Examining the impact of climate change on snowshoe hare demography and community interactions in the northern boreal forest

by

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Abstract

Ecologists are under increasing pressure to predict the influence of climate change on species demography along with the broader impacts on community and ecosystem structure. Predicting community responses to climate change, however, is a formidable challenge, that can be ameliorated by developing a better 1) mechanistic understanding of how climate influences community interactions, and 2) detailed understanding of the current factors limiting species abundance. Snowshoe hare (*Lepus americanus*) are an important prey species of the boreal forest that undergo 10 year population cycles. Hares are well-suited for snowy boreal winters, having large feet allowing for low foot loading and therefore improved flotation in deep, soft snow, giving them an advantage over their predators. In this thesis, I examine the potential impact of changes in winter climate on hare demography and community interactions, as well as the primary factors driving their fluctuations in abundance. I found that shallow snow reduced hare survival, to rates resembling those during cyclic population declines. This response was primarily driven through an increase in predation risk from coyotes (*Canis latrans*), as risk from their main predator Canada lynx (*Lynx canadensis*) was largely unaffected by snow depth. I further found that changes in hare density can influence community structure beyond predator-prey dynamics. The efficiency of the scavenging community was affected by hare density, with carcass persistence decreasing when snowshoe hare densities declined, mainly due to increased scavenging rates by their predator, the Canada lynx. In addition, scavenging rates in the boreal forest increased in warmer temperatures, suggesting climate change may increase scavenging efficiency in this system. Finally, I found that hare cycles may not be regulated by predator induced stress reducing reproductive output. Instead, changes in population growth following decline correspond with improved over-winter survival of juveniles, particularly for juveniles born earlier in the summer. However, the importance of changes in reproductive rates on hare demography should be investigated further, and I discuss potential experiments that may help decipher the role of predator fear regulating snowshoe hare populations. Overall, this thesis demonstrates that climate change can impact snowshoe hare demography indirectly through shifts in predation risk, and could have broad effects on community interactions in the northern boreal forest.

Preface

This thesis is an original work by Michael Peers. The research project, of which this thesis is a part, received research ethics approval from the University of Alberta Research Ethics Board, Project Name “Population dynamics of snowshoe hares”, AUP00001973, November 2016.

A version of Chapter 2 and 3 have been submitted to *Global Change Biology* and *Journal of Animal Ecology*, respectively. A version of Chapter 5 is published in *Ecology* as Peers et al. 2018. Quantifying fear effects on prey demography in nature. *Ecology* 99: 1716-1723. I was responsible for the writing of the manuscript with significant input from co-authors on the concept formation and manuscript revisions.

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Chapter 1

General Introduction

"When conditions are favourable, hares increase rapidly until they become very abundant. Then a mysterious disease breaks out and carries off such numbers that, in a year or two, they are very scarce."

~ J.F. Calvert & J.H. Cameron, Zoology for High School 1937

Predicting climate change impacts on species and communities

The recent increase in atmospheric concentrations of CO_2 and the subsequent changes in climate are undoubtedly impacting wildlife populations around the globe (Parmesan & Yohe 2003; Chen *et al.* 2011; Bellard *et al.* 2012). Ecologists are under increasing pressure to predict the influence of climate change on species demography along with the broader impacts on community and ecosystem structure. Sound predictions can provide important insight for strategically guiding conservation policy and future research directions. Predicting species responses to climate change, however, is a formidable challenge, given the numerous factors that could influence species demography and the complexity of ecological systems (Berteaux *et al.* 2006). Researchers commonly develop statistical models that define a relationship between current abundance/distribution and climate, and project this relationship under future climate scenarios (ex. Species Distribution Modelling; Thuiller 2004; Murray *et al.* 2017). Although these studies can provide important insight, their accuracy depends on the degree that models are built from cause-effect relationships, as opposed to spurious correlations (Berteaux *et al.* 2006). In theory, predictions of species abundance under climate change will be successful if:

i) Initial conditions of the system are thoroughly described
ii) No essential variable is excluded from the model
iii) The influence of climate on the key variables driving demography are known

Whether each of these conditions are met will never be known a priori. However, under this framework predictions of species responses to climate change will be improved by developing a 1) mechanistic understanding of how climate influences aspects of species demography known to influence abundance, 2) detailed understanding of the current factors limiting species abundance. Similar criteria can apply to linking climate effects on single species or larger ecological communities. My objective is to examine these two research areas to better understand the impact of climate change on snowshoe hares (*Lepus americanus*), and the boreal forest community.

Predator-prey dynamics under climate change

Examining the effect of climate on species demography remains challenging, due in part to the difficulty in understanding how climate disruption affects biotic interactions (Tylianakis *et al.* 2008; Heller & Zavaleta 2009; Walther 2010), such as predator-prey dynamics (Post *et al.* 1999; Zimova *et al.* 2016; Wilson *et al.* 2018). Predator-prey interactions are characterised by five stages (see Fig 1.1; adapted from Sih 2011), and the likelihood of a prey being consumed is determined by the frequency of encounters, and the conditional probability of each subsequent stage in the interaction. Therefore, climate change may reduce prey survival either by increasing encounter rates or the probability of any stage in the interaction (i.e. detection; Zimova *et al.* 2016). For example, deeper snow caused wolves (*Canis lupus*) to hunt in larger packs, improving hunting success which subsequently tripled kill rates on moose (*Alces alces*; Post et al., 1999). Furthermore, in northern pike (*Esox lucius*), warming temperatures increased their swimming speed relative to their prey, the brown trout (*Salmo trutta*), which increased hunting success (Ohlund *et al.* 2015).

Most systems, however, consist of multiple predator species, and climate change may alter the relative importance of different predators on prey mortality rates through differential influences on any stage in the interaction. This may in turn influence the effect of climate on future population dynamics of the prey. For instance, change in the environment may have opposing effects between two predator species, resulting in a neutral effect on overall prey mortality. In contrast, the variable may have similar effects on both species, or influence only a single predator species, causing either increased or decreased predation risk (Bastille-Rousseau *et al.* 2017). Understanding these patterns will provide important insight into how the predator community may be disrupted from climate change. These dynamics remain largely unexplored in wild populations, due to the difficulties of monitoring detailed changes in environmental conditions coupled with cause-specific mortality of the target species.

Vertebrate scavenging communities

Scavenging by vertebrates is an overlooked food web interaction that could have an important impact on ecological communities (Barton *et al.* 2013). Carrion availability can drive the population dynamics of both obligate and facultative scavengers (Pain *et al.* 2003; Wilmers *et al.* 2003), and vertebrates can consume up to 90% of available carrion, altering the distribution and availability of nutrients in comparison to carrion colonized by invertebrates and microbes (DeVault *et al.* 2011). Given the propensity for animals to consume carrion, scavenging contributes to a reticulate food web through the creation of numerous weak connections (Wilson & Wolkovich 2011), which can stabilize community dynamics by dampening the destabilizing effects of strong consumer-resource interactions (McCann 2000). Coupled with the retention of energy at higher trophic levels, vertebrate scavengers could have an important impact on food web stability and persistence (Dunne *et al.* 2002; Rooney *et al.* 2006). Despite this potential importance, classic food web theory has often ignored vertebrate scavenging dynamics (Wilson & Wolkovich 2011).

Carrion acquisition by vertebrates is strongly influenced by temperature, with reduced efficiency as temperature increases, due to increased microbial and invertebrate activity

(DeVault *et al.* 2004; Turner *et al.* 2017). As a result, temperature changes associated with climate change may impact carrion recycling rates and alter competitive interactions between vertebrates, invertebrates, and microbes (Beasley *et al.* 2018). However, the generality of these abiotic effects across a diverse range of ecosystems has not been tested (Sebastián-González *et al.* 2019). In addition, the importance of abiotic variables on scavenging rates could be minor relative to changes in biotic variables, such as the presence of competitors (Olson *et al.* 2012; Hill *et al.* 2018) or changes in carrion availability (Wilmers *et al.* 2003; Allen *et al.* 2015). Studies have often measured the effects of abiotic conditions without considering temporal changes in species demography (DeVault *et al.* 2004; Turner *et al.* 2017). Understanding these dynamics is important to forecast how future changes in the density of species, as well as climate and habitat change will impact food web structure (Bartley *et al.* 2019).

Demographic effects of predator fear

Over the last few decades, researchers have begun to appreciate the potential magnitude of prey demographic responses to the fear of predation (termed non-consumptive, indirect, or fear effects), whereby the presence of predators can reduce prey reproduction and survival through changes in behaviour and physiology (Creel & Christianson 2008; Peckarsky *et al.* 2008; Winnie & Creel 2017). For instance, interactions with predators may increase prey stress levels, causing reduced reproductive output through maternal effects (Boonstra *et al.* 1998; Sheriff *et al.* 2009). Similarly, avoidance of predators on the landscape may disrupt foraging rates or the use of high quality resources, impacting survival or reproduction (Creel *et al.* 2007, 2013). As a result, the demographic effect of predators may be larger than expected from purely consumption, and fear effects may be misidentified as bottom-up limitation if not adequately considered (Creel & Christianson 2008). As carnivore populations continue to undergo extirpation and re-establishment around the globe (Chapron *et al.* 2014; Ripple *et al.* 2014), coupled with variable impact of climate on food resources (Walsh *et al.* 1997), mistaking top-down (consumptive and fear effects) effects as bottom-up limitation will have significant impact on future projections of species demography.

Fear effects could be pervasive and have important demographic effects on prey species, limiting population abundance (Schmitz 1998; Preisser *et al.* 2005; Creel & Christianson 2008). That being said, quantifying the magnitude of fear effects on prey demography has primarily occurred in laboratory based "predator cue" experiments, where functional predators are removed but their presence is simulated (see examples in Preisser et al. 2005). In these cue experiments, consumptive effects of predators are eliminated in treatment groups (i.e. functional predators are eliminated) while fear effects are experimentally created either by the addition of non-functional predators (eg., mouthparts are glued shut or predators are separated from prey with a barrier; Schmitz 1998; Nelson *et al.* 2004) or by distributing a predator cue (e.g., kairomones, urine, feces, calls; Preisser *et al.* 2005). A fitness component of the prey, such as reproduction, is then typically compared between the cue treatment and a predator-free treatment containing no predators or cues, with the difference between treatment groups attributed to the fear effect. Quantifying the magnitude of fear effects in the wild remains relatively rare, and is still debated in most systems (Creel *et al.* 2007; Kauffman *et al.* 2010). Understanding the broad role of predator fear in limiting prey populations therefore requires further consideration of how accurately cue experiments represent prey demographic responses in the wild.

Snowshoe hares and the northern boreal forest

Snowshoe hares are an important prey species of the boreal forest (Krebs 2011), and experience regular population cycles that occur over 10 year periods (Krebs *et al.* 2001a). Snowshoe hare behaviour, physiology, and population dynamics are shaped heavily by predation, which can make up 85-100% of mortalities (Boutin *et al.* 1986; Boonstra *et al.* 1998; Hodges *et al.* 2001). Snowshoe hares are well-suited for snowy boreal winters, having large feet that contribute to low foot loading and therefore improved flotation in deep, soft snow (Murray & Boutin 1991). In the northern boreal forest, hares have two main predators: the Canada lynx (*Lynx canadensis*) and coyote (*Canis latrans*). Coyotes and lynx are similar in body mass, but because coyotes have much smaller feet, their foot loading is 4-8 times higher than that of lynx (Murray & Boutin 1991). As a result, coyotes tend to select boreal conditions with shallower or hard-packed snow, and pursue hunting strategies that limit chasing prey in deep snow (Murray & Boutin 1991; Murray *et al.* 1995).

Changes in winter climate and consequences on snow conditions could influence hare survival by altering predator hunting success (Stenseth *et al.* 2004), reducing the escape potential of hares (Post *et al.* 1999), or changing encounter rates (Vucic-Pestic *et al.* 2011). Specifically, reduced snow depth and increased snow hardness may amplify predation risk from coyote over lynx, altering predator-prey dynamics in this system (Penczykowski *et al.* 2017), which could ultimately impact cyclical dynamics (Cornulier *et al.* 2013). Snowshoe hares are a primary food source for numerous predators in the boreal forest, as they represent over 50% of available prey biomass at peak densities (Krebs *et al.* 2001b). As a result, the density of numerous predators are driven by the availability of hares (Boutin *et al.* 1995). If climate change reduces hare abundance or disrupts population cycles across their range, it could substantially impact the function of the boreal forest community (Humphries *et al.* 2017), a region that covers over half of Canada's land area.

Although the impact of hare abundance on predator species has been thoroughly investigated (Boutin *et al.* 1995; O'Donoghue *et al.* 1997, 1998; Humphries *et al.* 2017), the use of hare carrion by vertebrate scavengers has not been previously examined. Numerous species likely consume snowshoe hare carcasses, however, changes in carrion availability and hare biomass associated with their population cycles may be important drivers of temporal variation in scavenger efficiency and the diversity of vertebrate scavengers. More broadly, vertebrate scavenging dynamics in the northern boreal forest have not been examined (Sebastián-González *et al.* 2019), especially in regards to how abiotic and biotic variables influence the scavenging community. In northern systems, abiotic conditions could be important predictors of scavenging behaviour, especially in winter, as extreme cold temperatures may restrict access of carrion for smaller scavengers. The vertebrate scavenging community may also change among seasons, due to the arrival and departure of migrating and hibernating species (Krebs 2011; Humphries *et al.* 2017). Understanding the influence of these factors on scavenging communities of the boreal forest is critical, given the rapid increase in temperatures and changes in the biotic community expected in this region (Streicker 2016; Boonstra *et al.* 2018).

One of the most prominent concerns of cyclic small mammals under climate change is the apparent dampening of cycle amplitude associated with changes in winter snow conditions (Ims *et al.* 2008; Cornulier *et al.* 2013). In order to develop accurate predictions of how winter changes in predation risk associated with climate change may disrupt snowshoe hare cycles, we require a clear understanding of the demographic and external factors regulating hare densities.

Despite extensive research investigating the influence of external factors on snowshoe hare cycles (Keith 1983; Krebs *et al.* 1995; Sheriff *et al.* 2009), the primary drivers of their dynamics are still debated (Deangelis *et al.* 2015; Krebs *et al.* 2018a).

Snowshoe hares change reproductive rates across cycle phases. Hares reduce reproductive output prior to peak densities by approximately two years, and do not recover reproductive rates for several years following population decline (Cary & Keith 1979; Stefan & Krebs 2001). Explanations of the cycle have therefore featured direct, lethal effects of predators, in combination with a driver of the observed reproductive cut-back (Krebs *et al.* 2018a). The most widely accepted mechanism for the changes in reproduction are indirect effects of predators mediated through predator-induced stress (Boonstra *et al.* 1998; Sheriff *et al.* 2009, 2011). However, due to the difficulties of monitoring reproduction in this species, changes in reproduction and juvenile recruitment across cyclic phases have not been thoroughly investigated. Furthermore, the mechanistic link of reproductive output to non-lethal effects of predators has primarily occurred using standard cue experiments that may have exaggerated fear effects (Sheriff *et al.* 2009). The influence of predator fear and the associated change in reproduction on population dynamics in this species therefore requires further consideration.

Goal of the thesis

I structured this thesis as a series of stand-alone but inter-related chapters that will examine the potential impacts of climate change on snowshoe hares in the northern boreal forest, and the impact on the broader ecological community. I will improve our understanding of the association between climate variables, hare demography, and community interactions, such as predator-prey dynamics and vertebrate scavenging. I will also examine the primary demographic factors that change across hare cycles, and examine the potential that fear drives these patterns.

All of my work is conducted in the Kluane Lake region of southwestern Yukon, Canada (61 N, 138 W), in a broad glacial valley bounded by alpine areas and bisected by the Alaska Highway (Fig 1.2). The boreal forest in this area is comprised primarily of white spruce (*Picea glauca*) with smaller amounts of trembling aspen (*Populus tremuloides*) and balsam poplar (*Populus balsamifera*), and the shrub layer is dominated by areas of gray willow (*Salix glauca*) and dwarf birch (*Betula glandulosa*). The climate is cold continental, with snow cover occurring from October to May. July is the only snow-free month, and temperatures in February averaging –14.0 ºC during the four years of my thesis work (2015-2018).

Snowshoe hare densities in the region have been monitored since 1977 (see Fig 1.3), along with numerous other species, as part of the Community Ecology Monitoring Program (CEMP; http://www.zoology.ubc.ca/~krebs/kluane). During my work, snowshoe hare were at the increase, peak, and entering the decline phase of their cycle, and densities ranged between 0.49 and 1.82 snowshoe hares per hectare (Krebs *et al.* 2018b). Canada lynx and coyote are the two main predators of hares in the region with great-horned owl (*Bubo virginianus*) and goshawk (*Accipiter gentilis*) accounting for a smaller percentage of hare deaths. The Yukon in general has experienced drastic changes in climate with annual temperatures increasing by 2ºC over the last half-century (Streicker 2016) and spring snow-free periods have increased by ~11 days per decade between 1967-2008 in the most extreme regions of the territory (Brown *et al.* 2010).

In Chapter 2, I determine whether changes in winter weather conditions significantly impact predation risk in snowshoe hares, and the potential mechanisms driving changes in risk. Using the outcome of this analysis, I develop projections for the degree that prolonged winter weather conditions may impact hare survival. I further examine whether climate-mediated changes in risk differ between Canada lynx and coyote, their two main predators, to provide insight into how climate disruption may impact the predator-prey community. In Chapter 3, I first describe the vertebrate scavenging community of the northern boreal forest, by monitoring snowshoe hare carcasses with motion-triggered cameras. I then examine whether changes in carrion availability or prey biomass associated with snowshoe hare cycles, as well as abiotic variables such as temperature, influence community scavenging dynamics.

In Chapter 4, I examine how the presence and survival of late-litter juvenile hares varies with cycle phase. Snowshoe hares breed during the summer, with a maximum of four litters produced in a single year that are locally synchronous, creating distinguishable juvenile cohorts (O'Donoghue 1994). The majority of the reproductive collapse, in terms of number of offspring produced in a season, occurs via the cut-back of the third and fourth litters (Stefan & Krebs 2001). Specifically, fourth litters are thought to only occur in the late low and early increase phase, significantly increasing population growth during this time, whereas third litters are curtailed during the decline reducing recruitment and population recovery over the summer (Stefan & Krebs 2001). However, the demographic effect of this reproductive cut-back will depend on the consistency of this pattern across multiple cycles and the relative survival rate of late-litter juveniles in comparison to juveniles from earlier litters, which remains more constant across cycle phases.

In Chapter 5, I review the experimental evidence for demographic effects of predator fear on wild prey populations, and examine the limitations in common experimental approaches that may hinder interpretations of their results. I further suggest alternative experimental approaches that may improve our understanding of fear effects in nature, and discuss the potential for such experiments to determine the influence of predator fear on reproductive output in snowshoe hares.

Finally, in Chapter 6, I summarize the main findings of my thesis in regards to projections of hare abundance under climate change and the potential impact on the boreal forest community. However, given that the main findings are discussed in detail in each individual chapter, I spend the majority of Chapter 6 discussing what I view as the major outstanding questions in the broader topics related to my thesis.

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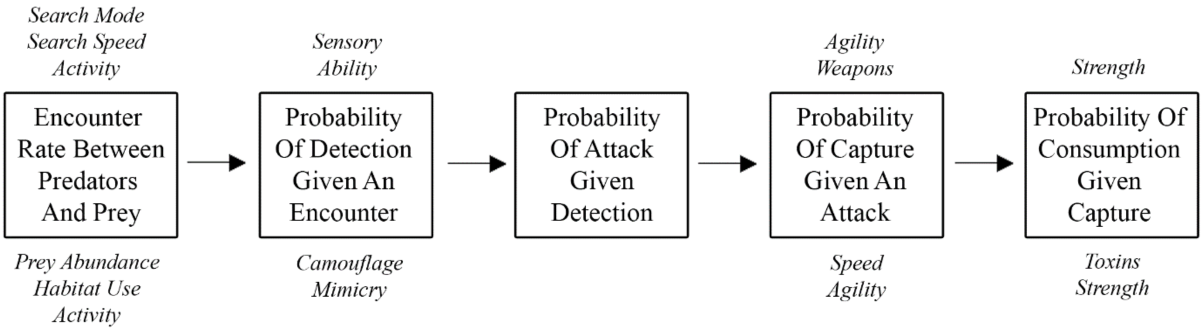

Figure 1.1. The sequence of a predator-prey interaction starting with encounters and proceeding to the consumption of prey (adapted from Sih 2011). Climate change could influence prey mortality rates by either increasing encounters with predators, or the probability of any subsequent stage in the interaction. Predator (top) and prey (bottom) traits that may influence these probabilities are listed.

Figure 1.2. Image of the Kluane Lake region in southwestern Yukon, Canada.

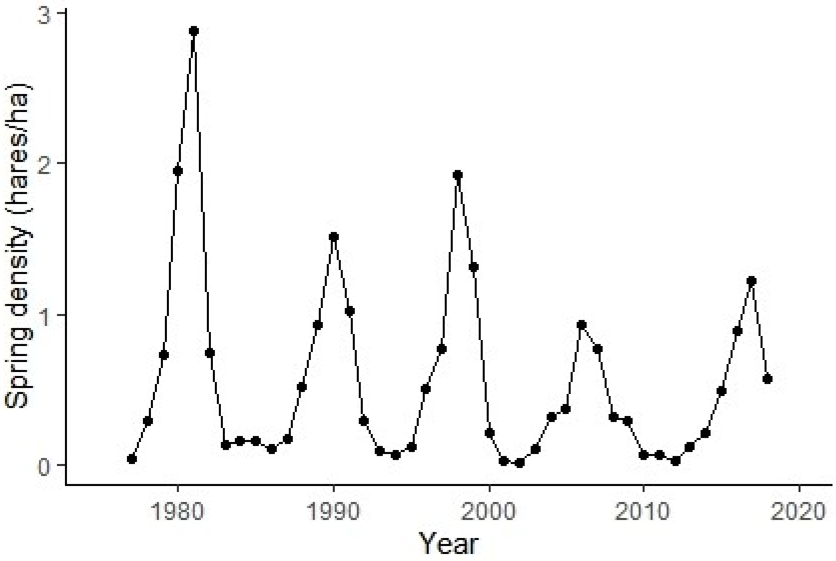

Figure 1.3. Spring snowshoe hare densities in the Kluane Lake region, southwestern Yukon from 1977-2018.

Chapter 2

The interplay between environmental conditions, predator species, and prey age affects predation risk for a keystone species

Submitted to *Global Change Biology*

"…humility is no doubt required for ecologists trying to anticipate climate change impacts on ecosystems"

~ Berteaux et al. 2017, Climate Research

Abstract

Predator-prey relationships may be strongly impacted by climate change, but predictions require improved understanding of how predation risk among multiple predator species shifts as a consequence of changing environmental conditions. Here, we demonstrate that the mortality risk of a winter-adapted mammal, the snowshoe hare, is strongly influenced by variation in snow conditions. Prolonged shallow snow can reduce monthly survival rates to those resembling populations during cyclic declines, and therefore are not sustainable. This response was primarily driven by an increase in coyote predation in shallow snow, as risk from their main predator, the Canada lynx, was largely unaffected by snow conditions. Variation in weather conditions had a larger effect on sub-adult than adult survival, suggesting climate-mediated predator-prey dynamics will influence species demography more strongly through recruitment. Our results demonstrate that climate change can impact species survival through shifts in predation risk, but patterns differ between predator species and prey age.

Introduction

Climate change is predicted to have major impacts on wildlife globally (Parmesan & Yohe 2003; Loarie *et al.* 2009; Chen *et al.* 2011), causing numerical declines and extinctions in species that are unable to adapt or move (McLaughlin *et al.* 2002; Wiens 2016). Predicting these effects on species or communities remains challenging, partly because of the complexities associated with how climate disruption affects not only a single species, but also the interactions amongst members of the community (Tylianakis *et al.* 2008; Kubelka *et al.* 2018; Romero *et al.* 2018). Predator-prey dynamics can be strongly impacted by climate (Post *et al.* 1999; Zimova *et al.* 2016), however, we lack knowledge for whether prolonged changes in daily weather conditions, and associated changes in risk, can result in severe impacts on species demography. As a result, consideration of predator-prey interactions in future population projections has only recently emerged (Bastille-Rousseau *et al.* 2017). Although studies conducted over long temporal scales can provide important insight on changes in these interactions over time (Kubelka *et al.* 2018), robust predictions require multi-species analyses examining changes in dynamics associated with current climate conditions (Blois *et al.* 2013). Such studies can help determine the direct and complex effects of climate on community interactions, which are critical to improve our predictive capacity.

Climate change could increase the functional response of predators by altering prey detection probability or hunting success (Stenseth *et al.* 2004; Dell *et al.* 2014; Zimova *et al.* 2016), when environmental conditions reach a threshold where predators outperform prey (Ohlund *et al.* 2015). However, prey and predator behaviour, such as foraging and movement rates, are also sensitive to changes in the environment, which could subsequently alter encounter rates and risk (Post *et al.* 1999; Atwood *et al.* 2007). For prey species, the predicted changes in population growth and abundance that are associated with environmental change will depend on the sensitivity and elasticity of the demographic variables that are impacted (Iles *et al.* 2019). For example, in many species population growth is especially sensitive to adult survival rather than juvenile recruitment, making environmental effects on the former cohort disproportionately impactful (Owen-Smith & Mason 2005; Doak & Morris 2010). Environmental conditions may impact the predation risk of age classes differently through a variety of mechanisms, including favouring predator species that target particular age groups (Husseman *et al.* 2003), or variation in behaviour and vulnerability between age classes (Lea & Blumstein 2011; Mumma *et al.* 2019).

Examining single species-climate or even predator-prey relationships is insufficient to predict future changes in community structure (Blois *et al.* 2013; Barton & Ives 2014). In most systems prey have multiple predators, and climate change may affect predation rates differentially among predator species (Bastille-Rousseau *et al.* 2017). For instance, environmental change may shift hunting advantages from one predator to another, with the species best adapted to past conditions being detrimentally affected and potentially displaced by species that have an advantage in altered environmental conditions (Fisher & Burton 2018). Understanding these patterns will provide important insight into how community composition, food web structure, and overall biodiversity will be affected by climate change, but such questions remain largely unexplored in wild populations because of the challenges in monitoring relevant changes in environmental conditions simultaneously with cause-specific mortality of prey.

Across North American boreal forests, Canada lynx (*Lynx canadensis*) and snowshoe hares (*Lepus americanus*) form a keystone predator-prey interaction, with both species exhibiting a 8-10 year population cycle (Krebs *et al.* 2001a) that exerts direct and indirect effects across the boreal vertebrate community (Krebs 2011; Boonstra *et al.* 2016). Snowshoe hare behaviour, physiology, and population dynamics are shaped heavily by predation, which can make up 85-100% of mortalities (Boutin *et al.* 1986; Boonstra *et al.* 1998; Hodges *et al.* 2001). Snowshoe hares and lynx are both well-suited for snowy boreal winters, having large feet that contribute to low foot loading and therefore improved flotation in deep, soft snow (Murray & Boutin 1991). Coyotes (*Canis latrans*) are a generalist predator that originates from the central prairies of North America, but expanded northward over the last century. Coyotes are not new arrivals to the northern boreal forests (Banfield 1974; Slough & Jung 2007), but rarely reach high abundance outside of disturbed landscapes (Crête & Larivière 2003; Kays *et al.* 2008). Coyotes and lynx are similar in body mass, but because coyotes have much smaller feet, their foot loading is 4-8 times higher than that of lynx (Murray & Boutin 1991). As a result, coyotes tend to select boreal conditions with shallower or hard-packed snow and to pursue hunting strategies that limit chasing prey in deep snow (Murray & Boutin 1991; Murray *et al.* 1995).

Changes in winter climate and the resulting changes in snow conditions could influence hare survival by altering predator hunting success and hare escape potential (Stenseth *et al.* 2004), or through changes in hare foraging rates that impact encounters (Vucic-Pestic *et al.* 2011). Specifically, reduced snow depth and increased snow hardness may amplify predation risk from coyote over lynx, altering predator-prey dynamics in this system (Penczykowski *et al.* 2017), which could ultimately impact cyclical dynamics (Cornulier *et al.* 2013). In addition, the environmental drivers of risk may differ between sub-adults and adults, as hares reproduce in the summer and juveniles enter the autumn with smaller body size, which likely affects foraging strategies and anti-predator behaviour (Hodges *et al.* 2006). Such variation could impact how climate affects population cycles in this species, given the differential influence of recruitment and adult survival on population growth across cyclic phases (Hodges *et al.* 2001).

We examined the effect of daily winter temperature and snow conditions on cause-specific mortality of snowshoe hares, to determine if changes in winter weather can significantly impact over-winter survival in this species. We examined how changing winter conditions differentially influenced lynx and coyote predation risk and thereby could alter predator prey dynamics in this system, and whether risk associated with these conditions differs across age classes. Finally, we examined the influence of temperature and snow conditions on hare foraging behaviour to determine potential mechanisms driving weather-related changes in risk, and differences between age groups. Ultimately, our study contributes to a currently depauperate body of literature on the complex relationship between environmental variation and predator-prey dynamics; we surmise that this effort will improve our ability to forecast the effects of environmental changes on community interactions (Post *et al.* 1999).

Material & Methods

Study area

Our study was conducted in southwestern Yukon, Canada (Lat: 60.9 N, Long: -138.0 W), where snowshoe hares have been studied for the last 40 years (Krebs *et al.* 2018a). The boreal forest in this region is comprised primarily of white spruce (*Picea glauca*), with smaller amounts of trembling aspen (*Populus tremuloides*) and balsam poplar (*Populus balsamifera*). The shrub layer is dominated by areas of gray willow (*Salix glauca*) and dwarf birch (*Betula glandulosa*). In addition to Canada lynx and coyote, other predators include great-horned owl (*Bubo virginianus*) and goshawk (*Accipiter gentilis*), which account for a smaller percentage of hare mortalities (Hodges *et al.* 2001). During this study (2015-2018), snowshoe hare populations were at their late increase, peak, and entering the early decline of their cycle (Krebs *et al.* 2018b).

Monitoring survival and daily weather

Between January 2015 and May 2018, we captured hares in Tomahawk live-traps (Tomahawk Live Trap Co. Tomahawk, WI, USA) on three different study areas within an ~ 8 km stretch of forest. Hares weighing > 1100g were fitted with VHF collars equipped with mortality sensors (Model SOM2380, Wildlife Materials Inc., USA, or Model MI-2M, Holohil, Canada; <40 g, <5% body weight). Handling and collaring procedures were approved by the University of Alberta Animal Care and Use Committee (Protocol: AUP00001973).

We monitored the survival of 321 individuals almost daily throughout the winter. We considered the winter season as December through March, which represented the months with continuous snow cover and average temperatures below 0 ºC throughout the four winters we monitored survival. When a mortality signal was detected, we located the kill site to determine cause of death, and identified the predator species responsible based primarily on the presence of predator tracks in snow, portions of the carcass remaining, and other field sign such as feathers, scat, and pellets (Hodges *et al.* 2001). We attempted to locate kill sites on the date the mortality signal was detected to reduce the potential for scavenging by predators to be misidentified as sign of predation. To further examine this possibility, we monitored hare carcasses in our study area using remote cameras, and determined scavenging as an unlikely bias in our designation of cause of death (M. Peers, unpubl.).

On each study area, we monitored snow conditions at three stations in relatively open forest: total snow depth was measured to the nearest 0.5 cm; snow hardness was determined by the sinking depth of a 250g cylinder penetrometer dropped from 50 cm above the snow (Murray & Boutin 1991); and daily snowfall was determined using plywood boards that were laid on the snow surface to capture snow that fell during the last 24 hrs. We determined daily temperature, using a minimum of 2 Ibuttons (DS1922L, Maxim Integrated, Whitewater, USA) on each grid, which took at least six temperature recordings per day. Locations where environmental data were recorded were fixed during the study. Across the study years, hardness and depth were recorded on >60% of days, and snowfall and temperature were recorded every day. Days with missing snow depth and hardness measurements were linearly interpolated using the "zoo" package in R (Zeileis *et al.* 2019).

Effects of environment on survival

We assessed the influence of environmental conditions on winter hare survival using semi-parametric Cox proportional hazards (CPH) models. Time intervals in our CPH models represented each telemetry check (68.8% 1 day, 97.0% within 3 days) and we excluded monitoring gaps that exceeded seven days. Daily weather values were averaged over monitoring intervals, and each hare was associated with weather conditions from its study area. We used a right-censored design with time-at-risk (days) based on time since the start of the season (Fieberg & Delgiudice 2009).

First, to examine the influence of weather conditions on overall hare mortality risk, we developed CPH models (hereafter referred to as all-cause model) that grouped all causes of death together (i.e., lynx, coyote, birds of prey, and unknown predator). Over the four years, we had a total of 153 predator-caused mortalities, and four mortalities that were attributed to starvation and subsequently censored. We censored 35 individuals because of either collar failure causing an unknown status (n=28), or the removal of their collar prior to the completion of the study (n=7). To ensure that informative censoring did not influence our results, we developed models (detailed below) on datasets that either censored missing individuals or treated them as mortality events (Murray *et al.* 2010). These models reveal qualitatively similar results (see supplementary material) implying our results are robust to informative censoring (Murray *et al.* 2010; Murray & Bastille-Rousseau 2019).

For our all-cause CPH model, we included average temperature, snow depth, and snow hardness as explanatory variables given their suspected impact on predator-prey interactions in our system (Murray & Boutin 1991; Stenseth *et al.* 2004), as well as our interests in their influence on risk. We then used a model selection approach to test the importance of daily snowfall, days since snowfall > 1 cm, and an interaction between snow depth and hardness (Burnham & Anderson 2002). This was done by including combinations of these variables with temperature, snow depth, and snow hardness (the core group of variables). Exploratory analysis revealed that sex was not influential to hare survival and was not considered further ($P=0.37$). Candidate survival models also considered random effects of year and study area. We determined hazard ratios for each variable in the all-cause model using our top model based on lowest AIC_c. For the top model, we assessed multicollinearity using a variance inflation factor (VIF; Graham 2003) and excluded variables with a VIF >2, except between main variables and those representing interactions between multiple variables. We further ensured the top model satisfied the proportionality assumption of CPH models (Murray & Bastille-Rousseau 2019). We used the predict function in R to examine the effect of prolonged weather conditions on monthly hare survival. We compared the effect of weather covariates from our top model to models built from 500 bootstrapped samples of our data to produce a measure of uncertainty on the effect of each covariate on monthly survival. Each bootstrapped dataset included resampled survival intervals, with replacement, until the number of intervals in the resample equaled the original dataset (McLellan 2015).

Next, we examined how our weather variables influenced risk from lynx and coyote using a competing-risk framework based on the data augmentation approach (Lunn & McNeil 1995; Murray & Bastille-Rousseau 2019). We replicated our dataset for each cause of death and a dummy variable was used to assign each risk to a specific cause (Bastille-Rousseau *et al.* 2016). Within each risk set, we identified death only for the appropriate cause (i.e. lynx or coyote), with all other entries being censored. Mortalities from goshawks and great-horned owls were not considered in the cause-specific analysis due to the limited sample sizes (i.e. 10 & 6 respectively). Unknown causes primarily occurred due to inclement weather limiting kill site classification (i.e. snowfall after mortality), and were suspected to consist largely of predation events from either lynx or coyotes. We therefore censored unknown mortality events in the cause-specific model as opposed to including them as an "other" classification. However, to ensure our results are not sensitive to this decision, we developed models including an "other" classification that failed to reveal qualitatively different results (see supplementary material), implying that our designation of only two mortality events are robust to the classification of unknown mortalities (Murray *et al.* 2010). We included two-way interaction terms between causes of death in the model to allow the effects of environmental covariates to vary based on predator species. We used AIC_c to identify the model that best explained variation in cause-specific mortality, and included combinations of variables from the all-cause model with an interaction term for cause of death. However, given the smaller sample size of predator-caused mortalities (lynx= 65; coyote= 27) we included only single effect terms to reduce the number of parameters in the model (Murray *et al.* 2019).

Finally, we examined whether hare survival between age classes is differentially affected by winter conditions, by splitting our dataset into sub-adults and adults. Adults consisted of tagged individuals known to be >1 yr old, while suspected sub-adults were individuals who were caught for the first time that autumn or summer, and weighed <1000 g if first capture occurred in June or July (as in Hodges *et al.* 1999). We restricted data used in age-specific models to study areas that were monitored over the previous year, which reduced our sample size to 236 individuals and 116 mortality events. Our classification of sub-adults therefore assumes that newly caught hares in the autumn represent juveniles as opposed to dispersing adults. We feel this approach is more accurate than purely body mass given: 1) The majority of individuals in the autumn population are juveniles (Hodges *et al.* 2001), and instances of adult dispersal over summer are relatively rare (Boutin *et al.* 1984), 2) hares have multiple litters per summer and early litter juveniles are indistinguishable from adults based on mass by autumn, therefore mass restrictions would remove early litter juveniles and potentially bias results to late litter juveniles which have relatively low survival (Gillis 1998). Furthermore, greater than 96% of individuals captured in May during our study were previously tagged by us (M. Peers, unpubl.), suggesting un-marked individuals on our study grid were rare at the beginning of the breeding season. We determined the top predictors of age-specific mortality by comparing CPH models in an AIC_c framework that included all causes of mortality, and variables were stratified by age-class. We further examined if cause of death between sub-adults and adults differed using a z test of proportions.

Effects of snow and temperature on hare foraging

A subset of the individuals monitored during our study (n = 137) were equipped with AXY-3 accelerometers (Technosmart Europe Srl., Rome, Italy). Accelerometers measure the acceleration of the body along three axes: anterior–posterior (surge), lateral (sway), dorso–ventral (heave), allowing for the characterization of different behavioural patterns (Graf *et al.* 2015). Accelerometers were attached to VHF collars on the dorsal side of the neck, and recorded at 1 Hz with a resolution of +/- 8 g-forces. Using behavioural classifications according to the decision tree developed for snowshoe hare accelerometers by Studd et al. (2019), we calculated the daily time spent foraging for each individual. The foraging behaviour represented feeding mixed with single hop movements, and was classified over 4 s intervals with an accuracy of 93.1% (Studd *et al.* 2019).

We examined the influence of weather variables on daily foraging rate (hours/day) using a linear mixed effects model that included individual ID and year as random effects. We considered the same combination of variables as our all-cause survival models, stratified by age-class.

Results

The majority of deaths where predator identity could be assigned were attributable to lynx (59.4 %) and coyote (25.5 %), with a smaller percentage to goshawks (9.4%) and great-horned owls (5.7 %; see Table 2.S7). Four-month over-winter survival was lowest during the winter of 2015-16 (0.37; 95% Confidence Intervals (CI): 0.28, 0.50), followed by 2017-18 (0.49: 0.37, 0.66), and 2016-17 (0.55: 0.45, 0.67; see Fig 2.S1).

Environmental drivers of hare mortality

The all-cause model with the strongest support consisted of our base weather variables along with an interaction between snow depth and snow hardness (*w*=0.38, see Table 2.S1). Hare mortality was influenced by snow hardness, with decreasing snow hardness (i.e., increasing sinking depth of the penetrometer) increasing overall mortality (HR=1.233, 95% Confidence Intervals (CI): 1.053, 1.445). However, this effect was only present in shallow snow, as increasing snow depth coinciding with decreasing snow hardness reduced overall mortality (HR=0.995, CI: 0.991, 0.999). Changes in temperature did not influence hare survival, whereas risk increased in shallow snow (Fig 2.1). Using coefficients from our top model, prolonged changes in winter snow conditions and associated risk could strongly influence 30-day hare survival (see Fig 2.1). Snow depths exceeding 60 cm (with other weather variables at their mean value) correspond to a mean 30-day survival rate of 0.97 (CI: 0.93, 0.99), while depths of 25 cm correspond to a mean survival probability of 0.87 (CI: 0.83, 0.91). When snow depth is 25 cm and the sinking depth of the penetromer is 20 cm, the survival probability is further reduced (0.77, CI: 0.69, 0.84; see Fig 2.1).

For cause-specific models, the top model included daily temperature, snow depth, and snow hardness (w=0.63, see Table 2.S2). Individual weather variables appeared to be more relevant to explaining changes in risk from each specific predator. Increasing temperature reduced predation risk from lynx (HR=0.960, CI: 0.920, 1.001), whereas snow depth (HR=0.992, CI: 0.959, 1.025) and hardness (HR=0.998, CI: 0.938, 1.063) had no influence on risk from lynx (see Fig 2.2). Increasing snow depth reduced risk from coyote (HR=0.866, CI: 0.776, 0.967) and decreasing snow hardness (i.e. increasing sinking depth of the penetrometer) increased risk

(HR=1.244, CI: 1.061, 1.459). Similar to the all-cause model, the influence of snow hardness on coyote risk appears driven by its effect in shallow snow (see Fig 2.2c).

Influence of environment on age-specific mortality and behaviour

The top model explaining age specific mortality across our predictor variables included temperature, snow depth, and snow hardness (w=0.60, see Table 2.S3). Increasing snow depth reduced mortality risk for both age classes, however, the effect size was larger for sub-adults (HR=0.935, CI: 0.889, 0.984) than for adults (HR=0.969, CI: 0.938, 1.002; Fig 2.3). Similar to the all cause model, reduced snow hardness, in shallow snow depth, resulted in higher mortality risk for both age classes, although the effect size was larger for sub-adults (Fig 2.4). Temperature had no influence on risk for sub-adults (HR=0.974, CI: 0.922, 1.028) or adults (HR=0.984, CI: 0.944, 1.025). Overall, survival was higher for adults than for sub-adults over our study (see Fig 2.S2). A qualitatively higher proportion of sub-adult (0.33) than adult (0.25) mortalities were attributable to coyote (z= 0.83, p=0.41; see Table 2.S7).

We monitored the winter foraging behaviour of 137 individual hares for a total of 4594 hare-days. Average foraging time per day during the winter was 10.2 h, with sub-adults foraging longer per day (10.8 h) than adults (10.1 h). Each covariate had similar influence on foraging for both age classes. Time spent foraging increased for both age groups when temperature increased and snow depth decreased (Fig 2.3). Snow softness decreased foraging rates for both age-classes, but only in shallow snow (Fig 2.4). Days since snowfall had a minor influence on hare foraging rates, with decreased foraging time on days with larger snowfall (see Fig 2.S3).

Discussion

Predator-prey relationships may be strongly impacted by climate change (Post *et al.* 1999; Zimova *et al.* 2016), but robust predictions require detailed understanding of how current climate conditions translate into changing risk from multiple predator species (Blois *et al.* 2013). Our results demonstrate that snow conditions significantly influence mortality risk of a winter adapted mammal, the snowshoe hare. Shallow snow increases risk of predation for hares, particularly when snow hardness decreases (Fig 2.2c). This response was primarily driven through an increase in coyote predation under shallow snow, as risk from Canada lynx was largely unaffected by snow depth (Fig 2.3). Furthermore, decreased snow depth had a larger effect on sub-adult than adult survival (Fig 2.3). Our study adds to the growing research documenting environmentally-driven variation in predator-prey dynamics (Post *et al.* 1999; Bastille-Rousseau *et al.* 2017), and further demonstrates that the predicted influence of climate on these dynamics should consider multiple predator species and prey age classes.

Variation in environmental effects on survival between age classes may be partially caused by differences in foraging requirements, as adults spend less time foraging per day across weather conditions (Fig 2.4 & 2.5). That being said, the effects of snow conditions on survival are likely caused by changes in predator mobility and hunting success, as opposed to changes in hare behaviour. Although hare foraging increases in shallow snow, coinciding with increased mortality risk, individuals also foraged longer per day during warmer temperatures, which did not coincide with a similar change in risk (Fig 2.4). Individuals reduced their foraging time similarly in shallow soft snow and deep snow, but only experienced increased mortality risk in shallow snow (see Fig 2.4 & 2.5). This indicates that a refuge from predation for hares occurs when snow reaches a depth sufficient to reduce mobility by their predators (Murray & Boutin

1991; Pozzanghera *et al.* 2016). In shallow snow, hare movement is hindered but predators retain their mobility until greater snow depths, due to their relatively long legs and chest height (Murray & Boutin 1991). Snow depths >35 cm (when risk is at baseline) reflect a threshold where hares begin to outperform their predators (Ohlund *et al.* 2015), which is approximately the average chest height for coyotes in our region (Murray & Boutin 1991).

Our models indicate prolonged changes in snow conditions can significantly alter monthly survival (Fig 2.2), as shallow snow resulted in survival rates resembling those observed during the decline phase of their cycle, while deeper snow depths corresponded to rates seen in periods of growth (Hodges *et al.* 2001). Such effects could therefore have pronounced impact on hare demography, regardless of cycle phase. Furthermore, recent evidence suggests a reduction in snow cover during the autumn and spring causes increased coat-colour mismatch in hares (Mills *et al.* 2013), which hinders camouflage and reduces individual survival (Zimova *et al.* 2016; Wilson *et al.* 2018). Coupled with the impact of snow depth and hardness on winter mortality (see Fig 2.2 & 2.3), snowshoe hares may be particularly vulnerable to changes in snow conditions associated with climate change. Although the predicted changes in climate vary across North America (Peacock 2012), much of the boreal forest is experiencing reduced snow cover duration (Brown & Mote 2009), which will likely result in lower hare abundance (Peers *et al.* 2014; Sultaire *et al.* 2016). That being said, the environmental drivers of predation risk may vary across their range due to differences in the predator community and climate conditions (Kielland *et al.* 2010; Feierabend & Kielland 2015). Increased hare foraging rates during warmer temperatures and shallow snow also indicate a potential for improved body condition, which may compensate for lower over-winter survival through increased reproductive output (Hamel *et al.* 2009; Reed *et al.* 2013). Forecasts of hare demography under climate change should consider this potential for demographic compensation, and examine the consistency of snow conditions on risk among populations that vary in predator communities.

Our cause-specific analysis suggests changes in snow conditions in North America may influence coyote demography more strongly across the boreal forest relative to lynx, and is a likely mechanism for the numerical response of coyote to changes in the North Atlantic Oscillation (NAO; Bowler *et al.* 2014). At a given hare density, coyote respond positively to a negative value of NAO (Bowler *et al.* 2014), which correspond to colder temperatures across northwestern Canada (Mysterud *et al.* 2003; Stenseth *et al.* 2004), and reduced snow depth in our study region (Krebs *et al.* 2001b). Reduced snow depth increased coyote kill rates (Fig 2.3a), which drives their numerical response (O'Donoghue *et al.* 1997). An association of NAO with lynx is less understood, with recent evidence suggesting a similar relationship with coyote (Hone *et al.* 2011; Yan *et al.* 2013) that contradicts earlier findings (Stenseth *et al.* 2004). Increased risk from lynx at colder temperatures may cause their response to the NAO, however, such changes could stem from purely energetic demands at temperatures below their thermal neutral zone, causing higher kill rates (St. Juliana & Mitchell 2016). Regardless, coyotes appear more responsive to changes in winter weather conditions, and continued range expansion of coyote northward (Chubbs & Phillips 2005) will be more strongly dependent on winter snow depth, as opposed to changes in snow hardness or temperature (Penczykowski *et al.* 2017). Furthermore, negative effects of altered snow conditions on lynx demography may stem from exploitative or agonistic competition with coyotes (Guillaumet *et al.* 2015), as they appear well-suited to hunt across a range of snow depths and hardness (Fig 2.2; Peers *et al.* 2012).

This work adds to a growing body of evidence that cyclic species at northern latitudes may be vulnerable to changes in winter snow conditions and the associated changes in predation risk (Ims *et al.* 2008; Cornulier *et al.* 2013). Environmental conditions monitored here had the largest effect on juvenile survival, suggesting climate change may disproportionately impact cyclic species during the increase phase of the cycle, where growth is more strongly dependent on recruitment (Krebs *et al.* 2001b). Indeed, peak densities of hares have declined in some regions (Sheriff *et al.* 2015), however, a clear link between peak abundance and climate is not clear (Yan *et al.* 2013; Krebs *et al.* 2014). Regardless, our results demonstrate that changes in weather conditions can have an important influence on predation risk that varies between age-classes. Future studies should scale the mechanistic changes in predation risk caused by abiotic conditions to differences in demography, and consider potential compensation that may limit a consistent climate-risk relationships over time.

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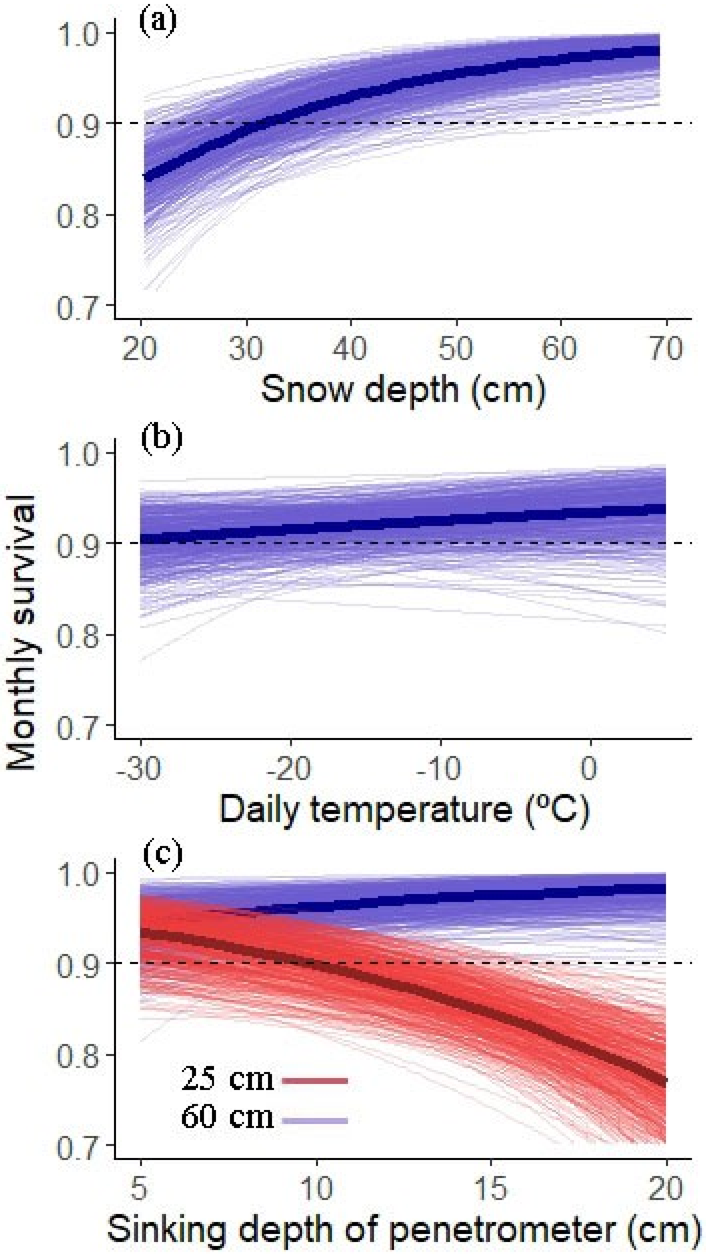

Figure 2.1. Modelled effect of a) snow depth, b) temperature, and c) snow hardness at 60 cm (blue) and 25 cm (red) snow depths (~ 90th percentiles of winter snow depth), on 30-day snowshoe hare (Lepus americanus) survival. Solid line represent covariate effects based on coefficients from the top model, and hollow lines represent coefficients from models built from 500 bootstrapped datasets. The dotted line at 0.90 survival is given for comparison between panels.

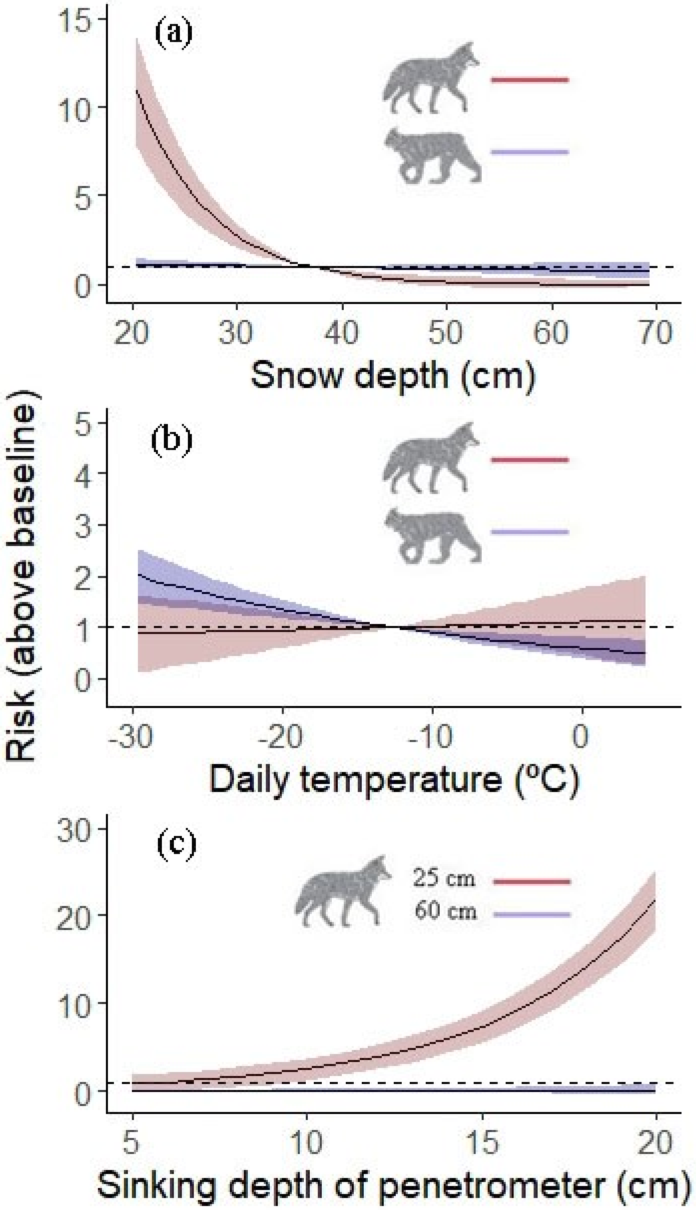

Figure 2.2. Modelled effect of a) snow depth on snowshoe hare (*Lepus americanus*) mortality risk from coyote (*Canis latrans*) and lynx (*Lynx canadensis*), b) temperature on hare mortality risk from coyote and lynx, and c) snow hardness on hare mortality risk from coyote at two different snow depths. Mortality risk is based on coefficients from the top model, and confidence bars represent predicted response standard errors. The dotted line represents baseline risk for hares.

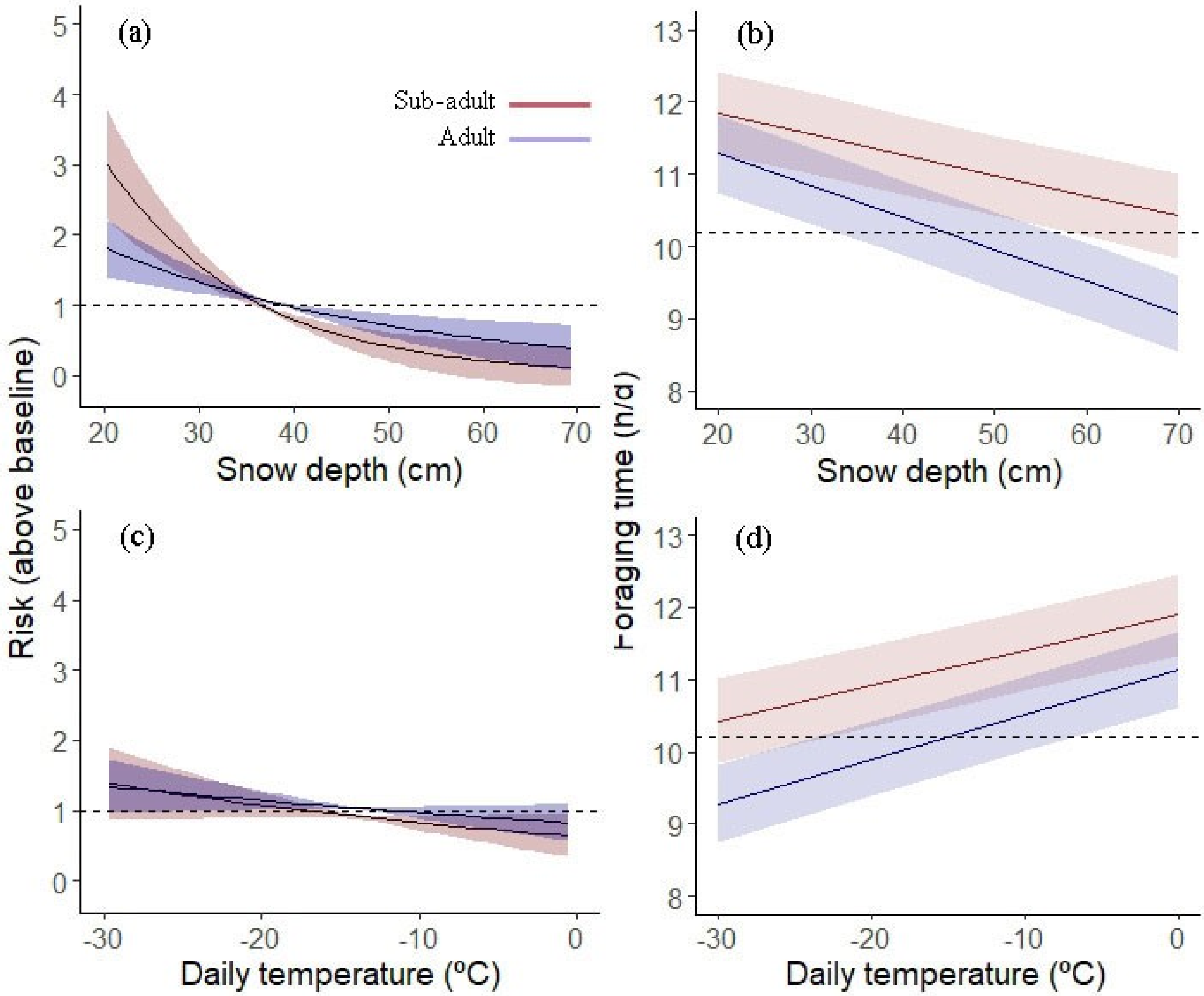

Figure 2.3. Modelled effect of snow depth (a, b) and temperature (c, d) on the mortality risk and daily foraging time for both sub-adult and adult snowshoe hare (*Lepus americanus*). Confidence bars represent predicted response standard errors, and the dotted line represents baseline mortality risk (a, c) or the average time spent foraging per day in hours across the winter (b, d).

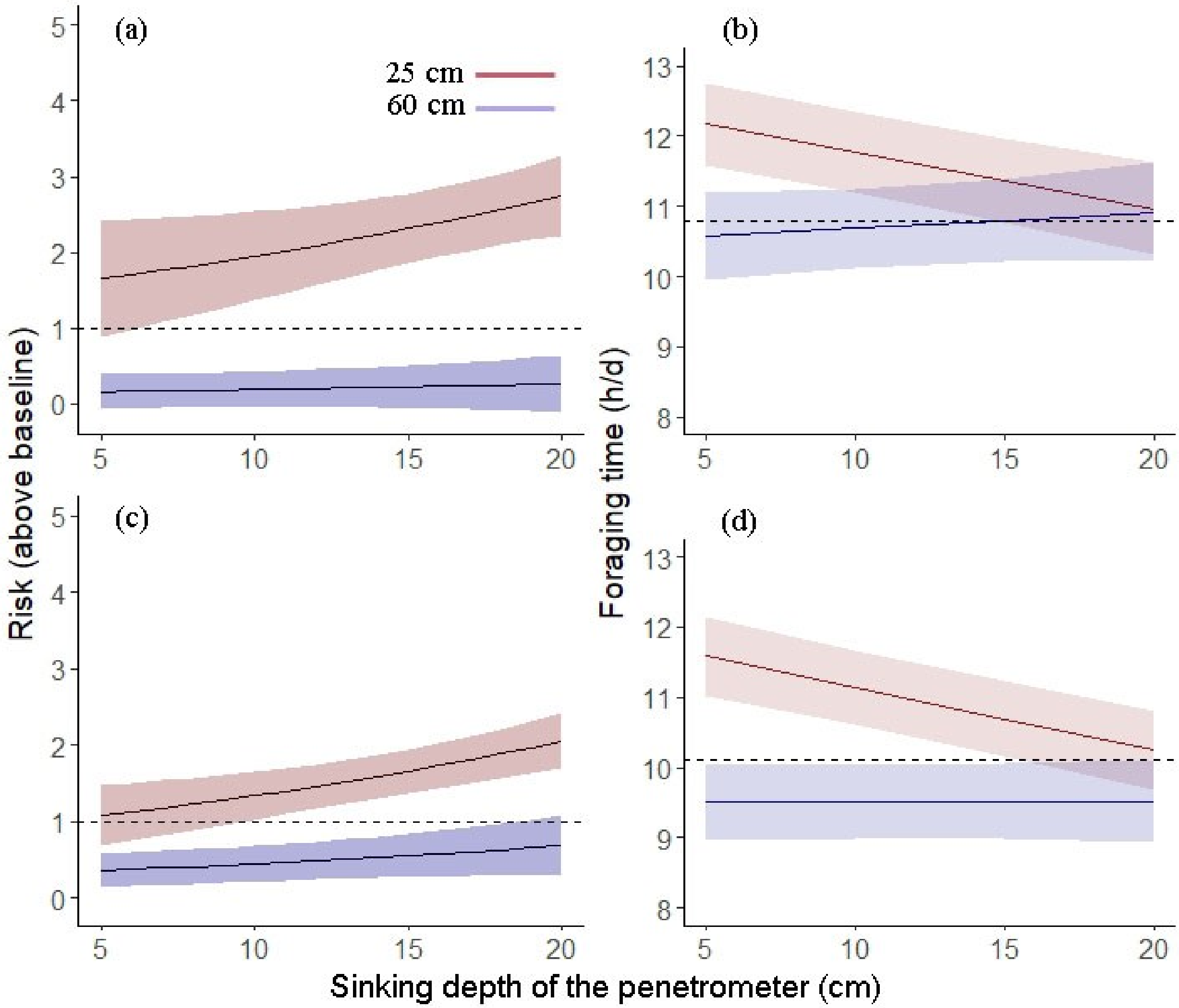

Figure 2.4. Modelled effect of snow hardness on mortality risk and daily foraging time for sub-adult (a, b) and adult (c, d) snowshoe hare (*Lepus americanus*) at two different snow depths. Confidence bars represent predicted response standard errors and the dotted line represents baseline mortality risk (a, c) or the average time spent foraging per day in hours across the winter for sub-adults (b) and adults (d).

Chapter 3

Prey availability and ambient temperature drive carrion persistence in the boreal forest

Submitted to *Journal of Animal Ecology*

"'…gyrfalcon is noble and this aristocratic bird lives only on warm-blooded living prey, preferably birds, and never eats carrion"

~ Unknown

Abstract

Scavenging by vertebrates can have important impacts on food web stability and persistence, and can alter the distribution of nutrients throughout the landscape. However, scavenging communities have been understudied in most regions around the globe, and we lack understanding of the biotic drivers of vertebrate scavenging dynamics. In this paper, we examined how changes in prey and carrion availability caused by population cycles of a primary prey species, the snowshoe hare (*Lepus americanus*), influenced scavenging communities in the northern boreal forest. We found that the efficiency of the scavenging community was affected by hare density, with carcass persistence decreasing when snowshoe hare densities declined, mainly due to increased scavenging rates by their predator, the Canada lynx (*Lynx canadensis*). However, prey density did not influence the number of species to scavenge a given carcass, suggesting prey abundance affects carrion recycling but not necessarily the number of connections in the food web. In addition, scavenging rates increased in warmer temperatures, and there were strong seasonal effects on the richness of the vertebrate scavenging community. Our results demonstrate that vertebrate scavenging communities are sensitive to changes in species' demography and environmental change, and that future assessments of the boreal forest food web should consider links established through scavenging.

Introduction

Scavenging by vertebrates is an overlooked food web interaction that could impact the structure and stability of ecological communities (Darimont *et al.* 2008; Barton *et al.* 2013; Schlacher *et al.* 2013). Carrion can be a valuable resource for a multitude of species, and can drive the population dynamics of both obligate and facultative scavengers (Pain *et al.* 2003; Wilmers *et al.* 2003; Smith *et al.* 2015). Vertebrates can consume up to 90% of available carrion, which alters the distribution and availability of nutrients in comparison to carrion colonized by invertebrates and microbes (DeVault *et al.* 2011). Given the propensity for animals to consume carrion, scavenging contributes to a reticulate food web through the creation of numerous weak connections (Wilson & Wolkovich 2011), which can stabilize community dynamics by dampening the destabilizing effects of strong consumer-resource interactions (McCann 2000). Coupled with the retention of energy at higher trophic levels, vertebrate scavengers could have an important impact on food web stability and persistence (Dunne *et al.* 2002; Rooney *et al.* 2006). Despite this potential importance, classic food web theory has often ignored scavenging (Wilson & Wolkovich 2011), and there remains a paucity of work examining the multitude of potential factors driving vertebrate scavenging dynamics.

Predator-prey dynamics are often drivers of carrion availability in ecosystems, which could influence scavenger behaviour (Wilmers *et al.* 2003; Perrig *et al.* 2017). Species commonly alter foraging strategies when food sources become readily available, and vertebrates switch to consuming carrion to take advantage of an abundant food source (Gleason *et al.* 2005). Therefore, changes in carrion availability associated with predator-prey dynamics may be an important influence on carrion recycling rates, or the number of scavengers in the community (Wilmers *et al.* 2003; Allen *et al.* 2015). Scavenging rates for predator species, however, are likely dependent on changes in the abundance of their prey, where carrion represent an alternate caloric resource when prey are scarce (Needham *et al.* 2014; Mattisson *et al.* 2016). If a predator species has a relatively large impact on the scavenging community, or multiple predators behaviourally respond to the same prey, temporal variation in prey density could be an important driver of vertebrate scavenging dynamics, but these effects of landscape-wide changes in prey or carrion availability on the vertebrate scavenging community remain unknown (Beasley *et al.* 2018).

Along with biotic factors, scavenging rates can be modulated by abiotic conditions, such as habitat and temperature (Smith *et al.* 2017; Turner *et al.* 2017). Acquisition of carrion by vertebrates is reduced as temperature increases, due to increased microbial and invertebrate activity at the carcass (DeVault *et al.* 2004). Forest openings also increase carrion detection and consumption, as dense canopy cover can obscure visibility from certain avian scavengers (Selva *et al.* 2005; Turner *et al.* 2017). However, the generality of these abiotic effects across a diverse range of ecosystems has not been tested (Sebastián-González *et al.* 2019), and species in a community likely differ in their response to these variables (Selva *et al.* 2005). Furthermore, the importance of abiotic variables on scavenging rates could be minor relative to changes in species density or carrion availability, as studies have measured the effects of abiotic conditions without considering temporal changes in species demography. Understanding these dynamics is important to forecast how future changes in the density of species, as well as climate and habitat change will impact food web structure (Bartley *et al.* 2019).

The boreal forest of North America is characterized by large-scale fluctuations of a dominant prey species, the snowshoe hare (*Lepus americanus*). Snowshoe hares undergo population cycles with an 8-11 year periodicity, with densities varying by over two orders of magnitude across the cycle (Krebs *et al.* 2001a). Snowshoe hares can account for >50% of the vertebrate biomass in the boreal forest, and their fluctuations drive the behaviour and abundance of several predator species (Boutin *et al.* 1995; Krebs 2011). Although the impact of these cycles on predator-prey dynamics and community interactions have been thoroughly investigated (Krebs 2011; Krebs *et al.* 2014), little is known about the impacts of snowshoe hare population dynamics on scavenging communities (O'Donoghue *et al.* 1998). Snowshoe hare carcasses likely represent a consistent food source for numerous species, however, changes in snowshoe hare carrion and biomass associated with their population cycles may be important drivers of temporal variation in scavenger efficiency and the diversity of vertebrate scavengers.

Scavenging dynamics in the boreal forest has been relatively understudied in comparison to other ecosystems around the globe (Sebastián-González *et al.* 2019). At northern latitudes, abiotic conditions could be important predictors of scavenging behaviour (Selva *et al.* 2005), and may impact scavenging rates differently than other systems given the relatively limited activity of invertebrates, particularly during winter months. The vertebrate community also changes among seasons due to the arrival and departure of migrating and hibernating species (Krebs 2011), which could cause strong seasonal patterns in the richness of vertebrate scavengers and scavenging rates (Sebastián-González *et al.* 2019). Understanding the influence of these factors on the vertebrate scavenging community of the boreal forest is critical, especially given the rapid increase in temperatures at northern latitudes due to climate change, and the potential destabilization of animal populations displaying cyclic patterns in abundance (Ims *et al.* 2008; Streicker 2016).

In this study, we monitored the vertebrate scavengers of the boreal forest of southwestern Yukon over four consecutive years, a region where scavenging dynamics have not yet been considered in studies of community interactions. The extensive research on the snowshoe hare cycle in this region provides a unique opportunity to examine the influence of changing prey abundance and carrion availability on community and species-specific scavenging rates. We monitored the density of snowshoe hares, as well as the availability of their carcasses, to test whether prey and carrion availability influence vertebrate scavenging communities relative to temperature, habitat and seasonal effects. For the primary scavengers, we developed species-specific scavenging models to examine variation on the effects of these factors across species, and determine which predator/scavenger species may be driving temporal patterns in the entire community. This research provides important insight into the mechanisms driving changes in the boreal forest food web, a system where scavenging communities have not been thoroughly examined (Sebastián-González *et al.* 2019).

Material &Methods

Study area

This study was conducted in the Kluane lake region of southwestern Yukon, Canada (61 N, 138 W), in a broad glacial valley bounded by alpine areas and bisected by the Alaska Highway. The boreal forest in this area is comprised primarily of white spruce (*Picea glauca*) with smaller amounts of trembling aspen (*Populus tremuloides*) and balsam poplar (*Populus balsamifera*), and the shrub layer is dominated by areas of gray willow (*Salix glauca*) and dwarf birch (*Betula glandulosa*) (Douglas 1974). The climate is cold continental, with snow cover occurring from Oct to May, with July being the only snow free month, and temperatures in February averaging –14.0 ºC during the four years of our study (between 2015-2018). During this study, snowshoe hare were at the increase, peak, and entering the decline of their cycle, and densities ranged between 0.49 and 1.82 snowshoe hares per hectare (Krebs *et al.* 2018).

Field methods and camera analysis

We opportunistically deployed 98 snowshoe hare carcasses during field-work in the region between Jan 2015 – May 2018. Carcasses were located during fieldwork (e.g., road-kill) or were donated from local trappers and/or researchers and were deployed continuously between September and May. We used carcasses immediately following discovery, or frozen and later thawed prior to deployment. Most carcasses were whole but some had external damage due to the cause of death. We deployed carcasses in forested or non-forested areas consisting of willow and open-fields. To limit pseudo-replication, we did not put out multiple carcasses within 1 km of each other, and no deployment occurred in the same location as a previous carcass (Turner *et al.* 2017). When carcasses were deployed, we recorded the time of deployment, habitat type (broad categories above), and canopy closure at the carcass to the nearest 10% measured by a spherical densiometer.

We monitored each carcass with one remote-sensing camera (no-glow, infrared PC900 Hyperfire^{TM} RECONYX, Inc., Holmen, Wisconsin, USA) set on a tree or shrub approximately 2-4 m from the carcass and 0.5 m off the ground. We set cameras to take 3 rapid-fire photographs when triggered, with a 15 s delay between subsequent triggers. We checked carcasses regularly (every 2-4 days) and left them in place until the carcass was removed or minimal edible remains were left. We did not secure carcasses to the ground to allow species to move the carcass to cover for consumption. If carcasses were moved slightly off-camera by a scavenger species, we adjusted the carcass position during our checks to ensure scavenging species were being detected on camera.

We downloaded images from the cameras after the conclusion of each deployment (i.e. once carcass was consumed or removed by a scavenger) and uploaded them to the Alberta Biodiversity Monitoring Institute website (www.abmi.ca) for image classification and analysis. In each photo, we identified the scavenger species and whether they were scavenging or not in the photo. We classified the observation as unknown if we could not determine the exact species responsible for the scavenging event. We further classified micromammals (*Myodes* sp., *Peromyscus* sp., and *Sorex* sp.) together as "small mammals" given the difficulty of distinguishing these species in photographs. We defined a scavenging event as any time a vertebrate consumed any part of the carcass, or if a disturbance or movement of the carcass was observed between two consecutive photos. For larger species such as Canada lynx (*Lynx canadensis*) or coyote (*Canis latrans*), we considered scavenging events to be either a) consumption of the carcass on site, or b) the carcass being carried off-screen by the scavenger (see Fig 3.S1). If the carcass was removed between a series of rapid-fire photos, we assumed the scavenger removed it during the 15-second delay. From the photographs, we also recorded the date and time of the first scavenging event on a given carcass, and when each carcass was removed or consumed. We did not attempt to quantify or describe any data on invertebrate scavengers. We acknowledge that scavenging rates in our study may be dependent on carcass condition (i.e. opened) and human presence at the site. However, these factors were consistent across deployments, and our primary goal was to determine how biotic and abiotic factors influenced changes in scavenging community efficiency and richness.

Monitoring snowshoe hare densities and carcass availability

We calculated monthly hare carrion availability in our study area throughout the four years as a function of biomass in g per km^2 using the following:

Monthly hare carrion availability (g/km^2) = hare density (km^2) * monthly mortality percentage * average carcass remaining (g)

We obtained density estimates for snowshoe hares from the Community Ecological Monitoring Program (CEMP; http://www.zoology.ubc.ca/~krebs/kluane), which has been estimating density of species in the Kluane Lake study area over the last four decades (Krebs *et al.* 2014, 2018). We monitored densities of snowshoe hare each autumn and spring using mark-recapture (see methods described in Krebs *et al.* 2001b). Between January 2015 and May 2018, we captured snowshoe hares continuously in Tomahawk live-traps (Tomahawk Live Trap Co. Tomahawk, WI, USA), and we fitted snowshoe hares weighing over 1100g with VHF collars equipped with mortality sensors (Model SOM2380, Wildlife Materials Inc., USA, or Model MI-2M, Holohil, Canada). Over the course of the study, we monitored a total of 458 individual snowshoe hares with VHF telemetry. VHF collars weighed less than 40g and were below the threshold of 5% of the individual body weight. The University of Alberta Animal Care and Use Committee (Protocol: AUP00001973) approved handling and collaring procedures. From these data, we calculated monthly survival rates using the Kaplan Meier estimator in the 'survival' package (Therneau 2019). Our average sample size for calculating monthly survival was 70.0 individuals (range 33-116). When a mortality signal was detected, we located the kill site to determine cause of death, and estimated the proportion of the carcass remaining (nearest 10%). In the above calculation, density was re-estimated at the beginning of each month based on the previous month's density and survival rate. We determined the average carcass remaining in grams for each year by multiplying the proportion remaining estimate by an approximate average mass of an adult snowshoe hare (i.e. 1500g).

Scavenger species richness and community efficiency

First, we calculated the number of species observed scavenging in each season, and the percentage of deployments each species was observed scavenging (i.e., deployments a given species was observed scavenging/total number of deployments). Seasons were defined as: autumn (Sep-Nov), winter (Dec-Feb), and spring (Mar-May).

We then examined the drivers of scavenging efficiency (i.e. carcass persistence and time until first scavenger) and scavenger species richness (i.e., the number of species scavenging during a single deployment) using generalized linear models (GLM) with a gamma or Poisson distribution in the program R (3.3.1). Time until first scavenger and carcass persistence were defined as the duration of time in decimal days between carcass placement and either the first scavenging event, or time at which all available flesh was consumed or the carcass was removed by a scavenger. For each analysis, we removed carcasses where cameras failed prior to complete carcass consumption. We used an information theoretic approach to determine which variables best-characterized community scavenging dynamics. Models consisted of combinations of the daily temperature on deployment date, canopy closure (nearest 10%), season (autumn, winter, spring), and either snowshoe hare density or carrion biomass, and we selected the top model using Akaike's Information Criterion, corrected for small sample sizes (AICc; Burnham & Anderson 2002). Covariates used for our analyses had a Pearson's correlation coefficient less than 0.60 (Dormann *et al.* 2013). For our analysis of the number of scavengers at each carcass, we further included time until carcass removal to the nearest day as a covariate, as longer deployments could have a larger number of species scavenging (Turner *et al.* 2017).

Drivers of species-specific scavenging

For our most frequent avian and mammalian scavengers (species that scavenged > 10 carcasses; see below) we constructed species-specific models to determine the factors driving their scavenging rates. We determined the effects of covariates on whether or not that species scavenged a carcass using a GLM with a binomial distribution and a logit link. For each avian species (i.e. black-billed magpie *Pica hudsonia*, common raven *Corvus corax*, and gray jay *Perisoreus canadensis*) we considered models using every combination of season, temperature, canopy closure, and carcass availability and selected the top model for scavenging rates based on AICc (Burnham & Anderson 2002).

For the most frequent mammalian scavengers (i.e. Canada lynx, North American red squirrels *Tamiasciurus hudsonicus*, and snowshoe hare), we included biotic variables in addition to abiotic variables, since reliable data for these species were available through concurrent ecological monitoring. For snowshoe hares, we included season, temperature, forest, and snowshoe hare density in our model selection, with models in our candidate set having a maximum of 3 covariates due to the smaller sample size (i.e. 12 scavenging events, Murray *et al.* 2019). For Canada lynx we included temperature, season, lynx density and prey density in our model selection. Indices of lynx abundance in the Kluane Lake region are determined each year through track transects, where tracks are counted along a 25-km transect that traversed our study area, on days after fresh snowfalls while tracks were distinguishable (Boutin *et al.* 1995). We considered food availability for Canada lynx as the density of snowshoe hare, determined using mark-recapture as mentioned above. We included a mid-winter density estimate (Jan 01) as the average between fall and spring densities of that winter, and assigned a snowshoe hare density to each carcass based on the nearest density estimate to the deployment date.

For red squirrels, candidate models included combinations of season, forest, temperature, squirrel density and food availability. Squirrel density was monitored in the fall and spring using a mark recapture as part of the CEMP (Krebs *et al.* 2001b). Food availability for red squirrels is primarily determined by white spruce cone production (Steele 1998). Each autumn, cone production is measured in the region by counting the number of cones in the top three meters of 100 individual trees on six different study grids according to the sampling protocol outlined and calibrated in LaMontagne et al. (2006). In our red squirrel model, we related food availability for each deployment as the mean cone production per tree in the previous summer. This is because red squirrels cache cones throughout the autumn as a food resource over the winter (Steele 1998). For species-specific models, we did not examine the time scavenging or time at carcass (as in Allen *et al.* 2015). Although we believe these variables are informative, time at the carcass in our study would be strongly dependent on whether or not an individual consumed the carcass on camera, or removed the carcass out of camera view.

Results

Community scavenging dynamics

In total, 24 different vertebrate species scavenged snowshoe hare carcasses during the four years we monitored carcasses. The top avian scavengers in our system determined as the proportion of carcasses that they scavenged, were gray jays (61.1%), common ravens (60.0%), and black-billed magpies (40.0%). Top mammalian scavengers were red squirrels (51.6%), Canada lynx

(25.3%), and snowshoe hares (12.6%). The number of scavenger species changed between seasons, with 11, 11, and 21 different species observed scavenging in the autumn, winter, and spring, respectively (see Table 3.1).

Mean persistence of carcasses was 5.53 days (95% Confidence Intervals (CI): 3.98, 7.08). Our top model explaining carcass persistence consisted of snowshoe hare density, temperature, and season (*w*=0.23), and the only other models within 2 ΔAICc included snowshoe hare density and season (*w*=0.14), or solely temperature (*w*=0.11, see Table 3.S2). Carcass persistence time was the highest during the winter compared to spring and autumn (see Fig 3.1), and increased with both decreasing temperature and increasing snowshoe hare density (see Fig 3.2).

The average time until first scavenger was 1.11 days (95 % CI: 0.72, 1.50) and were most often gray jays (36.4%), red squirrels (19.3%), and common ravens (17.0%). The top model explaining time until first scavenger consisted of canopy closure and season (*w*=0.18). However, season was the only variable included in all models within 2 ΔAICc (see Table 3.S3), with time until first scavenger being shorter in autumn than winter and spring. The mean number of species scavenging per carcass was 3.05 (95 % CI: 2.78, 3.35), and was best predicted by carcass persistence time (*w*=0.11) with longer carcass durations supporting more species at the carcass (Table 3.S4).

Species-specific scavenging

Abiotic and biotic factors driving scavenging dynamics differed between species. For the common raven, the top model predicting scavenging rates consisted of season, canopy closure, and carcass availability on the landscape (*w*=0.30; Table 3.S5). Scavenging probability for ravens were highest during autumn, in open canopy, and when there was more biomass of carrion on the landscape (see Fig 3.3). Several models were within 2 ΔAIC for predicting magpie scavenging, however, season was included in most of the top models with magpie scavenging being the highest during the autumn (Table 3.1). Gray jay scavenging was best supported by the null model, which suggests none of the covariates included in our model describe gray jay scavenging (see Table 3.S6).

The top model explaining red squirrel scavenging included season and their density (*w*=0.18), and these were the only covariates included in every model with ΔAIC <2. Scavenging by red squirrels was highest in autumn, and when their densities were high (Fig 3.3). The top supported model for Canada lynx scavenging consisted of season, daily temperature, and snowshoe hare density (*w*=0.50), with season and snowshoe hare density being the only variables included in all models with ΔAIC <2. Canada lynx scavenging was highest in the winter, and decreased with increasing hare density (Fig 3.3). Our best model for scavenging by snowshoe hares included only daily temperature (*w*=0.39); scavenging increased significantly with decreasing temperature (Fig 3.3).

Discussion

The role of scavenging in vertebrate food webs is governed by the efficiency at which carrion is transferred back into vertebrate communities, as well as the number of species that scavenge (Dunne *et al.* 2002; Wilson & Wolkovich 2011). We demonstrate that population cycles of a primary prey species can influence the efficiency of carrion recycling through their impact on vertebrate scavenging communities. Carrion persistence in our system decreased when snowshoe hare densities declined, likely through increased scavenging rates by their predators, in particular Canada lynx (see Fig 3.3). Although hare carrion may not impact lynx demography, change in lynx scavenging behaviour may reduce carrion available for other vertebrate species over-winter. Changes in prey abundance can therefore have a greater influence on food web dynamics than expected from purely a predator-prey framework, and these results may be broadly applicable as prey availability has been shown to impact the scavenging rates of several predator species (Needham *et al.* 2014; Mattisson *et al.* 2016). However, snowshoe hare density did not influence the number of vertebrate scavengers, indicating prey density can affect carrion recycling efficiency but not the number of connections in the food web established through scavenging. Vertebrate scavenger communities are therefore variable, and dependent on biological changes in the broader ecological community (see DeVault *et al.* 2011; Cunningham *et al.* 2018).

Changes in carcass availability were not a strong predictor of scavenging rates. Despite snowshoe hares being a large proportion of available prey biomass in the system, the majority of snowshoe hare mortalities are from predation, and predators consume a large percentage of their carcasses (Hodges 2000; Feierabend & Kielland 2015). Carrion from small herbivores likely have a lower impact on total available carrion, relative to larger herbivores that have higher starvation rates and more biomass remaining from predator-killed carcasses (Allen *et al.* 2015; Moleón *et al.* 2015). However, temporal changes in snowshoe hare carrion did influence the scavenging rates of ravens, through either behaviour or demographic changes (Fig 3.3). Raven densities are correlated with snowshoe hare cycles (Boutin *et al.* 1995), and during peak densities predator-killed snowshoe hare carcasses may represent a consistent food source for ravens throughout the winter (Wilmers *et al.* 2003). Many organisms use carrion as either a principle food source or a buffer when primary resources decline, and changes in consistent carrion can impact the demography of both obligate and facultative scavengers (Pain *et al.* 2003; Wilmers *et* *al.* 2003). In total, 24 species scavenged hare carcasses during our study indicating snowshoe hare may impact a plethora of vertebrate scavengers in the boreal forest not commonly associated with their population cycles (see Table 3.1). This adds to a growing body of research indicating that an omission of scavenging might substantially underestimate the connectedness of vertebrate food webs (Wilson & Wolkovich 2011). Future assessments of the boreal forest community should consider links established through scavenging, given the potential importance of weak interactions in food web stability (McCann 2000; McCann & Rooney 2009), coupled with the rich assemblage of scavengers documented in our study area relative to other systems (see Sebastián-González *et al.* 2019).

Several studies have demonstrated that carrion acquisition by vertebrates is highly influenced by temperature, with warmer temperatures decreasing vertebrate scavenging rates because of increased microbial and invertebrate activity (DeVault *et al.* 2004; Turner *et al.* 2017). As a result, it has been postulated that climate change may increase carrion decomposition rates (Parmenter & Macmahon 2009), and reduce the amount of carrion available to vertebrate scavengers (Beasley *et al.* 2012). In our system, however, vertebrate scavenging rates actually increased with increasing temperatures, which is likely driven by decreased accessibility to carrion at cold temperatures (i.e. <-20 ºC), as well as minimal competition with invertebrates over winter at northern latitudes. Our results indicate decreased carrion persistence with warmer temperatures, suggesting vertebrate scavenging may actually increase during the winter under climate change in the northern boreal forest. Although warmer temperatures also favour microbial and invertebrate activity (DeVault *et al.* 2004; Turner *et al.* 2017), the subsequent increase in vertebrate scavenging during the winter may reduce the proportion of carcasses that persist to the summer. This would limit the amount of carrion available for decomposers, however, the influence of temperature on the competitive interactions between vertebrates and decomposers in this system warrants further investigation.

As documented in other systems, we found strong seasonal differences in scavenging dynamics with carcasses persisting longer during the winter, likely driven by the influence of temperature (Turner *et al.* 2017). The longer persistence of carcasses during winter explained why winter supported more scavenger species per carcass, as persistence time was the strongest predictor of the number of species scavenging (see Table 3.S4). Detection times were lowest during the autumn season, which coincides with increasing scavenging rates for avian species and red squirrel (Table 3.1). The richness of the vertebrate scavenging community also varied among seasons. As would be expected, hibernators such as arctic ground squirrels (*Spermophilus parryii*) and black bears (*Ursus americanus*), and migratory birds such as the Northern harrier (*Circus cyaneus*) and red-tailed hawk (*Buteo jamaicensis*) were never observed scavenging in the winter (see Table 3.1). However, most of these species were still present but did not scavenge in autumn, indicating carrion may be a resource used by migrating or hibernating species prior to green up, when their primary food sources become more abundant. These seasonal changes in the scavenging community are likely consistent throughout the boreal forest, and could be incorporated into multi-season perspectives of food web dynamics in temperate ecosystems (see Humphries *et al.* 2017).

Although the processes governing scavenging rates within a community can be complex, they are not random and dependent on several extrinsic factors (Selva *et al.* 2005; Selva & Fortuna 2007; Turner *et al.* 2017). That being said, there was large variability in scavenging rates, and the number of species scavenging across predictor variables, potentially due to variance among species in the primary drivers of their behaviour. For instance, while warmer temperatures increased scavenging rates for the community, snowshoe hare scavenged (cannibalistically) more during colder periods which could be due to lower protein content of the woody browse species consumed in winter (Peers *et al.* 2018). Carrion consumption for Canada lynx, red squirrel, and raven were dependent on biotic factors that differed among species (Fig 3.3). Similarly, lynx appear to increase their use of carrion when resources decline (i.e. snowshoe hare), however, red squirrel scavenging was not related to white spruce cone abundance. This indicates that spatial and temporal patterns in community scavenging rates may be challenging to forecast, particularly in systems comprised of a diverse assemblage of facultative scavengers. This further implies that biotic variables not included in our models, such as the density of avian species, may be important predictors of species behaviour and could influence community scavenging rates across the boreal forest.

Our results demonstrate that in a community dominated by facultative scavengers, biotic and abiotic factors can modulate vertebrate scavenging dynamics. In particular, lower prey density on the landscape and warmer temperatures increased carrion recycling efficiency, indicating vertebrate scavenging communities are sensitive to changes in species' demography and environmental change (Beasley *et al.* 2018). Given that biotic factors influenced scavenging behaviour for multiple species considered here, scavenging rates in most systems are likely dependent on the population dynamics of species in the community (see DeVault *et al.* 2011; Cunningham *et al.* 2018). Scavenging rates established in previous studies are therefore dependent on the biotic conditions during the time of their study, and understanding the full suite of factors driving vertebrate scavenging communities across the globe requires continued investigation. Future studies should examine the influence of changes in prey density and carcass availability on community scavenging rates, particularly for large species that may contribute substantially to overall carrion biomass.

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Table 3.1. Percent of snowshoe hare carcasses scavenged (n) by season for each species observed scavenging between Jan 2015-May 2018 in the Kluane Lake region, Yukon.

Species	**Overall** (95)	**Season**		
		Autumn (34)	**Winter** (21)	**Spring** (40)
Avian				
Bald eagle (*Haliaeetus leucocephalus*)	4.2 (4)	9.0 (3)	0.0 (0)	2.5 (1)
Black-billed magpie (*Pica hudsonia*)	40.0 (38)	47.1 (16)	57.1 (12)	25.0 (10)
Black-capped chickadee (*Poecile atricapillus*)	1.1 (1)	0.0 (0)	0.0 (0)	2.5 (1)
Boreal chickadee (*Poecile hudsonicus*)	1.1 (1)	0.0 (0)	0.0 (0)	2.5 (1)
Common raven (*Corvus corax*)	60.0 (57)	73.5 (25)	57.1 (12)	25.0 (20)
Golden eagle (*Aquila chrysaetos*)	1.1 (1)	0.0 (0)	0.0 (0)	2.5 (1)
Gray jay (*Perisoreus canadensis*)	61.1 (58)	70.6 (24)	66.7 (14)	50.0 (20)
Northern goshawk (*Accipiter gentilis*)	7.4 (7)	8.8 (3)	9.5 (2)	5.0 (2)
Northern harrier (*Circus cyaneus*)	4.2 (4)	0.0 (0)	0.0 (0)	10.0 (4)
Northern hawk-owl (*Surnia ulula*)	1.1 (1)	0.0 (0)	0.0 (0)	2.5 (1)
Red-tailed hawk (*Buteo jamaicensis*)	1.1 (1)	0.0 (0)	0.0 (0)	2.5 (1)
Mammal				
Arctic ground-squirrel (*Spermophilus parryii*)	1.1 (1)	0.0 (0)	0.0 (0)	2.5 (1)
Black bear (*Ursus americanus*)	1.1 (1)	0.0 (0)	0.0 (0)	2.5 (1)
Canada lynx (*Lynx canadensis*)	25.3 (24)	8.8 (3)	42.8 (9)	30.0 (12)
Coyote (*Canis latrans*)	4.2 (4)	0.0 (0)	9.5 (2)	5.0 (2)
Grizzly bear (*Ursus arctos*)	3.2 (3)	8.8 (3)	0.0 (0)	0.0 (0)
Least chipmunk (*Tamias minimus*)	1.1 (1)	0.0 (0)	0.0 (0)	2.5 (1)
Northern flying squirrel (*Glaucomys sabrinus*)	2.1 (2)	0.0 (0)	9.5 (2)	0.0 (0)
Red squirrel (*Tamiasciurus hudsonicus*)	51.6 (49)	67.6 (23)	52.4 (11)	37.5 (15)

Small mammals (*Myodes; Peromyscus; Sorex*)	8.4 (8)	17.6 (6)	0.0 (0)	5.0 (2)
Snowshoe hare (*Lepus americanus*)	12.6 (12)	11.8 (4)	28.6 (6)	5.0 (2)
Short-tailed weasel (*Mustela erminea*)	9.5 (9)	8.8 (3)	14.3 (3)	7.5 (3)
Wolverine (*Gulo gulo*)	2.1 (2)	0.0 (0)	4.8 (1)	2.5 (1)

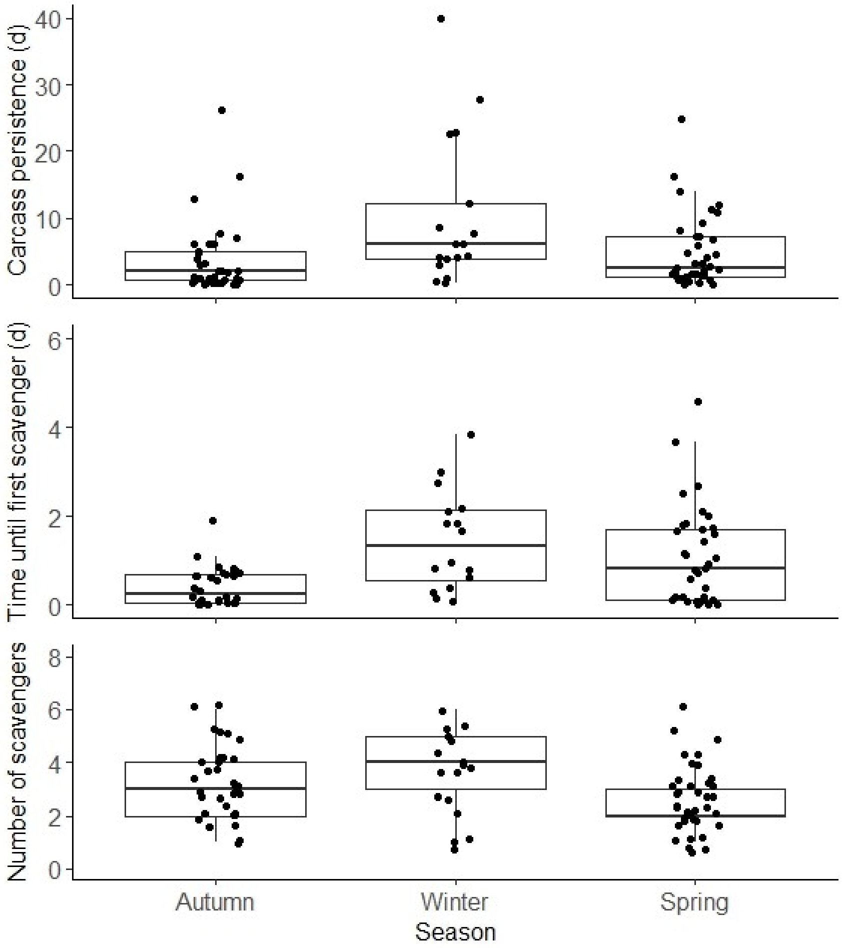

Figure 3.1. Boxplot and values for each carcass deployment comparing seasonal differences in a) carcass persistence time (days), b) time until the first scavenger (days), and c) number of scavenger species per carcass.

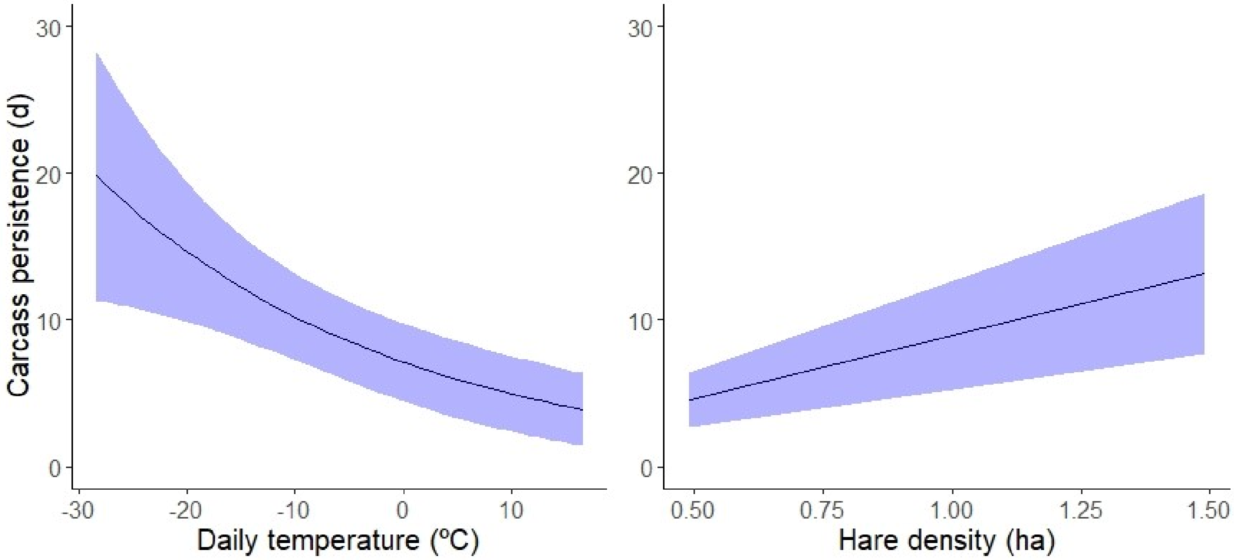

Figure 3.2. Modeled effect of daily temperature and snowshoe hare (*Lepus americanus*) density on carcass persistence (days) during the winter based on coefficients from the top model. Confidence bars represent predicted response standard errors.

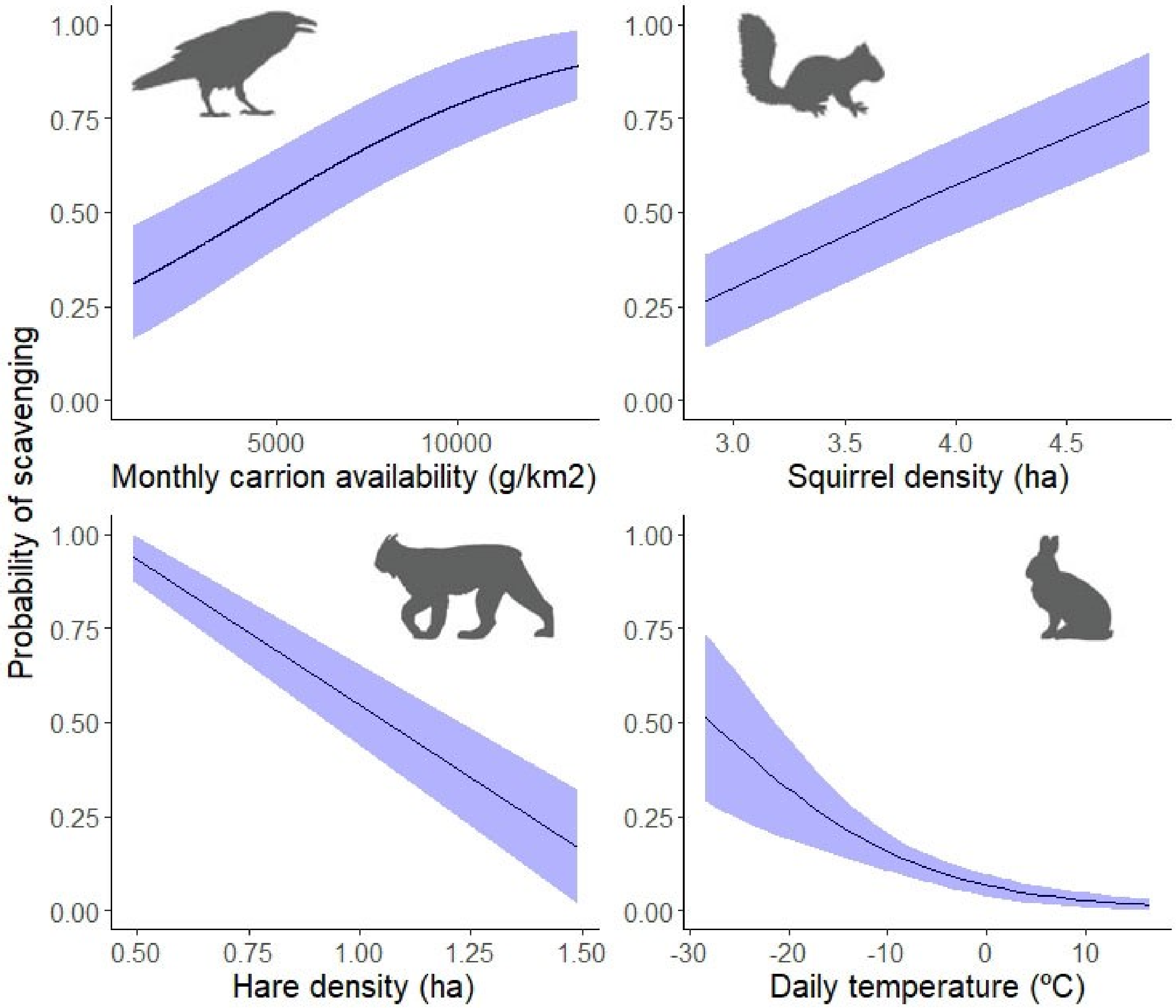

Figure 3.3. Modeled effect of biotic and abiotic predictors on the probability of scavenging for raven (*Corvus corax*), red squirrel (*Tamiasciurus hudsonicus*), Canada lynx (*Lynx canadensis*), and snowshoe hare (*Lepus americanus*) using coefficients from the strongest supported model. Confidence bars represent predicted response standard errors.

Chapter 4

Contribution of late-litter juveniles to the population dynamics of snowshoe hares

"The ten-year cycle; outstanding problem of Canadian conservation"

~ William Rowan, 1948

Abstract

Population cycles have interested ecologists for decades, however, the primary factors driving cyclic dynamics for most species are still debated. For snowshoe hares (*Lepus americanus*), explanations of their 10-year population cycles most commonly feature direct, lethal effects of predators, in combination with a driver of their observed reproductive cut-back. Hares reduce reproductive output prior to peak densities by approximately two years, and do not recover reproductive rates for several years following population decline. The majority of the reproductive collapse, in terms of number of offspring produced in a season, occurs via the cut-back of the third and fourth litters. However, the demographic effect of this reproductive cut-back will depend on the consistency of this pattern across multiple cycles, and the relative survival rate of late-litter juveniles in comparison to juveniles from earlier litters. These question remain unknown, due to the difficulty of monitoring reproduction and offspring survival in this species. We used long-term monitoring data on a snowshoe hare populations from southwestern Yukon, Canada, to provide insight into the role of late-litter juveniles on regulating hare cycles. We developed growth curves for juvenile hares and determined the suspected litter group for individuals caught in autumn based on body size and capture date. We found that fourth-litter juveniles occur consistently in the increase phase of the cycle, but have relatively low over-winter survival suggesting that the transition to population increase is unlikely caused by their occurrence. The proportion of third-litter juveniles captured in the autumn also remained relatively constant across cyclic phases. In contrast, apparent survival rates vary between phases particularly for early-litter juveniles. Juveniles from all litters were more likely to be recaptured in the spring during the increase and peak, and less likely during the low and decline. In

combination, these results suggest that the transition from low phase to population growth may stem in large part from changes in over winter-survival.

Introduction

Population cycles have interested ecologists for decades, and examining the drivers of species' cycles has been the subject of intense investigation, providing considerable knowledge on the factors regulating density (Myers 2018). Several external factors such as disease, food availability and predation have been proposed as mechanisms regulating population cycles, and numerous theoretical and experimental studies have tested the importance of these factors across species and populations (Krebs *et al.* 1995; Korpimäki *et al.* 2004; Redpath *et al.* 2006). However, the external factors driving cyclic dynamics for most species are still debated (Myers 2018). One approach to resolve such debate is to explore the density dependence of demographic variables, and determine which demographic variables change in accordance with cyclic phase (i.e. growth vs decline). Previous experimental results can then be placed in the context of the demographic parameters that appear to regulate species abundance.

The 10 year cycle of the snowshoe hare (*Lepus americanus*) across the boreal forests of North America is a prominent example of population cycles, with investigations into changes in their abundance dating back to the early 20th century (Green *et al.* 1939). The cycle is characterized into four phases: increase, peak, decline, and low (Keith 1990). The increase phase of their cycle is characterized by high survival and reproductive rates, whereas the decline phase is associated with low survival and reproductive rates (Hodges 2000; Krebs *et al.* 2001). This reduction in reproductive output, caused by changes in the number of leverets produced and pregnancy rates, precedes peak hare densities by approximately two years (Cary & Keith 1979; Stefan & Krebs 2001). As a result, explanations of the cycle most commonly feature direct, lethal effects of predators, in combination with a driver of the observed reproductive cut-back (Krebs *et al.* 2018). Changes in reproduction could be driven by variation in winter food availability or quality (Cary & Keith 1979; Deangelis *et al.* 2015), or indirect effects of predators mediated through predator-induced stress (Boonstra *et al.* 1998a; Sheriff *et al.* 2009, 2011), the latter of which is most widely accepted (Krebs *et al.* 2018).

Snowshoe hares breed during the summer, with a maximum of four litters produced in a single year that are locally synchronous, creating distinguishable juvenile cohorts (Cary & Keith 1979; O'Donoghue 1994). The majority of the reproductive collapse, in terms of number of offspring produced in a season, occurs via the cut-back of the third and fourth litters (Stefan & Krebs 2001). Specifically, fourth litters are thought to only occur in the late low and early increase phase, significantly increasing population growth during this time. Third litters are curtailed during the decline, reducing recruitment and population recovery over the summer (Stefan & Krebs 2001). First and second litters occur in each cycle phase, with second litter experiencing changes in the average litter size, whereas first litters remain relatively constant (i.e. 0.5 leveret variation; Hodges 2000).

Monitoring reproduction in hares requires considerable trapping effort (Hodges *et al.* 2001), especially during the low phase when researchers are limited by sample size (Gillis 1998; Hodges *et al.* 1999). Therefore, the consistency of their reproductive pattern, particularly in regard to the presence of a fourth litter, has not been examined across multiple cycles. The contribution of late-litter juveniles (i.e. third and fourth litters) to hare population growth will also depend on their survival rate relative to juveniles born earlier in the summer. Late-litter juveniles are born in late summer, and enter the autumn with smaller body mass (O'Donoghue & Krebs 1992), presumably having higher foraging requirements to accommodate growth which may reduce over-winter survival, particularly during autumn and early winter (Gillis 1998). However, due to high pre-weaning mortality rates of leverets (Stefan 1998), monitoring an adequate sample of juveniles from birth to autumn is difficult. As a result, we lack knowledge on relative survival rates of different juvenile cohorts, particularly in how survival varies across cyclic phase.

In this study, we tested the hypothesis that changes in reproduction are a primary driver for the transition among cyclic phases in snowshoe hare populations. We used long-term monitoring data on a snowshoe hare population from southwestern Yukon, Canada, to provide insight into several unresolved questions: 1) do hares have fourth litters consistently across cycles, 2) how does the proportion of late-litter juveniles (third and fourth litters) vary across phase of the cycle, 3) how does over-winter survival of juveniles from late litters compare to earlier litters, and 4) how does the survival of individuals from each litter vary among cyclic phases? We developed growth curves for juvenile hares and determined whether individuals caught in autumn were from early or late litters, or from fourth litters based on body size and capture date. Specifically, we tested whether fourth litters occurred solely during the low and increase phase across multiple cycles, and what their winter survival rate was relative to other juvenile cohorts. Further, we examined how survival rates differed between early and third-litter juveniles, and how this pattern varied during the increase, peak, decline, and low. If the low phase is determined by collapsed reproductive output, we predict the proportion of third-litter juveniles during this phase to be minimal in comparison to years of population growth. Furthermore, we predict survival rates of these juveniles to be relatively high during the low phase indicating changes are not driven by survival.

Material & Methods

Study area and trapping methods

This study was conducted in the Kluane lake region of Yukon, Canada (61ºN, -138ºW). The boreal forest in this area is comprised primarily of white spruce (*Picea glauca*) with smaller amounts of trembling aspen (*Populus tremuloides*) and balsam poplar (*Populus balsamifera*). The shrub layer is dominated by areas of gray willow (*Salix glauca*) and dwarf birch (*Betula glandulosa*). The main predators of hares in the region are Canada lynx (*Lynx canadensis*) and coyote (*Canis latrans*), with other predators including great-horned owl (*Bubo virginianus*) and northern goshawk (*Accipiter gentilis*). Snowshoe hares have been monitored in the region over the last four decades (Krebs *et al.* 2018).

We captured snowshoe hares using Tomahawk live traps (Tomahawk Live Trap Co., Tomahawk, WI) on several study grids that were either 10m x 10m or 20m x 20m with 30 m spacing between traps (Krebs *et al.* 2001, 2018). Sex, age, reproductive status, body mass and right hind foot length of each individual were recorded. Each hare received a Monel #3 eartag (National Band and Tag Co., Newport, KY) on the first capture and the identity of a previously marked hare was recorded in each subsequent capture. Trapping occurred between autumn 1977 and autumn 2017, and all data used in this study came from unmanipulated control grids.

Calculating growth rates and designating litter groups

Using 209 body mass measurements on 69 known age juveniles from earlier monitoring in the same population (O'Donoghue & Krebs 1992), we fit Gompertz growth curves using maximum likelihood, with log normal errors in the "grofit" package in R (Kahm *et al.* 2010). Due to the limited sample size, particularly for individuals older than 50 days, we combined juveniles from multiple litters in the same growth curve, and fixed the asymptotic growth rate as the average adult mass in December and January (1518 g; See Fig 4.1). We choose these dates for our average asymptotic mass as it represents when individuals will be adult size, but prior to over-winter mass loss (Hodges *et al.* 2006).

We used mass data for individuals captured between September-November to determine the presence of fourth litter juveniles each year. We classified suspected fourth litter hares as any individual who weighed less than the lower 95th confidence interval of a juvenile born on August 13th. This date represents the latest recorded birth date of a third litter, when hare reproduction was intensively monitored from 1988-1996 (Hodges *et al.* 2001).

We distinguished early (i.e. first and second) and third-litter juveniles based on body mass similar to above. Third-litter hares were classified as any individual who weighed less than the upper 95th confidence interval of an individual born on the earliest recorded date of a third litter, July 20th (Hodges *et al.* 2001). However, we restricted this analysis to trapping that occurred between the week of August 01 and September 18, the date where the Gompertz growth curve reaches 1000 g, as we considered hares larger than 1000 g impossible to designate into a litter group. Here, we are assuming individuals are most likely from a third litter if they weighed less than the maximum growth rate of an individual born after the earliest known third-litter. We determined early-litter juveniles during this same time period as any juvenile hare that was not considered late litter. Juveniles were classified as individuals who were caught for the first time that autumn or summer (as in Hodges *et al.* 1999). There is a potential that our classification of juveniles includes dispersing adults, however, this likely had minimal impact on our analysis as instances of adults dispersing into the population over the summer are rare (Hodges 1999). We included data in this analysis only from study grids where monitoring occurred in the previous year. To calculate the proportion of the autumn population that was from either early or third-litter juveniles, we included trapping records that occurred only between August 14 and

September 18, which represents the time period after the last known date of the third litter, and prior to the growth curve reaching 1000g.

Examining survival rates and the presence of fourth litters

First, we examined the cyclic phase of each year where fourth litter juveniles occurred, to determine their consistency across cycles. Cyclic phase was determined based on criteria from Keith (1990), where finite rate of annual change (spring to spring) less than 0.44 equals a decline, more than 1.89 equals an increase phase, and the years between these phases correspond to either peak or low. Next, we examined the over-winter survival probability for juveniles from each litter group (i.e. early, third, or fourth). For this analysis, we considered over-winter survival as any juvenile that was captured beyond March 01 the following spring (prior to the earliest date of the spring population census). We acknowledge this represents apparent survival, as loss will include both death and emigration (Sandercock 2019). However, we expect emigration to have limited impact on our results, as there is no suspected difference in dispersal rates between litter groups and cyclic phase (Boutin *et al.* 1984; Gillis & Krebs 1999), and our goal was to compare relative changes in winter survival between cohorts and cyclic phase (see further discussion below). For simplicity, we therefore refer to the probability of being captured the following spring as apparent survival for the rest of our analyses. We calculated the proportion of juveniles from each litter group that survived over winter by comparing the survival rates of 500 bootstrapped datasets of individuals within each litter group. Sample size of our bootstrapped datasets corresponds to the total number of individuals captured during the autumn for each litter group.

We then compared differences in apparent survival between early and third-litter juveniles, as well as adults, across cyclic phases. First, we assigned cyclic phase as the phase of the upcoming spring, as our goal was to determine survival rates that result in the post-winter phase (see supplement for results from other phase classifications). Given the low sample size within some years, calculating average survival for litter and cyclic phase as the mean across years was not feasible. Instead, we assessed relative differences in survival by comparing the survival rates of 500 bootstrapped datasets of individuals from each age-group and phase. Each bootstrapped dataset included resampled individuals, with replacement, until the number of individuals in the resample equaled the original dataset for each age group and cycle phase. We repeated this same analysis, including only years that represented transitions between cyclic phases to determine the demographic change that may signal such transitions.

We then examined the drivers of juvenile over-winter survival across our entire dataset using generalized linear models (GLM) with a binomial distribution and a logit link in the program R (3.3.1). We used an information theoretic approach to determine which variables best-characterized whether a juvenile hare was captured the following spring. Models consisted of all combinations of litter group, cycle phase, mass, and sex. We selected the top model using Akaike's Information Criterion, corrected for small sample sizes (AICc; Burnham & Anderson 2002). Covariates used for our analyses had a variance inflation factor less than 2 (Graham 2003), signifying covariates were not correlated in our models.

Results

We captured a total of 40 individual hares suspected to be from a fourth litter between September-November over the 42 years of monitoring in the region (3680 individuals captured between September-November). Fourth litter individuals were present in 12 years across the five cycles and occurred primarily during the low and increase phase of the cycle (11 cases) with a single case during the decline (Fig 4.2). Proportion of the autumn population (i.e. August 14-September 18) that was early or third-litter juveniles differed across cyclic phases (Fig 4.3). However, given the restricted trapping period included in the analysis, only 25 years had trapping data that could be included. Qualitatively, the proportion of the total hares caught during the autumn that were third-litter juveniles was largest during the low phase (0.36) and remained relatively constant during the increase (0.15), peak (0.21), and decline (0.15) phases of the cycle (Fig 4.3). For early-litter juveniles, proportions were highest during the increase (0.50), followed by the peak (0.47), decline (0.47), and low phases (0.36; Fig 4.3 & Table 4.S2). These patterns were similar whether cycle phase was considered to coincide with that autumn, the previous spring, or the following spring (Fig 4.S1).

Apparent survival rates varied among litter groups, with early-litter juveniles having higher survival (0.28, 95% CI based on bootstrap recruitment: 0.26, 0.31) than third-litter juveniles (0.06, 95% CI: 0.04, 0.08). Survival rates for fourth litter individuals were the lowest (0.05, 95% CI: 0.00, 0.10), as only two of the 40 individuals were recaptured the following spring (Fig 4.4a). Survival also varied between cycle phases, and each litter had qualitatively similar patterns. Lowest survival occurred during the decline and low phase for both early (Decline=0.18, CI: 0.15, 0.21; Low=0.14, CI: 0.06, 0.22) and third litters (Decline=0.02, CI: 0.00, 0.05; Low=0.03, CI: 0.00, 0.10). Apparent survival rates increased during the increase and peak phase for both early (Increase=0.39, CI: 0.34, 0.46; Peak=0.34, CI: 0.31, 0.37) and third litters (Increase=0.12, CI: 0.03, 0.21; Peak=0.07, CI: 0.04, 0.10; see Fig 4.4b). These patterns were similar in years that were transitions between the cyclic phases (Fig 4.S2). Over-winter survival appears less variable across phases for adults, with highest rates during the increase and peak (Fig 4.4b). Survival patterns across phase and age groups appear similar if examining yearly percentages as opposed to the pooled bootstrap models (Fig 4.S3), however, there is large variation among years within the same phase and age group. Yearly patterns should be taken with caution, as some years were severely limited by sample size (i.e. <5 individuals captured in the autumn).

Our top model explaining whether a juvenile was captured the following spring included cyclic phase, litter group, and body mass (*w*=0.79; Table 4.S1) and was the only model within 2 ΔAICc. Likelihood of being recaptured in the spring was higher for early-litter juveniles (1.35±0.26, z = 5.2, P < 0.01; Fig 4.5) and increased with larger body mass (0.002±0.0002, z = 4.6, P < 0.01). In reference to the decline phase, recapture rates were higher during the increase (1.18±0.20, z = 6.0, P < 0.01) and peak (0.77±0.154, z = 5.0, P < 0.01). Recapture rates in the low phase did not significantly differ from rates during the decline phase (-0.26±0.46, z = -0.6, P = 0.58; Fig 4.5).

Discussion

Our goal was to examine the presence and survival rate of juveniles from different litter groups to provide insight into the demographic variables most strongly influencing population cycles in this species. These results demonstrate that the 4th litters are present consistently across cycles, and primarily occur during the increase phase (see Fig 4.2; Stefan & Krebs 2001). However, given the relatively low probability that fourth litter juveniles were recaptured the following spring, it seems unlikely that the transition from a cyclic low to population increase is driven by the occurrence of this litter group. This suggests that a change in reproductive output is not the important driver of the increase phase of the cycle, as the increase in leverets produced per female during this period is largely driven by the occurrence of the 4th litter (Stefan & Krebs 2001). Furthermore, the proportion of third-litter juveniles captured in the autumn remains relatively constant across cyclic phases and is actually the highest in the low phase (see Fig 4.3 & Fig 4.S1). In contrast, apparent survival rates vary between phases particularly for early-litter juveniles (see Fig 4.4). Juveniles from all litters were more likely to be recaptured in the spring during the increase and peak, and less likely during the low and decline (see Fig 4.4). In combination, these results suggest that the transition from low phase to population growth may stem in large part from changes in over winter-survival; populations do not increase, following decline, until mortality rates have decreased, as opposed to changes in reproductive output.

We can think of two potential hypotheses that may drive this pattern. First, high predation risk during population declines causes higher stress levels in females (Boonstra *et al.* 1998a, b; Sheriff *et al.* 2011), which leads to lower reproductive rates and offspring quality (Sheriff *et al.* 2009). These offspring may have reduced over-winter survival, and continue to produce lower quality offspring through maternal effects (Sheriff *et al.* 2010). Recruitment of juveniles into the spring increases when stress levels are reduced and offspring quality improves, which subsequently improves survival. Second, predators exist at high enough densities following population decline to maintain similar consumption rates in proportion to prey density during the low phase. Predators such as great-horned owls that have a slower numerical response relative to other predators (O'Donoghue *et al.* 1997) may have a particularly important role during this phase of the cycle (Rohner *et al.* 2001; Tyson *et al.* 2010). Juvenile survival increases when relative consumption rates finally decrease, which causes population growth.

There are several key uncertainties and limitations in our data that should be considered for future research. The timing of reproduction in the spring may depend on yearly changes in climate (Visser *et al.* 2009), and leverets can vary in body size and growth rates (O'Donoghue & Krebs 1992), causing some individuals to be inaccurately classified as either early or late-litter individuals. Therefore, comparison of the proportion of individuals from each litter group should be taken with caution. For survival, our results clearly indicate that larger individuals in late summer/early autumn are more likely to be recaptured in the spring (see Fig 4.5), and that this pattern changes across the cycle. Most often, larger individuals at this time period will represent early as opposed to late-litter juveniles. These patterns are also consistent with earlier work examining juvenile survival rates between litter groups (Gillis 1998). Furthermore, our main goal was to compare survival rates and autumn proportions across cycle phases, which is more robust to the limitations outlined above. A more important uncertainty is the potential differences in dispersal rates that may bias our estimates of apparent survival. Although earlier work suggests juvenile dispersal does not differ between litter groups and cycle phase, these results are based on low sample sizes (Boutin & Krebs 1986; Gillis & Krebs 1999). Future studies should examine whether late-litter juveniles disperse at higher rates, and whether this pattern is dependent on population density, as changes in survival rates between phases may represent differences in dispersal. That being said, the proportion of individuals caught in spring that are new hares does not vary widely across cycle phases (Hodges *et al.* 2001), suggesting higher survival in the increase versus low phases is not driven by differences in dispersal.

This research indicates that snowshoe hare populations may transition from the low to increase phase due to improvement in over-winter survival for juveniles (see Fig 4.4, 4.5). This contradicts earlier suggestions that the low is caused by a delay in reproductive output following population decline (Boonstra *et al.* 1998a; Sheriff *et al.* 2010, 2015). Indeed, reproduction changes throughout the cycle (Cary & Keith 1979; Stefan & Krebs 2001), however, we did not find evidence that the low phase is characterized by a reduced proportion of third-litter juveniles, nor that population increase coincides with a higher proportion. Modelling exercises are therefore required to estimate the degree that the autumn populations could be changed had females produced at their maximum capacity. That being said, the main change in reproductive output between the low and increase phase in our population is caused by the occurrence of the 4th litter (Stefan & Krebs 2001), and given the low survival rate relative to early-litter juveniles, it seems unlikely population growth at this phase is driven by their occurrence. Instead, changes in reproduction may be indicative of overall patterns in individual condition (i.e. stress; Sheriff *et al.* 2009), which influences offspring quality and likelihood of survival, as the low to increase phase corresponds with changes in relative survival (see Fig 4.4b). These patterns resemble environmental canalization; fitness or demographic components whose variation has greater effects on overall fitness or population growth should be less variable across time (Gaillard & Yoccoz 2003). The third and fourth litters have greater temporal variation relative to early litters, due to their lower contribution to fitness and demography (Pfister 1998). However, given the uncertainty in our estimates of survival and classification of litter groups, as well as the limited sample size within phases, we strongly recommend future studies investigate late-litter survival and reproduction during the low and increase phase of the snowshoe hare cycle. Although such studies will always be limited by sample size, they will provide critical information of population dynamics at this important phase of the cycle.

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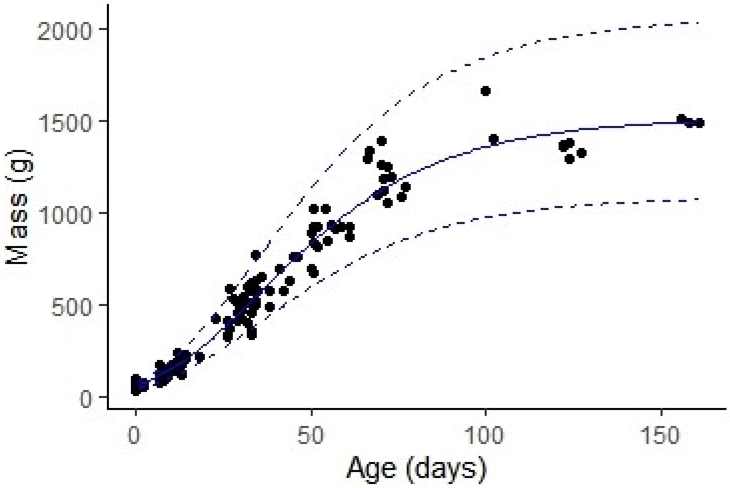

Figure 4.1. Gompertz growth curves (solid) and 95% CIs for juvenile snowshoe hare fit using maximum likelihood with log normal errors. Each point represent the 209 mass measurements recorded for 69 known-age individuals.

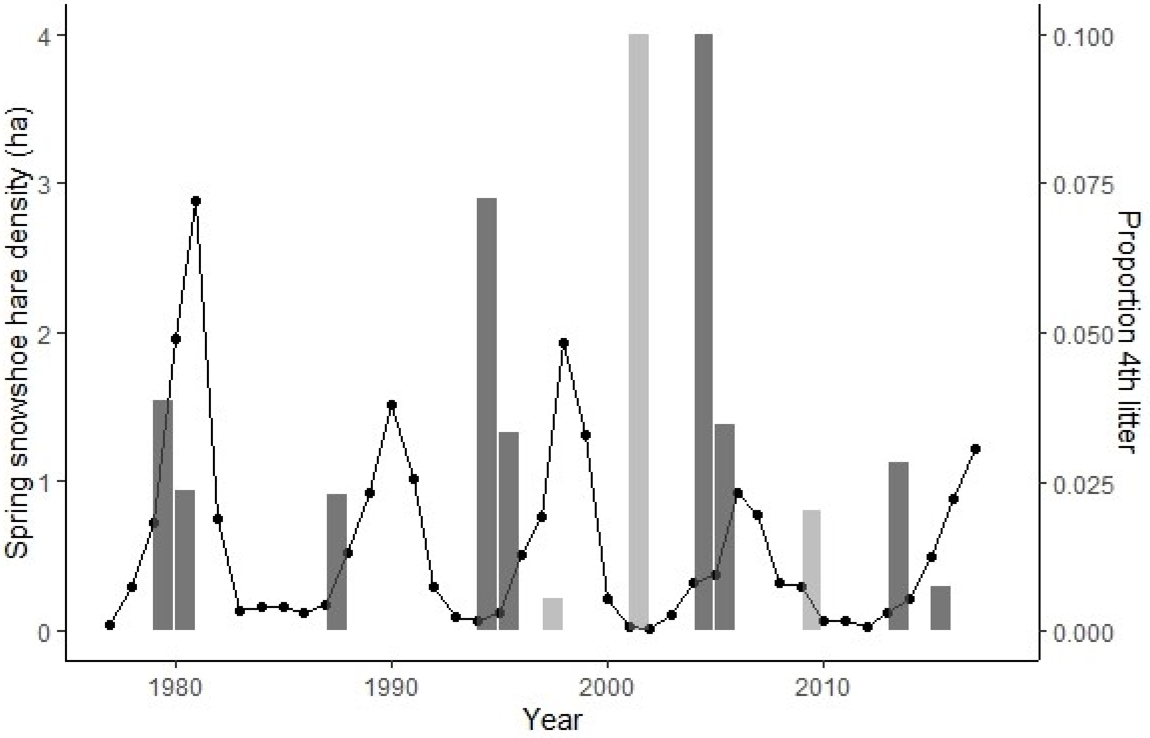

Figure 4.2. Spring snowshoe hare density (dotted line) in southwestern Yukon since 1977 with the proportion of the total individuals captured in September-November that were suspected to be from a fourth litter (gray bars). Light gray bars represent years where only one individual fourth-litter juvenile was captured.

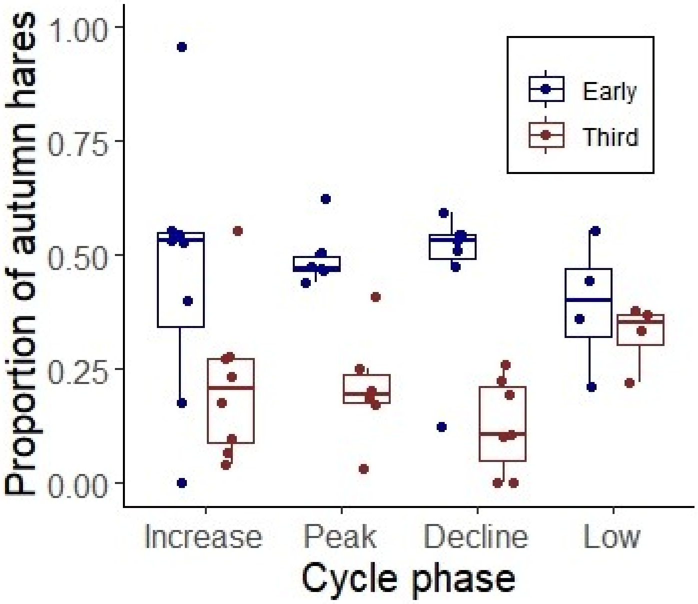

Figure 4.3. Boxplot of the proportion of the autumn population that were either early-litter (blue), or third-litter (red) juveniles for each phase of the cycle. Individual dots represent the values for each year that correspond to the cycle phase and litter group.

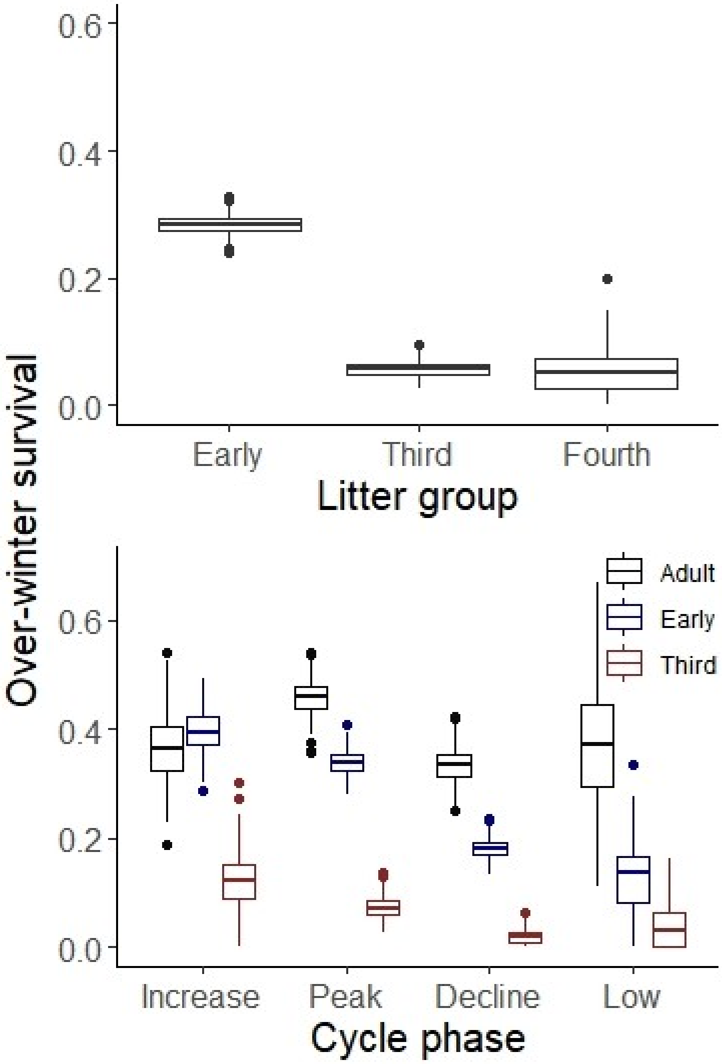

Figure 4.4. The probability of being captured the following spring among a) litter groups, and b) cycle phase for adults (black), early-litter (blue), and third-litter (red) juveniles, based on recapture rates from 500 bootstrapped datasets.

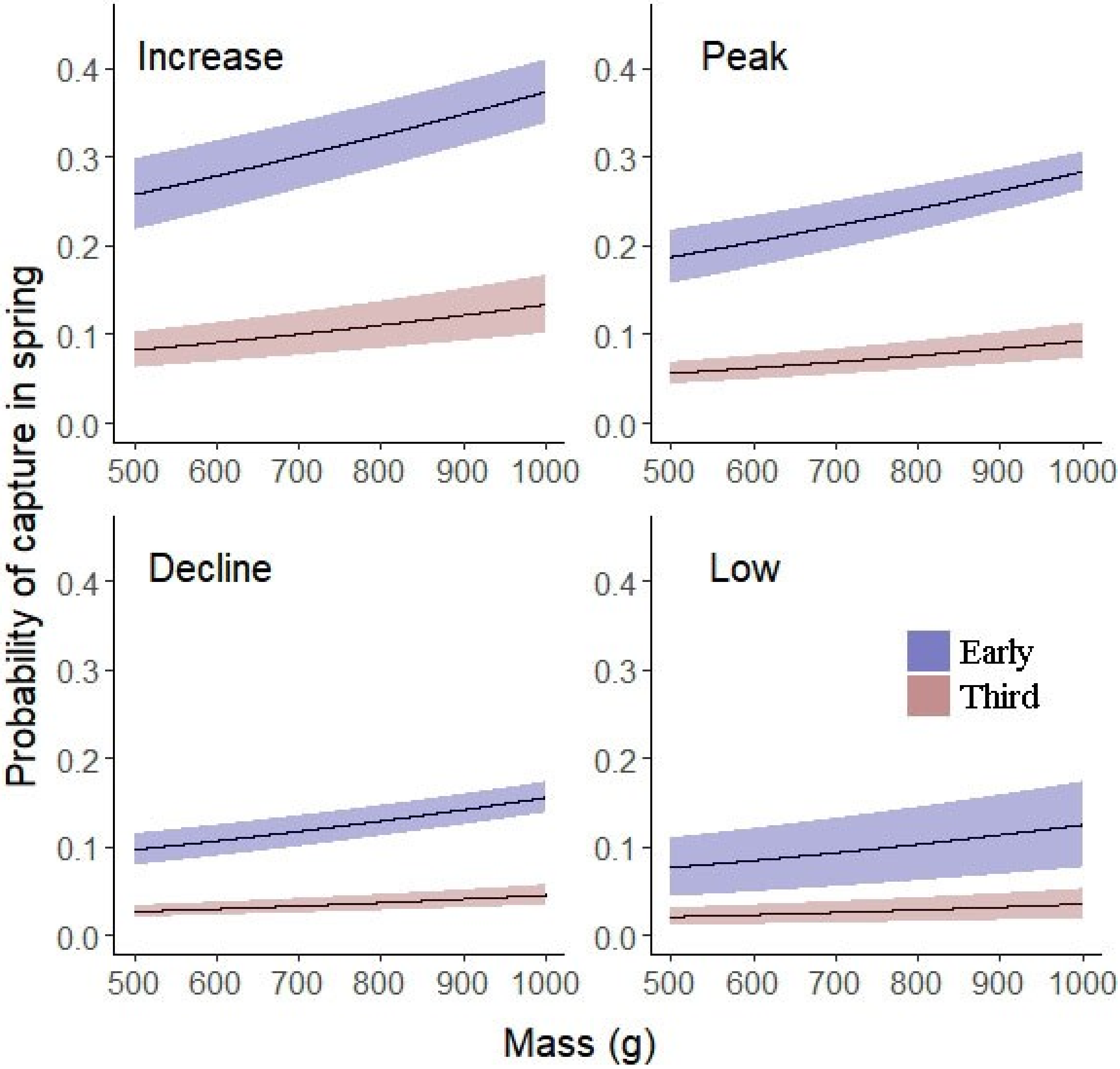

Figure 4.5. Modelled effect of body mass at first capture on the probability of being captured the following spring for early (blue) and third (red) litter juveniles across each phase of the cycle, using coefficients from the strongest supported model. Confidence bards represent predicted response standard errors.

Chapter 5

Quantifying fear effects on prey demography in nature

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“Whatever else may be said of predation, it does draw attention”

~ Paul L Errington, 1947

Abstract

In recent years, it has been argued that the effect of predator fear exacts a greater demographic toll on prey populations than the direct killing of prey. However, efforts to quantify the effects of fear have primarily relied on experiments that replace predators with predator cues. Interpretation of these experiments must consider two important caveats: 1) the magnitude of experimenter-induced predator cues may not be realistically comparable to those of the prey's natural sensory environment, and 2) given functional predators are removed from the treatments, the fear effect is measured in the absence of any consumptive effects, a situation which never occurs in nature. We contend that demographic consequences of fear in natural populations may have been overestimated because the intensity of predator cues applied by experimenters in the majority of studies has been unnaturally high, in some instances rarely occurring in nature without consumption. Furthermore, the removal of consumption from the treatments creates the potential situation that individual prey in poor condition (those most likely to contribute strongly to the observed fear effects via starvation or reduced reproductive output) may have been consumed by predators in nature prior to the expression of fear effects, thus confounding consumptive and fear effects. Here, we describe an alternative treatment design that does not utilize predator cues, and in so doing, better quantifies the demographic effect of fear on wild populations. This treatment substitutes the traditional cue experiment where consumptive effects are eliminated and fear is simulated with a design where fear is removed and consumptive effects are simulated through the experimental removal of prey. Comparison to a natural population would give a more robust estimate of the effect of fear in the presence of consumption on the demographic variable of interest. This approach represents a critical advance in quantifying the mechanistic pathways through which predation structures ecological communities.

Discussing the merits of both treatments will motivate researchers to go beyond simply describing the existence of fear effects and focus on testing their true magnitude in wild populations and natural communities.

Introduction

The landscape of fear experienced by prey in response to their predators has emerged as a potential fundamental ecological process influencing many aspects of prey biology. Consequently, there is growing interest in the magnitude of prey demographic responses to the fear of predation (termed non-consumptive or fear effects), whereby the mere presence of predators causes declines in reproduction and survival through changes in prey behaviour and physiology (Fig 5.1; Creel & Christianson 2008; Peckarsky *et al.* 2008; Winnie & Creel 2017). A growing number of laboratory and field experiments suggest that the fear of predators could have limiting effects on prey populations that rival the classic "consumptive" effects of predators (Schmitz *et al.* 1997; Creel *et al.* 2007; Zanette *et al.* 2011). If fear effects are pervasive and large, our fundamental understanding of the mechanisms and magnitude by which predators limit prey populations and the potential cascading effects of predators on ecosystems would need to be thoroughly revised (see Ford *et al.* 2014; Suraci *et al.* 2016). As carnivore populations continue to undergo extirpation and re-establishment around the globe (Chapron *et al.* 2014; Ripple *et al.* 2014), determining the magnitude of their fear effects on prey demography could greatly improve the efficacy of conservation initiatives.

Quantifying the magnitude of fear on prey demography in the wild remains rare. Perhaps the most high profile example involves the reintroduction of wolves (*Canis lupus*) to Yellowstone National Park and the subsequent influence on elk (*Cervus canadensis*) foraging patterns, leading to reduced reproductive output and population declines over and above what could be attributed to consumptive effects (i.e. direct killing; Creel *et al.* 2005, 2007). The demographic link to fear has been challenged by others citing problems with measures of predation risk and pregnancy rates, and potential confounds with environmental factors such as drought and winter severity (Kauffman *et al.* 2010; Boonstra 2013; Peterson *et al.* 2014; Ford & Goheen 2015). Furthermore, recent studies have found limited evidence for reproductive suppression caused by predator fear (Middleton *et al.* 2013; Proffitt *et al.* 2014). Despite the Yellowstone system arguably being the best example of the true magnitude of fear effects on prey demography in the wild (see Christianson & Creel 2014), substantial uncertainty remains in understanding the role of fear in this system.

Despite the clear potential for observational studies to quantify fear effects (as in Christianson & Creel 2014), much of our understanding of the strength of fear versus consumptive effects on prey demography has come from "predator cue" experiments (hereafter cue experiments), where functional predators are removed but their presence is simulated (see examples in Preisser *et al.* 2005). In these cue experiments (Fig 5.2a), consumptive effects of predators are eliminated in treatment groups (i.e. functional predators are eliminated) while fear effects are experimentally created either by the addition of non-functional predators (eg., mouthparts are glued shut or predators are separated from prey with a barrier; Schmitz 1998; Nelson *et al.* 2004) or by distributing a predator cue (e.g., kairomones, urine, feces, calls; Preisser *et al.* 2005). A fitness component of the prey such as reproduction is then typically compared between the cue treatment and a predator-free treatment containing no predators or cues, with the difference between treatment groups attributed to the fear effect (Fig 5.2a). In studies focused on population growth (Nelson *et al.* 2004), a third treatment (natural) is sometimes included in the experiment in which functional predators are present, and the difference between the natural-cue and cue-predator free treatments is considered to establish the consumptive and fear effect, respectively. Although most experiments are lab-based, in some cases, cues are applied to wild individuals over and above ambient levels but using a similar experimental design (Fuelling & Halle 2004; Zanette *et al.* 2011). In many instances, however, these classical cue experiments may not accurately quantify the magnitude of fear effects on natural prey demography, for reasons discussed in the following two sections.

1. Unknown realism in cue treatments

A key assumption in all cue experiments quantifying the demographic effect of fear is that the "cue" administered by the experimenter is a realistic depiction of the cues that actually create the landscape of fear. Approaches have varied from diffusing predator kairomones to prey in aquatic media (Preisser *et al.* 2005), to playing auditory recordings of common predators of the prey species from nearby speakers (Zanette *et al.* 2011; LaManna & Martin 2016). The "dose" of predator cues administered, relative to natural conditions, is crucial to interpreting how the magnitude of fear effects observed under experimental conditions applies to natural conditions. For example, presenting prey with very intense predator cues will increase the likelihood of large fear effects (see Mappes *et al.* 1998), just as artificially increasing predator densities above natural levels would greatly exaggerate the magnitude of consumptive effects on prey populations.

In natural systems, cues that create the landscape of fear are diverse and encompass scents, sounds, and visual stimuli which vary in magnitude, duration, and spatial distribution (Parsons *et al.* 2017). Detection of cues and the perceived threat level are further complicated by the background environment (ex. water turbidity; Ellrich & Scrosati 2016) as well as several properties of the predator which encode information about threat level (ex. size, diet, hunger; Chivers *et al.* 2001; Bell *et al.* 2006; McCoy *et al.* 2012; Weissburg & Beauvais 2015). In contrast to this, predator cues in experiments measuring demographic effects are usually delivered in isolation, at high intensity, and in relatively simplistic ways that do not reflect the complex timing, distribution, and fluctuations of natural predator cues (Weissburg *et al.* 2014). As a result, the degree to which the treatment represents a realistic level of perceived threat is unknown for the majority of cue experiments, and it is therefore difficult to relate the observed demographic responses to those of natural fear effects. This is further complicated because prey assessment of risk is a multi-modal process (i.e. prey use multiple cues), and altering cue modalities and their interactions results in varying behavioural responses of prey (Chivers *et al.* 2001). That being said, use of cues that demonstrate a high certainty of immediate threat (e.g. multiple speakers playing predator calls in close proximity; LaManna & Martin 2016), should elicit a maximum behavioural response in the prey, which would be expected to exaggerate fear effects if the cue occurs more frequently or more intensely than expected in nature.

Measuring the natural level of complex predator cues, in order to contextualize experimentally derived fear effects, is virtually impossible because investigators must then know all of the sensory cues involved in creating the landscape of fear for the target species, as well as the distribution and intensity of each cue in the environment (Ferland-Raymond *et al.* 2010). Even simple measures of fear such as predator-prey encounter rates have proven challenging as exemplified by the controversy over how to calculate wolf-elk encounter rates in Yellowstone (Creel *et al.* 2013; Middleton *et al.* 2013). Researchers must further understand the relevant properties of each cue that are vital for an individual's assessment of threat (Parsons *et al.* 2017). Finally, natural landscapes of fear (i.e. the distribution and intensity of cues) are produced by interacting predator communities which would differ to an unknown degree from those created from single predator species (Hoverman & Relyea 2016). It is therefore difficult to determine whether the magnitude of predator cues simulated in the majority of experimental situations is relevant to the natural world. In some systems, however, cues have been more accurately replicated (such as flow through chambers in aquatic environments; Cowan & Peckarsky 1994) and the demographic responses in such studies should be more resilient to the complexities in natural cue distribution and intensity (see Pangle & Peacor 2006; Pangle *et al.* 2007).

2. Demographic effects of fear in cue experiments could be inflated due to the absence of consumptive effects

In cue experiments, consumption is eliminated in both the cue and predator-free treatments and thus the magnitude of fear effects measured must carry the caveat that these effects were measured in the absence of any consumption (Fig 5.2a), a situation that is highly unlikely to occur in nature. Removal of consumption from the treatments creates the potential situation that individual prey in poor condition (those most likely to contribute strongly to observed fear effects via starvation or reduced reproductive output) may have been consumed by predators in nature before the fear effects would be expressed, thus confounding consumptive and fear effects (Abrams 2007, 2008). Essentially, cue treatments may over-estimate fear effects by allowing fear-caused mortality and reproductive effects that would have never occurred. Even if predation is random with respect to prey characteristics, some portion of the treatment individuals would naturally be preyed upon, and an unknown component of the fear effect will always be confounded in cue experiments.

In some instances, a large portion of the measured fear effect may simply be an artifact of the experiment if the cue applied rarely occurs naturally without consumption. This may be particularly true in treatments where prey are exposed to predators rendered non-lethal (Schmitz 1998; Nelson *et al.* 2004). For example, Nelson et al. (2004) exposed pea aphid (*Acyrthosiphon* *pisum*) populations to two predatory damsel bug (*Nabis spp.*) treatments: one with damsel bugs rendered non-lethal due to mouthpart manipulations and another with damsel bugs as functional predators. Behavioural observations indicated that mouthpart manipulations did not alter predator behaviour, as both predator types displayed similar time active, resting and handling prey (i.e. grappling with aphids for non-lethal damsel bugs and feeding for lethal ones). The authors concluded that 39-80% of the predator effects on population growth were attributed to fear. However, in our view the behavioural observations demonstrate that a significant component of the fear effect may be artificial. Assuming that aphids grappled by the non-lethal damsel bugs would normally be consumed (i.e. if the predator was not manipulated), the downstream fear effects (i.e. reduced growth and reproduction) expressed by these individuals would not be observed in nature because they would have been killed in the initial interaction. Simply put, a large percentage of "grappling" interactions between prey and non-lethal predators would have resulted in consumption; allowing such individuals to remain in the experimental population creates the opportunity for downstream fear effects to be manifested. The net result would be to increase the proportion of the full predator effect ascribed to fear (or at least considered compensatory with fear; Schmitz *et al.* 1997), while reducing the magnitude of consumptive effects. This makes it difficult to measure the true magnitude of fear effects from such experiments as an unknown component of the demographic effect attributed to fear never occurs in the wild due to the original consumption of the prey by the predator. This problem is not restricted to treatments using non-lethal predators, as fear effects derived from any cue treatment targeted at individuals are difficult to isolate without knowing the frequency at which the treatment occurs naturally without consumption.

Exaggerated fear effects from cue experiments

Previous research has clearly demonstrated that predator fear influences individual prey behaviour and physiology, affecting fitness and ultimately demography (Cowan & Peckarsky 1994; Eggers *et al.* 2006; Pangle & Peacor 2006; Creel *et al.* 2007). Cue experiments conducted over the last several decades have significantly advanced our understanding of community structure, population dynamics and trophic interactions (Belovsky *et al.* 2011; Suraci *et al.* 2016; Voelkl *et al.* 2016; Elliott *et al.* 2017). However, due to the reasons outlined above, it remains difficult to determine whether experimentally induced fear effects on prey demography in each study represent an over or under estimation of the true magnitude of fear in nature.

Despite this uncertainty, it is our contention that, given common experimental procedures, there is high risk that cue administration (and the resulting demographic effects) in a large portion of studies represent extreme scenarios unlikely to occur in nature. The bulk of our knowledge on the demographic effects of fear is derived from small-scale laboratory experiments that inflate cue intensity and persistence, likely elevating prey response (Weissburg *et al.* 2014). Furthermore, experiments conducted in the wild have often used treatments administering single cues at unnaturally high intensity (such as Zanette *et al.* 2011) which only represent a realistic increase in perceived threat if we assume natural cues are fully additive, and therefore the treatment compensates for the cues that are missing. Finally, fear effects derived in most cue studies are at least partially confounded (and in some cases artificial) due to the absence of consumption. The suggestion that the demographic effects of fear equal or surpass the consumptive effect may therefore be incorrect (see Preisser *et al.* 2005) and the true magnitude of fear on prey population distribution and abundance in nature remains unresolved.

Future cue experiments, particularly in the wild, would be improved by the inclusion of variable cue treatment levels to determine the degree the demographic response is dependent on the intensity of the treatment (akin to risk response curves; Fraker 2008). Such experiments could be initially targeted at previous systems with fear effects already documented (such as Sheriff *et al.* 2009; Zanette *et al.* 2011). Although this would aid in determining how much the intensity of the treatment influences the demographic response, it does not eliminate the challenge of establishing where the cue treatment falls within the context of fear cues in the wild, or the potential confounds caused by a lack of consumption in the experimental treatments. As a cautionary example, several experiments conducted on bank voles (*Clethrionomys glareolus*) applied predator odour continuously to individuals in small enclosures, demonstrating breeding suppression caused by predator fear (Ylonen 1989; Ronkainen & Ylonen 1994; Ylonen & Ronkainen 1994). However, later studies in larger, more natural outdoor environments (although maintaining intense odour cues) did not find significant effects, casting doubt that fear induced breeding suppression is critical to the population dynamics of voles (Wolff & Davis Born 1997; Mappes *et al.* 1998).

The "fear removal" treatment to quantify fear effects in wild populations

We argue that a more diverse methodological repertoire is required to help resolve debate regarding the magnitude of the natural landscape of fear on prey demography in the wild. Here we describe an alternative treatment to isolate fear effects in wild populations that avoids the challenge of determining if the predator cue applied by the experimenter is a reasonable approximation of the natural environment, as well as the potential confounds caused by a lack of predator consumption (termed "fear removal" treatment; Fig 5.2b). Rather than manipulating the type and amount of cues applied we recommend that they be removed completely and the focus should shift to a treatment simulating the consumptive effects of predation. This simple change substitutes the traditional cue experiment where consumptive effects are eliminated and fear is simulated, for a design where fear is eliminated and consumptive effects are simulated through the removal of individual prey by the researcher. This conceptual shift echoes earlier lab-based studies examining the relative roles of trait- and density-mediated indirect interactions (i.e. trophic cascades; Griffin & Thaler 2006; Trussell *et al.* 2006), that we believe could be readily conducted in wild populations specifically examining the effect of fear on prey demography and behaviour.

The most documented and logical path for fear to impact prey demography is through reduced reproductive output (i.e. pregnancy rates, litter size, juvenile growth and survival; Creel *et al.* 2007; Preisser & Bolnick 2008; Sheriff *et al.* 2009; Zanette *et al.* 2011; Dudeck *et al.* 2018) and we begin with a description of how the fear removal treatment could be utilized in experiments aimed at understanding the degree to which fear is currently limiting reproduction in a wild population. We have provided a conceptual description of our fear removal design in Figure 5.2 using reproduction as the response variable, although other response variables affected by fear could be examined (i.e. foraging rates, stress levels, growth rates, body condition). The experiment would consist of two groups; 1) a natural population with functional predators and prey at natural densities, and 2) a fear removal treatment consisting of prey at natural densities but in the absence of predators. Consumption rates observed in the natural treatment would be simulated in the fear removal treatment by the researcher removing individual prey to match the losses observed in the natural treatment leading to similar densities in each treatment and, eliminating potential density-dependent confounds in the interpretation of results.

In the natural population, prey would be exposed to both consumptive and fear effects whereas in the fear removal treatment, prey would still be exposed to the consumptive effect (through culling or removal of individuals by the researcher), but would not be exposed to the fear effect due to the removal of the predator and its associated cues (Fig 5.2b). The design creates two treatments experiencing consumptive effects but only one treatment experiencing fear effects (natural). The difference in the response variable between the natural and fear removal treatments provides the magnitude of fear effects in the presence of consumptive effects. In essence, if we exclude predators to remove fear from the equation and simultaneously remove individuals to match prey densities in the natural population, individuals in the fear removal treatment should show increased performance in any response variable previously limited by fear.

This design has two advantages over cue experiments: it experimentally removes the effect we are interested in quantifying (fear) rather than attempting to simulate natural fear effects through the application of simplified cues, and it isolates the fear effect while maintaining the presence of the consumptive effect (i.e. fear is isolated in the natural population). It is argued that fear effects could be missed or ascribed to other factors (i.e. food limitation) when we focus solely on consumption (see Creel & Christianson 2008; Winnie & Creel 2017). However, cue experiments do not asses this potential given large components of the fear effect derived may be encompassed naturally within the predation rate (due to confounds mentioned above). The fear removal treatment is not confounded in this manner.

Conducting the fear removal experiment has two main technical challenges; creating a predator-free environment and simulating losses due to predation that are similar to those in a natural population without creating human-caused fear effects. Many cue experiments have worked with small-scale lab or field systems using natural predator-prey treatments and predator-free treatments (Feltmate & Williams 1991; Schmitz *et al.* 1997; Nelson *et al.* 2004). It would be relatively straightforward to create the fear removal treatment in any of these systems provided experimental environments are at a large enough scale to reduce the exaggeration of fear effects that occur in small-scale enclosures (see Weissburg *et al.* 2014). The creation of predator-free environments under large-scale field conditions is clearly more challenging, but has been done previously: Krebs et al. (1995) built two 1 km2 exclosures to protect snowshoe hares (*Lepus americanus*) from mammalian predators; Huitu et al. (2005) built 1 ha exclosures to protect field voles (*Microtus agrestis*) from weasels; and Fauteux et al. (2016) built 9 ha exclosures to protect brown lemmings (*Lemmus trimucronatus*) from both avian and terrestrial predators. In some cases predators could be excluded through targeted removals (see examples in Salo *et al.* 2010) and islands or other natural barriers restricting access by predators could be utilized (Ekerholm *et al.* 2004).

While simulating consumptive effects, it will be important to reduce the potential for human-caused fear effects as fear of humans can influence prey behaviour and stress (Clinchy *et al.* 2016; Zbyryt *et al.* 2017), which could ultimately affect reproductive rates. However, in most studies, individuals must be captured and handled to measure physical condition, reproduction and monitor population size. Given this, it would be relatively straightforward for researchers to cull individuals rather than releasing them during these monitoring events. This does not entirely remove the potential for fear effects due to handling but it does control for these effects across treatments.

We provide an example of how the fear removal experiment could be used to disentangle the role of fear on reproduction in wild populations, using the snowshoe hare, a species we are familiar with. Snowshoe hares undergo 10-year population cycles (Krebs *et al.* 2001) and evidence suggests that predator-induced fear plays an integral role in the population dynamics of the species (Boonstra *et al.* 1998), reducing reproductive output prior to peak densities, and delaying recovery during the low phase of the cycle (summarized in Krebs *et al.* 2018). Sherriff et al. (2009) conducted a standard cue experiment whereby females were transferred into pens and exposed to a trained dog every other day during gestation. Females exposed to the dog exhibited reduced reproductive output over controls (Sheriff *et al.* 2009).

In our alternative approach, a fear removal treatment would be created by excluding predators from designated areas by means of exclosures (Krebs *et al.* 1995) or removing them from small islands (Marcstrom *et al.* 1989) prior to the winter season during the late increase, peak, or decline phase of the cycle. Over the course of the winter hares would be removed from the fear removal treatment at rates matching those observed in natural treatment areas, as inferred through monitoring mortality and its causes via telemetry (Boutin *et al.* 1986; Feierabend & Kielland 2015). Age, sex, and body condition of the individuals selected for removal could be matched to those killed by predators. This would result in natural and fear removal treatments having similar densities prior to summer breeding, except hares in the fear removal treatment would have experienced no exposure to predators (or fear) over winter. Any reproductive differences observed between individuals in the two treatments (fear removal and natural) could therefore be attributed to the fear effect and the magnitude of such effects could be compared to those observed in the cue experiment conducted by Sheriff et al. (2009). In our view, similar experiments could be performed in the wild across numerous species where fear is considered to have an important limiting effect on reproduction, behaviour, or stress levels.

The "fear removal" experiment to isolate fear effects on population growth

One of the fundamental goals of previous cue research is to determine the component of the full predator effect on population growth that is attributed to fear (see Preisser et al. 2005 and Fig 5.2a). Although the fear removal experiment outlined above would provide insight into the effect of fear on reproduction in nature, such effects may not strongly influence population growth in nature due to potential demographic compensation (Bonenfant *et al.* 2009). However, the fear removal treatment could be designed to isolate such an effect by conducting fear removal, natural, and predator-free treatments over multiple generations. In this experimental design, the difference in density (final or trajectory) between the predator-free treatment and the natural treatment provides a measure of the full predation effect (i.e. both consumption and fear), while the difference between the natural and fear removal treatment establishes the contribution of the fear effect alone (Fig 5.2b).

Although fully isolating fear and consumptive effects on population growth is not possible because the two pathways of predation are interacting (Okuyama & Bolker 2007), the fear removal experiment still provides more informative value for deciphering the role of fear on prey population growth, relative to the cue experiment. Apart from the advantage of being able to more accurately quantify (and therefore simulate) predation rates in numerous systems, this experimental design would establish the fear effect that is separate from consumption (i.e. difference between natural and fear removal; Fig 5.2b). This is because fear is isolated in our natural population where functional predators are also present, and any strong fear effect observed will not be artificial or confounded due to a lack of predator consumption. Isolating this more direct effect of fear is the critical goal for wildlife management if we argue demographic components of predators are missed when we focus solely on predation rates (Creel & Christianson 2008; Winnie & Creel 2017).

Implementing this experiment is clearly more challenging as culling would not be done to control for density dependent effects but rather to directly simulate the numbers and types of individuals (age classes etc.) consumed in the natural treatment. In addition, the experiment would have to be conducted over multiple generations to allow time for the population trajectories to run their course and mitigate transitory effects on inference (Abrams 2008; Kimbro *et al.* 2017).

Ideally, this experiment would be conducted on a wild population to estimate the extent fear is currently limiting population density in nature. Information required to perform the treatment could be measured in the wild through mortality studies using radio telemetry to track the fates of individuals, which can then be simulated in a population where predators have been excluded. It should be possible to perform the experiment in smaller-scale systems, where predation rates are either known or can be determined and simulated. However, enclosed artificial populations could be established for a variety of species (see Peacor & Werner 2001), specifically examining the effect on prey density (see Alto *et al.* 2012), as these experiments would provide an important contrast to cue experiments that attempt to measure the fear effect on population growth. For instance, Schmitz et al. (1997) created replicated treatments that contained densities of grasshoppers (*Melanoplus femurrubrum*) and spiders (*Pisurina mira*) that approximated natural densities, and the fates of all spiders and grasshoppers were followed over a 30 day period (Schmitz *et al.* 1997). Consequently, it should be possible to create a fear removal treatment in this system by excluding spiders, and simultaneously removing prey at rates that approximate the disappearance of grasshoppers in the natural treatment. Similarly, the fear removal treatment could be applied in aphid populations, given the ability to exclude predators as well as quantify predation rates from damsel bugs (Nelson *et al.* 2004). As mentioned earlier, a few systems have conducted similar treatments to examine the relative roles of trait- and density-mediated indirect interactions (Griffin & Thaler 2006; Trussell *et al.* 2006). Although technically challenging, this alternative approach will provide more information regarding the role of fear in limiting population growth than can be determined from cue experiments alone.

Moving forward

To date, experimental studies on the landscape of fear have focused on resolving whether predators have the potential to limit prey demography through fear effects, with many studies suggesting this to be the case. The true magnitude of such effects however, remains unknown, due to criticisms of common experimental procedures outlined above. Therefore, arguments that predator-induced fear has population-limiting effects that rival those of consumptive effects should be taken with caution. If the majority of predator cue experiments continue without major adjustments, our understanding of fear effects will continue to rely on untested assumptions with minimal scope for addressing the ultimate question of what role fear has in limiting prey populations in the wild. Moving forward, future research should utilize alternative experimental approaches that strive to answer this question, such as those presented here. Furthermore, researchers could pre-emptively monitor prey populations to critically assess potential fear effects from future predator reintroductions (similar to Christianson & Creel 2014). A multitude of approaches will provide a more robust understanding of fear effects in wild populations than can be determined from predator cue experiments alone. At a minimum, future cue additions should more critically evaluate how their treatment resembles the sensory environment of the prey, and include multiple treatment levels to determine the sensitivity of fear effects to the accuracy of the manipulation.

We recognize the difficulties of our alternative approach, especially in accurately replicating predator consumption over long time spans in a wild population. However, in our view this alternative experiment more accurately isolates the influence of fear on prey limitation, and discussing its merits will at a minimum allow researchers to critically examine the common cue approach and the questions they address, stimulating discussion in a field that is currently at an impasse. We hope researchers will be motivated to go beyond simply describing the existence of fear effects and focus on testing the magnitude of this phenomenon in wild populations and natural ecosystems.

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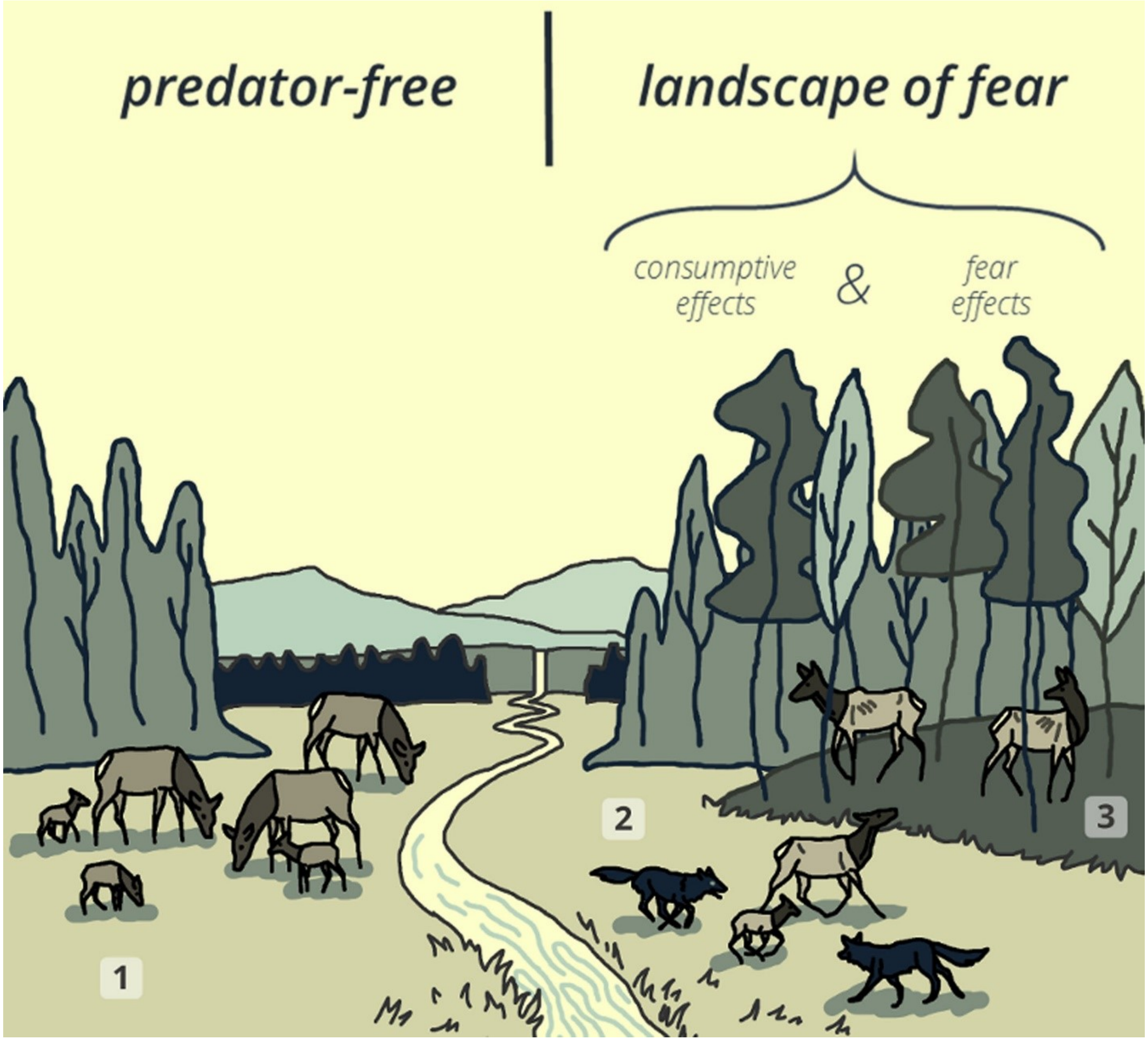

Figure 5.1. A diagram describing the limiting potential of consumptive and fear effects of predation on prey populations. Under no predation (1), prey can select higher quality habitat, forage at higher rates and have lower stress levels which leads to higher reproduction, survival and densities. In the presence of predators, prey suffer higher mortality (2) in high quality habitat and increased fear of predators can result in prey moving to poorer habitat to avoid predators, or increased vigilance and chronic stress levels resulting in higher starvation and/or reduced reproductive output (3). The net result is reduced prey abundance through decreased survival and reproduction.

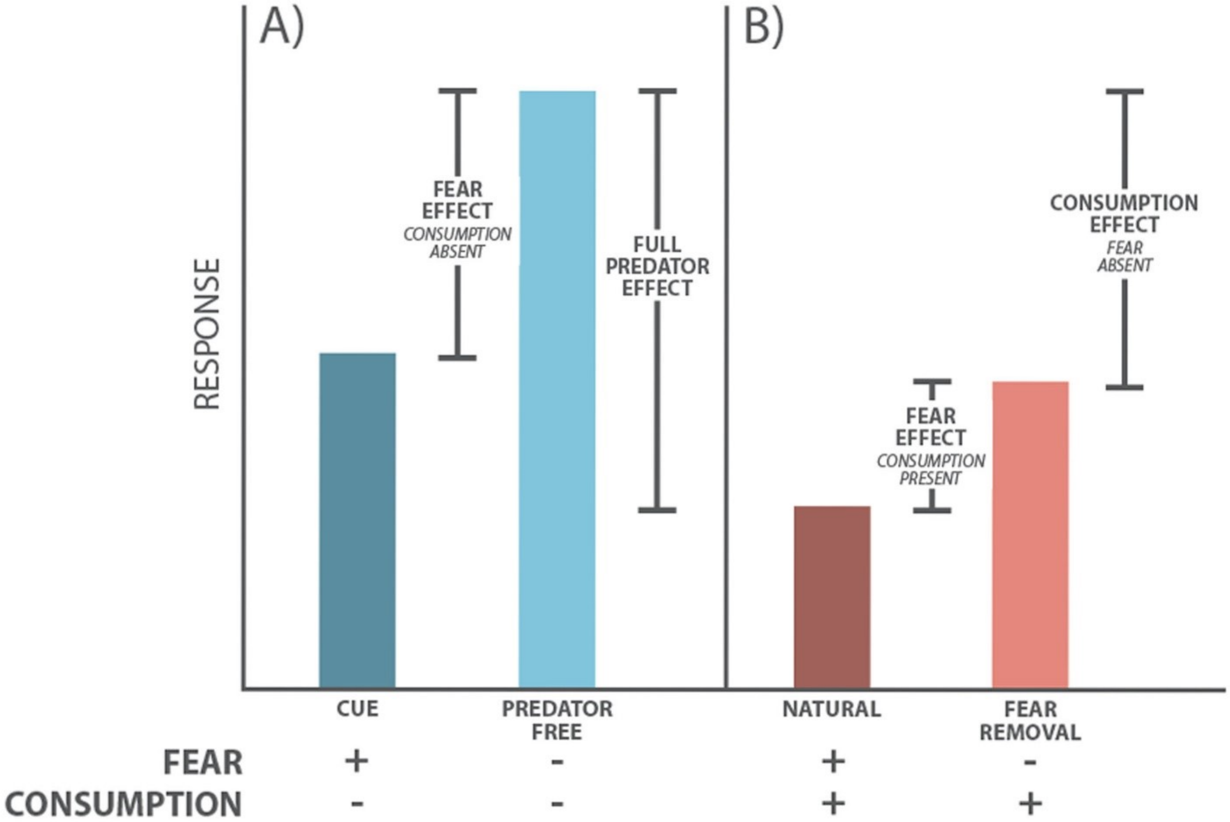

Figure 5.2. Contrasting the methodological approaches to measuring fear effects on individual reproduction in the wild. NATURAL, is an unmanipulated prey population where predators exert both consumptive and fear effects, CUE is a prey population free of real predators but exposed to experimenter imposed predator cues, FEAR REMOVAL is a prey population free of predators but where experimenters remove prey to match consumption rates when exposed to real predators, and PREDATOR-FREE is a prey population free of predators. In the CUE experiment (a), a demographic effect of fear is quantified by the difference in a response variable (i.e. reproduction) between the CUE and PREDATOR-FREE treatments. This fear effect is measured in the absence of any potential consumptive effects because predators are removed from both the cue and predator-free treatments. In the case of the FEAR REMOVAL experiment (b), differences in reproductive output between the FEAR REMOVAL treatment and NATURAL population represent the magnitude of the fear effect. The fear effect in this alternative approach is not dependent on how “fear” was simulated and is estimated in the presence of consumption.

Chapter 6

General Discussion

"In ecology we might achieve generality at the local level, possibly only at the population level, and only when the number of ecologists in the world exceeds the number of lawyers and the budget for ecological research exceeds that of the military."

~ Charles Krebs, Australian Zoologist 2017

Synthesis of results and broader significance

Predicting the effects of climate change on species is challenging, and requires detailed understanding of how climate affects biotic interactions, as well as the primary external factors influencing species abundance. My thesis examined both of these factors on snowshoe hare populations in the northern boreal forest to better understand the potential impact of climate change on their demography. Furthermore, I examined the impact of snowshoe hare abundance, as well as climate conditions, on other ecological processes to estimate how changes in hare demography coupled with climate may affect the broader ecological community.

I found that winter snowshoe hare survival was significantly impacted by snow conditions. Specifically, shallow snow reduced hare survival to rates resembling those during cyclic population declines. This response was primarily driven through an increase in predation risk from coyotes, since risk from their main predator, Canada lynx, was largely unaffected by snow depth. These results demonstrate that changes in snow conditions could impact hare demography, and alter the predator-prey community of the boreal forest. Negative effects of climate change on lynx demography across the boreal forest may therefore stem from increased exploitative competition from coyotes, as opposed to changes in hunting success (Guillaumet *et al.* 2015). Coyotes appear well suited to changes in snow conditions predicted across the boreal forest (Peacock 2012). If coyote density and distribution is limited by hunting success, they will likely increase their abundance throughout the boreal forest, and continue to expand their range northward (Chubbs & Phillips 2005; Hody & Kays 2018). How this may impact predator-prey communities and specifically snowshoe hare cycles should be a focus of future research.

Winter-weather conditions also had a larger effect on juvenile than on adult survival, and was likely driven by differences in foraging. In Chapter 4, I found that the increase phase of the cycle corresponded with improvement in over-winter survival of juveniles, particularly those from early litters. During population decline and the low phase, over-winter survival of juveniles was relatively low. This indicates that climate change may disproportionately impact hare populations during the increase phase of their cycle. Indeed, this may be a mechanism influencing the collapse of population cycles in other small mammals (Ims *et al.* 2008; Kausrud *et al.* 2008), and may explain the lack of population growth following declines in Norwegian lemmings (*Lemmus lemmus*) where cycles appeared to have ceased (Kausrud *et al.* 2008).

Changes in hare demography significantly affect community dynamics, as they are a primary food source for predators in the boreal forest (Krebs 2011; Humphries *et al.* 2017) and influence the density of several predator species (Boutin *et al.* 1995). However, results from Chapter 3 suggest changes in hare biomass can have a greater influence on food web dynamics than expected from purely a predator-prey framework, due to their potential impact on vertebrate scavenger communities. I found that the efficiency of the scavenging community was affected by hare density, with carcass persistence decreasing when snowshoe hare densities declined, mainly due to increased scavenging rates by their predator, the Canada lynx. Although hare carrion is not available at high enough biomass to impact lynx demography, changes in lynx scavenging behaviour may influence other vertebrate scavengers that rely on carrion as a resource over-winter (i.e. gray jays, magpies, ravens). Snowshoe hare carrion likely represents a minor portion of the total carrion available (Barton *et al.* 2019), however, the behavioural response of predators to changes in hare density may be consistent across carcass types. The patterns found in Chapter 3 could therefore be applicable to the broader scavenging community, although this requires further consideration.

The efficiency of the scavenging community was also differently affected by temperature in comparison to other systems that have been monitored, potentially from inactivity of invertebrates in cold northern winters. Specifically, vertebrate scavenging rates in our system increased with increasing temperature, most likely through improved access to the carcasses for smaller vertebrate species, or temperature driven changes in movement rates and carcass detection (Selva *et al.* 2005). This suggests vertebrate scavenging may increase during the winter at northern latitudes under climate change, which could subsequently reduce the proportion of carcasses that persist to the summer and become available for invertebrates and microbes (Beasley *et al.* 2018).

Finally, the results from Chapter 4 and 5 suggest the mechanistic drivers of hare population cycles may need to be revisited. I found that the over-winter survival of fourth-litter juveniles was negligible, suggesting their influence on hare demography during population increase may be minimal relative to the changes in survival of earlier litters. There was also no apparent change in the proportion of third-litter juveniles across cycle phases. Furthermore, predator cue experiments, such as those conducted in snowshoe hare (Sheriff *et al.* 2009; Boudreau *et al.* 2019), may have exaggerated fear effects on prey demography, due in part to the intensity of the treatment administered. That being said, substantial research is required during the low phase of the cycle and the role of predator fear on snowshoe hares, which I discuss in more detail below.

Emerging thoughts during long, remote winters

Predator-prey dynamics and climate change

My results suggest predator-prey dynamics can be strongly impacted by changes in climate. However, there are several important considerations for determining how changes in predation risk associated with climate change may alter future species demography. One important consideration is how climate determinants of risk vary across seasons, and how this impacts projections of yearly survival. In snowshoe hares, reduced snow depth and cover may have significant impacts on yearly survival because the changes in winter mortality risk found here may occur in tandem with increased mortality risk in the autumn and spring due to increased coat-colour mismatch (Sultaire *et al.* 2016; Zimova *et al.* 2016; Wilson *et al.* 2018). However, snowshoe hares in the Kluane region experienced improved survival rates during the summer (Fig 6.1), similar to other hare populations at northern latitudes (Feierabend & Kielland 2015). Increased mortality risk appears to coincide with the presence of snow (Peers, unpublished). Therefore, increased snow-free periods associated with climate change may improve survival during this seasons, and extend higher survival rates into the spring and autumn. The degree that improved survival during the summer under climate change can compensate increased mortality during the winter should be examined for hare populations in the northern regions of their range.

Furthermore, projections of predation risk under climate change assume that interactions distinct from those involving climatic conditions, predators, and prey remain static through time; an assumption that is highly unlikely (Zimova *et al.* 2016; Bastille-Rousseau *et al.* 2017). Adequate prediction of future predation rates for species requires explicit consideration for the simultaneous effects among multiple-changing drivers (Tylianakis *et al.* 2008). For instance, environmental change may impact food resources for numerous species, as forage quality, abundance, and availability are affected by climate (Walsh *et al.* 1997; Mallory & Boyce 2018).

Changes in resource availability may alter prey foraging behaviour or body condition, which could influence predator encounters, detection probability, or prey escape potential (see Fig 1.1; Sih 2011). As a result, climate-risk relationships developed from current monitoring studies may not accurately represent future patterns. The inaccuracy of projections will depend on the relative magnitude of each factor on survival, and whether simultaneous change in these predictors causes an additive effect, or a disrupted climate-risk relationship. Similarly, changes in food availability may compensate for lower over-winter survival through increased reproductive output (Hamel *et al.* 2009; Reed *et al.* 2013). The sensitivity of climate-mediated changes in risk to simultaneous change in other variables therefore requires further consideration.

Finally, our results indicate that climate conditions influence the functional response of predators. Linking such changes to future demography of predators and prey in any system will depend on continued increase in per capita kill rates, and the degree predator density changes with higher predation rates (i.e. numerical response; O'Donoghue *et al.* 1997; Redpath & Thirgood 1999). When predators become satiated, handling time increases (Li *et al.* 2018) and consumption rates decrease altering the functional response (Jeschke 2007). Within a single year, prolonged weather conditions may not continuously increase risk if predators satiate and predation risk is therefore reduced (Jeschke 2007). Across years, continuous change in climate will only cause a proportional increase in predation rates if predators are below the asymptote of their functional response, or can increase numerically (Redpath & Thirgood 1999). Although predation rates can be affected by climate, linking these effects to changes in demography is challenging, particularly for cyclic species (Abrams *et al.* 2003). For snowshoe hares, coyotes seem able to increase both their functional and numerical response with improved hunting success, with per capita kill rates increasing linearly across a wide range in hare densities

(O'Donoghue *et al.* 1997, 1998). Therefore, coyotes may be able to increase predation rates on hares proportional to changes in weather conditions, suggesting predictions of Chapter 2 may be realised.

Understudied scavenging communities

I found that 24 species scavenge hare carcasses in our system, making it the second most diverse scavenging community previously documented (Sebastián-González *et al.* 2019). Although the northern boreal forest may not be commonly considered as a rich scavenging community, limited food availability over winter (Campbell *et al.* 2005; Humphries *et al.* 2017) may cause species to more readily consume carrion in comparison to populations or similar taxa at southern latitudes (i.e. snowshoe hares; Peers *et al.* 2018). In general, detailed studies across vertebrate scavenging communities have only recently emerged (Mateo-Tomás *et al.* 2019; Sebastián-González *et al.* 2019), and primarily have occurred in communities that contain dominant obligate scavengers, such as vultures (Mateo-Tomás *et al.* 2019). In our system, dominant obligate scavengers that occur in the boreal forest, such as turkey vultures (*Cathartes aura*), or wolverine (*Gulo gulo*), are absent or occur at low densities. Despite this, carcass persistence was similar to other regions monitored (Sebastián-González *et al.* 2019). The factors driving scavenging communities in systems dominated by facultative scavenging should be considered further. The change in predator behaviour found in our study may be indicative of the dynamics of many scavenging communities, as several predators are known to increase carrion use during periods of lower prey abundance (Needham *et al.* 2014; Mattisson *et al.* 2016). In order to develop a comprehensive understanding of the factors driving carrion recycling rates around the globe, continued research into carrion use is required across a diverse range of ecosystems.

Demographic drivers of the snowshoe hare cycle

In my view, the timing of reproductive changes in snowshoe hare populations is one of the critical knowledge gaps for understanding the primary demographic variables regulating their abundance. Even though reproduction has been monitored in the Kluane region (Stefan & Krebs 2001), the reproductive rates during the first year of the low phase are unknown due to the limitations of monitoring hares during extremely low densities. If females restore their third litter during the first year of the low, then the delay in reproduction following population decline is entirely driven by the occurrence of the fourth litter (Cary & Keith 1979). The relatively low recruitment rate of fourth-litter juveniles relative to earlier litters suggest they have a minor influence on population growth.

Similarly, the cut-back in reproduction prior to peak densities is also primarily driven by the cessation of the fourth litter (Stefan & Krebs 2001). Future work should investigate whether densities during population declines would be significantly impacted had hares maintained a third litter. As a conceptual example, consider Jacquot Island in the Kluane Lake region where hare densities have also been minored over the last four decades (Krebs *et al.* 2002). Over a single year, hare population abundance on the island was reduced from ~106 individuals in August 2016, to only 4 individuals the following year (Krebs *et al.* 2018). In my opinion, if a cut-back in third litters occurred on this island during this summer, as opposed to the previous year, it would have no influence on the population decline caused by intense predation, and the population would have been driven into the low regardless of changes in reproduction. That being said, this population could have experienced severe predation that is unlikely to occur in non-island populations.

Role of fear on species demography

Chapter 5 suggests the broad effects of predator fear on prey demography may have been exaggerated by predator cue experiments. The experiment laid out in Chapter 5 would be difficult to implement in many systems, and has its own potential confounds that would need to be thoroughly considered. However, such experiments would provide important insight on the magnitude of fear effects in wild populations (Fauteux *et al.* 2016), since results from cue experiments would be considered more robust if independently validated through multiple modes of inference.

Furthermore, results from cue experiments in isolation are difficult to fully interpret. For instance, the primary link of reproductive changes in snowshoe hares occurs through experimental manipulations of predation risk using cue experiments. Sheriff et al. (2009) conducted a standard cue experiment whereby females were transferred into pens and exposed to a trained dog every other day during gestation. Females exposed to the dog exhibited reduced reproductive output over controls, and had substantially higher fecal cortisol metabolites (i.e. 214-837% higher; Sheriff *et al.* 2009). It could be argued that the "cue" administered in this experiment is unnaturally high, and exaggerated by captivity (Weissburg *et al.* 2014). These potential concerns resulted in a more recent study that conducted a cue experiment on wild individuals to represent a more natural increase in predation risk (Boudreau *et al.* 2019). In this study, individual hares were chased by a trained dog 3 times per week throughout the summer, and researchers compared a suite of measurements between treatment and control hares.

Although treatment had significant impacts on cortisol levels, effect sizes were less than those determined in the earlier experiment (Boudreau *et al.* 2019).

Given the hunting success of their primary mammalian predators (31.7-38.1%; O'Donoghue *et al.* 2001), the likelihood of individuals being chased at such high rates is unlikely. The "cue" administered in the Boudreau et al. (2019) experiment may still be unnaturally high, potentially exaggerating fear effects. Indeed, if a reactive response of hares to visual encounters and chases is the primary mechanism driving an increase in stress (Creel 2018), it may be reasonable to surmise this type of treatment exaggerates fear effects. In contrast, the relative infrequency of encounters suggest chases may not be a primary mechanism that individuals use to assess risk (Weissburg *et al.* 2014). If hares also respond pro-actively, additional predator cues may be used to indicate changes in risk on the landscape (i.e. feces, urine, etc.; Preisser *et al.* 2005; Preisser & Bolnick 2008), and manipulating these cues may cause a higher treatment effect on behaviour and physiology. Therefore, interpreting results from previous cue experiments on hares is difficult without knowing the primary sensory modalities, or combination of them, that individuals use to asses risk (Weissburg *et al.* 2014). In regards to snowshoe hare research, the path forward could be to 1) continue to implement cue treatments at various levels to determine the degree that the demographic response is dependent on the intensity of the treatment (akin to risk response curves; Fraker 2008), 2) attempt to simulate a plethora of cues at their accurate densities (which may be impossible), or 3) use the fear removal experiment described in Chapter 5 and measure reproductive performance and stress physiology (Fauteux *et al.* 2016). In my view, despite the latter experiment requiring considerable effort, it can provide a more robust picture of the demographic effects of predator fear.

Final thoughts

Future projections of species demography improve our ability to mitigate and adapt to climate change. However, the quality of these projections will undoubtedly depend on our understanding of the factors governing species abundance, and their interactions amongst members of the community. If researchers and funding agencies only prioritize studies examining correlations between climate variables and species demography, we will have a strong understanding of how demographic variables correlate with climate, but limited capacity to predict future changes.

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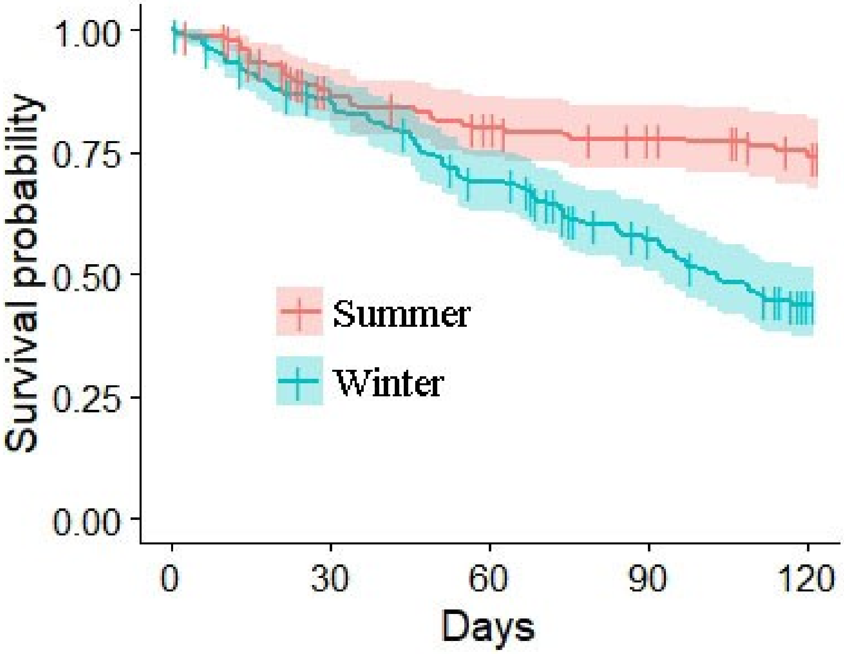

Figure 6.1. Kaplan-Meier four-month survival curves for snowshoe hares in the Kluane Lake region for the winter (blue) and summer (red) seasons.

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Appendix A: Supplementary material for Chapter 2

Table 2.S1. Model selection of Cox proportional hazard models on overwinter hare survival showing the number of parameters (*k*), change in AIC_c from the best ranked model (ΔAIC_c), and Akaike model weights (*w*).

Model	k	ΔAIC_c	*w*
Temp + SD + SH + SD:SH	4	0	0.38
Temp + SD + SH + SD:SH + DSF	5	1.53	0.18
Temp + SD + SH + SD:SH + Days Since	5	1.89	0.15
Temp + SD + SH	3	2.76	0.10
Temp + SD + SH + SD:SH + DSF + Days Since	6	3.24	0.08
Temp + SD + SH + DSF	4	4.07	0.05
Temp + SD + SH + Days Since	4	4.46	0.04
Temp + SD + SH + DSF + Days Since	5	5.44	0.03
~1	0	17.89	0.00

Weather variables are: average daily temperature (Temp), snow depth (SD), sinking depth of the penetrometer (SH), daily snowfall (DSF), days since snowfall (Days Since), and an interaction between snow depth and hardness (SD:SH).

Table 2.S2. Model selection of Cox proportional hazard models stratified by mortality risk from lynx and coyote showing the number of parameters (*k*), change in AIC_c from the best ranked model (ΔAIC_c), and Akaike model weights (*w*).

Model	k	ΔAIC_c	*w*
Temp + SD + SH	6	0	0.63
Temp + SD + SH + DSF	8	1.87	0.25
Temp + SD + SH + Days Since	8	3.95	0.09
Temp + SD + SH + DSF + Days Since	10	5.58	0.04
~1	0	27.02	0.00

Table 2.S3. Model selection of Cox proportional hazard models stratified by age showing the number of parameters (*k*), change in AIC_c from the best ranked model (ΔAIC_c), and Akaike model weights (*w*).

Model	k	ΔAIC_c	*w*
Temp + SD + SH	6	0	0.60
Temp + SD + SH + Days Since	8	2.10	0.21
Temp + SD + SH + DSF	8	3.19	0.12
Temp + SD + SH + DSF + Days Since	10	4.63	0.06
~1	0	9.30	0.01

Table 2.S4. Modelled hazard ratios and 95% confidence intervals for each weather variable from the top all-cause and cause-specific models based on AICc. Bolded values indicate significant effects and italicized represents P values < 0.1.

Variable	All-Cause	Coyote	Canada lynx
Temp	0.987 (0.959, 1.016)	1.008 (0.917, 1.108)	*0.960 (0.920, 1.001)*
SD	1.019 (0.957, 1.077)	**0.866 (0.776, 0.967)**	0.992 (0.959, 1.025)
SH	**1.233 (1.053, 1.445)**	**1.244 (1.061, 1.459)**	0.998 (0.938, 1.063)
SD:SH	**0.995 (0.991, 0.999)**	NA	NA

Table 2.S5. Modelled hazard ratios and 95% confidence intervals for each weather variable on sub-adult and adult mortality risk from the top age-specific model based on AICc. Bolded values indicate significant effects and italicized represents P values < 0.1.

Variable	Sub-adult	Adult
Temp	0.974 (0.922, 1.028)	0.984 (0.944, 1.025)
SD	**0.935 (0.889, 0.984)**	*0.969 (0.938, 1.002)*
SH	1.035 (0.951, 1.125)	1.044 (0.986, 1.106)

Table 2.S6. Modelled hazard ratios and 95% confidence intervals for each weather variable from the top all-cause model treating missing individuals as mortality events, and cause-specific model that included unknown mortalities. Bolded values indicate significant effects and italicized represents P values < 0.1.

Variable	All-Cause	Coyote	Canada lynx
Temp	*0.974 (0.947, 1.001)*	1.008 (0.917, 1.108)	*0.960 (0.921, 1.001)*
SD	1.020 (0.968, 1.074)	**0.867 (0.778, 0.968)**	0.992 (0.960, 1.025)
SH	**1.260 (1.084, 1.464)**	**1.242 (1.060, 1.457)**	0.999 (0.938, 1.063)
SD:SH	**0.995 (0.991, 0.999)**	NA	NA

Table 2.S7. Proportion of mortalities during the winter from each cause of death for all individuals and separated by age-class. Not included are four mortalities suspected to have occurred from starvation. Values in brackets for each predator represent the proportion of mortalities where cause of death could be identified.

Group	Canada lynx	Coyote	Goshawk	Great-horned owl	Unknown Predator
All mortalities (153)	0.41 (0.59)	0.18 (0.25)	0.07 (0.09)	0.04 (0.06)	0.31
Sub-adult (47)	0.36 (0.52)	0.23 (0.33)	0.06 (0.09)	0.04 (0.06)	0.30
Adult (69)	0.51 (0.67)	0.19 (0.25)	0.03 (0.04)	0.03 (0.04)	0.25

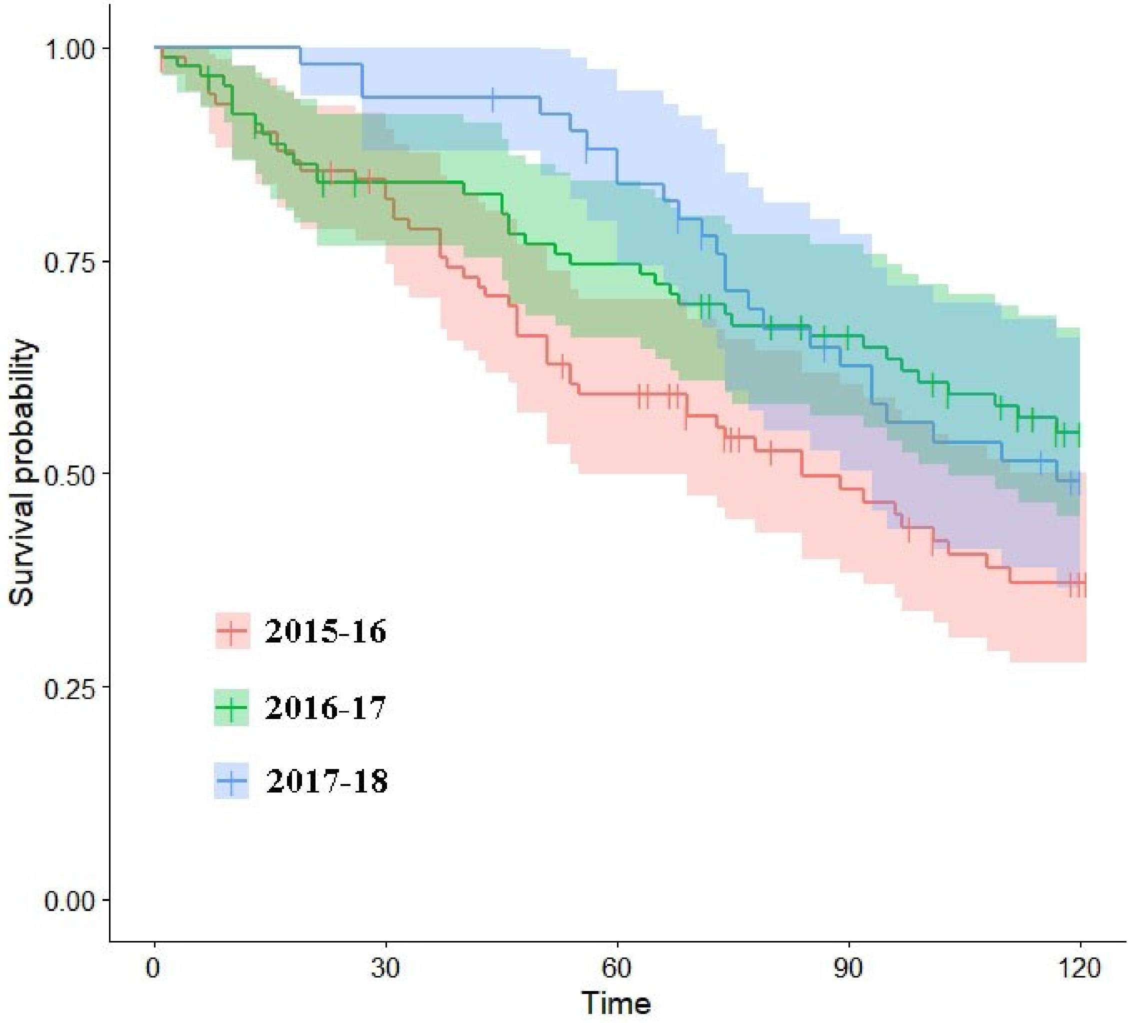

Figure 2.S1. Kaplan-Meier four-month survival curves for snowshoe hare in the Kluane Lake region across the three winters we monitored survival from December until March.

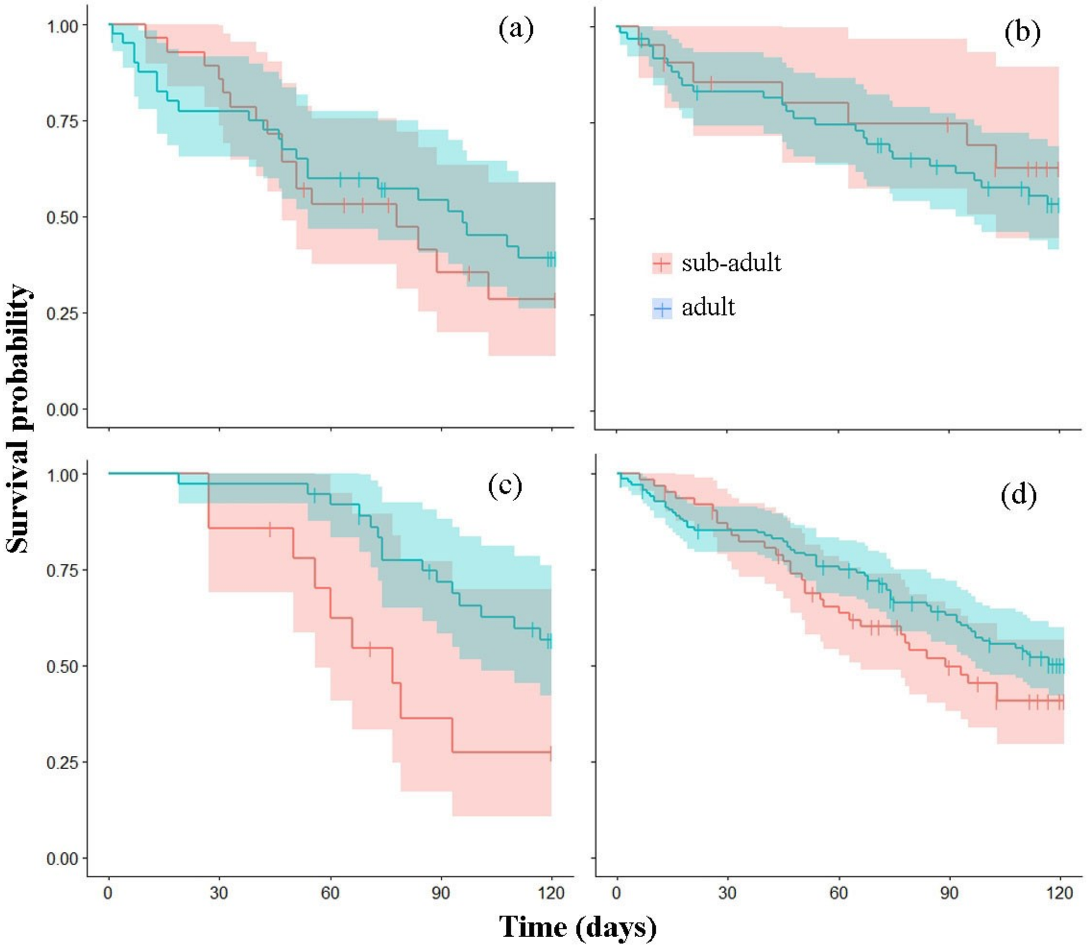

Figure 2.S2. Kaplan-Meier four-month survival curves for sub-adult (red) and adult (blue) snowshoe hares during the winter of a) 2015-16, b) 2016-17, c) 2017-18, and d) all years combined.

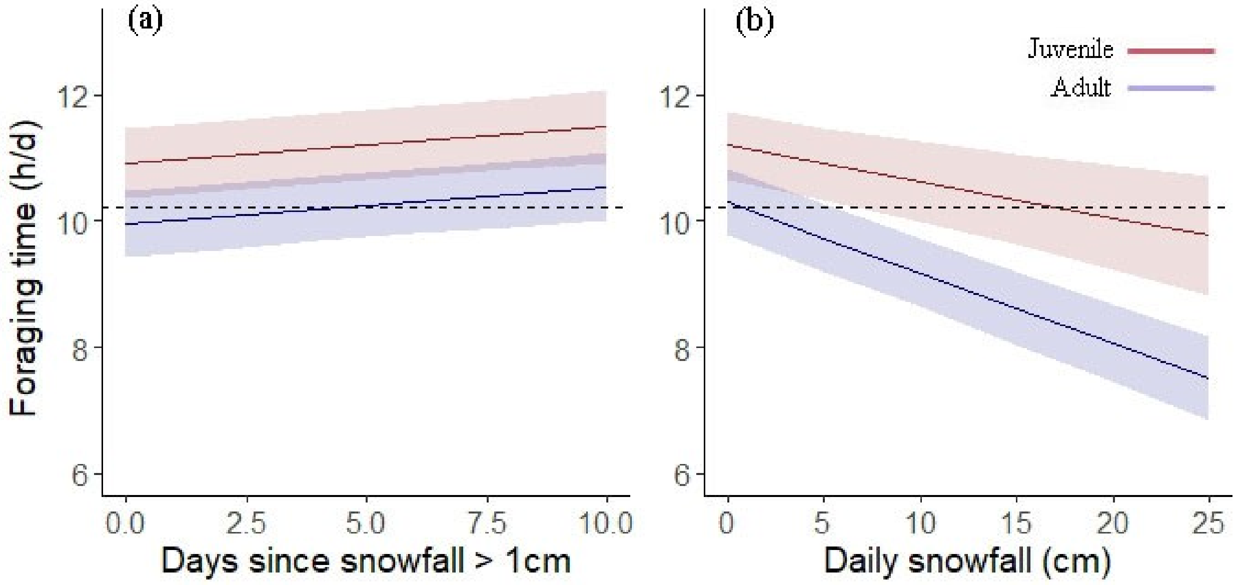

Figure 2.S3. Modelled effect of (a) days since snowfall, and (b) daily snowfall on daily foraging time for sub-adult (red) and adult (blue) snowshoe hare. Confidence bards represent predicted response standard errors and dotted line represents the average time spent foraging per day during the winter.

Appendix B: Supplementary material for Chapter 3

Table 3.S1. Model selection of GLMs on carcass persistence showing the number of parameters (*k*), change in AIC_c from the best ranked model (ΔAIC_c), and Akaike model weights (*w*) from the top 8 models.

Model	k	ΔAIC_c	*w*
Temperature + Hare Density + Season	3	0	0.23
Hare Density + Season	2	0.96	0.14
Temperature	1	1.42	0.11
Temperature + Hare Density	2	2.37	0.07
Temperature + Closure + Hare Density + Season	4	2.37	0.07
Temperature + Carrion Biomass	2	2.99	0.05
Closure + Hare Density + Season	3	3.14	0.05
Season	1	3.17	0.05

Table 3.S2. Model selection of GLMs on time until first scavenger showing the number of parameters (*k*), change in AIC_c from the best ranked model (ΔAIC_c), and Akaike model weights (*w*) for the top 8 models.

Model	k	ΔAIC_c	*w*
Closure + Season	2	0	0.18
Closure + Hare Density + Season	3	0.51	0.14
Hare Density + Season	2	0.51	0.14
Season	1	0.70	0.12
Temperature + Hare Density + Season	3	1.57	0.08
Carrion Biomass + Closure + Season	3	2.05	0.06
Temperature + Closure + Season	3	2.15	0.06
Carrion Biomass + Season	2	2.17	0.06

Table 3.S3. Model selection of GLMs on the number of scavenger species per carcass showing the number of parameters (*k*), change in AIC_c from the best ranked model (ΔAIC_c), and Akaike model weights (*w*) for the top 8 models.

Model	k	ΔAIC_c	*w*
Carcass Persistence	1	0	0.11
Carcass Persistence + Temperature	2	0.62	0.08
Carcass Persistence + Season	2	1.09	0.06
Carcass Persistence + Hare Density	2	1.48	0.05
Temperature	1	1.60	0.05
Carcass Persistence + Hare Density + Temperature	3	1.72	0.05
Carcass Persistence + Carrion Biomass	2	1.83	0.04

Carcass Persistence + Temperature + Season	3	2.14	0.04

Table 3.S4. Model selection of GLMs on common raven scavenging showing the number of parameters (*k*), change in AIC_c from the best ranked model (ΔAIC_c), and Akaike model weights (*w*) for the top 8 models.

Model	k	ΔAIC_c	*w*
Carrion Biomass + Closure + Season	3	0	0.30
Carrion Biomass + Closure	2	1.44	0.15
Carrion Biomass + Season	2	2.08	0.11
Carrion Biomass + Closure + Season + Temperature	4	2.31	0.10
Carrion Biomass	1	3.08	0.07
Closure	1	3.24	0.06
Carrion Biomass + Closure + Temperature	3	3.26	0.06
Carrion Biomass + Closure + Season	3	4.28	0.04

Table 3.S5. Model selection of GLMs on gray jay scavenging showing the number of parameters (*k*), change in AIC_c from the best ranked model (ΔAIC_c), and Akaike model weights (*w*) for the top 8 models.

Model	k	ΔAIC_c	*w*
~1	0	0	0.18
Season	1	0.17	0.17
Closure	1	1.39	0.09
Temperature	1	1.45	0.09
Season + Closure	2	1.63	0.08
Carrion Biomass	1	1.93	0.07
Carrion Biomass + Season	2	2.24	0.06
Temperature + Season	2	2.26	0.06

Table 3.S6. Model selection of GLMs on black-billed magpie scavenging showing the number of parameters (*k*), change in AIC_c from the best ranked model (ΔAIC_c), and Akaike model weights (*w*) for the top 8 models.

Model	k	ΔAIC_c	*w*
Season	1	0	0.17
Temperature	1	0.54	0.13
Carrion Biomass + Season	2	1.28	0.09
~1	0	1.33	0.09
Temperature + Season	2	1.45	0.08
Closure + Season	2	1.87	0.07

Carrion Biomass + Temperature	2	2.13	0.06
Carrion Biomass	1	2.31	0.05

Table 3.S7. Model selection of GLMs on red squirrel scavenging showing the number of parameters (*k*), change in AIC$_c$ from the best ranked model (ΔAIC$_c$), and Akaike model weights (*w*) for the top 8 models.

Model	k	ΔAIC$_c$	*w*
Squirrel Density + Season	2	0	0.17
Squirrel Density + Season + Forest	3	0.71	0.12
Squirrel Density + Temperature	2	1.16	0.10
Squirrel Density + Season + Forest + Temperature	4	1.69	0.08
Squirrel Density + Season + Spruce Cones	3	2.16	0.06
Spruce Cones + Season + Forest	3	2.70	0.04
Spruce Cones + Season	2	2.70	0.04
Season + Forest	2	2.81	0.04

Table 3.S8. Model selection of GLMs on Canada lynx scavenging showing the number of parameters (*k*), change in AIC$_c$ from the best ranked model (ΔAIC$_c$), and Akaike model weights (*w*) for the top 8 models.

Model	k	ΔAIC$_c$	*w*
Hare Density + Season + Temperature	3	0	0.50
Hare Density + Season	2	1.37	0.25
Hare Density + Lynx Density + Season	3	3.59	0.08
Hare Density	1	3.61	0.08
Hare Density + Lynx Density	2	5.74	0.03
Hare Density + Temperature	2	5.76	0.03
Season	1	7.67	0.01
Hare Density + Lynx Density + Season	3	7.94	0.01

Table 3.S9. Model selection of GLMs on snowshoe hare scavenging showing the number of parameters (*k*), change in AIC$_c$ from the best ranked model (ΔAIC$_c$), and Akaike model weights (*w*) for the top 8 models.

Model	k	ΔAIC$_c$	*w*
Temperature	1	0	0.39
Temperature + Forest	2	2.11	0.14
Temperature + Hare Density	2	2.14	0.13
Temperature + Season	2	3.59	0.06
~1	0	3.89	0.06

Temperature + Hare Density	2	4.31	0.05
Season	1	4.47	0.04
Forest	1	5.55	0.02

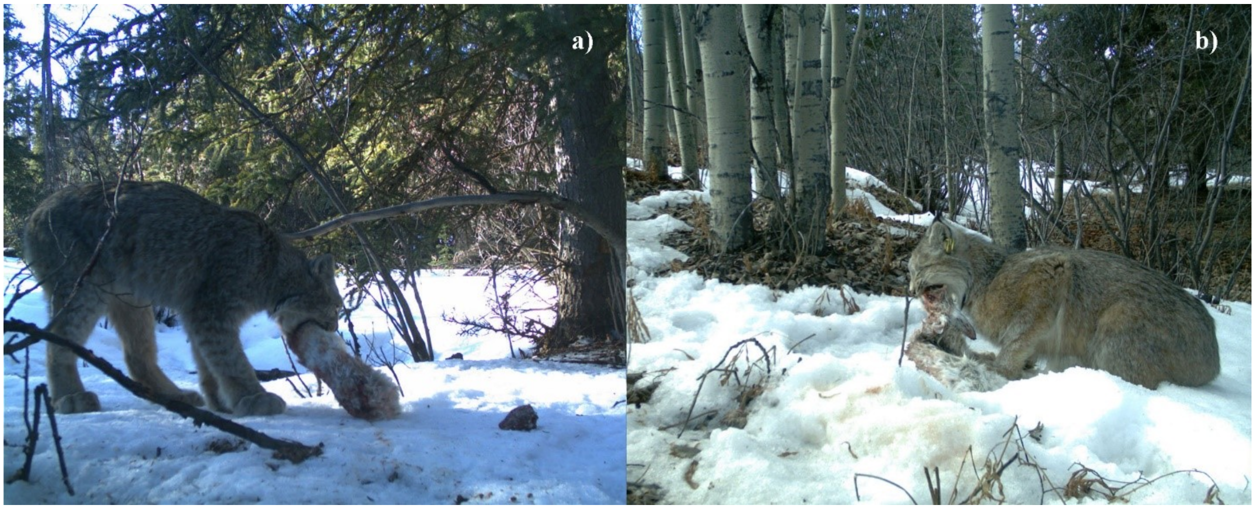

Figure 3.S1. Images depicting a Canada lynx a) removing a carcass from the deployment site or b) consuming the carcass on site.

Appendix C: Supplementary material for Chapter 4

Table 4.S1. Total hares caught (number that recruited) between Aug 01 and Sep 18 on control grids suspected to be early or third-litter juveniles for each phase of the cycle.

Litter Group	Low	Increase	Peak	Decline	Total
Early	36 (5)	175 (69)	554 (187)	415 (75)	1180 (336)
Third	31 (1)	33 (4)	195 (14)	109 (2)	368 (21)

Table 4.S2. Number of suspected early and third-litter juveniles captured (proportion of autumn hares) between Aug 14 and Sep 18 on our control girds for each phase of the cycle.

Litter Group	Low	Increase	Peak	Decline	Total
Early	31 (0.36)	114 (0.50)	439 (0.47)	405 (0.47)	989 (0.49)
Third	31 (0.36)	34 (0.15)	198 (0.21)	118 (0.15)	381 (0.19)
Total hares	87	229	932	764	2012

Table 4.S3. Model selection of generalized linear models on spring recapture rates showing the number of parameters (*k*), change in AIC$_c$ from the best ranked model (ΔAIC$_c$), and Akaike model weights (*w*). Only the five models with the lowest AICc are listed.

Model	k	ΔAIC$_c$	*w*
Litter + Cycle Phase + Mass	6	0	0.79
Litter + Cycle Phase + Mass + Sex	8	2.64	0.21
Litter + Cycle Phase	5	19.74	0.00
Litter + Cycle Phase + Sex	7	23.16	0.00
Cycle Phase + Mass	5	29.35	0.00

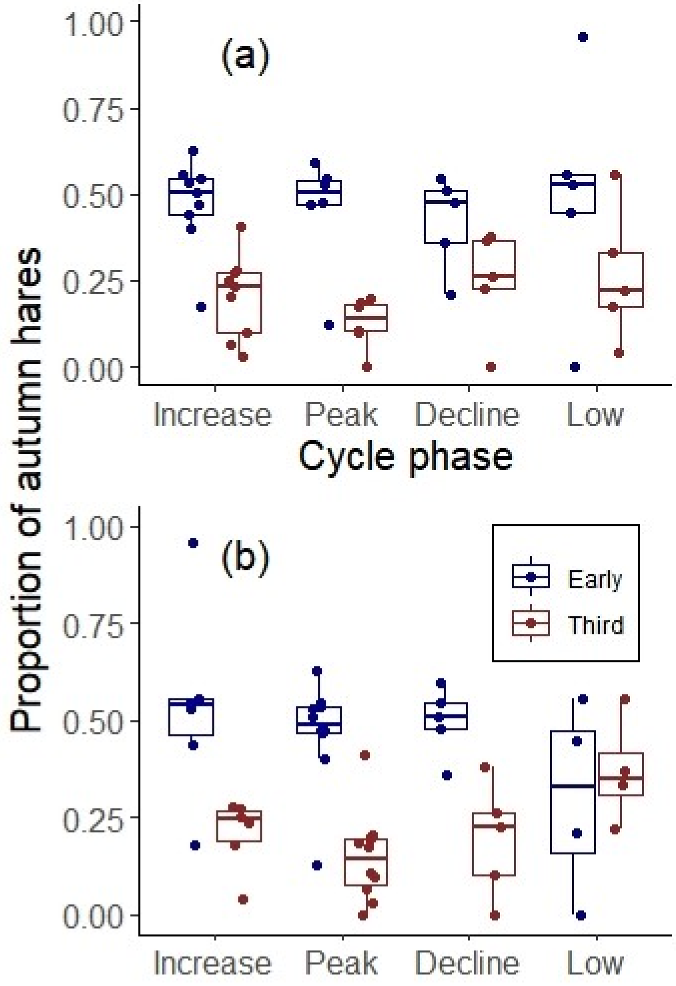

Figure 4.S1. Boxplot of the proportion of the autumn population that were either early-litter (blue), or third-litter (red) juveniles for each phase of the cycle. Individual dots represent the values for each year that correspond to the cycle phase and litter group. Cycle phase in this figure represents the phase a) from the previous spring, or b) the autumn.

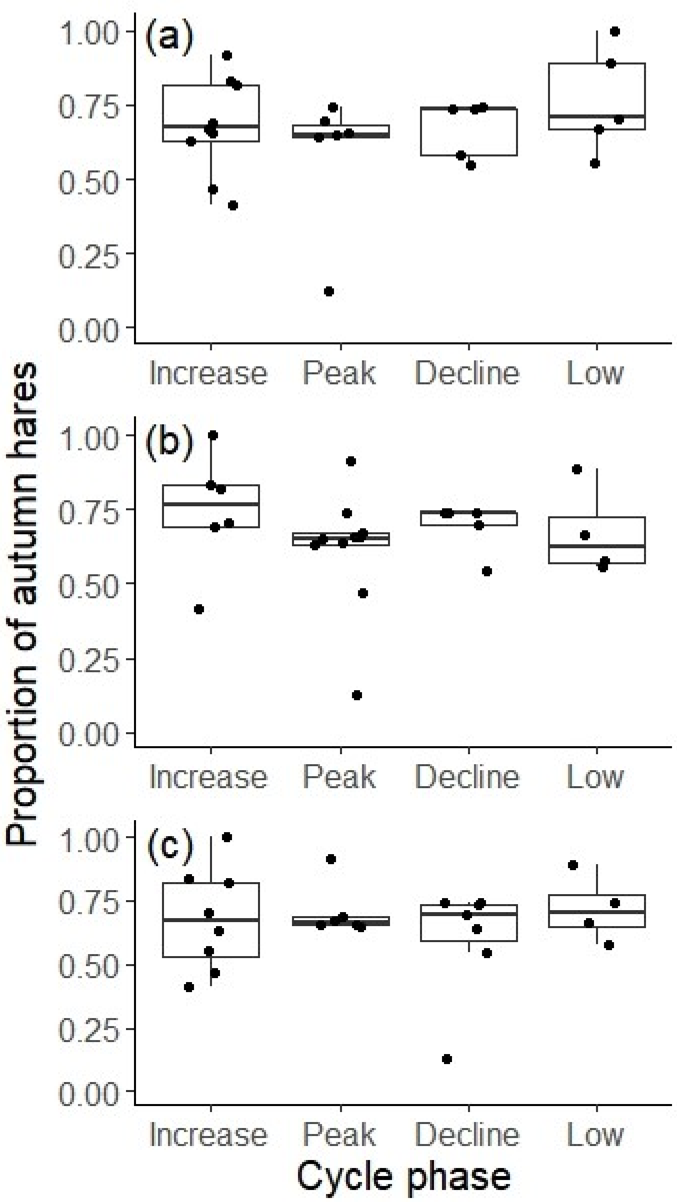

Figure 4.S2. Boxplot of the proportion of the autumn population that were considered juveniles (i.e. first capture occurred this summer/autumn) for each phase of the cycle. Individual dots represent the values for each year that correspond to the cycle phase. Cycle phase in this figure represents the phase a) from the previous spring, b) the autumn, or c) the following spring.

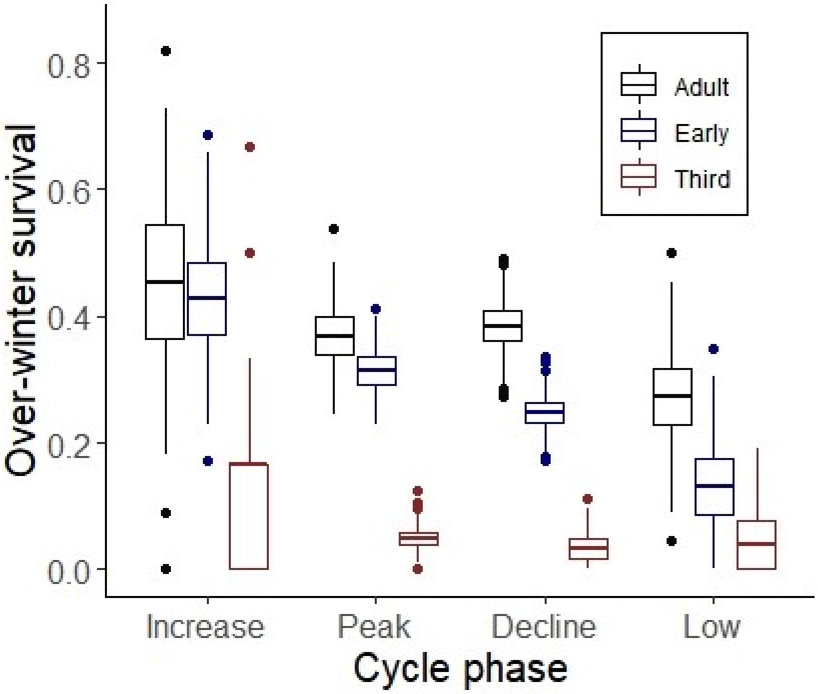

Figure 4.S3. Apparent over-winter survival by cycle phase for adults (black), early (blue), and third (red) litter juveniles, based on recruitment rates from 500 bootstrapped datasets. Only years that represent the transition between these cyclic phases are included.

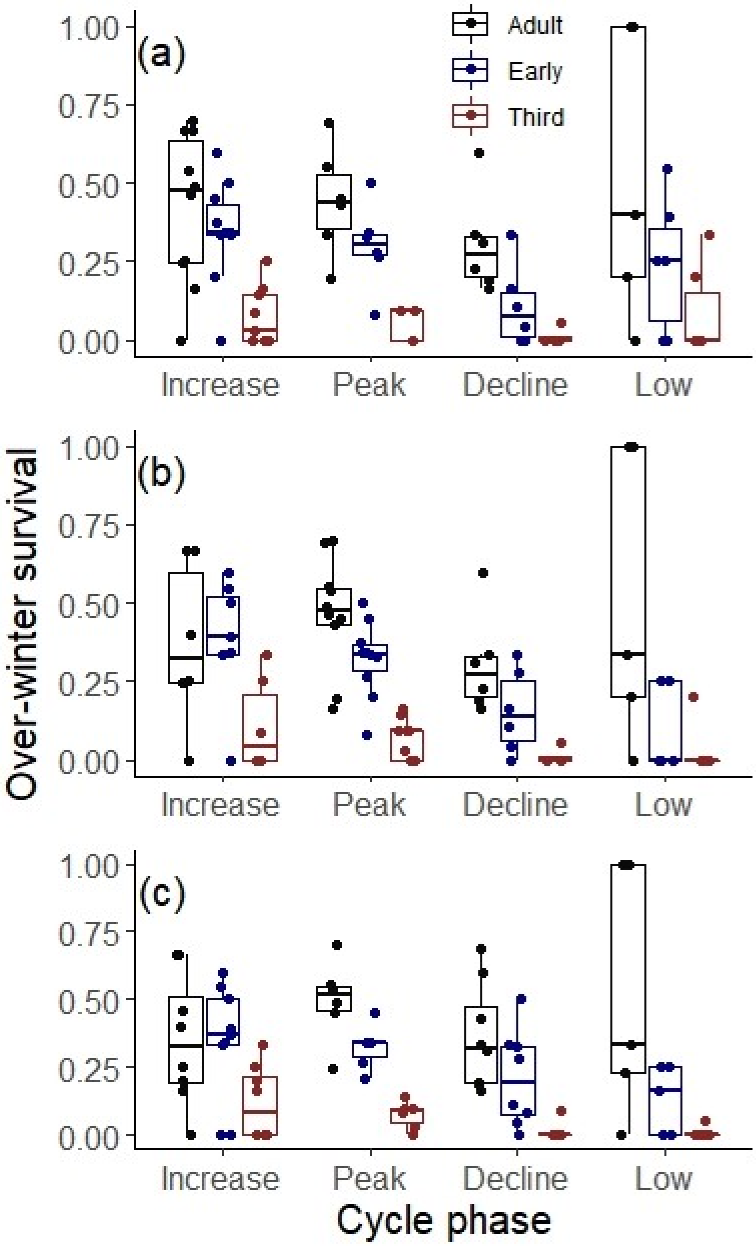

Figure 4.S4. Apparent over-winter survival for each age group, for each year that trapping occurred during the time when individuals could be classified as early or third-litter juveniles (August-September 18). Cycle phase in this figure represents the phase a) from the previous spring, b) the autumn, or c) the following spring.