

Examining predation risk and antipredator responses of snowshoe hares in Northern
Canada's boreal forest

by

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Abstract

Predators limit prey populations not only through direct killing of prey but also through changes in behavior due to predation risk and negative fitness consequences that result. Prey species are known to respond to both predictable (e.g. risky times and places) and unpredictable variation (e.g. predator encounters) in predation risk by adopting proactive and reactive antipredator responses respectively, but proactive and reactive antipredator responses have been rarely examined simultaneously in a single study. Snowshoe hares (*Lepus americanus*) which are known for their 10-year population cycle are the major prey for multiple predator species and thus a keystone herbivore in North America's boreal forest. The hare population cycle is known to be driven by predators directly through predation but may also be potentially influenced by non-consumptive effects of predators such as physiological stress negatively affecting body condition and reproduction of hares. In this thesis, I (1) investigate a reactive antipredator response (reduction in foraging) of hares to unpredictable (acute) predation risk and (2) identify temporal patterns of hare predation and behavioral patterns of hares before predation, aiming to contribute to a more comprehensive understanding of predation risk and antipredator responses.

In chapter 1, I examined the effects of food availability and long-term predation risk, by manipulating food availability for hares via individual-based food supplementation and by monitoring two-month mortality rate of hares. I found that hares reduced foraging time as a reactive antipredator response after lynx encounters and the magnitude of the response was affected by the interaction between food availability and long-term predation risk. In chapter 2, I examined risky time and behavior for hares. Daytime and bright moonlit nights

could be the riskiest time for hares, but hares were killed frequently both during the daytime and the night/dawn/dusk, possibly because different predator species preyed upon hares at different times of day; lynx and great horned owl predation occurred almost equally during the day and the night/dawn/dusk, and coyote and goshawk predation occurred mostly during the daytime. Hares did not show higher foraging rate before predation than their average foraging rate, and this finding imply that hares are exposed to high risk of predation regardless of whether they are foraging or not. Considering that hares spend most of their time and are killed by predators mostly in a spruce forest and that hare habitat is relatively homogeneous in Northern Canada's boreal forest, spatiotemporal refugia may not be common for hares. Overall, my research revealed that hares are experiencing both predictable and unpredictable variation in predation risk, and are potentially responding to both types of variation in predation risk simultaneously by adopting proactive and reactive antipredator response respectively. I suggest that future studies should both proactive and reactive antipredator responses simultaneously, to better understand non-consumptive effects of predators on prey populations.

Preface

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General introduction

Prey modify their behavioral patterns to minimize the risk of predation, by altering habitat use, increasing vigilance, or reducing activity level (Creel 2018). These antipredator responses usually impose nutritional or physiological costs on prey, thereby negatively affecting future survival and reproduction (Boonstra et al. 1998, Lima 1998, Creel and Christianson 2008). Therefore, predators limit prey populations not only through direct killing of prey (consumptive effect) but also through predation risk (non-consumptive effect) (Werner and Peacor 2003, Preisser et al. 2005).

Prey species are known to respond to both predictable and unpredictable variation in predation risk (Creel 2018). Predictable variation in predation risk is exemplified by habitat/area-specific predation risk (Kotler et al. 2004, Gehr et al. 2018) and risky times determined by diel activity patterns of predators (Kohl et al. 2018, 2019, Smith et al. 2019) or the lunar cycle (Kotler et al. 2002, 2010). Prey proactively respond to this type of variation in predation risk (proactive antipredator response, Creel 2018) by avoiding risky places (Fortin et al. 2005, Hebblewhite et al. 2005, Valeix et al. 2009), being vigilant (Fortin et al. 2004), or allocating risk behaviors (i.e. foraging) to safe times (Kotler et al. 2002, Courbin et al. 2019, Smith et al. 2019). On the other hand, unpredictable variation in predation risk represents acute predation risk such as predator presence in close proximity or predator encounters (Creel 2018, Valeix et al. 2009), and prey reactively respond to this type of risk (reactive antipredator response, Creel 2018) by increasing vigilance level (Dröge et al. 2017) or temporarily modifying movement patterns (Middleton et al. 2013, Oates et al. 2019). Surprisingly, proactive and reactive antipredator responses are rarely

examined simultaneously in a single study (but see Gehr et al. 2018). To reveal the overall costs of antipredator responses and non-consumptive effects of predators on prey demography, it is crucial to examine how prey respond to predictable and unpredictable variation in predation risk simultaneously by adopting different types (proactive and reactive) of antipredator responses.

Snowshoe hares (*Lepus americanus*) are a keystone herbivore in North America's boreal forest, and are consumed by various predator species (Krebs et al. 2018, Peers et al. 2020) and it is widely known that their population density fluctuates in a cyclic manner with a 9 to 11 -year periodicity (Krebs et al. 2014). In the Kluane Lake region, Yukon, Canada (61°N, 138W⁰), hares are the major prey species for four predator species, Canada lynx (*Lynx canadensis*), coyotes (*Canis latrans*), northern goshawks (*Accipiter gentilis*) and great horned owls (*Bubo virginianus*) (Krebs et al. 2001). Predators have been revealed to drive the hare population cycle (Krebs et al. 2018) as the majority of hare mortality is caused by predation (Krebs et al. 2001) while physiological stress induced by predation risk negatively affects reproduction and recruitment of hares (Boonstra et al. 1998, Sheriff et al. 2009). Despite the potential importance of the non-consumptive effect of predators in the hare population cycle, antipredator responses of hares and their potential costs have not been thoroughly examined (but see Hik 1995). Hares forage almost exclusively at night and dawn/dusk but reduce foraging on nights of bright moonlight (Studd et al. 2019), probably because they are proactively responding to predictable temporal variation in predation risk by allocating risky behavior (i.e. foraging) to safer times. Previous studies experimentally tested physiological response of hares to simulated unpredictable (acute) predation risk

(Sheriff et al. 2009, Boudreau et al. 2019), but hares' reactive antipredator response in natural conditions has never been examined.

In this thesis, I aim to deepen our understanding how prey in a multi-predator system simultaneously deal with two different types of variation (predictable and unpredictable) in predation risk by thoroughly investigating predation risk and antipredator responses of snowshoe hares in Northern Canada's boreal forest. The data on hares and predators on which my thesis is based were collected in the Kluane Lake region, Yukon, Canada in the winters from 2015-2016 to 2018-2019, when the hare population was at the increase, peak, and decline phases of the population cycle and experienced various levels of long-term risk (e.g. predator-hare ratio). In chapter 1, I investigate a reactive antipredator response of hares to unpredictable (acute) predation risk, by examining (1) if hares show behavioral response (reduction in foraging) following an encounter with their major predator (lynx), and (2) if so, what determines the magnitude of the response. In chapter 2, I try to identify temporal patterns of hare predation and behavioral patterns of hares before predation, aiming to examine predictable variation in predation risk for hares and risky behaviors for hares in a multi-predator system. Overall, this thesis contributes to a more comprehensive understanding of predation risk and antipredator responses.

Chapter 1: The interaction between food supply and long-term predation risk on antipredator response to acute predation risk

Abstract

Revealing the mechanisms that determine the magnitude and costs of antipredator responses is crucial to understanding their potential demographic effect on prey populations. Food availability and temporal variation in predation risk are both important determinants of the magnitude of antipredator responses, but their effects have rarely been examined simultaneously. Here, to reveal how food availability and long-term predation risk affect antipredator responses to acute predation risk, we examined the reactive antipredator response of snowshoe hares (*Lepus americanus*) to an encounter with Canada lynx (*Lynx canadensis*) by monitoring long-term variation in predation risk (two-month mortality rate of hares) and manipulating food availability of targeted hares. Snowshoe hares reduced foraging time for up to 10 hours after lynx came within 75 m as a reactive antipredator response. Food-supplemented hares reduced foraging time more after a lynx encounter than control hares, when long-term risk was low. Most strikingly, however, control hares increased the magnitude of antipredator response to a lynx encounter as long-term risk increased, whereas food-supplemented hares showed the opposite pattern. Here, we show evidence for an interaction effect between food availability and long-term predation risk on the magnitude of reactive antipredator response to acute predation risk.

Introduction

Prey need to balance the trade-off between energy intake and antipredator responses to minimize the risk of death (McNamara and Houston 1986, 1987, Lima and Dill 1990). Antipredator responses such as increased vigilance, reduced foraging, or habitat selection result in lower energy intake (Fortin et al. 2005, Winnie and Creel 2007, Barnier et al. 2014) and can negatively affect the future survival and reproduction of prey (Lima 1998). Prey populations can thus be limited by predators not only through direct predation losses but also through fitness costs of antipredator responses (Werner and Peacor 2003, Preisser et al. 2005, Creel and Christianson 2008). Therefore, it is crucial to reveal the mechanisms that define the magnitude and costs of antipredator responses, to better understand the indirect effects of predators on prey populations.

Foraging behavior generally exposes prey to higher risk of predation, and thus prey should stop foraging once the cost of foraging (risk of predation) starts to exceed the benefit of foraging (energy intake and its effect on fitness) (Brown 1992, Kotler 1997). Therefore, food availability and predation risk interactively affect time allocation of prey between foraging and predator avoidance, thereby determining the magnitude of antipredator responses (Kotler 1997, Kotler et al. 2004). High food availability, and consequentially better nutritional state, allow prey to allocate more time to antipredator responses by reducing foraging time (Bachman 1993, Kotler et al. 2004). However, when food is scarce and thus prey are in poor nutritional state, the risk of starvation outweighs that of predation, thus requiring maintenance of foraging time at the cost of limited

antipredator responses even under high predation risk (Lima 1998), as shown by empirical studies (Sinclair and Arcese 1995, Brown and Kotler 2004, Oates et al. 2019).

Predation risk varies at various time scales (Lima and Bednekoff 1999), but it can be broken down into long-term and short-term risk. Long-term risk represents the background level of predation risk such as habitat/area-specific predation risk (Kotler et al. 2004, Creel 2018, Gehr et al. 2018) or proportion of time prey spend being exposed to the immediate risk of predation (Lima and Bednekoff 1999). Under high long-term risk, prey are exposed to chronic risk of predation. Prey can respond to this type of risk proactively (Creel 2018), by avoiding risky habitats (Fortin et al. 2005, Hebblewhite et al. 2005) or areas where predator occurrence is common (Valeix et al. 2009), or by being vigilant and scanning for predators (Fortin et al. 2004). On the other hand, short-term risk represents acute risk of predation such as predator presence in close proximity or predator encounters (Creel 2018, Valeix et al. 2009). Prey reactively respond to this acute risk by modifying their behaviors (e.g. increased movement or vigilance) (Middleton et al. 2013, Dröge et al. 2017, Oates et al. 2019) and habitat use (Valeix et al. 2009).

According to the risk allocation hypothesis, the level of antipredator responses to acute risk is affected by long-term risk (Lima and Bednekoff 1999, Ferrari et al. 2009). Prey generally allocate foraging to safe situations (= low acute risk) and antipredator behaviors to dangerous situations (= high acute risk) in the starvation-predation trade-off, but they should lessen the magnitude of antipredator response even under high acute risk when long-term risk is high as safe situations are infrequent (Lima and Bednekoff 1999).

However, studies testing this hypothesis have produced contradictory results (Ferrari et al. 2009); some studies reported that prey previously exposed to higher long-term risk showed a greater magnitude of antipredator response to acute risk (Giles and Huntingford 1984, Ferrari et al. 2007), whereas other studies found a reduced response to acute risk than individuals exposed to lower long-term risk (Sih and McCarthy 2002, Brown et al. 2006, Creel et al. 2008). Therefore, the effect of long-term risk on antipredator responses to acute risk is still unclear. In addition to long-term risk, food availability, and consequentially nutritional state of prey, should also affect how prey allocate foraging time between low- and high-acute risk situations (McNamara and Houston 1986, Kotler 1997, Lima and Bednekoff 1999). The determinants of the magnitude of antipredator response to acute risk is a critical knowledge gap in the study of predator-prey relationship, and examining the effects of food and long-term risk simultaneously may be an important step to fill this gap.

Here, we examined the effect of food availability and long-term risk on the reactive antipredator response of snowshoe hares to acute predation risk by Canada lynx with a food supplementation experiment on free-ranging hares over 4 winters of varying mortality rates in Northern Canada's boreal forest. Hares are known for their 10-year population cycle (Krebs et al. 1995), which comprises 4 different phases in terms of population change; the peak, decline, low, and increase (Krebs et al. 2001). Since the densities of major predators follow the hare cycle with 1- or 2-year time lag (Hik 1995, Krebs et al 2001), the predator-hare ratio and adult predation mortality of hares fluctuate annually (Hik 1995, Krebs et al. 2001, Krebs et al. 2018). The predator-hare ratio should also change from early to late winter due to constant predation loss of individuals from hare populations, and thus long-

term predation risk for hares varies annually and seasonally. Overwinter body mass loss of hares (Hodges et al. 2006) implies that hares are potentially food-limited and their antipredator responses can be constrained by food availability and nutritional condition. Therefore, our system was ideal for testing how the level of food availability and long-term risk interactively affect the magnitude of antipredator responses. We hypothesized that (1) hares lessen the magnitude of antipredator response (reduction in foraging time) to acute risk (predator encounter) when long-term risk (two-month mortality rate of hares) is high, because low-acute risk situation is infrequent and thus they need to forage even under high acute risk (Lima and Bednekoff 1999), but (2) food supplementation facilitates higher food intake rate and shortened foraging time (Kotler 1997), thereby allowing hares to respond to acute risk more strongly even when long-term risk is high. Based on the hypothesis, we predicted that (1) control hares would reduce foraging time after a lynx encounter only when two-month mortality rate is low, while (2) food-supplemented hares would consistently reduce foraging time more than control hares after a lynx encounter and would still show the response even when two-month mortality rate is high.

Methods

Study area

Our study was conducted in the Kluane region, southern Yukon, Canada (61⁰N, 138W⁰) in 4 winters between 2015-2016 and 2018-2019, spanning from the increase to the decline of the hare cycle. The area is mainly occupied by white spruce (*Picea glauca*)

dominant boreal forest with interspersed aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*), and shrub understory comprised of bog birch (*Betula glandulosa*) and grey willow (*Salix glauca*) (Boonstra et al. 2016). Lynx, coyotes (*Canis latrans*), northern goshawks (*Accipiter gentilis*) and great horned owls (*Bubo virginianus*) are the major predator species for hares in our study area (Krebs et al. 2001).

Data collection

We live-trapped hares using Tomahawk live-traps (Tomahawk Live Trap Co., Tomahawk, WI, USA) on 5 trapping grids (600 × 600 m) which are located within 5 km from each other (Krebs et al. 2001), between November and April in each winter. Individual ID on the ear-tag, body weight, and sex were recorded for each capture. We deployed VHF collars with mortality sensors (Model SOM2380, Wildlife Materials Inc., USA, or Model MI-2M, Holohil, Canada) on hares, to monitor their daily survival throughout the winter. Once we detected a mortality signal, we located the hare carcass and recorded the cause of death. Selected females also received GPS units (Technosmart Europe Srl., Rome, Italy) and AXY-3 accelerometers (Technosmart Europe Srl., Rome, Italy) attached to VHF collars, to obtain location and behavioral data. GPS fix rates were set at 5, 15, or 30 minutes, and GPS error was around 15m. VHF collars and GPS/accelerometer/VHF collars (both < 40g) were deployed on hares heavier than 1100g, so that the weight of the collar was less than 5% of the hare's body weight. Accelerometers were put on VHF collars so that they were on the dorsal side of the neck of hares, and

recorded body acceleration at 1 Hz frequency with +/- 8 g forces along 3 axes (dorso-ventral, anterior-posterior, and lateral) (Graf et al. 2015). Acceleration was classified into not foraging (including travelling, sprinting and resting), and foraging (feeding and travel with one hop) with a hierarchal decision tree for hares developed by Studd et al. (2019) that had an accuracy of 93.1%. See Studd et al. (2019) for more detailed information on data collection by accelerometers and behavioral classification of snowshoe hares. Throughout the 4 winters, we monitored 128 female hares with GPS units and accelerometers for potential interactions with lynx (2015-2016 = 36, 2016-2017 = 37, 2017-2018 = 44, 2018-2019 = 45), and 505 (male = 197, female = 308) hares with VHF tags for daily survival (including females monitored with GPS units; 2015-2016 = 185, 2016-2017 = 130, 2017-2018 = 96, 2018-2019 = 94) which included individuals monitored across multiple winters.

Throughout each winter, we supplemented selected female hares with commercial rabbit chow ad libitum (2015-2016 = 13, 2016-2017 = 17, 2017-2018 = 24, 2018-2019 = 16). The selected females were given microchip pit tags on the VHF/GPS/accelerometer collars, which allowed them to access feeders deployed on the study grids, thus hares without pit tags (i.e. control hares) did not have access to the feeders. We selected food-supplemented hares and deployed feeders so that home ranges of multiple food-supplemented hares would overlap, to maximize the experimental treatment. We deployed motion triggered cameras (no-glow, infrared PC900 Hyperfire™ RECONYX, Inc., Holmen, Wisconsin, USA) by the feeders to monitor if the targeted hares deployed with pit tags were visiting the feeders and eating chow. Food-supplemented hares consistently showed higher body mass and survival rate than control hares in all the 4 winters, showing

that manipulation of the availability and quality of food consistently facilitated better nutritional state of food-supplemented hares (Majchrzak, *unpublished data*).

We live-trapped lynx between November and April with custom-made box traps (Kolbe et al. 2003) which were baited with meat (road kill) and castor, and set along snowmobile trails or the edge of the Alaska Highway in the study area. Lynx were immobilized with a combination of ketamine, dexmedetomidine, and atipamezole and we deployed a GPS collar (Telemetry Solutions remote download model (350g) or Followit Iridium GPS (400g)), on all lynx over 7 kg. GPS fix rates were set at 15 minutes. We monitored 53 lynx in total with GPS collars in the 4 winters, some of which were monitored across multiple winters (2015-2016 = 14, 2016-2017 = 21, 2017-2018 = 24, 2018-2019 = 15).

Identification of hare-lynx interactions and response of hares

We monitored interactions between 162 female hares (323618 GPS locations) and 18 lynx (115907 GPS locations) that overlapped the hares in the 4 winters. To avoid failing to detect potential close hare-lynx interactions, we conducted linear interpolation of each movement step between two consecutive GPS points at 1 minute intervals for hare and lynx GPS points using the *redistraj* function of *adehabitatLT* package in R (Calenge 2006). We did not apply the interpolation to the cases where the time interval between the two consecutive GPS points was longer than 60 minutes. We identified simultaneous GPS points of hares and lynx within 100m with *wildlifeDI* package in R (Long et al. 2014). We

used the closest interaction in the analysis, when there were multiple simultaneous GPS points of the same hare-lynx pair within 100m during the previous/following 24 hours. When a hare interacted with multiple lynx within 24 hours (8 out of 253 cases), we included only the closer interaction in the analysis. We calculated foraging time of the hare during 24 hours before and after each hare-lynx interaction in 2 hour-increments, to examine if hares reduce foraging time after lynx presence. Foraging behavior of hares was detected as feeding and travel with one hop by accelerometers (Studd et al. 2019).

Long-term predation risk

We used two-month mortality rate of control hares in the study area (2015-2016 = 185, 2016-2017 = 130, 2017-2018 = 96, 2015-2016 = 94) as the measure of long-term predation risk for hares, considering that hare mortality is almost exclusively due to predation and hares are exposed to multiple predator species in the system (Krebs et al. 2001, Krebs et al. 2018). We first estimated two-month survival rate of hares (November-December, January-February, March-April) for each winter by the Kaplan-Meier method accounting for left-truncation with *survival* package in R (Therneau 2015), and then calculated mortality rate by subtracting survival rate from 1. Hares that survived were censored on the last day for each monitoring period (2 months) and lost hares were censored on the day we lost the signal from the VHF tags deployed on them.

Statistical analysis

We calculated foraging time of hares during 24 hours before (pre-lynx foraging time) and after lynx presence (post-lynx foraging time) in 2-hour increments, and then calculated the change in foraging time by subtracting pre-lynx foraging time from post-lynx foraging time for each 2-hour time window. We conducted a one-tailed paired t-test to examine if hares significantly reduced foraging time after a lynx encounter, comparing pre- and post-lynx foraging time of each hare.

To examine the factors and their effects on the amount of reduction in foraging time of hares during 10 hours after a lynx encounter, we used linear mixed effects models (LMM) taking the total amount of change in foraging time of hares (in minutes) during 10 hours after lynx encounters. We chose 10 hours for the analysis because hares showed no significant decrease in foraging time 10-12 hours after a lynx encounter (Figure. 1.1.). To examine the factors and their effects on the duration of reduction in foraging time of hares after a lynx encounter (how long hares continued reducing foraging time after lynx encounters as a categorical variable, 1: no response, 2: 0-8 h, 3: 0-8 and 8-16 h, 4: 0-8, 8-16 and 16-24 h), we used ordinal logistic regression models (OLS). In both analyses, candidate models included different combinations of long-term risk (two-month mortality rate of hares), food supplementation (0: control, 1: food-supplemented), interaction between long-term risk and food supplementation, and the distance to lynx as the main predictor variables. We also included time of day (daytime, night, and dawn/dusk), time of winter (the number of days since November 1st), and pre-lynx foraging time of hares (over 24

hours) in all the candidate models as control variables, to control for their potential effects on nutritional state and antipredator response of hares. All the candidate models included individual hare ID as a random intercept, because some individuals were sampled multiple times. To make the effect size of predictor variables directly comparable to each other, all the continuous variables (two-month mortality rate of hares, the distance to lynx, time of winter, and pre-lynx foraging time of hares) were standardized by mean-centering and dividing by their standard deviation. Food supplementation and time of day were treated as categorical variables. We constructed LMMs by *lmerTest* package in R (Kuznetsova et al. 2017), and homogeneity of residual variance and normality of residual variance were tested by model validation plots using *performance* package in R (Lüdtke et al. 2020). We did not find any issues in model validation. We used *ordinal* package for constructing OLSs (Christensen 2019). We checked collinearity of the predictor variables by calculating the variance inflation factor (VIF), setting 3 as the threshold value for excluding variables. We conducted model selection using the corrected Akaike Information Criterion for small sample size (AICc) (Burnham and Anderson 2002, Harrison et al. 2018) with *MuMIn* package in R (Barton 2012), to identify the most parsimonious model. The software R 3.6.1 (R Core Team 2019) was used for all the statistical analyses.

Results

Over 4 winters there were 245 events where GPS collared lynx came within 100 m of a snowshoe hare equipped with a GPS/accelerometer collar (defined as a lynx encounter hereafter, 2015-2016 = 42, 2016-2017 = 39, 2017-2018 = 129, and 2018-2019 = 35). Two-

month mortality rates of hares ranged 2.7-fold from 0.176 to 0.475 (Table 1.1.). On average, hares reduced foraging time for up to 10 hours after a lynx encounter (0-2 hours; by 5.36 ± 2.51 minutes [11.59 ± 5.42 % $t = -4.19$, $df = 244$, $P < 0.001$], 2-4 hours; by 2.01 ± 2.46 minutes [4.16 ± 5.09 % , $t = -1.61$, $df = 244$, $P = 0.055$], 4-6 hours; by 2.45 ± 2.25 minutes [5.03 ± 4.62 % $t = -2.13$, $df = 244$, $P = 0.017$], 6-8 hours; by 2.81 ± 2.20 minutes [5.87 ± 4.60 % $t = -2.50$, $df = 244$, $P = 0.007$], 8-10 hours; by 2.66 ± 2.49 minutes [5.77 ± 5.40 % $t = -2.09$, $df = 244$, $P = 0.019$]) and resumed foraging normally 10-12 hours after a lynx encounter ($t = -0.46$, $df = 244$, $P = 0.32$) (Figure 1.1.). Hares reduced foraging time by 15.28 ± 7.08 minutes in total over 10 hours after a lynx encounter on average ($t = -4.25$, $df = 244$, $P < 0.001$), which was 6.44 ± 2.98 % of the mean foraging time during the same 10-hour time window on the day before the encounter.

A reduction in foraging time of hares during 10 hours after a lynx encounter was observed when the distance to lynx was 0-25 m ($t = -2.82$, $df = 58$, $P = 0.003$), 25-50 m ($t = -3.04$, $df = 77$, $P = 0.002$), and 50-75 m ($t = -1.59$, $df = 64$, $P = 0.059$), but was not observed when the distance to lynx was > 75 m ($t = -0.64$, $df = 42$, $P = 0.26$) (Figure 1.2.). Given this we used only lynx encounters within 75 m in the following analysis.

To measure the magnitude of hares' antipredator response, we examined the total amount of reduction in foraging time of hares during 10 hours after a lynx encounter. Both of the two models including the interaction between long-term risk and food supplementation were selected as the top models ($\Delta AICc < 2$), with the most parsimonious model including the distance to lynx as one of the predictor variables as well (Table 1.2.).

Control hares increased the magnitude of antipredator response as long-term risk increased; they reduced foraging time more as two-month mortality rate increased (Table 1.3., Figure 1.3.). Food supplementation did not have a significant main effect on the magnitude of hares' antipredator response, but it had a significant effect through an interaction with long-term risk (Table 1.3., Figure 1.3.). Contrary to control hares, food-supplemented hares decreased the magnitude of antipredator response as long-term risk increased. Food-supplemented hares reduced their foraging time more than control hares after a lynx encounter when two-month mortality rate was low, but they decreased the amount of reduction in foraging time with the increase in two-month mortality rate (Table 1.3., Figure 1.3.). Consequently, food-supplemented hares showed a greater magnitude of antipredator response than control hares under low long-term risk, but control hares showed stronger antipredator response when long-term risk was high (Figure 1.3.). Hares tended to decrease the magnitude of the response as the distance to lynx increased, but the effect was not significant (Table 1.3.). As for the control variables, hares had a stronger response to a lynx encounter when foraging time in the previous 24 hours was longer, whereas time of day and time of winter did not have a significant effect on hares' antipredator response (Table 1.3.).

We also examined what factors would affect the duration of hares' response (length over which hares continued reducing their foraging time following a lynx encounter, 1: no response, 2: 0-8 h, 3: 0-8 and 8-16 h, 4: 0-8, 8-16 and 16-24 h). No models were selected over the null model ($\Delta\text{AICc} < 2$) (Table 1.4.), and thus we did not obtain parameter estimates.

Discussion

Snowshoe hares reduced foraging time for up to 10 hours after lynx came within 75 m, as a reactive antipredator response to acute predation risk. Food-supplemented hares reduced foraging time after a lynx encounter more than control hares under low long-term risk. However, contrary to our hypothesis and prediction, control hares increased the magnitude of the response to acute risk with increasing long-term risk, whereas food-supplemented hares reduced the magnitude of the response as long-term risk increased. Our study shows that food availability (and consequential nutritional state of prey) and long-term risk interactively affect the magnitude of antipredator response to acute risk.

Prey are generally expected to forage under low acute risk and to stop foraging and increase the level of antipredator response when acute risk is high (e.g. when predator is present in close proximity), but as long-term risk increases, the proportion of time prey spend being exposed to high acute risk increases and thus they need to lessen antipredator response to forage and avoid the risk of starvation even with high acute risk (Lima and Bednekoff 1999). Based on this risk allocation hypothesis, we predicted that 1) control hares would decrease the magnitude of antipredator response to acute risk (predator encounters) as long-term risk (two-month mortality rate) increases, but 2) higher food intake rate and shortened foraging time facilitated by food supplementation would allow hares to maintain a high level of antipredator response even under high long-term risk.

Against our prediction, control hares increased the magnitude of the response with increasing two-month mortality rate, by reducing foraging time more after a lynx encounter (Figure 1.3.). This result is consistent with some previous studies which reported greater magnitude of antipredator response to acute risk under high long-term risk. Giles and Huntingford (1984) found that sticklebacks (*Gasterosteus aculeatus L.*) living under high long-term risk showed greater magnitude of antipredator response to actual (fish predators) and simulated acute risk (bird models) than those from the areas of low long-term risk. Similarly, Ferrari et al. (2007) reported that mosquito (*Culex restuans*) larvae exposed to high long-term risk showed heightened antipredator response to acute risk (alarm cues) compared to those exposed to low long-term risk.

The greater magnitude of response in food supplemented hares to a lynx encounter than control hares under low two-month mortality is consistent with previous theoretical (McNamara and Houston 1986, 1987) and empirical research (Bachman 1993, Kotler 1997, Oates et al. 2019) which reported that the magnitude of antipredator response is positively affected by food availability and nutritional state of prey. Unexpectedly, however, food-supplemented hares reduced the magnitude of the response under high two-month mortality rate. This is probably because food-supplemented hares already reduced their daily foraging time as a proactive response to predation risk and thus they could not afford to reduce foraging further under high acute risk. Kotler et al. (2004) showed that food-supplemented Allenby's gerbils (*Gerbillus andersoni allenbyi*) reduced foraging even when predators were absent and did not reduce foraging further when predators were present. High food availability (in quality and quantity) is expected to allow prey to reduce foraging time to

reduce the risk of predation proactively, by facilitating high food intake rate and better nutritional state (Brown 1992, Kotler 1997), and our data show that food-supplemented hares actually showed shorter daily foraging times and higher level of vigilance while maintaining larger body mass than control hares throughout the winter (Majchrzak, *unpublished data*). In addition, since feeders were placed on the same locations throughout the winter, food-supplemented hares were also expected to shorten search time. Therefore, food-supplemented hares strongly responded to acute risk by reducing foraging time under low long-term risk probably because they could still allocate foraging to relatively frequent low-risk situations, even though their daily foraging time was already shortened compared to control hares. However, once long-term risk heightened and low-risk situations became infrequent, they probably could not reduce foraging further in response to acute risk. Finding that snowshoe hares in natural condition increased the magnitude of antipredator response to acute risk as long-term risk heightened but food supplementation reversed the pattern implies that food availability and long-term risk interactively affect antipredator responses to acute risk.

Another important aspect of antipredator responses to acute predation risk is how prey perceive acute risk and how long they respond to the risk. Considering that acute risk represents the immediate risk of predation such as predator presence in close proximity (Creel 2018), the distance to a predator should affect perception of acute risk by prey. Previous studies on antipredator response to acute risk in mammalian predator-prey system were conducted almost exclusively in ungulate-predator system, where prey perceive presence of predator from relatively long distance (Middleton et al. 2013, Dröge et al. 2017,

Oates et al. 2019). For example, elk (*Cervus elaphus*) responded when wolves (*Canis lupus*) were present within 1 km by increasing movement rate and the distance of displacement (Middleton et al. 2013), and moose *Alces alces* showed increased movement rate when wolves were present within 500 m (Oates et al. 2019). In our study, snowshoe hares reduced foraging time when lynx came within 75 m, showing that the threshold distance for hares to perceive predator presence is much shorter compared to ungulates. Interestingly, however, the distance to lynx did not have a significant effect when we analyzed the magnitude of hares' response to a lynx encounters within 75 m. This suggests that once a predator is perceived by a hare, the distance to the predator has little impact on the magnitude of the response (i.e. hares express an all or nothing response to acute risk). In terms of the duration of antipredator response to acute risk, hares in our study showed a pattern which is consistent with that of elk reported by Middleton et al. (2013). Our results show that hares retained their normal foraging time by 10-12 hours after a lynx encounter on average, and Middleton et al. (2013) also found that the effect of a wolf encounter on the movement rate of elk faded away within the next 24 hours. Previous studies suggested that the cost of antipredator response to acute risk is not food-mediated but stress-mediated (Creel 2018). Middleton actually reported that elk did not reduce feeding rate after wolf encounters and elk-wolf encounter rate was not frequent (less than 1 encounter per 10 days), suggesting that nutritional cost of antipredator response to acute risk may be negligible. However, our finding shows that hares reduced foraging time in response to lynx encounters, and even though the average duration of the response was 10 hours, food mediated effect of the response would not be negligible if hares experience lynx encounter

frequently or if hares respond to encounters with other predator species in the same way. Therefore, it is crucial to examine how frequently prey encounter predators (all the predator species in the system if possible) and how prey behaviorally respond to predator encounters, to appropriately evaluate the food mediated costs of reactive antipredator response on prey demography. We also examined what factors affect the duration of hares' response, but no predictor variables (long-term risk, food supplementation and the distance to lynx) and control variables (pre-lynx foraging time, time of day and time of winter) were found to have an effect.

Understanding the determinants of antipredator responses is crucial in ecological studies, considering that the demographic costs of antipredator responses on prey populations have not been fully understood (Creel et al 2007, White et al. 2011, Middleton et al. 2013). Our study provides the first evidence that the magnitude of antipredator response to acute predation risk is affected by the interaction between food availability and long-term predation risk. In addition, our results show that antipredator response to acute risk may impose nutritional cost on prey, contradicting previous studies (Middleton et al. 2013, Creel 2018). Previous studies showed that acute risk often triggers physiological stress response of prey and thereby negatively affecting survival and reproduction of prey (Boonstra et al. 1998, Bonier et al. 2009, Creel et al. 2009). We suggest that future studies should examine both behavioral and physiological aspects of reactive antipredator response, to reveal the overall effects of acute predation risk on prey demography. We focused on the reactive antipredator response to acute risk in our study, but prey also proactively respond to long-term risk and this proactive antipredator response generally

impose nutritional costs on prey (Creel 2018). For example, prey select safer but less favorable foraging habitat (Fortin et al. 2005) or reduce foraging activity under the bright moonlight (Kotler et al. 2010, Studd et al. 2019). For the next step to better understand non-consumptive effects of predators on prey populations, we also suggest that researchers should consider both proactive and reactive antipredator responses simultaneously but separately, to reveal how the magnitude and costs of each type of response are determined.

Table 1.1. 60-day mortality rate of snowshoe hares in winter between 2015-2016 and 2018-2019 in Kluane Lake region, Yukon, Canada, calculated by subtracting survival rate estimated by Kaplan-Meier method from 1. CI is confidence interval.

Year	Time	Mortality rate (95% CI)
2015-2016	Nov-Dec	0.405 (0.296, 0.498)
	Jan-Feb	0.475 (0.362, 0.567)
	Mar-Apr	0.279 (0.158, 0.383)
2016-2017	Nov-Dec	0.219 (0.127, 0.301)
	Jan-Feb	0.216 (0.123, 0.299)
	Mar-Apr	0.336 (0.215, 0.439)
2017-2018	Nov-Dec	0.176 (0.057, 0.280)
	Jan-Feb	0.328 (0.191, 0.441)
	Mar-Apr	0.356 (0.211, 0.475)
2018-2019	Nov-Dec	0.269 (0.120, 0.393)
	Jan-Feb	0.455 (0.306, 0.571)
	Mar-Apr	0.358 (0.211, 0.477)

Table 1.2. Comparison of candidate linear mixed effects models predicting the amount of change in foraging time of hares during 10 hours after a lynx encounter within 75 m (n=202 from 54 female hares). Risk is chronic predation risk (60-day mortality rate of hares), Dist is the distance to lynx, Food is food supplementation, TOD is time of day (daytime, night, and dawn/dusk), PF is pre-lynx foraging time (over the 24 hours before a lynx encounter) of hares, and Winter is time of winter (the number of days since November 1st). All models included individual hare ID as a random intercept. k is the number of parameters including an intercept, ΔAICc is the change in AICc from the most parsimonious model, and w is Akaike model weight. All the continuous predictor variables (Risk, Dist, PF, and Winter) were standardized (mean-centered and divided by a standard deviation).

Model	K	ΔAICc	w
Risk*Food + Risk + Food + Dist + TOD + PF + Winter	11	0.00	0.428
Risk*Food + Risk + Food + TOD + PF + Winter	10	0.46	0.340
TOD + PF + Winter	7	3.32	0.082
Food + TOD + PF + Winter	8	5.26	0.031
Risk + TOD + PF + Winter	8	5.44	0.028
Food + Dist + TOD + PF + Winter	9	5.55	0.027
Risk + Dist + TOD + PF + Winter	9	5.73	0.024
~ 1	3	6.09	0.020
Risk + Food + TOD + PF + Winter	9	7.43	0.010
Risk + Food + Dist + TOD + PF + Winter	10	7.71	0.009

Table 1.3. Parameter estimates from the most parsimonious model of the amount of change in foraging time of hares during 10 hours after a lynx encounter within 75 m (n=202 from 54 female hares). Risk is two-month mortality rate of hares, Food is food supplementation, TOD is time of day (daytime is the reference category), PF is pre-lynx foraging time (over the 24 hours before a lynx encounter) of hares, and winter is the number of days since November 1st. β is the parameter estimate, SE is the standard error, CI is 95% confidence interval, t is the t-value, and p is the p-value. All the numeric predictor variables (Risk, PF, and Winter) were standardized (mean-centered and divided by a standard deviation). Individual hare ID was included in the linear mixed effects model as a random intercept.

Fixed effects	B	CI	SE	t	p
(Intercept)	-9.96	(-24.67, 4.68)	7.73	-1.29	0.20
Risk	-11.20	(-23.19, 0.99)	6.32	-1.77	0.08
Food	-4.83	(-21.09, 11.41)	8.58	-0.56	0.58
Dist	6.49	(-1.23, 13.90)	3.90	1.66	0.10
TOD: twilight	-4.61	(-32.01, 22.78)	14.21	-0.32	0.75
TOD: night	-6.48	(-22.29, 9.31)	8.21	-0.79	0.43
PF	-13.39	(-21.23, -4.90)	4.10	-3.27	0.001
Winter	-0.28	(-10.03, 9.13)	4.97	-0.06	0.96
Risk*Food	24.83	(9.58, 40.21)	8.00	3.10	0.002

Table 1.4. Comparison of candidate generalized linear mixed effects models predicting the duration of reduction in foraging time of hares after a lynx encounter within 75 m (n=202 from 54 female hares). Risk is chronic predation risk (60-day mortality rate of hares), Dist is the distance to lynx, Food is food supplementation, TOD is time of day (daytime, night, and dawn/dusk), PF is pre-lynx foraging time (over the 24 hours before a lynx encounter) of hares, and Winter is time of winter (the number of days since November 1st). All models included individual hare ID as a random intercept. k is the number of parameters including an intercept, ΔAICc is the change in AICc from the most parsimonious model, and w is Akaike model weight. All the continuous predictor variables (Risk, Dist, PF, and Winter) were standardized (mean-centered and divided by a standard deviation).

Model	K	ΔAICc	w
TOD + PF + Winter	8	0.00	0.267
Food + TOD + PF + Winter	9	0.56	0.202
Risk + TOD + PF + Winter	9	1.50	0.126
Risk + Food + TOD + PF + Winter	10	1.96	0.100
~ 1	4	1.97	0.100
Food + Dist + TOD + PF + Winter	10	2.76	0.067
Risk*Food + Risk + Food + TOD + PF + Winter	11	3.38	0.049
Risk + Dist + TOD + PF + Winter	10	3.70	0.042
Risk + Food + Dist + TOD + PF + Winter	11	4.30	0.031
Risk*Food + Risk + Food + Dist + TOD + PF + Winter	12	5.63	0.016

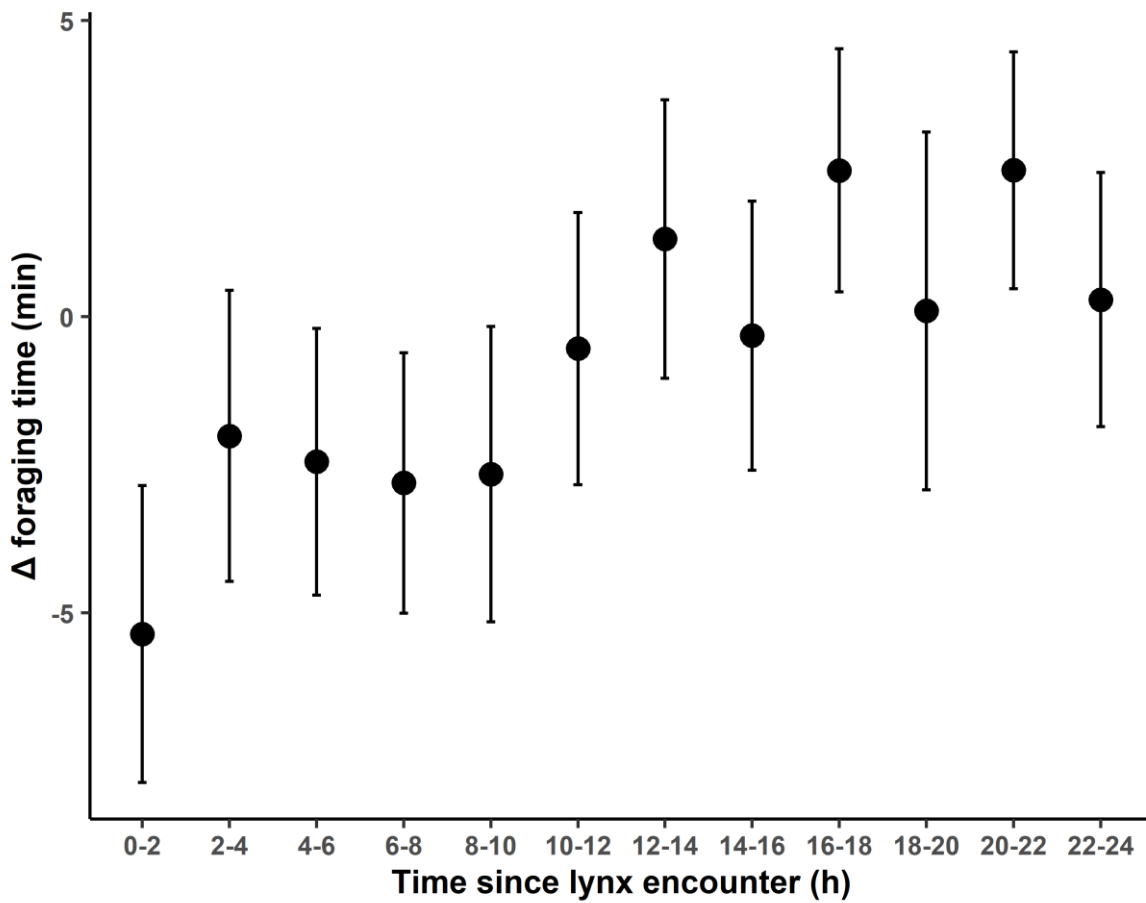


Figure 1.1. Change in foraging time of female hares during 24 hours after a lynx encounter within 100m in 2 hour-increments ($n = 245$ from 59 hares). Negative values mean that hares reduced foraging time from the same 4-hour time window during 24 hours before a lynx encounter. Error bars represent 95% confidence intervals.

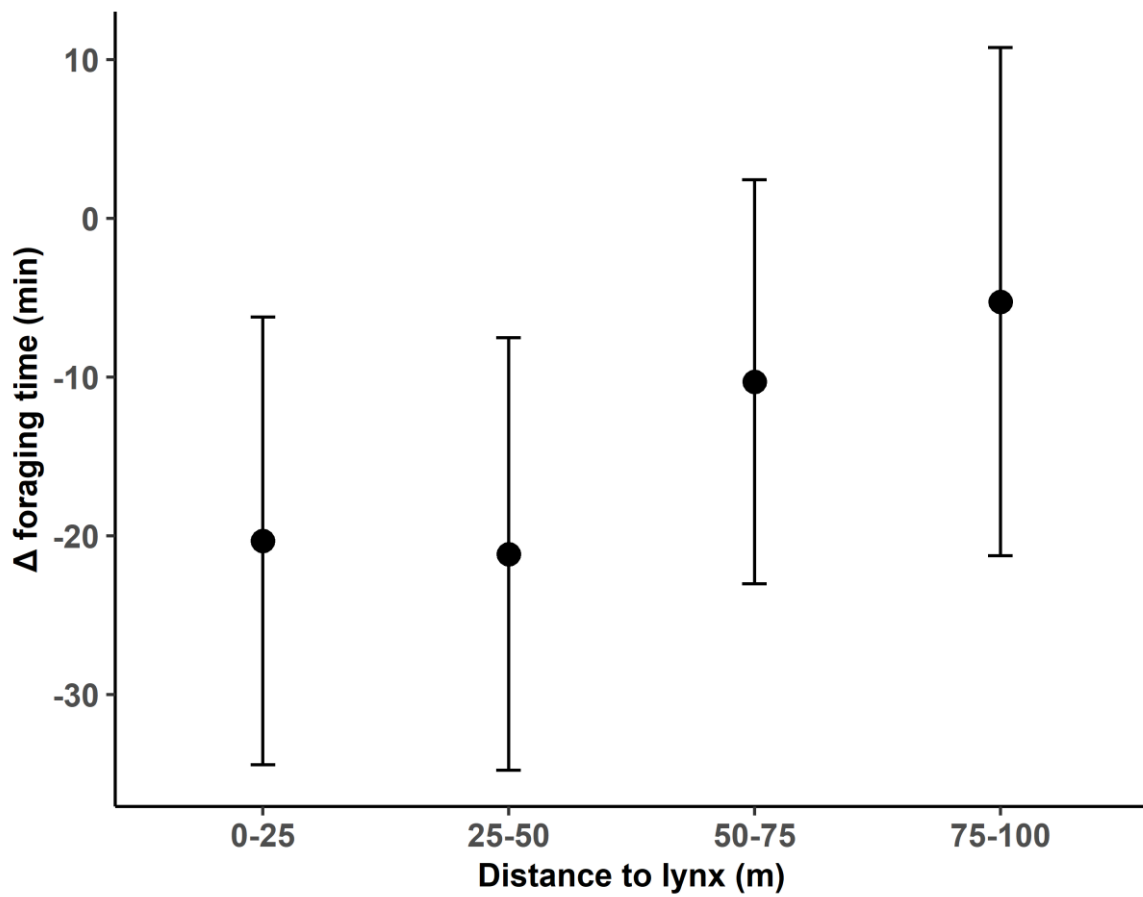


Figure 1.2. Total amount of change in foraging time of female hares during 10 hours after a lynx encounter for different classes of the distance to lynx (0-25 m: n = 59, 25-50 m: n = 78, 50-75 m: n = 65, 75-100 m: n = 43). Error bars represent 95% confidence intervals.

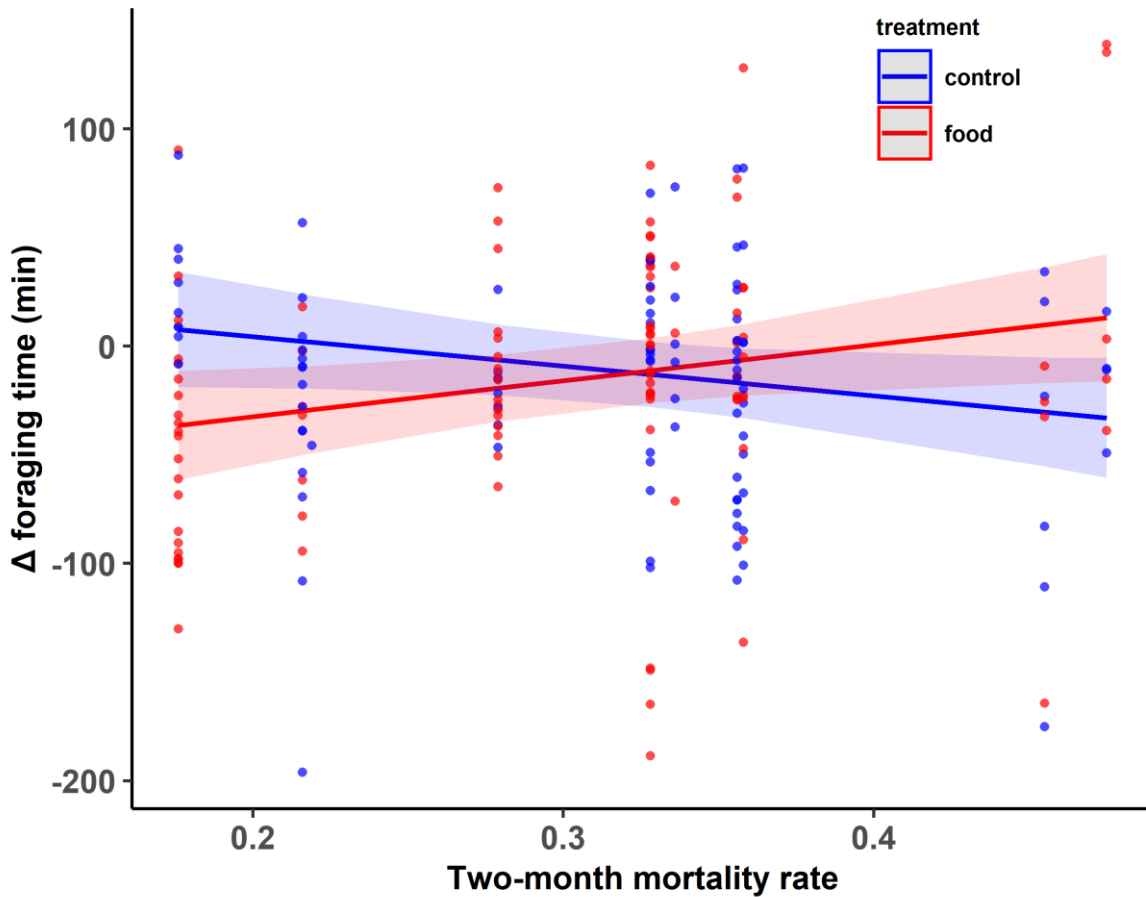


Figure 1.3. Interaction effect between chronic risk (60-day mortality rate of hares) and food supplementation on the total amount of change in foraging time of hares during 10 hours after a lynx encounter with 95% confidence intervals predicted by the most parsimonious models with raw data points ($n = 202$ from 54 hares). Time of day, time of winter, and pre-lynx foraging time are controlled for, and the models include individual hare ID as a random intercept. All the continuous predictor variables (chronic risk, time of winter, and pre-lynx foraging time) are back-transformed to the original means and scales.

Chapter 2: Identifying the time of snowshoe hare predation and their behavioral patterns before predation in a multi-predator system

Abstract

To better understand antipredator responses and non-consumptive effects of predators, it is important to understand how prey proactively respond to predictable spatial and temporal variations in predation risk. This is challenging in multi-predator systems because different behavioral patterns of different predator species complicate variations in predation risk, and identification of patterns of predation can be an important first step. Here, we examined temporal patterns of snowshoe hare (*Lepus americanus*) predation by multiple predator species and hares' behavioral patterns before predation in Northern Canada's boreal forest, aiming to identify temporal variations in predation risk and risky behavioral patterns for hares. We found that hare predation occurred during the daytime more frequently than expected, and hares were exposed to high predation risk by both of their major predators, lynx (*Lynx canadensis*) and coyote (*Canis latrans*), during the daytime. We also found that night-time hare predation mainly occurred on nights of bright moonlight, and these findings suggest that daytime and nights of bright moonlight are riskier times for hares. However, hares were killed frequently both during the daytime and the night/dawn/dusk, and different predators killed hares at different times of day. Foraging rate of hares before predation did not deviate from their normal behavioral patterns. Overall, our results suggest that hares living in a homogeneous habitat (spruce forest)

where they are exposed to multiple predator species are experiencing high risk of predation mortality at any time regardless of their activity level. Therefore, spatiotemporal refugia may not be available for hares and higher foraging rate may not necessarily increase the risk of predation for hares. Since factors such as the number of predator species or behavioral patterns of predators and prey can vary among different systems, it is important for researchers to study interactions between prey and multiple predators in diverse systems, to deepen our understanding of predation risk and non-consumptive effects of predators.

Introduction

Prey populations are limited by predators directly through predation and indirectly through the negative fitness consequences of predation risk (Werner and Peacor 2003, Preisser et al. 2005, Creel and Christianson 2008). The indirect effect of predators, by which predators affect prey behaviors via predation risk and thereby negatively impacting prey fitness, has been gaining researchers' attention as a non-consumptive effect (Preisser et al. 2007, Say-Sallaz et al. 2019). Predation risk triggers antipredator responses, which usually impose fitness costs on prey such as poor body condition, lower survival, and reduced reproductive output through physiological stress or nutritional deficits (Creel 2018). One famous example is that predation risk by wolves (*Canis lupus* causes) elk (*Cervus elaphus*) to reduce foraging, thereby negatively affecting body condition and reproduction of elk in the Yellowstone ecosystem (Creel et al. 2005, Winnie and Creel 2007, Creel et al. 2009).

It is well acknowledged that prey perceive and respond to spatial variation in predation risk, as represented by the concept of “landscapes of fear” (Laundré et al. 2001, Gaynor et al. 2019). For example, prey sacrifice foraging efficiency and increase vigilance in the areas with high predation risk (Brown 1999, Laundré et al. 2001, Kotler et al. 2004). Prey also proactively respond to spatial variation in predation risk by avoiding risky areas/habitats (Fortin et al. 2005, Valeix et al. 2009, Gehr et al. 2018). Browsing ungulates in Africa avoid the areas where lions (*Panthera leo*) are frequently present (Valeix et al. 2009) or European roe deer (*Capreolus capreolus*) avoid the areas with higher chance of an encounter with Eurasian lynx (*Lynx lynx*) (Gehr et al. 2018). However, recent studies have revealed that prey can still forage in risky habitats by finding temporal refugia during which predators are not active, suggesting that considering only spatial variation in predation risk and ignoring its temporal variation may lead to overestimation of non-consumptive effect of predators (Kohl et al. 2018, 2019, Smith et al. 2019). Previous studies reported that prey can perceive and respond proactively to temporal variation in predation risk, by allocating risky behavior (mainly foraging) to relatively safe times and antipredator responses to risky times (Brown et al. 1999, Lima and Bednekoff 1999). For example, it has been found that Vicunas (*Vicugna vicugna*) avoid risky habitat and reduce activity level at night when pumas (*Puma concolor*) are active (Smith et al. 2019), and that zebras (*Equus quagga*) forage in a risky habitat only during the daytime when lions are inactive (Courbin et al. 2019). Desert gerbils were found to increase vigilance and reduce foraging in the night of bright moonlight (Kotler et al. 2002, 2010). Therefore, it is important to examine how prey proactively respond to predictable spatial and temporal variations in predation risk to better

understand antipredator responses and non-consumptive effects of predators. This is especially challenging in multi-predator systems in which different behavioral patterns (e.g. diel activity and habitat use patterns, hunting mode, etc.) of different predator species complicate spatial and temporal variations in predation risk in the system, and identifying patterns of predation such as time of predation (risky time), habitat type (risky place), and risky behavior of prey can be an important first step.

In this study, we monitored snowshoe hares (*Lepus americanus*) with accelerometers attached to VHF collars over 4 winters in Northern Canada's boreal forest, aiming to identify patterns of hare predation by multiple predator species. Habitat of hares in this region is relatively homogeneous and dominated by a spruce forest (Boonstra et al. 2016) in which they spend most of their time (73.4% of daytime when they are inactive and 75.2% of night/dawn/dusk when they are active), and the majority of hare predation occurred in a spruce forest (72% of the detected winter hare predation events from 2015-2016 to 2018-2019) (*our unpublished data*). Therefore, we considered only time of hare predation and behavioral patterns of hares before predation in this study. Hares in the region are exposed to 4 major predator species, Canada lynx (*Lynx canadensis*), coyotes (*Canis latrans*), northern goshawks (*Accipiter gentilis*) and great horned owls (*Bubo virginianus*) (Krebs et al. 2001). Time of predation can be estimated based on predators' movement and behavioral patterns by using GPS data (Merrill et al. 2010), but this method is applicable only when body size of prey is large (Webb et al. 2008) and no method has been available for identifying time of predation for mid-small-bodied prey. Therefore, we developed a new method to identify time of predation for mid-small-bodied prey by using

temperature and behavioral data of prey collected by accelerometers. To examine behavioral patterns of hares before predation, we calculated the proportion of time hares spent foraging during short time intervals before the estimated time of predation. We predicted that predation on hares would occur mainly during the daytime on a diel scale and night-time hare predation would occur mainly during bright moonlit nights, because we hypothesized these are risky times for hares based on the fact that hares allocate foraging almost exclusively to the night/dawn/dusk and reduce night-time foraging when moonlight is bright (Studd et al. 2019). We also predicted that hares showed abnormally high foraging rate before predation, based on the basic theory that foraging behavior exposes prey to high risk of predation (McNamara and Houston 1987, Brown and Kotler 2004).

Materials and methods

Study area and data collection

Our research was conducted in the Kluane region, southern Yukon, Canada (61°N, 138W⁰) in 4 winters (October-April) between 2015-2016 and 2018-2019. Canopy cover in this area mainly comprises white spruce (*Picea glauca*) interspersed with aspen (*Populus tremuloides*) and balsam poplar (*Populus balsamifera*), and the shrub understory is composed primarily of bog birch (*Betula glandulosa*) and grey willow (*Salix glauca*) (Boonstra et al. 2016).

Each winter, we live-trapped hares using Tomahawk live-traps (Tomahawk Live Trap Co., Tomahawk, WI, USA) on 5 trapping grids (600 × 600 m). During each capture,

we recorded individual ID (using ear-tags), body mass, and sex. We deployed VHF collars with mortality sensors (Model SOM2380, Wildlife Materials Inc., USA, or Model MI-2M, Holohil, Canada) on hares, to monitor their daily survival throughout the winter. Once we detected a mortality signal, we located the hare carcass and recorded GPS coordinates (longitude and latitude) of the kill site and the cause of death based primarily on predator tracks in snow and the portions of the carcass remaining. We attached AXY-3 accelerometers (Technosmart Europe Srl., Rome, Italy) to VHF collars to obtain temperature and behavioral data. Accelerometer/VHF collars (both < 40g) were deployed on hares heavier than 1100g, so that the collar weighed less than 5% of the hare's body mass. Accelerometers recorded body acceleration along 3 axes (dorso-ventral, anterior-posterior, and lateral) at 1 Hz frequency with +/- 8 g forces, which were classified into 4 behavioral categories (resting, hopping, sprinting, and foraging) at 93.1 % accuracy using the hierarchical decision tree developed by Studd et al. (2019). Throughout the 4 winters, we monitored 505 (male = 197, female = 308) hares with VHF tags for survival (2015-2016 = 185, 2016-2017 = 130, 2017-2018 = 96, 2018-2019 = 94) which included individuals monitored across multiple winters, and detected 223 predation mortality events where predator species could be identified. Throughout the 4 winters, we monitored 216 hares with accelerometer/VHF collars (2015-2016 = 56, 2016-2017 = 57, 2017-2018 = 53, 2018-2019 = 50), and obtained temperature and behavioral data around the time of predation from 95 individuals. We excluded 31 out of the 95 hare mortalities from the analysis, because we could not distinguish cause of death between avian or mammalian predators.

Data analysis

During the winter, temperature recorded on the accelerometers are warmer than ambient temperature as they are influenced by the body heat of the hare. To estimate the time of predation, we first identified the time when the temperature measured on the accelerometer began to drop drastically towards ambient temperature. This time point is visible when plotting temperature against time (see Figure 2.1.a), and we considered this as the time when an accelerometer/VHF collar was no longer being warmed by the hare. We then considered the time of predation as the first identified sprinting behavior of the hare during 60 minutes before the sudden drop in temperature (see Figure 2.1.b). This time span was chosen because it usually takes ~ 20-45 minutes for lynx to consume a hare (Studd, *unpublished data*). We did not have data on handling time of other predator species (coyote, goshawk, and great horned owl), but we assumed consumption rates were less than 60 minutes from the time of chase. Since hares do not sprint frequently (92.37 ± 1.27 second/24 hours, *our unpublished data*), we believe it is reasonable to consider sprinting behavior during 60 minutes before the sudden drop in temperature as the sign of a chase by a predator. No sprinting behavior of hares was detected in 25 of the 64 mortalities, and we therefore considered these predation mortality events occurring without a chase. For these cases, we estimated the time of predation by subtracting the mean time gap (= time gap between the time of temperature drop and the estimated time of predation) calculated for each predator species based on the other 39 cases where sprinting was detected. Calculated

mean time gap was 23 mins 58 sec for lynx, 45 mins 7 sec for coyote, 20 mins 2 secs for avian predators (goshawk, great horned owl, and unidentified avian were combined), and 28 mins 7 secs for mammalian predators (lynx, coyote, and unidentified mammal were combined).

Once we estimated the time of predation, we assigned time of day to all mortalities ($n = 64$), and the fraction of the moon illuminated to mortality events occurring during the night ($n = 25$). We categorized time of day into day, night, and civil dawn/dusk, and the fraction of the moon illuminated into bright (> 0.66), moderate ($0.33-0.66$), and dark (< 0.33). We conducted Chi-square goodness of fit tests to test if any specific time of day is riskier for hares. We estimated expected values based on the proportion of each time of day over the entire study period (849 days, October 1st - April 30th from 2015-2016 to 2018-2019). The estimated proportion of each moon phase was; 0.391 for day (7961.7 h), 0.541 for night (11027.9 h), and 0.068 for dawn/dusk (1386.2 h). To test if bright moonlight enhances the risk of predation for hares, we conducted Chi-square goodness of fit tests. We estimated expected values based on the proportion of each moon phase over the entire study period (849 days, October 1st - April 30th from 2015-2016 to 2018-2019). The estimated proportion of each moon phase was; 0.389 for bright (330 days), 0.211 for moderate (179 days), and 0.400 for dark moon phase (340 days).

For each of the hare predation mortality events, we calculated (1) the proportion of time the killed hare spent foraging during 15, 30, 45, and 60 minutes before the estimated time of predation, and (2) the mean proportion of time hares that were not preyed upon

spent foraging during the same time of day as the estimated time of predation (daytime, night, or dawn/dusk) over the previous 7 days as the baseline foraging rate. We then compared (1) and (2) by conducting a one-tailed paired t-test, to examine if the proportion of time the killed hares spent foraging before predation deviated from the normal behavioral patterns of hares, expecting that the killed hares would show higher foraging rate than the baseline foraging rate. We only used the hares which received the same treatment (control or food-supplemented) as the killed hare for calculating the baseline foraging rate for each predation event, because control and food-supplemented hares showed different daily foraging rate (Majchrzak, *unpublished data*). In this behavioral analysis, we only included female hares due to the small sample size of males monitored with accelerometers and excluded the predation events where the baseline foraging rate could not be obtained due to the lack of data, decreasing the sample size from 64 to 49.

Results

Over the 4 winters (October-April) from 2015-2016 to 2018-2019, we obtained temperature and behavioral data of hares from 64 predation events in the 4 winters (Table 2.1.), and sprinting behavior of hares was detected in 39 of the 64 predation mortalities. Overall, the majority of predation occurred during the daytime (53.1 %) and night (39.1 %), and a small fraction of predation occurred during the dawn or dusk (7.8 %) (Figure 2.2.). A significantly higher proportion occurred during the daytime than expected ($\chi^2 = 5.99$, $df = 2$, $P = 0.050$). Lynx predation occurred almost equally during the daytime (47.2 %) and

during the night/dawn/dusk (52.8 %), whereas most of coyote predation occurred during the daytime (72.7 %). Avian predation also occurred equally during the daytime (50 %) and during the night/dawn/dusk (50 %), but goshawk predation (n = 3) only occurred during the daytime. There were only 2 great horned owl predations, one of which occurred during the daytime and the other occurred during the night.

Of the 25 predation events that occurred during the night, a significantly higher proportion occurred when moonlight was bright (fraction of the moon illuminated > 0.66) than expected ($\chi^2 = 8.92$, $df = 2$, $P = 0.012$). 68.0 % of the night-time predation events occurred on nights with bright moonlight, while 12.0 % and 20.0 % occurred on nights of moderate (fraction of the moon illuminated = 0.33-0.66) and dark moonlight (fraction of the moon illuminated < 0.33), respectively (Figure 2.3.). In addition, a larger proportion (66.7%) of lynx predation events that occurred at night were on nights of bright moonlight (Figure 2.3.).

The proportion of time killed hares spent foraging did not deviate from the baseline foraging rate (calculated as the mean foraging rate of hares which were not preyed upon) either during 15 (t = -1.62, $df = 48$, $P = 0.94$), 30 (t = -0.61, $df = 48$, $P = 0.73$), 45 (t = -0.08, $df = 48$, $P = 0.53$), or 60 minutes (t = -0.34, $df = 48$, $P = 0.63$) before predation.

Discussion

To better understand antipredator responses and non-consumptive effects of predators in multi-predator systems, it is crucial to reveal proactive antipredator responses

to predictable variations (spatial and temporal) in predation risk and identifying patterns of predation in terms of time, habitat type, and behavior of prey can be an important first step. Snowshoe hares in Northern Canada's boreal forest inhabit a relatively homogeneous habitat (spruce forest) and are exposed to four main predator species, lynx, coyotes, northern goshawks, and great horned owls (Krebs et al. 2001). We found that hare predation occurred during the daytime more frequently than expected. In addition, combining the fact that lynx and coyote were the majority of the known causes of hare predation mortalities during our study period (88.7% of 194 predation mortalities, *our unpublished data*) with our finding that both of them often killed hares during the daytime (Figure 2.2.), the daytime can be considered as the riskiest time for hares as we expected. We also found that night-time hare predation occurred mostly when moonlight was bright (Figure 2.3.), which was also consistent with our expectation. Studd et al. (2019) found that snowshoe hares allocate foraging almost exclusively to dark times (night, dawn, and dusk) but they reduce night-time foraging under bright moonlight and show compensatory foraging in the following morning (i.e. early daytime). Therefore, hares may be proactively responding to temporal variations in predation risk by allocating foraging to relatively safe times (Lima and Bednekoff 1999). At the same time, however, hares were killed both during the daytime and during the night/dawn/dusk, and different predator species killed hares at different times of day (Table 2.1., Figure 2.2.). Considering that hares are inactive/resting during the daytime whereas they forage almost exclusively during the night/dawn/dusk (Studd et al. 2019), our results suggest that hares are preyed upon regardless of whether they are active or inactive. Our behavioral analysis also showed that

foraging rate of hares before predation did not deviate from the normal behavioral patterns of hares, which is against the general theory that higher foraging rate exposes prey to higher risk of predation (McNamara and Houston 1987, Brown and Kotler 2004). To summarize, our results imply that hares are basically exposed to high risk of predation at any time (possibly except during the nights of dark moonlight) regardless of what they are doing, though we could not examine behavioral patterns of hares besides foraging such as habitat use or movement rate. Previous studies reported that prey can minimize the risk of predation while meeting their foraging requirement by finding a spatiotemporal refugia even in a multi-predator system, and thus behaviorally mediated non-consumptive effects of predators can be limited (Kohl et al. 2018, 2019, Smith et al. 2019). However, our findings suggest that this may not apply when prey inhabit a relatively homogeneous habitat (i.e. lack of alternative foraging habitat) where they are exposed to different predator species at different times of day, and allocating foraging to relatively safe times may be the only option for prey in such cases.

Time of predation is often identified by examining movement and behavioral patterns of predators based on predators' GPS location data collected with high sampling frequencies, but this method tends to fail to detect predation events when prey body size is small due to short handling time of predators (Webb et al. 2008, Merrill et al. 2010). In the present study, we developed a method to identify the time of hare predation by using temperature and behavioral data collected by accelerometers. This is the first study (to our knowledge) which identified time of predation for mid-small-bodied prey, and we believe that our method is widely applicable to various predator-prey systems as long as body

temperature of prey can be consistently recorded by accelerometers. As we did in the present study, temporal patterns of predation by different predator species can be revealed when researchers can identify predator species at kill sites even if predators are not monitored with remote sensing devices. In addition, collecting short-interval GPS data (e.g. 5 minutes) with accelerometer data can potentially facilitate identification of predation site and habitat information with high accuracy, which is difficult especially for small-bodied prey because their carcasses can be easily moved after they are killed by predators.

Non-consumptive effects formed by multiple predator species have been a critical knowledge gap in the study of predator-prey relationships (Say-Sallaz et al. 2019, Montgomery et al. 2019), and identifying patterns of predation by different predator species can contribute to understanding how antipredator responses and consequential non-consumptive effects of predators are determined in multi-predator systems. We identified temporal patterns of snowshoe hare predation and behaviors of hares before predation in a multi-predator system by using accelerometer data, and our results suggest that spatiotemporal refugia may not exist for hares and higher foraging rate does not necessarily increase the risk of predation. Considering that the number of predator species, behavioral patterns of predators (e.g. diel activity and habitat use patterns, hunting mode, etc.), or habitat availability/heterogeneity for prey can be different in different systems, it is important for researchers to study interactions between prey and multiple predators in diverse systems (Say-Sallaz et al. 2019), to deepen our understanding of non-consumptive effects of predators.

Table 2.1. Snowshoe hare predation in relation to time of day and moon phase in winter from 2015-2016 to 2018-2019 in the Kluane Lake region, Yukon, Canada (n = 64). Moon phase was categorized into 3 based on the fraction of the moon illuminated; bright (> 0.66), mid (0.33-0.66), and dark (< 0.33) phase.

Predator	n	Time of day	Moon (night predation)
Lynx	36	Day: 17	Bright: 12
		Night: 18	Mid: 2
		Dawn/Dusk: 1	Dark: 4
Coyote	11	Day: 8	Bright: 0
		Night: 1	Mid: 0
		Dawn/Dusk: 2	Dark: 1
Goshawk	3	Day: 3	Bright: 0
		Night: 0	Mid: 0
		Dawn/Dusk: 0	Dark: 0
Great horned owl	2	Day: 1	Bright: 1
		Night: 1	Mid: 0
		Dawn/Dusk: 0	Dark: 0
Mammal	56	Day: 30	Bright: 15
		Night: 22	Mid: 2
		Dawn/Dusk: 4	Dark: 5
Avian	8	Day: 4	Bright: 2
		Night: 3	Mid: 1
		Dawn/Dusk: 1	Dark: 0
Total	64	Day: 34	Bright: 17
		Night: 25	Mid: 3
		Dawn/Dusk: 5	Dark: 5

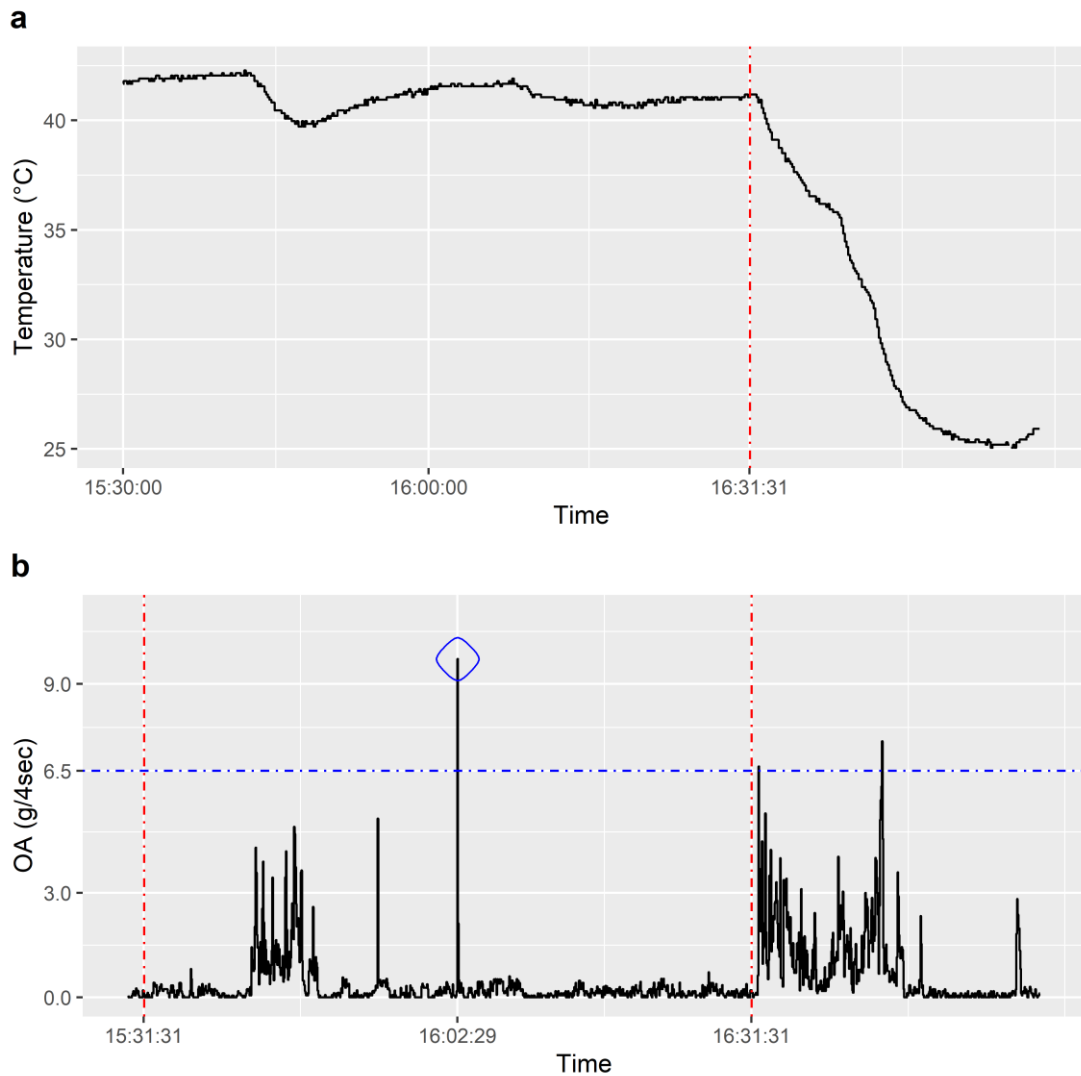


Figure 2.1. Example plots of changes in temperature (a) and body acceleration of a hare (b) with time around the time of predation, based on the accelerometer data collected from a hare (ID 25695) which was killed by a lynx on April 3rd 2019. A red dotted line in (a) denotes the time when the temperature began to drop (16:31:31). Sprinting behavior of a hare is identified as a value of overall acceleration (OA) greater than 6.5g-forces over 4 seconds, which is denoted as a blue dotted line and a blue circle in (b).

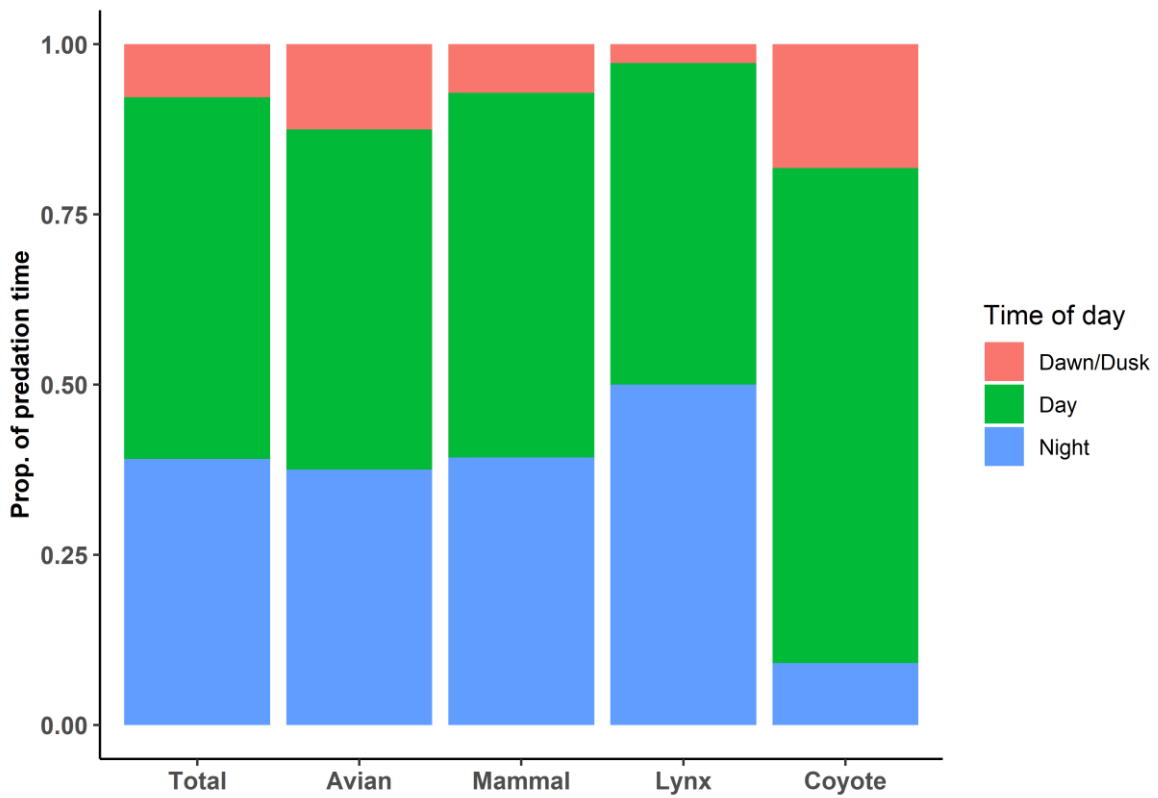


Figure 2.2. Time of predation on snowshoe hares in winter from 2015-2016 to 2018-2019 in the Kluane Lake region, Yukon, Canada (n = 64). Avian predators (n = 8) include goshawk (n = 3), great horned owl (n = 2), and unidentified avian (n = 3), and mammalian predators (n = 56) include lynx (n = 36), coyote (n = 11), and unidentified mammals (n = 9).

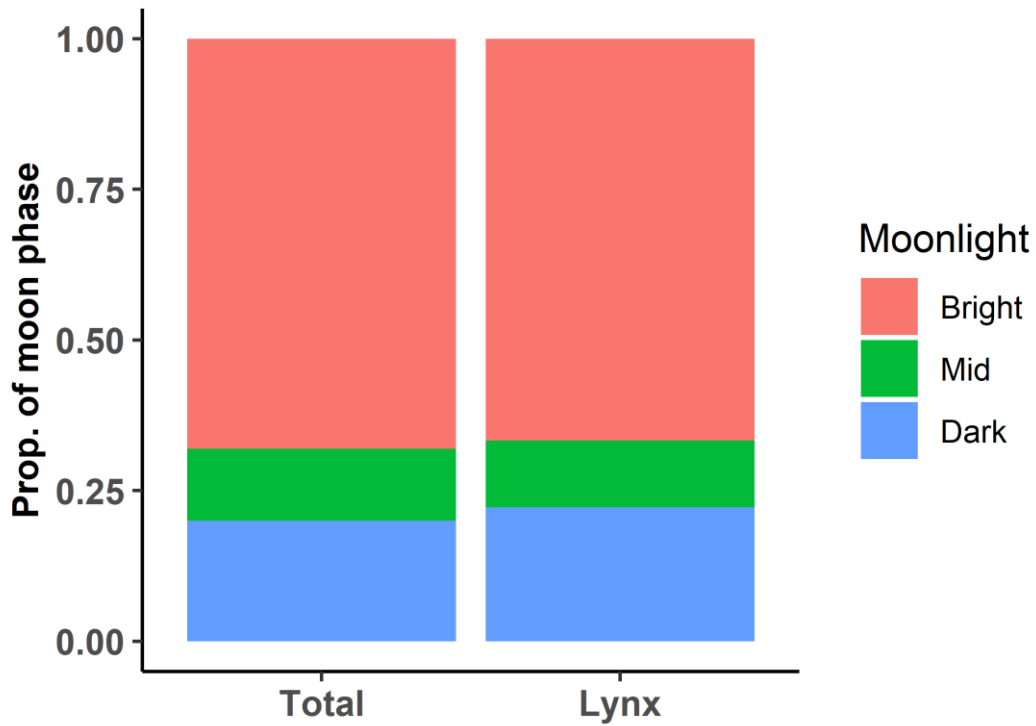


Figure 2.3. Proportion of different levels of moon illumination in night-time predation on snowshoe hares (total: $n = 25$, lynx: $n = 18$). The level of moonlight illumination represents the fraction of the moon illuminated; bright (>0.66), mid ($0.33-0.66$), and dark (<0.33).

Conclusion

Predators limit prey populations not only through direct predation, but also through negative fitness consequences of antipredator responses, and these non-consumptive effects of predators has been an important area of research (Werner and Peacor 2003, Preisser et al. 2005, Creel and Christianson 2008, Preisser et al. 2007). A critical knowledge gap in the study of predator-prey relationships is how prey balance their response to both predictable and unpredictable variation in predation risk, and how the magnitude of non-consumptive effects of predators is determined. To fill this knowledge gap, I investigated both predictable and unpredictable variation in predation risk for snowshoe hares and their reactive antipredator response to acute predation risk in Northern Canada's boreal forest, where hares are exposed to multiple predator species. More specifically, I examined the reactive antipredator response of hares to a lynx encounter (acute risk) and the effects of long-term predation risk and food availability on the magnitude of hares' reactive antipredator response (Chapter 1), and identified temporal patterns of hare predation by multiple predator species and behavioral patterns of hares before predation (Chapter 2).

In Chapter 1, I found that snowshoe hares reduced foraging time as a reactive antipredator response for up to 12 hours after lynx encounters within 75 m (acute predation risk). Under low long-term predation risk (chronic risk: two-month mortality rate of hares), food-supplemented hares reduced foraging more and for longer after a lynx encounter than control hares. However, opposite to my prediction, control hares increased the magnitude of their response to a lynx encounter with the increase in long-term risk, whereas food-

supplemented hares showed the opposite pattern. These findings suggest that food availability and long-term predation risk interactively affect the magnitude of hares' reactive antipredator response to acute predation risk.

In Chapter 2, I found that daytime on a diel scale and bright moonlit nights could be the riskiest time of hares, because they were exposed to high risk of predation by both lynx and coyote which are their major predators during the daytime, and night-time hare predation occurred mostly on nights of bright moonlight. However, hares were killed equally during the daytime and the night/dawn/dusk and hare predation by different predator species occurred at different times of day. Another interesting finding was that hares did not show higher foraging rate before predation than their normal behavioral patterns. Combining these results with the fact that hares spend most of their time in a spruce forest and hare predation mortalities are detected mostly in a spruce forest, it can be concluded that spatiotemporal refugia may not exist for hares and higher foraging rate does not necessarily increase the risk of predation. This is probably because hares in the region inhabit a homogeneous habitat (spruce forest) and are exposed to the risk of predation by multiple predator species at different times. Considering that the number of predator species or behavioral patterns of predators and prey are different in different systems, researchers need to investigate interactions between prey and multiple predators in diverse systems, to better understand spatiotemporal variations in predation risk and non-consumptive effects of predators.

Overall, key findings of this thesis are (1) hares are experiencing both predictable and unpredictable variation in predation risk, and are potentially responding to both types of variation in predation risk simultaneously by adopting different types (proactive and reactive) of antipredator response, (2) the magnitude of hares' reactive antipredator response to unpredictable (acute) predation risk is affected by the interaction between food availability and long-term predation risk, and (3) efficiency of proactive antipredator response of hares to predictable variation in predation risk is potentially limited by the lack of spatiotemporal refuge due to the homogeneous habitat and existence of multiple predator species. These findings suggest that it is important to examine how prey simultaneously respond to predictable and unpredictable variation in predation risk by proactive and reactive antipredator responses, to better understand non-consumptive effects of predators on prey populations.

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