Ecology, 0(0), 2021, e03456

Food availability and long-term predation risk interactively affect antipredator response

Shotaro Shiratsuru,[1,5] Yasmine N. Majchrzak,[1] Michael J. L. Peers,[1] Emily K. Studd,[1,2]
Allyson K. Menzies,[2] Rachael Derbyshire,[3] Murray M. Humphries,[2] Charles J. Krebs,[4]
Dennis L. Murray,[3] and Stan Boutin[1]

[1] *Department of Biological Sciences, University of Alberta, Edmonton, Alberta T6G 2R3 Canada*
[2] *Department of Natural Resource Sciences, McGill University, St-Anne-de-Bellevue, Québec H9X 3V9 Canada*
[3] *Department of Biology, Trent University, Peterborough, Ontario, Canada*
[4] *Department of Zoology, University of British Columbia, Vancouver, British Columbia, Canada*

Citation: Shiratsuru, S., Y. N. Majchrzak, M. J. L. Peers, E. K. Studd, A. K. Menzies, R. Derbyshire, M. M. Humphries, C. J. Krebs, D. L. Murray, and S. Boutin. 2021. Food availability and long-term predation risk interactively affect antipredator response. Ecology 00(00):e03456. 10.1002/ecy.3456

Abstract. 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, particularly in wild prey. Here, we determine how food availability and long-term predation risk affect antipredator responses to acute predation risk by monitoring the foraging response of free-ranging snowshoe hares (*Lepus americanus*) to an encounter with a Canada lynx (*Lynx canadensis*) in Yukon, Canada, over four winters (2015–2016 to 2018–2019). We examined how this response was influenced by natural variation in long-term predation risk (2-month mortality rate of hares) while providing some individuals with supplemental food. On average, snowshoe hares reduced foraging time up to 10 h after coming into close proximity ($\leq$75 m) with lynx, and reduced foraging time an average of 15.28 ± 7.08 min per lynx encounter. Hares tended to respond more strongly when the distance to lynx was shorter. More importantly, the magnitude of hares' antipredator response to a lynx encounter was affected by the interaction between food-supplementation and long-term predation risk. Food-supplemented hares reduced foraging time more than control hares after a lynx encounter under low long-term risk, but decreased the magnitude of the response as long-term risk increased. In contrast, control hares increased the magnitude of their response as long-term risk increased. Our findings show that food availability and long-term predation risk interactively drive the magnitude of reactive antipredator response to acute predation risk. Determining the factors driving the magnitude of antipredator responses would contribute to a better understanding of the indirect effects of predators on prey populations.

Key words: antipredator response; food availability; Lepus americanus*;* Lynx canadensis*; nonconsumptive effect; predation risk; predator–prey.*

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 but also through fitness costs of antipredator responses (Werner and Peacor 2003, Preisser et al. 2005, Creel and Christianson 2008). In order to understand the consequences of indirect effects of predators on prey populations better, we need to determine the factors that affect the magnitude of antipredator responses.

Foraging behavior generally exposes prey to higher risk of predation, and thus prey should reduce foraging once the costs (risk of predation) start to exceed the benefits (energy intake and its effect on fitness) (Brown 1992, Kotler 1997). High food availability and consequentially better nutritional state allow prey to allocate more time to antipredator responses such as reduced 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,

Manuscript received 1 October 2020; revised 1 April 2021; accepted 13 May 2021. Corresponding Editor: Marco Festa-Bianchet.

[5] E-mail: shiratsu@ualberta.ca

Oates et al. 2019). This trade-off between starvation and predation risk implies that food availability and predation risk should interactively determine the magnitude of antipredator responses by affecting time allocation of prey between foraging and predator avoidance (McNamara and Houston 1987, Kotler 1997, Kotler et al. 2004).

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, which varies because of overall changes in predator density or predator–prey ratio (Lima and Bednekoff 1999), habitat/area–specific 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 (e.g., depending on predator density or predator–prey ratio) (Lima and Bednekoff 1999). 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 through vigilance and scanning for predators (Fortin et al. 2004). On the other hand, short-term risk represents acute risk of predation such as predator encounters (Valeix et al. 2009, Creel 2018). Prey reactively respond to this acute risk by modifying their behavior (e.g., movement away from the immediate risk or increased vigilance) (Middleton et al. 2013, Dröge et al. 2017, Oates et al. 2019).

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 behavior to dangerous situations (=high acute risk) in the starvation–predation trade-off, but they should lessen the magnitude of antipredator response to high acute risk when long-term risk is high (i.e., when prey experience chronic predation risk), as safe situations for foraging 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 the opposite response (Sih and McCarthy 2002, Brown et al. 2006, Creel et al. 2008). Therefore, the effect of long-term risk on the response 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). However, the effect of food availability and nutritional state of prey on the reactive antipredator response to acute risk has not been thoroughly examined (but see Oates et al. [2019]). The determinants of the magnitude of antipredator response to acute risk is a critical knowledge gap in the study of predator–prey relationships, and examining the effects of food and long-term risk simultaneously is 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 (*Lepus americanus*) to acute predation risk by Canada lynx (*Lynx canadensis*). We conducted an individual-based food supplementation experiment on free-ranging hares over four winters with varying mortality rates associated with changing predator and hare densities. Hares are known for their 10-yr population cycle (Krebs et al. 1995), which comprises four different phases in terms of population change; the peak, decline, low, and increase (Krebs et al. 2001). Because the densities of major predators follow the hare cycle with a 1- or 2-yr time lag (Boutin et al. 1995, Krebs et al. 2001), the predator–hare ratio and predation rate on hares fluctuate annually (Hik 1995, Krebs et al. 2018). The predator-hare ratio also increases from early to late winter because of constant predation of hares during this time, 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, the snowshoe hare–lynx 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 (2-month mortality rate of hares) is high, because low acute risk situations for foraging are infrequent (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 long-term risk is low, and (2) food-supplemented hares would consistently reduce foraging time regardless of long-term risk.

METHODS

Study area

Our study was conducted in the Kluane region, southern Yukon, Canada (61° N, 138° W) in four winters between 2015 and 2016 and 2018 to 2019, spanning the increase to the decline phase of the hare cycle. The study area is mainly occupied by white spruce (*Picea glauca*) dominant boreal forest with interspersed aspen (*Populus tremuloides*) and balsam poplar (*Populus balsamifera*). The shrub understory is comprised of bog birch (*Betula glandulosa*) and gray willow (*Salix glauca*) (Krebs and Boonstra 2001). 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, Peers et al. 2020).

Data collection

We live-trapped hares using Tomahawk live-traps (Tomahawk Live Trap Co., Tomahawk, Wisconsin, USA) on three separate trapping areas (which include seven 600 × 600 m trapping grids in total) which are located within 8 km from each other (Boutin et al. 2001), between November and April in each winter. Individual ID on the ear-tag, body mass, and sex were recorded for each capture. We deployed either VHF collars with mortality sensors (Model SOM2380, Wildlife Materials Inc., United States, or Model MI-2 M, Holohil, Canada) or a combination collar consisting of a GPS (Technosmart Europe Srl., Rome, Italy), accelerometer (AXY-3, Technosmart Europe Srl.), and VHF on hares heavier than 1,110 g (collar weight <5% hare weight). GPS fix rates were set at 5, 15, or 30 min, and GPS error was ˜15 m. 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 three axes (dorso–ventral, anterior–posterior, and lateral [Graf et al. 2015]). Acceleration was classified into not foraging (including traveling 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%. See Studd et al. (2019) for more detailed information on accelerometer data collection and behavioral classification of snowshoe hares.

Throughout the four winters, we monitored the daily survival of 481 (male = 158, female = 323) individual hares using VHF telemetry (2015–2016 = 212, 2016–2017 = 158, 2017–2018 = 130, 2018–2019 = 113), which includes individuals monitored across multiple winters. We monitored 110 females in total with GPS units and accelerometers for potential interactions with lynx (2015–2016 = 30, 2016–2017 = 34, 2017–2018 = 38, 2018–2019 = 45) on five of our study grids. Once we detected a mortality signal, we located the hare carcass and recorded the cause of death.

Throughout each winter, we supplemented a subset of female hares with commercial rabbit chow (crude protein 17%, crude fat 2%, and 2,320 kcal/kg) ad libitum (Majchrzak 2020). The selected females (2015–2016: November–December = 12, January–February = 12, March–April = 11, 2016–2017: November–December = 17, January–February = 15, March–April = 13, 2017–2018: November–December = 23, January–February = 21, March–April = 18, 2018–2019: November–December = 12, January–February = 14, March–April = 7) were given microchip pit tags on the VHF/GPS/accelerometer collars, which allowed them to access feeders deployed on the study grids, whereas hares without pit tags (i.e., control hares) did not have access to the feeders. Overall, 43 unique food-supplemented females were monitored with the VHF/GPS/accelerometer collars, and 16 of them were monitored across multiple winters. All supplemented hares had 1–3 feeders within their home range, but feeders were placed such that multiple hares could use the same feeders (Majchrzak 2020). Feeders held roughly 200 g of rabbit chow, and we replaced food every 2–3 d. We deployed motion triggered cameras (no-glow, infrared PC900 HyperfireTM RECONYX, Inc., Holmen, Wisconsin, USA) at the feeders to monitor if hares deployed with pit tags were eating the supplemental food, and only included hares that accessed the feeders in the food-supplemented treatment. Winter energy expenditure of hares in our study area is around 230 kcal/d (Sheriff et al. 2009), and food-supplemented hares spent on average <1 h/d at the feeders (see Majchrzak [2020]). Food-supplemented hares consistently had higher body mass in all four winters than control hares, and had higher survival rate in all but 2018–2019, showing that manipulation of the availability and quality of food consistently facilitated higher nutritional state (Majchrzak 2020). Predator presence around the feeders was rarely detected on cameras, suggesting that feeders were not significantly attracting predators to the food supplementation sites (Y. N. Majchrzak, *unpublished data*).

We live-trapped lynx between November and April in our study area with custom-made box traps (Kolbe et al. 2003), which were baited with meat (road kills) and beaver castor, and set along snowmobile trails or the edge of the Alaska Highway. Lynx were immobilized with a combination of ketamine, dexmedetomidine, and midazolam and we deployed a GPS collar (Telemetry Solutions remote download model [350 g] or Followit Iridium GPS [400 g]), on all lynx over 7 kg. GPS fix rates were set at 15 min. We monitored 18 lynx that overlapped with collared hares over four winters, some of which were monitored across multiple winters (2015–2016 = 4, 2016–2017 = 7, 2017–2018 = 8, 2018–2019 = 6).

Identification of hare–lynx interactions and response of hares

We compared all hare and lynx GPS locations (n_{hare} = 315,706; n_{lynx} = 115,907) in time and space to identify potential hare–lynx interactions. 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-min intervals for hare and lynx GPS points using the *redisltraj* 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 min. We identified simultaneous GPS points of hares and lynx within 100 m 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 100 m during the previous/following 24 h. When a hare interacted with multiple lynx within 24 h (8 out of 253 cases), we included only the closest interaction in the analysis. We calculated foraging time of the hare during 24 h before and after each hare–lynx interaction, to examine if hares reduced foraging time after lynx presence. Foraging time was calculated as the sum of all foraging regardless of whether it was at a feeder or on natural browse for food-supplemented hares.

Long-term predation risk

We used 2-month mortality rate of control hares (including both male and female hares) as the baseline 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, 2018). We did not have data on predator encounter rate of hares, which we consider as the best indicator of long-term risk, but we assumed that this 2-month mortality rate reasonably reflects predator encounter rate and lethality of predator encounters. During the study, winter mortality rates were 0.180/28 d (95% confidence interval [CI]: 0.154, 0.205) and 0.067/28 d (95% CI: 0.046, 0.088) for control female hares (2015–2016 = 109, 2016–2017 = 81, 2017–2018 = 60, 2018–2019 = 57) and food-supplemented female hares (2015–2016 = 27, 2016–2017 = 28, 2017–2018 = 35, 2018–2019 = 19), respectively. For more detailed information on survival rates of control and food-supplemented hares, see Majchrzak (2020). We could determine the cause of mortality for 160 of the 200 mortalities during the four winters; 97.5% of them were attributed to predation, and this pattern held for both food-supplemented ($n = 37$) and control hares ($n = 163$) (Majchrzak 2020). Although we could not attribute cause of mortality for the unknown cases, we are confident that these individuals did not die of starvation because we regularly found mortalities within 24–48 h after death and we rarely found intact carcasses. Therefore, 2-month mortality rate of control hares should reflect the baseline long-term predation risk for snowshoe hares in our study area, regardless of sex or treatment group. We first estimated 2-month (November–December, January–February, March–April) survival rate of hares (2015–2016 = 185, 2016–2017 = 130, 2017–2018 = 95, 2015–2016 = 94) for each winter using 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 they went missing.

Statistical analysis

We calculated foraging time (in minutes) of hares during 24 h before (pre-lynx foraging time) and after lynx presence (post-lynx foraging time) in 2-h increments, and then calculated the change in foraging time by subtracting pre-lynx foraging time from post-lynx foraging time for each 2-h 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. By conducting this approach, we could examine both the reduction in foraging time (in minutes) in response to lynx presence, and the duration of their response.

To examine the factors and their effects on the reduction in foraging time of hares during 10 h after a lynx encounter within 75 m, we used linear mixed-effects models (LMM). We chose 10 h (duration of the response) and 75 m (distance to lynx) for the analysis because hares showed no significant decrease in foraging time 10–12 h after a lynx encounter (see Fig. 1), and this reduction was only observed when the distance to lynx was ≤75 m (based on a one-tailed paired *t*-test; see Results and Fig. 2). Candidate models included different combinations of long-term risk (2-month mortality rate of hares), food supplementation (0: control, 1: food-supplemented), an 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 1 November), and pre-lynx foraging time of hares (over 24 h) in all the candidate models 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, the continuous variables (monthly mortality rate of hares, distance to lynx, and baseline foraging time) were standardized by mean-centering and dividing by two times their standard deviations, and the binary variable (treatment: control = 0, and food = 1) was centered to have mean zero (Gelman 2008). Time of day was treated as a categorical variable. We constructed LMMs by *lme4* package (Bates et al. 2015) and tested significance of parameter estimates 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 (Lüdecke et al. 2020). We did not find any issues in model validation. We checked collinearity of the predictor variables by using the variance inflation factor (VIF), setting 2 as the threshold value for excluding variables (Zuur et al. 2010). We conducted model selection using the corrected Akaike information criterion for small sample size ($\mathrm{AIC_c}$) (Burnham and Anderson 2002, Harrison et al. 2018) with *MuMIn* package in R (Barton 2012), to identify the best-supported model. The software R 3.6.1 (R Development Core Team 2019) was used for all the statistical analyses.

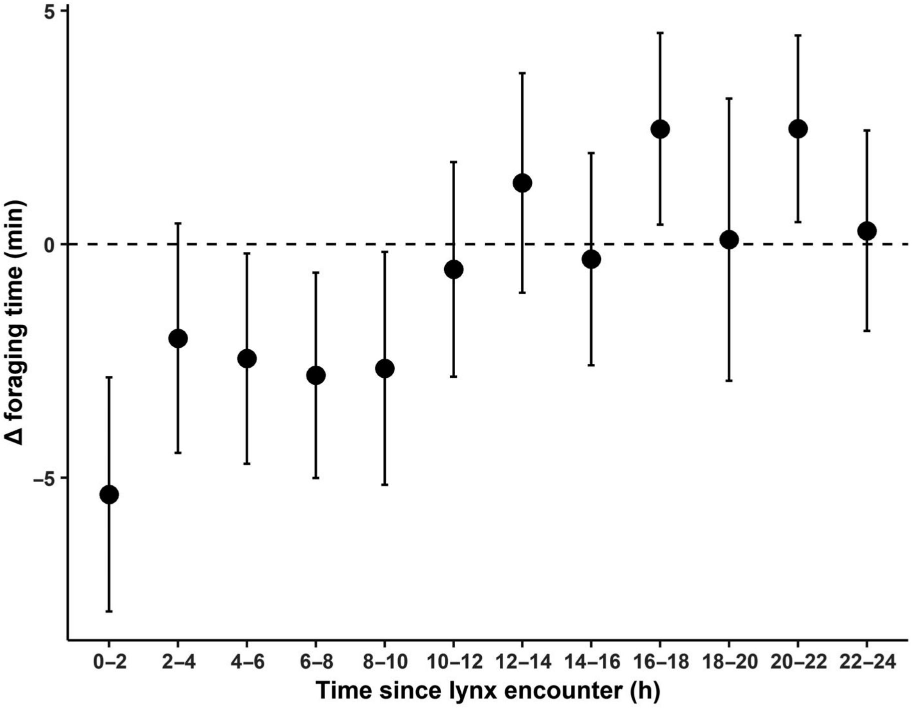

FIG. 1. Change in foraging time of female hares during 24 h after a lynx encounter within 100 m in 2-h increments (n = 245 from 59 hares). Negative values mean that hares reduced foraging time from the same 2-h time window during 24 h before a lynx encounter. Error bars represent 95% confidence intervals.

RESULTS

Over four 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). Over this same time period, 2-month mortality rates of hares ranged 2.6-fold from 0.181 to 0.475 and was highly variable (Appendix S1: Table S1). Two-month mortality rate of hares was highest during late winter (March–April) in the 2016–2017 and 2017–2018 winters, whereas it was highest during midwinter (January–February) in the 2015–2016 and 2018–2019 winters.

The average foraging time of hares was 9.32 ± 0.32 h for control hares (n = 120) and 8.64 ± 0.27 h for food-supplemented hares (n = 125) during 24 h before a lynx encounter, and 9.08 ± 0.35 h for control hares and 8.55 ± 0.30 h for food-supplemented hares during 24 h after a lynx encounter. On average, hares reduced foraging time for up to 10 h after a lynx encounter (0–2 h: −5.36 ± 2.52 min, t = −4.19, df = 244, $P < 0.001$; 2–4 h: −2.01 ± 2.47 min, t = −1.61, df = 244, P = 0.055; 4–6 h: −2.45 ± 2.26 min, t = −2.13, df = 244, P = 0.017; 6–8 h: −2.81 ± 2.21 min, t = −2.50, df = 244, P = 0.007; 8–10 h: −2.66 ± 2.51 min, t = −2.09, df = 244, P = 0.019) and resumed foraging normally 10–12 h after a lynx encounter (t = −0.46, df = 244, P = 0.32; Fig. 1). Combined, this equated to a reduction in foraging time of 15.28 ± 7.08 min over the 10 h following a lynx encounter (t = −4.25, df = 244, $P < 0.001$), which was 2.84 ± 1.32% of the overall mean pre-lynx daily foraging time.

Hares significantly reduced foraging time during 10 h after a lynx encounter when the distance to lynx was 0–25 m (t = −2.82, df = 58, P = 0.003) and 25–50 m (t = −3.04, df = 77, P = 0.002), and still tended to reduce foraging time when the distance to lynx was 50–75 m (t = −1.59, df = 64, P = 0.059; Fig. 2). The reduction in foraging time was greater when the distance to lynx was 0–25 m (−20.32 ± 14.41 min) and 25–50 m (−21.15 ± 13.84 min), compared to when the distance was 50–75 m (−10.29 ± 12.96 min). Reduction in foraging time was not observed when the distance to lynx was >75 m (−5.26 ± 16.47 min, t = −0.64, df = 42, P = 0.26; Fig. 2), and given this we used only those lynx encounters within 75 m in the following analysis (n = 202).

To measure the magnitude of hares' antipredator response, we examined the total reduction in foraging time of hares during 10 h 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 ($\Delta AIC_c < 2$), with the best-supported model including the distance to lynx as one of the predictor variables (Appendix S1: Table S2). Both long-term risk (β = 4.82, 95% CI = [−13.81, 23.96], t = 0.49, P = 0.63) and food supplementation (β = −4.72, 95%

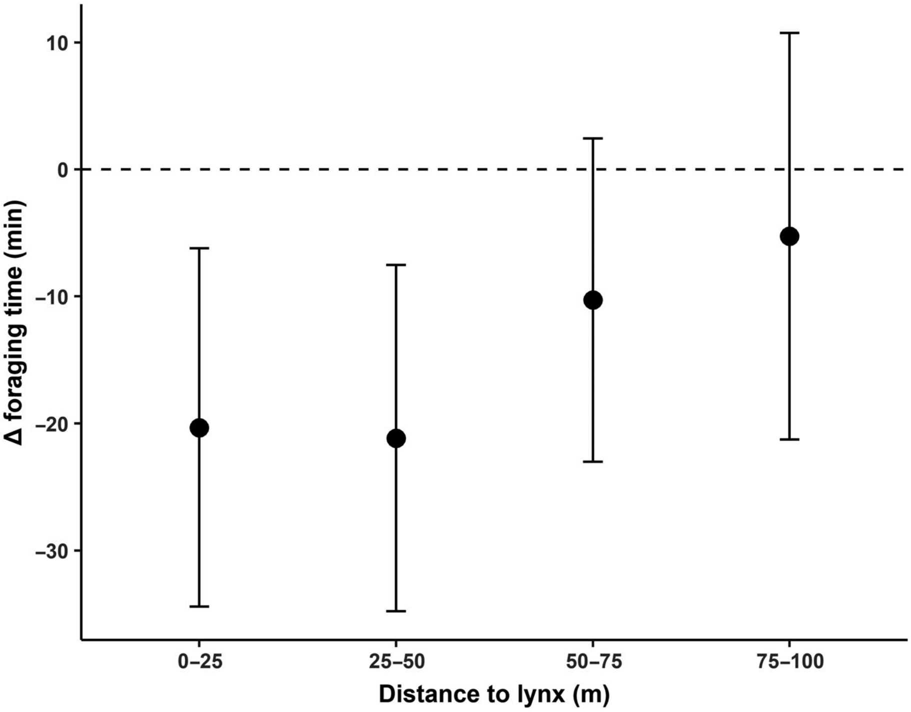

FIG. 2. Total change in foraging time of female hares during 10 h after a lynx encounter for different proximity to lynx (0–25 m: n = 59, 25–50 m: n = 78, 50–75 m: n = 65, 75–100 m: n = 43). Error bars represent 95% confidence intervals.

CI = [−20.99, 11.55], t = −0.55, P = 0.59) had a weak and insignificant main effect, but their interaction had a strong and significant effect on the magnitude of the hares' antipredator response (β = 49.16, 95% CI = [18.66, 79.86], t = 3.07, P = 0.002; Table 1). Control hares increased the magnitude of antipredator response as long-term risk increased; they reduced foraging time more as 2-month mortality rate increased (Fig. 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 2-month mortality rate was low, but they decreased the amount of reduction in foraging time with the increase in 2-month mortality rate (Fig. 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 (Fig. 3). This direction of the interaction effect between food supplementation and long-term risk on hares' response stayed the same when the same model was fitted to the data, which includes short-distance lynx encounters such as ≤60 m (Appendix S1: Table S3, Fig. S1) and ≤50 m (Appendix S1: Table S4, Fig. S2), though the effect became weaker. Hares tended to decrease the magnitude of the response as the distance to lynx increased, but the effect was not very strong (β = 13.01, 95% CI = [−2.44, 27.84], t = 1.67, P = 0.098; Table 1). As for the control variables, hares had a stronger response to a lynx encounter when they foraged more during the previous 24 h (β = −26.69, 95% CI = [−42.35, −9.69], t = −3.26, P = 0.001), whereas neither time of day nor time of winter had an effect on hares' antipredator response (Table 1).

DISCUSSION

Snowshoe hares reactively responded to acute predation risk, and individuals reduced foraging time for up to 10 h after encountering a lynx (Fig. 1). This response was influenced by the interaction between food availability and long-term risk. However, contrary to our prediction, control hares increased the magnitude of their response to acute risk with increasing long-term risk, whereas food-supplemented hares reduced the magnitude of their response (Fig. 3). Our study shows that food availability 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 stop foraging when acute risk is high (e.g., when predator is close by). As long-term risk increases, however, the proportion of time prey are exposed to high acute risk increases, and individuals thus lessen antipredator responses to avoid the risk of starvation (Lima and Bednekoff 1999). Based on this risk-allocation hypothesis, we predicted that (1) control hares would decrease the magnitude of antipredator response

TABLE 1. Parameter estimates from the best-supported model of the total change in foraging time (min) of hares during 10 h after a lynx encounter within 75 m (n = 202 from 54 female hares).

Fixed effects	β	CI	SE	t	P
(Intercept)	−12.66	(−24.51, −0.83)	6.25	−2.03	0.047
Risk	4.82	(−13.81, 23.96)	9.85	0.49	0.63
Food	−4.72	(−20.99, 11.55)	8.60	−0.55	0.59
Dist	13.01	(−2.44, 27.84)	7.81	1.67	0.098
TOD: twilight	−4.51	(−31.94, 22.87)	14.22	−0.32	0.75
TOD: night	−6.24	(−22.05, 9.55)	8.21	−0.76	0.45
PF	−26.69	(−42.35, −9.69)	8.20	−3.26	**0.001**
Winter	−0.85	(−20.28, 17.91)	9.92	−0.09	0.93
Risk * Food	49.16	(18.66, 79.86)	15.99	3.07	**0.002**

Notes: Risk is 2-month mortality rate of hares, Food is food supplementation, Dist is the distance to lynx, TOD is time of day (daytime is the reference category), PF is pre-lynx foraging time (over the 24 h before a lynx encounter) of hares, and winter is the number of days since 1 November. β is the parameter estimate, SE is the standard error, CI is 95% confidence interval, t is the t-statistic, and P is the P value. All the numeric predictor variables (Risk, PF, and Winter) were standardized (mean centered and divided by 2 standard deviations) and the binary variable (Food: control = 0 and food = 1) was centered to have mean zero. Individual hare ID was included in the linear mixed-effects model as a random intercept. Bold values represent statistically significant fixed effects ($P < 0.05$).

to acute risk (predator encounters) as long-term risk (2-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. Contrary to our prediction, control hares increased the magnitude of the response with increasing long-term risk, by reducing foraging time more after a lynx encounter (Fig. 3). This result is consistent with some previous studies. 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 relative to controls under low long-term risk is consistent with previous theoretical (McNamara and Houston 1986, 1987) and empirical research (Bachman 1993, Kotler 1997, Oates et al. 2019) where the magnitude of antipredator response is positively affected by food availability and the nutritional state of prey. However, food-supplemented hares unexpectedly reduced the magnitude of the response under high 2-month mortality rate. This is potentially because food-supplemented hares already reduced their daily foraging time as a proactive response to predation risk and could not afford to respond further in response to 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 change it further when predators were present. High food availability (in quality and quantity) is expected to allow prey to reduce foraging time proactively to risk by facilitating high food intake rate and better nutritional state (Brown 1992, Kotler 1997). Indeed, food-supplemented hares foraged less per day while maintaining larger body mass than control hares throughout the winter (Majchrzak 2020). 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. Overall, the pattern of the response between food-supplemented and control hares indicates 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. 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 systems were conducted almost exclusively in ungulate–predator systems, 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 (Fig. 2), showing that the threshold distance for hares to perceive predator presence is much shorter compared to ungulate prey. The magnitude of hares' response was qualitatively different, with hares reducing foraging time more when the distance to lynx was ≤50 m (Fig. 2), and the best supported model of the magnitude of the response also showed that a closer lynx encounter tended to trigger stronger response of hares, though the effect was minimal (Table 1).

Previous studies suggested that the cost of antipredator response to acute risk is not food mediated, but stress mediated (Creel 2018). Middleton et al. (2013) reported that elk did not reduce feeding rate after wolf encounters and elk–wolf encounter rate was not frequent (less than one encounter per 10 d), suggesting that nutritional cost of antipredator response to acute risk may be negligible. Our finding shows that hares reduced foraging time in response to lynx encounters, but the average duration of the response was 10 h and the amount of reduction in foraging time may be small relative to their

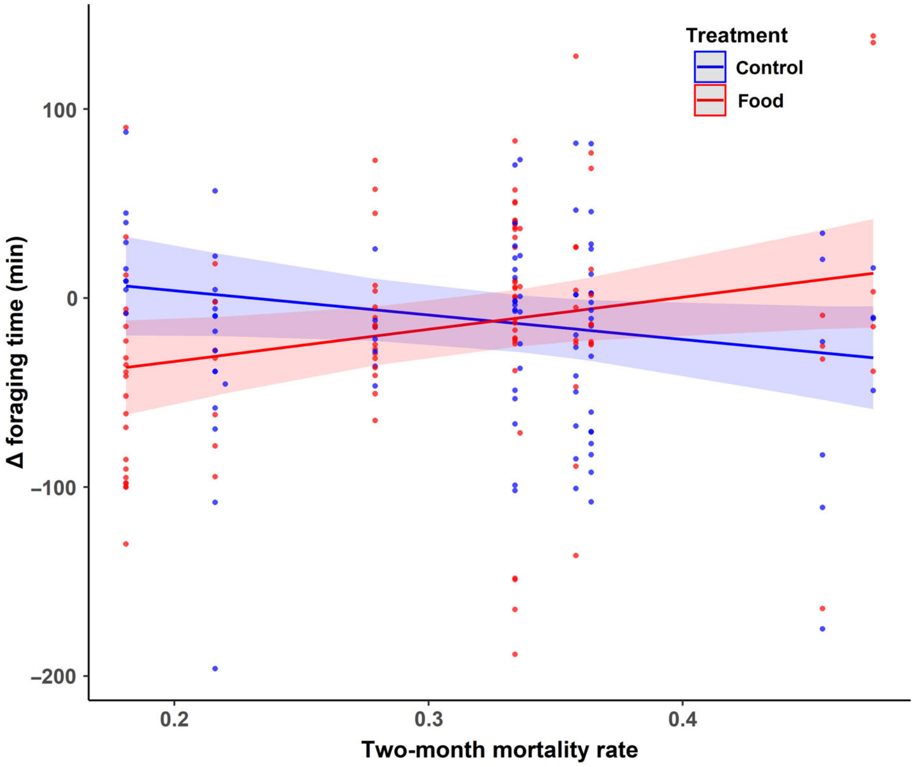

FIG. 3. Interaction effect between long-term risk (2-month mortality rate of hares) and food supplementation on the total change in foraging time of hares during 10 h after a lynx encounter with 95% confidence intervals predicted by the best-supported models with raw data points (*n* = 202 from 54 hares). 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 (long-term risk, time of winter, and pre-lynx for aging time) and the binary predictor variable (treatment: control = 0, and food = 1) are backtransformed to the original means and scales.

daily foraging time (9.32 ± 0.32 h for control hares). However, considering that hares are exposed to four major predator species in our study region (Krebs et al. 2001), hares may experience predator encounters frequently (e.g., once a day) when long-term risk is high (i.e., high predator–hare ratio and consequently high predator encounter rate). In addition, we found that control hares reduced foraging time more in response to a lynx encounter when long-term risk was high. Therefore, in the natural condition, the overall food-mediated cost of hares' antipredator response to acute risk may not be negligible under high long-term risk, such as during the decline phase of the hare cycle. We suggest that 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 those predator encounters, to evaluate the food-mediated costs of reactive antipredator response on prey populations appropriately. Previous studies tended to underestimate predator–prey encounter rate due to sampling biases (Creel et al. 2013), and thus it is important to design studies that account for these biases and accurately estimate predator-encounter rates.

Understanding the determinants of antipredator responses is crucial in ecological studies, considering that the demographic costs of such responses on prey populations have not been fully understood (Creel et al 2007, White et al. 2011, Middleton et al. 2013). Our study provides 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 suggest that antipredator response to acute risk may impose nutritional cost on prey depending on the level of long-term risk. Previous studies have mainly focused on the physiological (stress) cost of antipredator response to acute risk response and its negative effect on survival and reproduction of prey (Boonstra et al. 1998, Creel et al. 2009). However, researchers should examine both behavioral and physiological aspects of reactive antipredator response, in order to reveal the overall effects of acute predation risk on prey demography. In this study, we focused on the reactive antipredator response to acute risk in our study, but it is important to note that prey also proactively respond to long-term risk and this proactive antipredator response generally imposes nutritional costs on prey (Creel 2018). For example, prey select safer but less favorable foraging habitat (Fortin et al. 2005). For the next step to understand nonconsumptive effects of predators on prey populations better, we suggest that both proactive and reactive antipredator responses be simultaneously but separately considered to understand how the magnitude and costs of each type of response are determined.

ACKNOWLEDGEMENTS

We thank all the field technicians who trapped and monitored hares and lynx throughout the study. We also thank Agnes MacDonald and her family for long-term access to her trap line, and the Champagne and Aishihik First Nations for allowing us to conduct research within their traditional territory. This research was funded by the Natural Sciences and Engineering Research Council of Canada (NSERC), Northern Studies Training Program, the University of Alberta Northern Research Award program, the Association of Canadian Universities for Northern Studies, the Wildlife Conservation Society Canada, The W. Garfield Weston Foundation, the Killam Laureates program, Government of Yukon, and Earth Rangers.

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Open Research

Data (Shiratsuru et al. 2021) are available on the Dryad data repository (https://doi.org/10.5061/dryad.41ns1rndc).