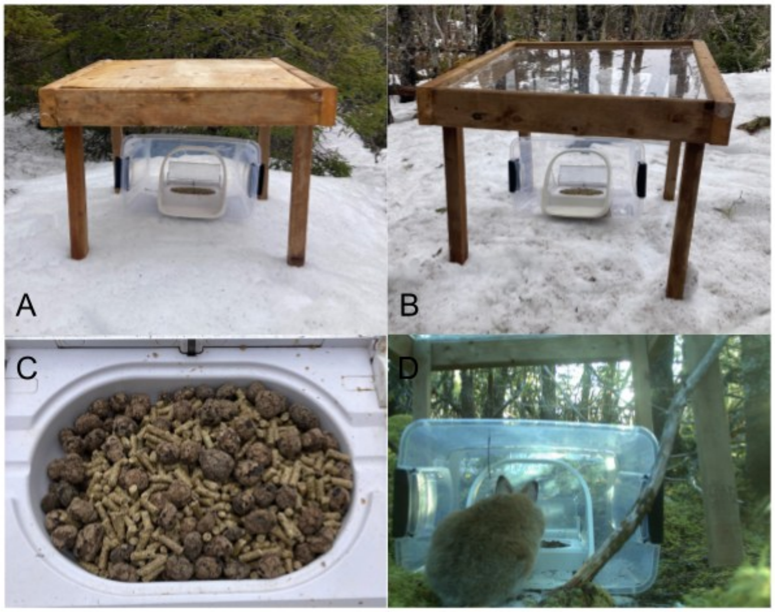

Figure 3.1. Photographs detailing our experimental set-up. Panels A and B depict the small wooden tables with changeable table tops made from wood or plexiglass. An electronic feeder is under each table, sheltered from the elements in a small plastic tub laid on its side. Panel C shows the mixture of commercial rabbit chow and clay gardening balls, which slowed foraging from the feeders. Panel D shows the experimental set-up with a collared hare actively eating from a feeder, though parts of the table are not in frame.

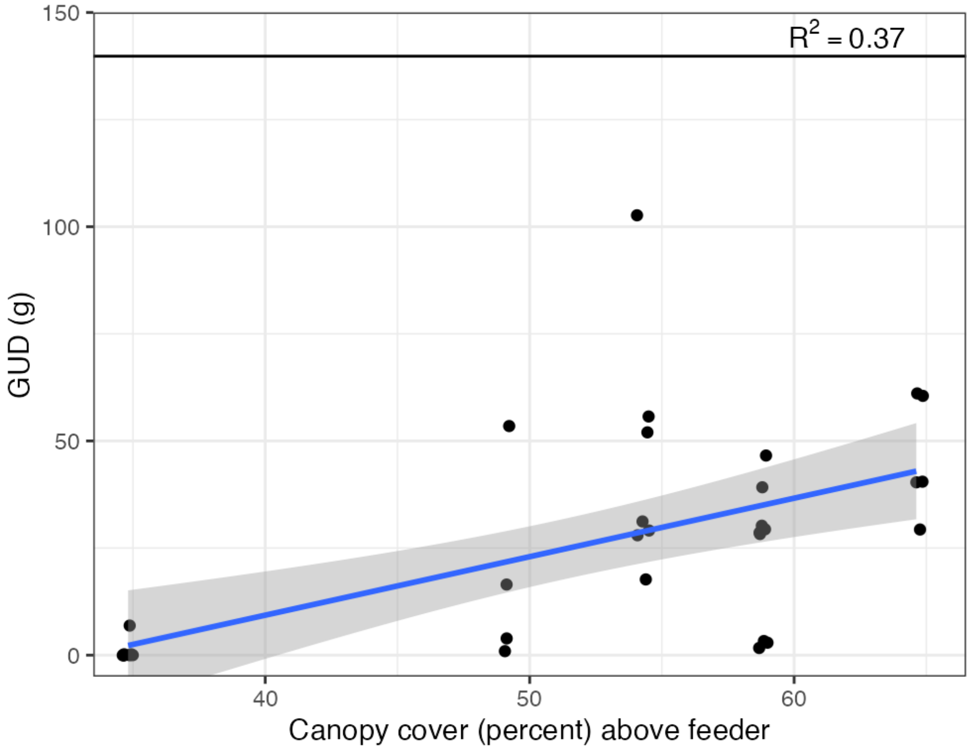

Figure 3.2. Giving up density (GUD) from electronic feeders over each two-night trial by individual snowshoe hares in May 2023. Canopy cover had a significant negative effect on the amount of food consumed in each two-night trail, where GUD increased with canopy cover. Five canopy cover values are represented, as individual feeders were not moved during the experiment and were associated with one canopy cover value. Each slightly jittered black dot represents one trail, while the black horizontal line represents the total quantity of food available. Black dots at zero indicate a hare consumed all food available in that trail. The blue line represents the model regression with an R^2 of 37%, and the grey band represents the standard error.

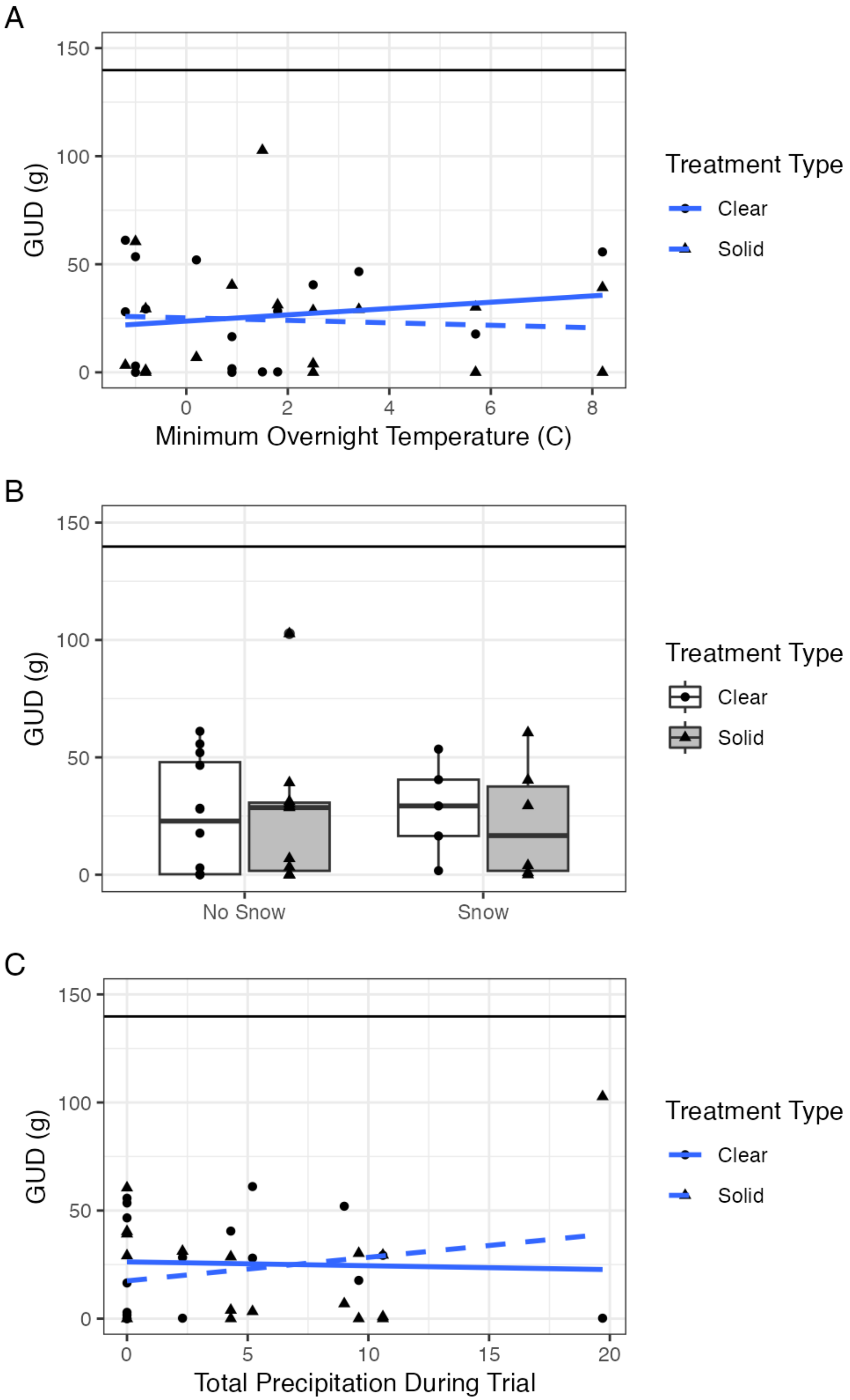
A
GUD (g)
150
100
50
0
0
2
4
6
8
Minimum Overnight Temperature (C)
Treatment Type
Clear
Solid
B
GUD (g)
150
100
50
0
No Snow
Snow
Treatment Type
Clear
Solid
C
GUD (g)
150
100
50
0
0
5
10
15
20
Total Precipitation During Trial
Treatment Type
Clear
Solid

Figure 3.3. Giving up density (GUD) from electronic feeders over each two-night trial by individual snowshoe hares in May 2023 and environmental variables. Feeders were placed under small wooden tables with either a clear top to simulate high risk or a solid top to simulate lower risk during each trial. (a) Minimum overnight temperature, (b) snow presence, and (c) total precipitation were not included in the highest ranking model, and did not have a significant impact on risk taking behaviour while foraging. Each black dot or triangle represents one trail, while the black horizontal line represents the total quantity of food available. Black dot or triangle centered on zero indicates a hare consumed all food available in that trail. Blue lines represent non-significant regression models.

CHAPTER 4. EPILOGUE

4.1 Summary

Animals must balance consuming food for adequate energy against the risk of predation. Additional variables, such as climatic factors, can tip the scales of this balance between energy and risk (Lima and Dill 1990; Verdolin 2006). In my thesis, I investigated how climate variables influence the balance between foraging and predation risk for snowshoe hares. I first (Chapter 2) tested how winter coat colour mismatch and weather variables influence foraging behaviour and survival. I specifically tested the camouflage hypothesis using a combination of data from accelerometer data loggers and telemetry, as well as weather data. Then, I used a novel experiment (Chapter 3) to examine how environmental variables influenced risk taking behaviours, testing the Risk Allocation Hypothesis in the context of climate factors. I showed that there is not likely to be a single mechanism behind snowshoe hare survival and behaviour, and that the balance between energy and risk is context dependent. Instead, my results point to both similarities and differences across the hare range that will help resolve how temperature and snow influence the balance between energetics and risk.

In Chapter 2, I used natural variation in weather conditions that created periods of match and mismatch to directly investigate how camouflage mismatch influenced the balance of energy gain and predation risk in winter. I showed that on the Island of Newfoundland, the camouflage hypothesis is not supported; snowshoe hares mismatched in winter had lower mortality risk than matched hares. Mismatch also had no effect on foraging behaviour. Instead, both survival and foraging behaviour were influenced by temperature and snow depth. Taken together, the results suggest that mechanisms such as temperature driven energetics or snow-depth mediated risk drive snowshoe hare survival and behaviour. While negative survival effects have been found in other regions, the drivers of winter survival I found are the same as those found in the Yukon Territory, suggesting the potential for unified snow depth and temperature mechanisms. The similarities and differences in results across the hare range underscores the necessity of finding common underlying mechanisms to explain range-wide responses.

In Chapter 3, I used a novel foraging experiment to stimulate different levels of altered risk in a wild setting to test how hares allocate risks while balancing energy intake and predation. Hares did not allocate risk based on our experimental simulated risk or under naturally changing weather conditions. Instead, we found that hares were risk averse as a function of the local-environment, or canopy cover. These results suggest that not all temperatures and other weather conditions will impact the balance between energy gain and risk, but that other factors of the environment may contribute towards shifting this energy-risk scale.

Both Chapters 2 and 3 demonstrate that external factors impact the balance between consuming food for energy and the risk of predation. Temperature impacts energetics, while snow depth and canopy cover have direct implications on predation risk. The range of temperatures in Chapter 2 were much colder than those in Chapter 3, and may indicate that only very cold temperatures represent an energetic challenge where effects can be detected. The conditions in Chapter 3 may have been too warm to detect energetic effects similar to those in Chapter 2. The specific conditions where snow depth and temperatures impact the balance between energetics and risk provides context to the result comparisons made across the hare range in Chapter 2.

4.2 Addressing the idiosyncrasies of place

It is often the goal of ecological study to make conclusions applicable to a scale larger than that of the individual study. However, most species occupy large ranges, and field research studies take place on a small and local scale. It is thus imperative to consider how the idiosyncrasies of place may contribute to broader ecological generalizations (Billick, Price, and Rocky Mountain Biological Laboratory 2010). We must consider both what makes our place unique, as well as what makes it generalizable across time and space. Snowshoe hares have been studied across their wide range in Northern North America, and as in many other systems have been found to do different things in different places. The hare range is highly varied climatically with slightly varied species assemblages, putting different pressures on local populations. Diving deeper into these idiosyncrasies of place can help uncover hidden mechanisms and put seemingly different results into a broader context.

In both of my data chapters I propose energetics as one potential mechanism behind my results or hypotheses. Simply put, it is harder to be an animal on a very cold day than when the temperature is well within the animal's thermal neutral zone. However, the minimum temperatures experienced by hares in different regions of their range can vary dramatically (see Figure 1.1). The minimum recorded temperature in Chapter 2 was -19 °C, and in my springtime Chapter 3 was -2 °C. While these minimum temperatures do not reflect the averages experienced by a hare in Newfoundland, they do represent the most energetically challenging conditions a hare experienced during my study. These temperatures are in stark contrast to the minimum temperatures of -40 to -50 °C a hare in the Yukon Territory may experience. The lower critical temperature for snowshoe hares is between -10 and -15°C (Sheriff et al. 2009), however this was measured in the Yukon territory at the northern extent of the hare range. Hare study sites in the Yukon Territory experience far more days below this lower critical temperature (annual average days below -10°C = 155.6) (Environment Canada 2019a) than my site in Newfoundland does (annual average days below -10°C = 34.9) (Environment Canada 2019b). Given such a stark regional difference in extreme cold, we should question if the expectation for this lower critical temperature to remain consistent is valid.

We know that individuals can shift their resting metabolic rate and thermal neutral zones with seasonal changes in temperature (Haim et al. 1991; Sheriff et al. 2009). We should then entertain the idea that populations across a broad range may have different thermal neutral zones in a given season. Snowshoe hares in the southern extent of their range have shorter, less dense, less white, and lower pelage temperatures in winter coats than hares in the North, indicating a geographic adaptation for the range of temperatures experienced in an average winter (Gigliotti, Diefenbach, and Sheriff 2017). With these differences in winter coats, a hare in the Yukon Territory likely experiences a winter temperature of -10 °C differently than a hare in Pennsylvania or Newfoundland. Additionally, from Chapter 2 we know that hares in Newfoundland experience a higher proportion of winter mismatched than has been reported elsewhere in the southern extent of their range; regardless of the direct impacts of mismatch on hares, we can use this as a visually obvious cue that hares have different winter experiences and are being impacted by climate change differently across the range. If seasonal energetic demands are not uniform for a species across its range, then we must consider these idiosyncratic elements of place when making generalizations or comparisons. I encourage future work to measure the lower critical temperature of hares in a winter white coat in multiple other regions of the range to more fully understand the intensity of local temperature pressure.

Beyond differences in local temperature exposure, hares across the range are predated on by differing predator guilds. Lynx were not detected in my study sites, and predation is believed to be driven by coyotes, red fox, and goshawks. However, lynx are prominent drivers of snowshoe hare population dynamics in the Yukon territory, where my Chapter 2 results are most similar. In contrast, southern regions like Montana have lynx present in the system, but also are home to predators with a more southern distribution in North America like bobcat. Different predators use different strategies to predate upon hares, which will interact with climate change differently. For example, snow depth was found to be important in Chapter 2, and I discussed how coyotes increase predation on hares in shallow snow. Lynx, in contrast, do not show strong snow depth trends, and so the driver of snow depth may be less important in regions where lynx are a larger cause of mortality than coyotes (Peers et al. 2020).

I encourage readers of my thesis, especially Chapter 2, to focus not on differences in results across time and place, but instead on common threads and influences that may deepen our general understanding of winter in the boreal forest. Differences in results from different locations, and even those that seem to be in opposition, are not new to ecological study. In searching for generality, Pulliam and Waser proposed three hypotheses to guide thinking about variable niche expression: 1. Differential methods, 2. Variation in the realized niche, and 3. Variation in the fundamental niche (Pulliam and Waser 2010). Considering many distributed place-based experiments can help reconcile local findings; thus, drilling down beyond initial reactions to local differences can foster the uncovering of a set of rules that govern species responses (Pulliam and Waser 2010). With the place-based research in this thesis, I encourage future hare researchers to strengthen the interplay between the knowledge of a particular system or region with general ecological theory; local knowledge can push conceptual frameworks, while general ecological theory informs local experimentation and pattern recognition (Price and Billick 2010). The greatest advances in ecology come when we can bridge the divide between place-based empirical knowledge and place-less theory and consider multiple ecological perspectives at the same time (Krebs 2010).

4.3 Future Directions

The work in my thesis provides another perspective on seasonal mismatch and the balance of energetics and risk, and expands on previous work elsewhere in the hare range. However, as with all field-based studies, our work was limited by practical and logistical constraints. Limited sample sizes, logistical constraints on field efforts, and stochastic weather conditions limited the strength and generalizability of our conclusions. Additionally, the limited depth of contextual regional knowledge at my study site introduced assumptions into my study design and hypotheses, and makes finding underlying common mechanisms with other regions more challenging. However, my results contribute to the growing body of knowledge about coat colour-changing species and provide a launch point for potential future research across geographies. I identify key similarities in winter behaviour and survival mechanisms with previous hare work that should be investigated further. I provide recommendations for future work rooted in both the successes and limitations of this place-based thesis that may help identify rules governing species responses, as well as additional conceptual and theoretical frameworks to address the idiosyncrasies of place (Billick and Price 2010; Price and Billick 2010; Pulliam and Waser 2010).

In all empirical studies, a large sample size is ideal to best represent the greater population and detect small effects. Indeed, across many studies, a failure to detect significant relationships is partly owing to the limited power of small sample sizes (Jennions and Moller 2003). Chapter 2 was limited logistically by the number of collars and accelerometers accessible for use in the study, and suffered from a significant number of collar failures in the second winter. Not all hares had accelerometers, and thus some mortality dates were less accurate than others as they were dependent on human investigation timing. Additionally, the weather in both winters did not provide the quantity of winter mismatch we anticipated. Anecdotally, recent winters in the region had less persistent snow and more snow-free periods throughout the winter season. We hoped to detect winter mismatch across many snow-to-no-snow switches, but were not afforded this opportunity. Though our sample size of mismatch days was lower than expected, we were still able to detect relationships and show a greater quantity of mismatch than has previously been reported. Future work would benefit from a long-term study in the region to capture the stochasticity of winter weather patterns. Chapter 3 was more limited by sample size than Chapter 2. The experimental design introduced a number of limitations that decreased the sample size from our initial target value - individual hare choice, feeder failure, and non-target animal interference all contributed to the small sample size. With only five individuals studied and a high number of variables considered, it is impossible to rule out the effect of individual differences and other stochastic elements. We encourage future research to work from our novel design with a greater number of feeders and animals. Additionally, we encourage future work with feeders to plan for a relatively high failure rate when selecting a target sample size.

The concept of predation risk is central to the motivations and design of my thesis. The experimental design in Chapter 3, as well as my hypotheses and predictions in both Chapters 2 and 3 made several assumptions about how hares perceive risk. However, despite a heavy reliance on the concept of predation risk, we know relatively little about the actual risk experienced by hares in my study site. A detailed accounting of species specific predation risk could inform the types of behaviour and habitat features that may induce higher levels of predation in certain regions or times of year. Our knowledge of the predator regime in Butter Pot

Provincial Park came from personal observations by long term park staff and our small number of field cameras (n=4). This knowledge, however, may be biased towards canid predators, and does not provide adequate information on predator density. Our mortality investigations were also insufficient to detect predation rates by specific species. Limitations in field personnel and collar movement by scavengers that reset the mortality sensor caused us to detect the mortality signal days after the predation event; we frequently could not identify the predator based on the remaining carcass if more than the collar existed at the kill site at all. An ideal future study would more fully quantify risk via targeted camera trapping efforts to provide density information, as well as with greater species specific predation rate data from rapid mortality investigations. Coupled with information like species specific risk in shallow vs deep snow (Peers et al. 2020), robust predator regime knowledge could provide insight into niche expression to better understand seemingly different results across locales (Pulliam and Waser 2010).

Beyond information about which predators are most likely to kill hares in winter, studies investigating hypotheses similar to the Camouflage and Risk Allocation Hypotheses would benefit from more detailed knowledge on why a hare is predated in a given place at a given time. Predictions from the Camouflage and Risk Allocation Hypotheses make assumptions based in general theory about what may cause an individual hare to be predated, as well as expected responses from the individual to avoid predation. However, we know from previous place-based research that habitat type can impact the source of predation more than immediate cover (Feierabend and Kielland 2015). In a Wisconsin study, hares had differential survival in different habitat types, and mismatch did not negatively impact survival in one of those habitat types (Wilson et al. 2019). Differences in risk based on habitat type may help explain and unite some differences between place-based studies across the hare range. We also know very little about what cues predators detect from prey, and how they use those cues in a successful hunt. A considerable body of work has examined cues used by prey species to avoid predators (e.g. Kuijper et al. 2014; Mitchell et al. 2015; Luttbeg et al. 2020; Jones et al. 2024), but comparably few studies focus on predators and how they successfully detect, recognize, and hunt prey (Staddon and Gendron 1983; Hansen, Holen, and Mappes 2010; Geller and Parker 2022). Fewer still consider colour-camouflage detection by predators or consider conspicuousness of prey (Staddon and Gendron 1983; Théry et al. 2005; Merilaita and Dimitrova 2014; Atmeh, Andruszkiewicz, and Zub 2018). One study used decoys to assess predator response to colour-mismatch, and found that predators better detected high contrast models (Atmeh, Andruszkiewicz, and Zub 2018). However, we still lack knowledge about both how predators perceive coat-colour mismatch in moving animals, as well as what other viaual, auditory, or chemical cues supplement colour contrast in each predator species. Diving deeper into the mechanisms behind predation events may help develop rules governing species responses, as well as conceptual frameworks that bolster general ecological theory to address the idiosyncrasies of place (Billick and Price 2010; Price and Billick 2010; Pulliam and Waser 2010).

One of the strengths of place-based research is that both common and differing results in different regions can lead to a robust mechanistic understanding of phenomena. My results and proposed temperature and snow depth mechanisms represent this strength of place-based work, despite logistical limitations. My results and conclusions are similar to studies in the Yukon territory (Peers et al. 2020; Kennah et al. 2022), which has very different climate and biotic pressures from the Island of Newfoundland. Similarities across results in different geographies reinforce the validity of proposed mechanisms in each study, and bring us closer to identifying unified mechanisms. Using this thesis and work in the Yukon as a starting point, future studies should work to uncover why previous results from parts of the Southern portion of the hare range are different are different from what I found in Chapter 2 (Mills et al. 2013; Zimova, Mills, and Nowak 2016; Wilson et al. 2019). I identified that temperature is a potential driver of behaviour and mortality, but responses may be limited outside of energetically challenging conditions. Measurement of thermal neutral zones across the hare range could provide a place-based theoretical foundation to investigate what constitutes an energetic challenge for hares and inform a unified temperature mechanism. Additionally, future work can integrate snow depth into considerations of species-specific predation risk; future work should record the snow depth, snow hardness, and predator species at any winter kill site to further evaluate snow mediated risk mechanisms. Mechanistic concepts of temperature and snow depth could then be expanded beyond snowshoe hares to similar seasonally coat-colour changing species to evaluate and predict responses to climate change across geographies.

4.4 Conclusion

The balance between energy gain through foraging and predator avoidance due to predation risk is impacted by factors like temperature, snow-pack, and local habitat features. These external forces are grounded by local context, but have important common threads with and distinctions from other regions that can push our conceptual understanding of ecological theory. My thesis contributes to mismatch and behavioural frameworks by providing evidence for how snowshoe hares respond to realized and experimentally manipulated predation risk. Additionally, my results provide context for how hares and other seasonally colour-changing species may respond to climate change as temperatures warm, snowpack declines, and winter mismatch increases. I present a potential launch point for future research to identify unified temperature and snow depth mechanisms that drive the balance between energetics and risk across the hare range.

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APPENDIX 1: CHAPTER 2 COAT COLOR “CUT-OFF VALUE” COMPARISON

The snowshoe hare literature differs slightly in what has been used as the cutoff for considering an individual as winter white, as detailed in the main text. To ensure our results are robust and can be directly compared to other studies, we tested two cutoffs for what is considered a white hare. Here, we compare an 80% and 50% white cutoff for all analyses. We only use the first winter of data in this comparison, as the first winter included very frequent trapping that provides a precise timeline of the molt. The second year of data has fewer observations, and interpolation assumptions could bias this comparison. Because we are using one year of data, the results of each model will differ slightly to what is reported in the main text.

In the 2022-2023 winter monitoring period, there was a total difference of 23 days between the 50% and 80% white cutoffs. In the autumn, using a 50% white cutoff rather than 80% increases the monitoring period by 14 days; hares were 50% white on November 24th, and were 80% white on December 8th 2022. In the spring, a 50% cutoff increases the monitoring period for hares by nine days; hares were 80% white on April 19th, and 50% white on April 28th. There were no additional mortality events when comparing a 50% cutoff compared to an 80% cutoff in either the autumn or spring. However, due to equipment availability there were no mortality checks done on collars prior to December 8th in the first year. In the survival analyses here, we do not adjust this date even though no collared animals died between collaring in early autumn and the first mortality check to avoid introducing bias. Survival analyses are thus limited to comparing the nine-day difference in the spring. Foraging behaviour analyses do capture the full 23 days difference between cutoffs.

In the analysis of survival, there is no difference between a 50% and 80% white cutoff, though the analysis is limited to capturing spring differences (Figure A1). In fact, the outcomes of Cox proportional hazard models are identical across the two cutoffs, despite the 50% white model suite including more survival checks. This is expected, as there were no additional mortalities when expanding the monitoring from the period when hares were 80% white to 50% white. Identical model selection outcomes for the 50% and 80% cutoffs are shown in Table A1, while identical model predictions appear in Figure A2.

In the comparison of foraging between the 50% and 80% white monitoring periods, the full difference of 23 days is represented. In the analysis of foraging time, the model with snow depth and temperature predictors is the top model selected using either a 50% or 80% white cutoff (Table A2). Mismatch is not included as a predictor variable when using either cutoff, nor does foraging time differ between match and mismatch (Figure A3). When evaluating the top temperature and snow depth model for each cutoff, there is no difference in results in the first winter. A one centimeter increase in snow depth is associated with 66.60 fewer seconds foraging in the model representing 80% white monitoring period, while the 50% cutoff is 64.52 fewer seconds (Figure A4). Similarly, an increase in temperature by one degree Celsius is associated with a decrease in foraging of 270.44 sec in the 80% white monitoring period, and 257.58 sec in the 50% white monitoring period (Figure A4). The difference in foraging time outcomes between an 80% and 50% white cutoff is less than 5%, and indicates that selecting one monitoring period over another is unlikely to greatly impact results.

We evaluated two different winter monitoring lengths that represent a 50% and 80% white cutoff. Our results from one winter indicate there is no difference in survival or foraging result outcomes when using an 80% white or 50% white cutoff. While it is important to consider season specific pressures in the shoulder seasons, we show that whole winter outcomes are not impacted by a total of ~3 weeks of differential data inclusion depending on which white cutoff is used. Our result provides confidence when comparing studies that use slightly different thresholds for considering an animal winter white. A robust result will not be impacted by slight definition changes, and we encourage a focus on larger overall winter trends when looking at individual studies or comparing results across time and space.

Table A1. Model comparison using multiple modes of inference of Cox's proportional hazard regression for snowshoe hare survival data in the winter of 2022-2023. All models are shown using both a 50% and an 80% white cutoff, representing a larger and smaller monitoring period, respectively. Predictors include multiple climatic variables including mismatch (i.e. snow presence for a completely white hare). Model outcomes are identical between the 50% and 80% monitoring periods, as no additional mortality events were captured in the 50% white monitoring period compared to the 80% period.

Model Predictors	AIC	Δ AIC	AIC Weight	BIC	Δ BIC	BIC Weight	Concordance
50% White							
Mismatch + Snow Depth	34.98	0.00	0.43	35.14	0.00	0.43	0.51
Mismatch	36.35	1.38	0.22	36.43	1.30	0.22	0.58
Mismatch + Temperature	37.62	2.65	0.12	37.78	2.65	0.11	0.64
Snow Depth	38.02	3.04	0.094	38.10	2.96	0.097	0.51
Temperature + Snow Depth	38.52	3.54	0.073	38.68	3.54	0.072	0.66
Temperature	38.64	3.66	0.069	38.72	3.58	0.071	0.64
80% White							
Mismatch + Snow Depth	34.98	0.00	0.43	35.14	0.00	0.43	0.51
Mismatch	36.35	1.38	0.22	36.43	1.30	0.22	0.58
Mismatch + Temperature	37.62	2.65	0.12	37.78	2.65	0.11	0.64
Snow Depth	38.02	3.04	0.094	38.10	2.96	0.097	0.51
Temperature + Snow Depth	38.52	3.54	0.073	38.68	3.54	0.072	0.66
Temperature	38.64	3.66	0.069	38.72	3.58	0.071	0.64

Table A2. Model comparison of generalized linear models using multiple modes of inference for snowshoe hare foraging data in the winter of 2022-2023. All models are shown using both a 50% and an 80% white cutoff, representing a larger and smaller monitoring period, respectively. Models predictors include multiple climatic variables including mismatch (i.e. snow presence for a completely white hare). In addition to listed model predictors, we included individual hare ID and month as random effects in each model. Using either a 50% or 80% white cutoff, the model including both snow depth and temperature is ranked highest when considering metrics from AIC and BIC values, and explains the most data via R^2 statistics.

Model Predictors	AIC	Δ AIC	AIC Weight	BIC	Δ BIC	BIC Weight	R^2 Marginal	R^2 Conditional
50% White								
Snow Depth + Temperature	1839.28	0	0.97	1866.59	0	0.77	0.10	0.33
Temperature	1846.28	7	0.029	1869.03	2.45	0.23	0.066	0.28
Mismatch + Temperature	1850.94	11.66	0.003	1878.25	11.66	0.002	0.066	0.28
Mismatch + Snow Depth	1871.63	32.35	9.1E-08	1898.94	32.35	7.8E-08	0.043	0.27
Snow Depth	1876.64	37.36	7.5E-09	1899.4	32.81	5.8E-08	0.044	0.28
Snow Depth + Temperature + Mismatch	1874.02	34.74	2.8E-08	1901.32	34.74	2.2E-08	0.06	0.22
Mismatch	1885.03	45.75	1.1E-10	1907.79	41.2	8.7E-10	0.006	0.23
80% White								
Snow Depth + Temperature	1774.76	0	0.99	1801.85	0	0.91	0.12	0.35
Mismatch + Snow Depth	1783.82	9.06	0.011	1806.39	4.55	0.093	0.068	0.27
Snow Depth	1788.48	13.72	0.001	1815.57	13.72	0.001	0.069	0.28
Snow Depth + Temperature + Mismatch	1807.4	32.64	8.1E-08	1834.49	32.64	7.4E-08	0.055	0.28
Temperature	1813.16	38.41	4.5E-09	1835.74	33.89	4.0E-08	0.055	0.29
Mismatch + Temperature	1811.62	36.86	9.8E-09	1838.7	36.86	9.0E-09	0.062	0.22

Mismatch	1822.72	47.96	3.8E-11	1845.29	43.45	3.3E-10	0.006	0.22

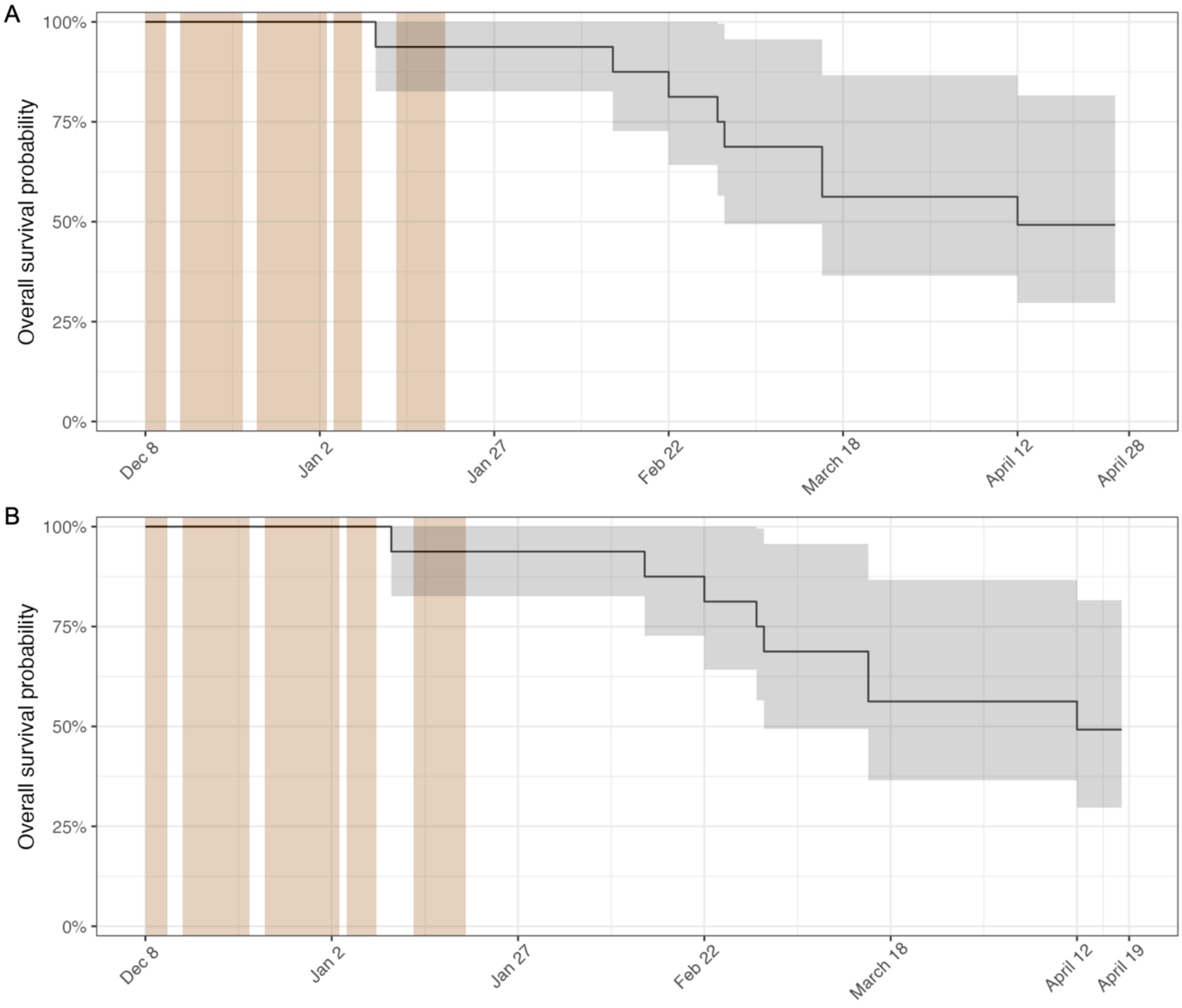

Figure A1. Kaplan-Meier survival plots showing overwinter mortality of collared snowshoe hares in Butter Pot Provincial Park in Newfoundland, Canada from A) 50% spring white monitoring period from December 8th 2022 through April 28th 2023 and B) 80% spring white monitoring period from December 8th 2022 to April 19th 2023. Brown overlaid rectangles indicate periods of no snow when all hares were mismatched, while a white background indicates snow cover when hares were matched. The gray band represents the 95% confidence interval around the survival probability. No additional mortality events occurred when using the longer 50% white spring monitoring period (B).

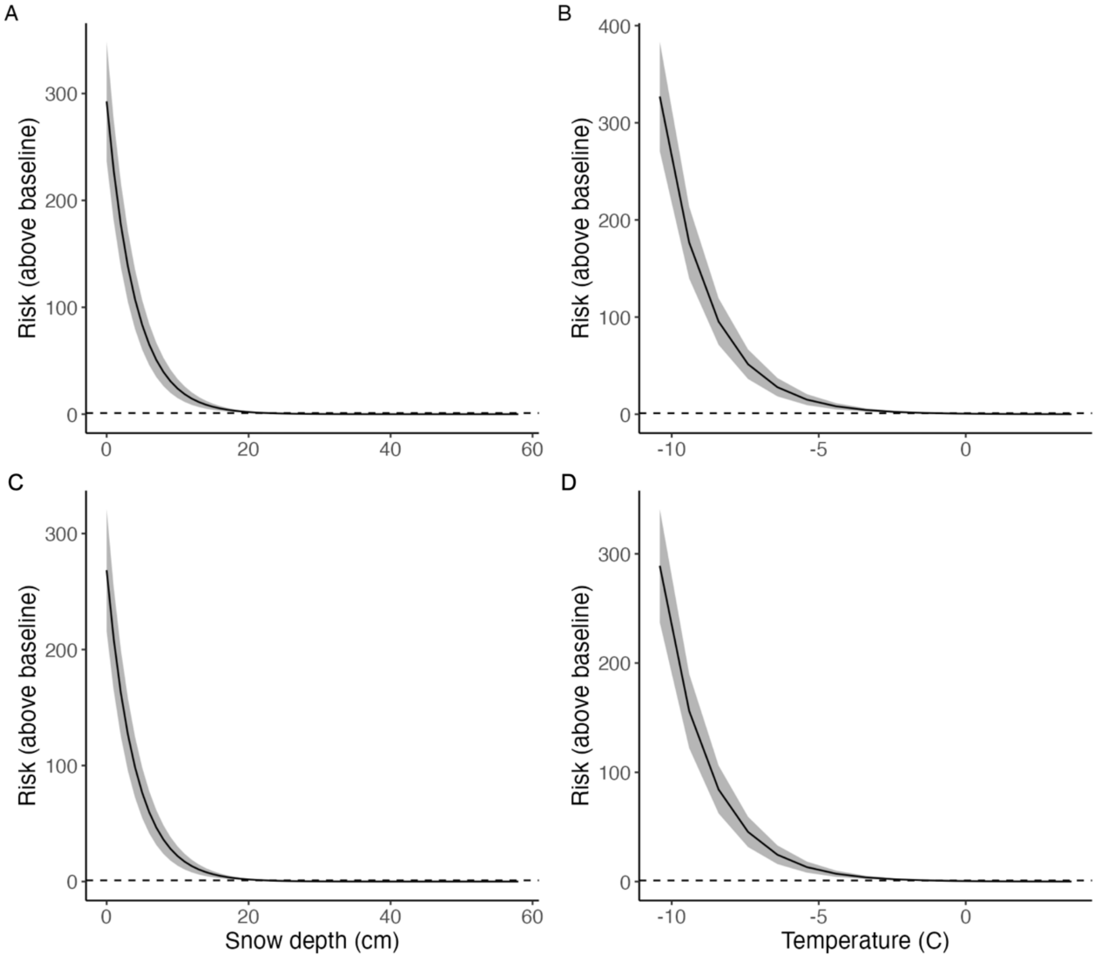

Figure A2. Predicted mortality risk (Hazard Ratio) of snowshoe hares in winter in Butter Pot Provincial Park in Newfoundland, Canada. Panels A and B show predicted hazards for hares 50% white or greater, representing the longer monitoring period, while panels C and D show the predicted hazard for hares monitored while 80% white or greater. Dashed lines represent baseline mortality risk (i.e., Hazard Ratio = 1), while the gray shaded areas represent predicted standard errors. Predictions are based on the model including both snow depth and temperature as predictors. We held the non-focal covariate from the model at zero for each prediction. There is no difference between predicted hazards from models using the 50% white monitoring period compared to the 80% period, as no additional mortality events occurred.

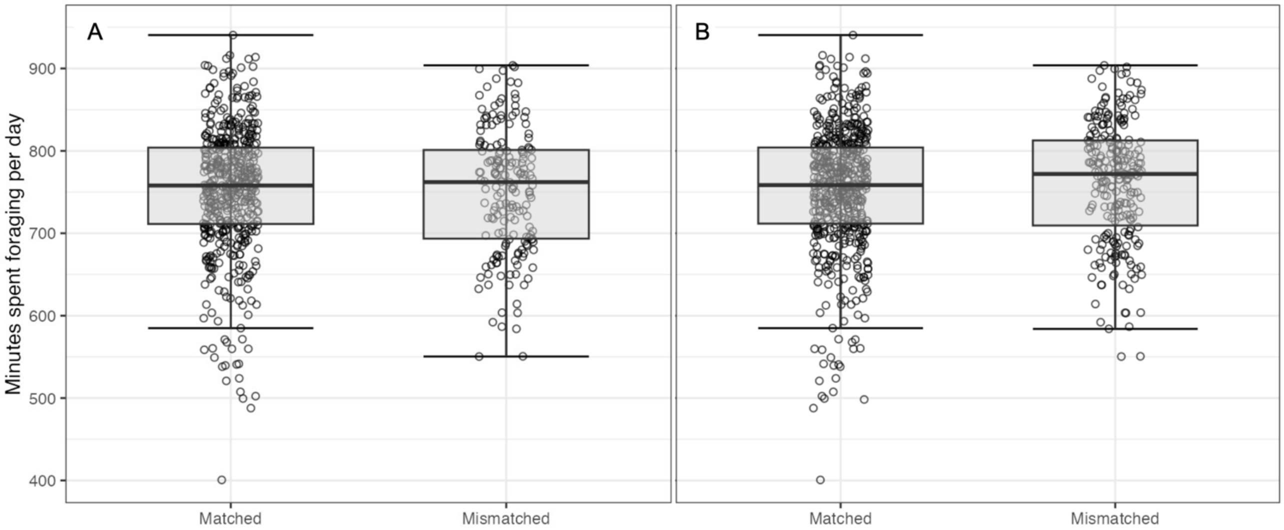

Figure A3. Minutes spent foraging per day by snowshoe hares in winter while matched or mismatched to the landscape using A) a 50% white cutoff or B) an 80% white cutoff. Open circles represent an individual's daily average foraging in minutes. Horizontal lines within the box represent the median. The light gray box displays the upper 75th and lower 25th percentiles of the interquartile range, while whiskers represent the largest and smallest values within 1.5 times the interquartile ranges above or below the grey box. There is no difference between foraging time using the 50% white monitoring period compared to the 80% period.

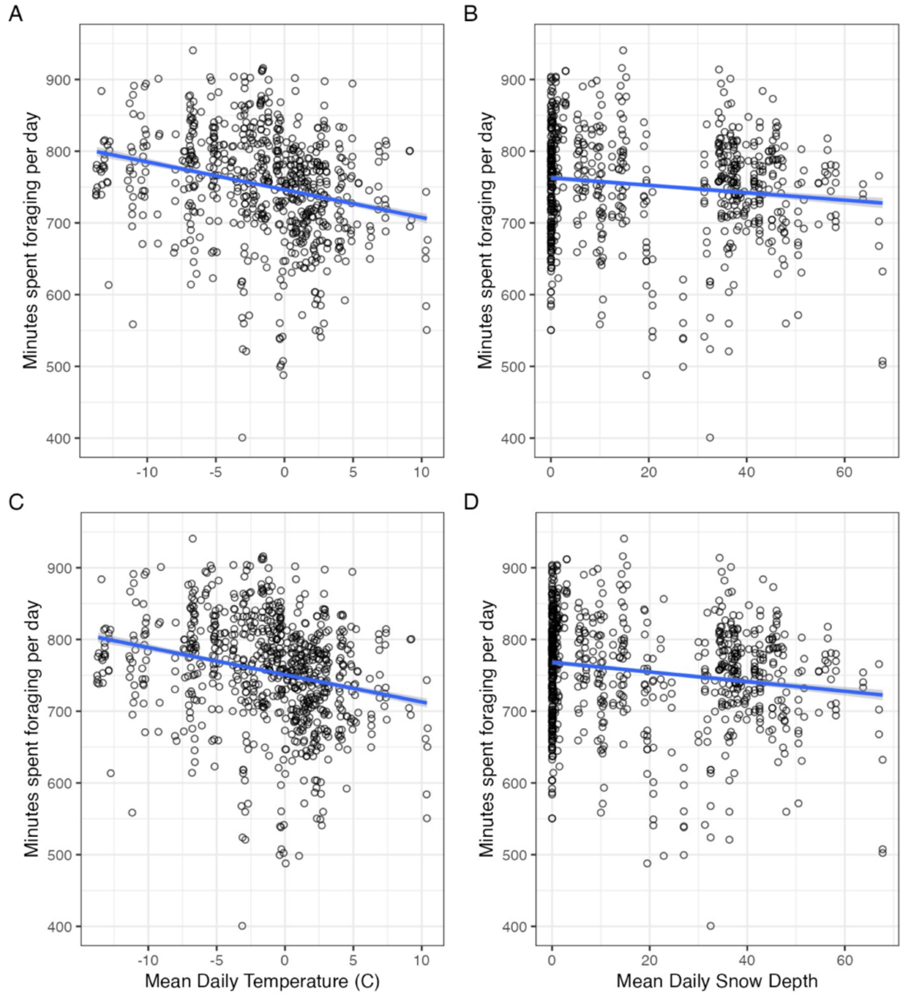

Figure A4. The relationship between A and C) mean daily temperature (°C) and B and D) snow depth (cm) and minutes spent foraging per day for snowshoe during the 2022-2023 winter in Butter Pot Provincial Park in Newfoundland, Canada. Panels A and B use a 50% white cutoff, while panels C and D use an 80% white cutoff. The blue regression line represents the predicted values from a gaussian linear mixed model with snow depth and temperature as predictor variables, individual ID and month as random variables, and scaled seconds spent foraging per day as the response variable. The predicted fit was converted to minutes spent foraging. Open circles represent the minutes spent foraging in one day by one individual, corresponding to the A and C) mean temperature or B and D) mean snow depth that day. There is less than a 5% difference in effect size of both temperature and snow depth when comparing the 50% cutoff to the 80% cutoff.