



Climate change increases predation risk for a keystone species of the boreal forest

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Canada lynx (*Lynx canadensis*) and snowshoe hares (*Lepus americanus*) form a keystone predator–prey cycle that has large impacts on the North American boreal forest vertebrate community. Snowshoe hares and lynx are both well-suited for snowy winters, but climate change-associated shifts in snow conditions could lower hare survival and alter cyclic dynamics. Using detailed monitoring of snowshoe hare cause-specific mortality, behaviour and prevailing weather, we demonstrate that hare mortality risk is strongly influenced by variation in snow conditions. Although predation risk from lynx was largely unaffected by snow conditions, coyote (*Canis latrans*) predation increased in shallow snow. Maximum snow depth in our study area has decreased 33% over the last two decades and predictions based on prolonged shallow snow indicate that future hare survival could resemble that seen during population declines. Our results indicate that climate change could disrupt cyclic dynamics in the boreal forest.

How climate influences biotic interactions is an urgent question and is critical for predicting climate change effects on species or communities^{1,2}. Climate change could impact predator–prey dynamics by altering prey detection probability or predator hunting success^{3,4}, or through changes in behaviour altering prey encounter rates by predators⁵. For prey species, the influence of climate change on risk will depend on the degree to which prolonged changes in weather can influence survival rates, as well as the sensitivity and elasticity of the demographic variables that are impacted⁶. For predator communities, climate change may shift hunting advantages from one predator to another, with the species best-suited to past conditions being disadvantaged relative to species that more effectively respond to new environmental conditions⁷. Understanding these patterns will provide critical insight into how community composition will be affected by climate change but such mechanisms remain largely unexplored in wild populations because of the challenges in monitoring relevant changes in environmental conditions simultaneously with cause-specific mortality of prey.

Population cycles are among the most intriguing and studied ecological phenomena⁸. Perhaps the most famous example is the 8–10-yr cycle of snowshoe hares (*Lepus americanus*) across the boreal forest of North America. Snowshoe hares can represent over 50% of prey biomass and changes in their abundance drive that of numerous predator species, including the Canada lynx (*Lynx canadensis*)⁹. Snowshoe hares and lynx have large feet that contribute to low foot-loading and both are well-suited for boreal winters with deep snow. Coyotes (*Canis latrans*) are a generalist predator throughout the boreal region that originate from the central prairies of North America and have four to eight times higher foot-loading than lynx¹⁰. Changes in winter climate and the resulting changes in

snow conditions could influence hare survival by altering predator hunting success and hare escape potential³. Specifically, reduced snow depth and increased snow hardness may amplify predation risk from coyote over lynx, altering predator–prey dynamics in this system¹¹. This could ultimately impact cyclical dynamics^{12–14}, as winter mortality is an important driver of cycle phase^{15,16} and substantial changes in snowfall and cover are expected across North America over this century¹⁷. Indeed, snowshoe hare populations that have been monitored for multiple cycles have potentially declined in amplitude¹⁸ and broad-scale climate has been linked to fluctuations in the number of harvested hares and lynx¹⁹.

In this study, we test the prediction that changes in winter snow conditions can impact over-winter survival in snowshoe hares. We also examine whether winter conditions differentially influenced mortality caused by lynx and coyote predation, which would indicate the degree to which predator communities in this system may be altered by climate change. We further used consistent snow depth measurements taken in our study region to determine whether snow depth has changed over the last two decades. This will aid our understanding of how snow depth may be impacted by climate change in the region, given that future projections are challenging¹⁷. Finally, we examine the influence of temperature and snow conditions on the foraging behaviour of hares to determine potential mechanisms driving weather-related changes in risk and differences between age groups. Ultimately, our study contributes to a currently limited body of literature on the complex relationship between environmental variation and predator–prey dynamics. We surmise that this effort will improve our ability to forecast the effects of environmental changes on community interactions⁵, in particular the influence of climate change on cyclic dynamics in these important boreal species.

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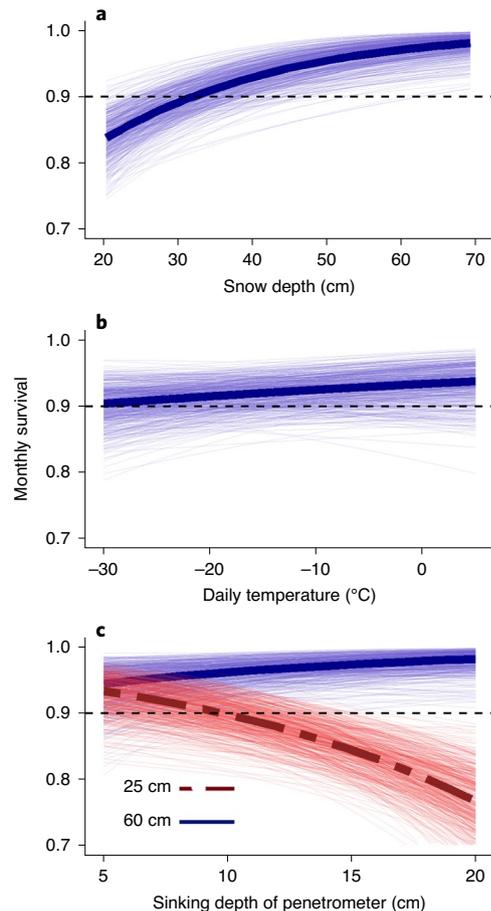


Fig. 1 | Predicted effect of climate on monthly hare survival. a–c. Modelled effect of snow depth (a), temperature (b) and snow hardness at 25 cm (red, dashed) and 60 cm (blue, solid) snow depths (~90th percentiles of winter snow depth) (c), on monthly snowshoe hare (*L. americanus*) survival. Solid lines represent covariate effects based on coefficients from the best supported CPH model and hollow lines represent coefficients from models built from 500 bootstrapped datasets. The dotted line at 0.90 survival is given for comparison between panels.

We monitored the daily survival and cause-specific mortality of 321 snowshoe hares across four winters (2015–18) in southwestern Yukon, along with daily changes in temperature and snow conditions (see Supplementary Fig. 1 for map of study area). These years represented the increase (2015–16), peak (2016–17) and decline (2017–18) phases of the hare cycle (Extended Data Fig. 1). In total, we had 153 predator-caused mortalities, with lynx (59.4%) and coyote (25.5%) representing most predation events, and a smaller percentage to goshawks (*Accipiter gentilis*, 9.4%) and great-horned owls (*Bubo virginianus*, 5.7%; Supplementary Table 1). On the basis of results from survival modelling, hare mortality risk was strongly influenced by snow conditions (Supplementary Tables 2 and 5). Prolonged changes in winter snow conditions and associated risk are predicted to strongly influence hare survival (Fig. 1). Snow depths >60 cm (with other weather variables at their mean value) correspond to a mean 30-d survival rate of 0.97 (95% confidence intervals (CI): 0.93, 0.99), whereas depths of 25 cm correspond to a mean survival probability of 0.87 (95% CI: 0.83, 0.91). When the sinking depth of a penetrometer used to measure snow compaction is 20 cm during shallow snow depth (that is, soft and shallow snow), survival probability is further reduced (0.77, 95% CI: 0.69, 0.84; Fig. 1). This indicates that prolonged changes in snow

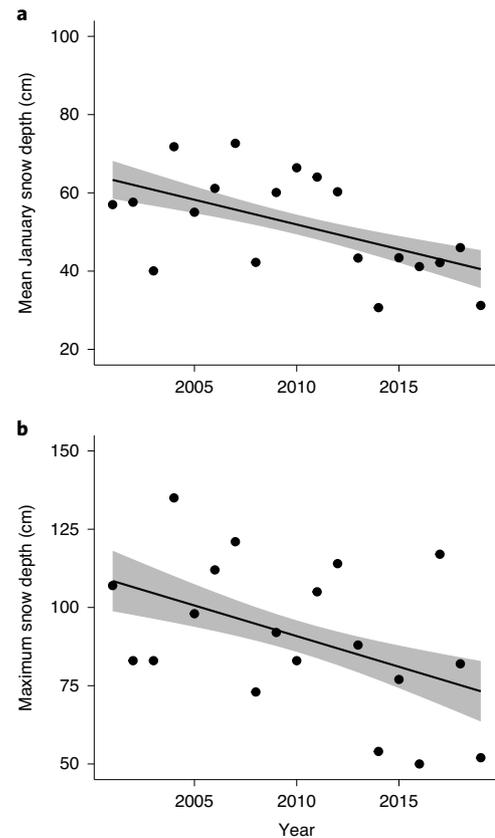


Fig. 2 | Snow depth change over the last two decades. a, b. The effect of year on average snow depth in January (cm) (a) and maximum winter snow depth (cm) (b) from 2001 to 2019 in the Kluane Lake region, Yukon. Shaded areas represent predicted response standard errors. Snow depth measurements were recorded throughout the winter (November–March) at nine consistent locations, <72 h following snowfall events.

conditions can substantially alter hare demography, since winter survival rates in shallow soft snow resemble those observed during the decline phase of the hare cycle (~0.8); deeper snow corresponds to rates seen during periods of population growth (>0.9), irrespective of snow hardness¹⁵.

Over-winter survival significantly differed across the 3 years (2015–16 [0.35; 95% CI: 0.26, 0.48]; 2016–17 [0.54; 0.44, 0.66]; 2017–18 [0.49; 0.35, 0.69]; Extended Data Fig. 2). Survival was lowest in the winter of 2015–16, relative to 2016–17 and 2017–18 ($P=0.05$), while survival did not differ significantly between the last two winters ($P=0.86$). This was unexpected, as the winter of 2015–16 represents the population-increase phase of the cycle, where survival is expected to be highest¹⁶. However, this winter coincided with the longest duration of time where snow depth was shallower than 35 cm, which represents a snow depth threshold above which mortality risk is reduced (that is, baseline mortality risk; Extended Data Fig. 3). Predictions of over-winter survival under shallow snow and low survival rates we observed during the increase phase, may become common in our study region, as snow depth has significantly declined over the last two decades (Fig. 2). Mean January snow depth has declined 36.0% since 2001 (-1.27 ± 0.46 , $P=0.014$), while maximum snow depth over-winter has declined 32.5% (-1.96 ± 0.92 , $P=0.048$).

The influence of snow on hare mortality appeared to be driven by its influence on risk from coyotes. Decreasing snow hardness (increasing sinking depth of the penetrometer) increased risk from coyote (hazard ratio (HR) = 1.244, 95% CI: 1.060, 1.456), whereas

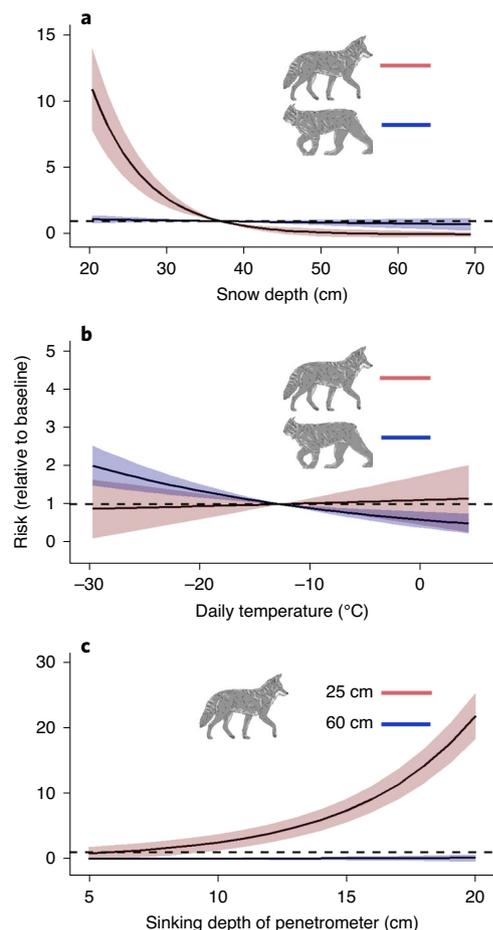


Fig. 3 | Relationship between cause-specific mortality and climate.

a–c, Modelled effect of snow depth on snowshoe hare (*L. americanus*) mortality risk from coyote (*C. latrans*) and lynx (*L. canadensis*) (**a**), temperature on hare mortality risk from coyote and lynx (**b**) and snow hardness on hare mortality risk from coyote at two different snow depths (**c**). Mortality risk is based on coefficients from the best supported CPH model and shaded areas represent predicted response standard errors. The dotted line represents baseline risk for hares.

increasing snow depth reduced risk from coyote (HR = 0.866, 95% CI: 0.776, 0.967). Although the effect of snow hardness on risk from coyote is contrary to expectations, it appears to be driven by its effect in shallow snow (Fig. 3c). Risk from coyotes is highest in shallow soft snow; however, in deep snow, risk increases as snow hardness increases. In contrast, lynx predation risk appeared less affected by changes in the environment, with variation in snow depth (HR = 0.992, 95% CI: 0.959, 1.025) and hardness (HR = 0.998, 95% CI: 0.938, 1.063) having no influence; increasing ambient temperature qualitatively reduced predation risk from lynx (HR = 0.960, 95% CI: 0.920, 1.001; Fig. 3). Differences between predators in the influence of snow conditions is further demonstrated when examining snow conditions at the kill site. Coyotes killed hares in areas of shallow and hard snow, relative to lynx (see Extended Data Fig. 4).

Snow depth had a comparable effect on mortality risk for both adults and sub-adults; however, the effect size was larger for sub-adults (HR = 0.935, 95% CI: 0.889, 0.984) than for adults (HR = 0.969, 95% CI: 0.938, 1.002; Fig. 4). Snow hardness, as measured by sinking depth of the penetrometer, did not differentially affect mortality of sub-adults (HR = 1.035, 95% CI: 0.951, 1.125) and adults (HR = 1.044, 95% CI: 0.986, 1.106). Similarly, temperature

did not influence risk for sub-adults (HR = 0.974, 95% CI: 0.922, 1.028) or adults (HR = 0.984, 95% CI: 0.944, 1.025), with adults having an overall higher survival rate during our study (see Extended Data Fig. 5). There was no difference in the proportion of sub-adult (0.33) and adult (0.25) mortalities attributable to coyote ($z = 0.83$, $P = 0.41$; Supplementary Table 1).

Changes in hare behaviour associated with environmental conditions did not drive winter mortality rates. We equipped 137 individual hares with accelerometers for a total of 4,530 hare-days and classified daily time spent foraging using behavioural classifications according to a decision tree distinguishing their foraging time every 4 s at 93.1% accuracy²⁰. Adults spent less time foraging per day (10.1 h) across all weather conditions than sub-adults (10.8 h; Fig. 4), indicating that variation in environmental effects on survival between age classes may be partially caused by differences in foraging requirements. However, the effect of snow conditions on hare survival are probably caused by changes in predator mobility and hunting success. Although hare foraging increases in shallow snow (sub-adult: -0.06 ± 0.008 , $t = -7.36$; adult: -0.07 ± 0.007 , $t = -10.2$), coinciding with increased mortality risk, individuals also forage for longer per day during warmer temperatures (sub-adult: 0.05 ± 0.006 , $t = 8.39$; adult: 0.06 ± 0.003 , $t = 21.9$), which did not coincide with a similar change in risk (Fig. 4). Individuals reduced their foraging time similarly in shallow soft snow and deep snow but only experienced increased mortality risk in shallow snow (Extended Data Fig. 6). This may be caused by a discrepancy in the impact on hare and coyote mobility. When snow is soft, hare mobility is reduced similarly, regardless of depth (see Extended Data Fig. 6b,d). However, in shallow soft snow coyotes retain their mobility due to their relatively long legs and chest height¹⁰. Indeed, the snow depth where hares begin to outperform predators (35 cm) is approximately the average chest height for coyotes in our region¹⁰.

Recent evidence suggests that a reduction in snow cover during the autumn and spring causes increased coat-colour mismatch in hares²¹, which hinders camouflage and reduces individual survival^{4,22}. Coupled with the impact of snow depth and hardness on winter mortality demonstrated here, in addition to the significant decrease in snow depth that we observed, snowshoe hares may be particularly vulnerable to climate change. Our results further indicate that coyotes will be more responsive to changes in winter weather conditions than lynx and negative effects of altered snow conditions on lynx demography may stem from exploitative or agonistic competition with coyotes²³, as lynx appear well-suited to hunt across a range of snow depths and hardness (Fig. 3; ref. ²⁴). The decrease in snow depth occurring across the boreal zone¹⁷ and observed in our study region (Fig. 2) may shift competitive advantages in favour of coyotes over lynx. Indeed, coyote density responds positively to a negative value of the North Atlantic Oscillation (NAO)²⁵, which corresponds to reduced snow depth in our region²⁶. Increased kill rates in shallow snow may be a potential mechanism for the effect of the NAO, as increased kill rates drive coyote numerical response²⁷.

Our research adds to a growing body of evidence that cyclic species at northern latitudes may be vulnerable to changes in winter snow conditions and the associated changes in predation risk^{12,14}. Monthly survival rates of 0.9 are required to sustain population growth in snowshoe hares²⁸. Our models predict that prolonged periods of shallow snow can significantly reduce hare winter survival, to rates observed during cyclic declines (~0.8; ref. ¹⁵). Therefore, reductions in snow depth may limit population increase, reducing peak amplitudes. Our results probably reflect broad-scale patterns across the boreal forest, as the demographic processes driving cyclic dynamics are consistent among populations^{16,28} and much of the biome is experiencing reduced snow cover duration²⁹. Furthermore, models containing solely weather variables outperformed those consisting of year or cycle phase (Supplementary Table 8), suggesting that these patterns can emerge despite large changes in predator

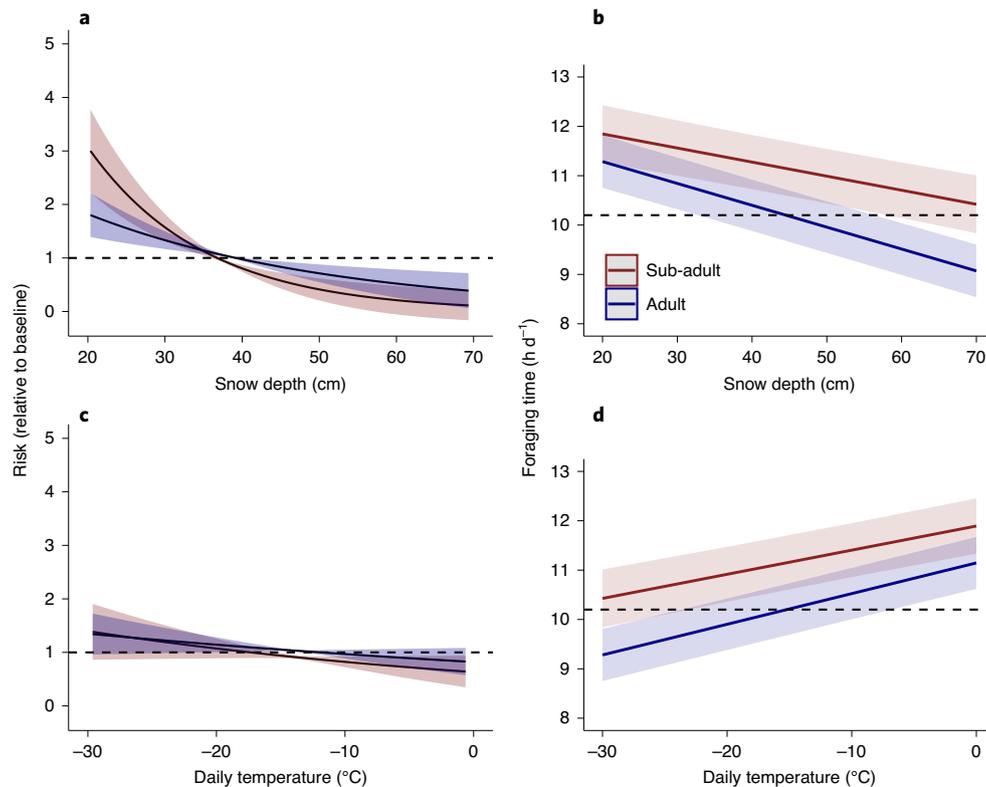


Fig. 4 | Effect of climate on age-specific mortality risk and foraging behaviour. **a–d**, Modelled effect of snow depth (**a,b**) and temperature (**c,d**) on the mortality risk and daily foraging time for both sub-adult and adult snowshoe hares (*L. americanus*). Shaded areas represent predicted response standard errors and the dotted lines represent baseline mortality risk (**a,c**) or the average time spent foraging per day in hours across the winter (**b,d**).

and prey densities (see Extended Data Figs. 1 and 7). That being said, future work should examine the degree these effects vary across snowshoe hare populations with different predator communities or local climate conditions^{30,31} and similar studies should be continued across multiple cycle phases. Regardless, our results demonstrate that changes in weather conditions can have an important influence on cause-specific mortality risk. Given that snowshoe hares represent a primary food source for numerous species in the boreal region^{9,32,33}, climate change could substantially influence the boreal forest community.

Online content

Any methods, additional references, Nature Research reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at <https://doi.org/10.1038/s41558-020-00908-4>.

Received: 9 January 2020; Accepted: 12 August 2020;

Published online: 14 September 2020

References

- Romero, G. Q. et al. Global predation pressure redistribution under future climate change. *Nat. Clim. Change* **8**, 1087–1091 (2018).
- Ims, R. A. et al. Arctic greening and bird nest predation risk across tundra ecotones. *Nat. Clim. Change* **9**, 607–610 (2019).
- Stenseth, N. et al. Snow conditions may create an invisible barrier for lynx. *Proc. Natl Acad. Sci. USA* **101**, 10632–10634 (2004).
- Zimova, M., Mills, L. S. & Nowak, J. J. High fitness costs of climate change induced camouflage mismatch in a seasonally colour moulting mammal. *Ecol. Lett.* **19**, 299–307 (2016).
- Post, E., Peterson, R. O., Stenseth, N. C. & McLaren, B. E. Ecosystem consequences of wolf behavioural response to climate. *Nature* **401**, 905–907 (1999).
- Iles, D. T., Rockwell, R. F. & Koons, D. N. Shifting vital rate correlations alter predicted population responses to increasingly variable environments. *Am. Nat.* **193**, E57–E64 (2019).
- Fisher, J. T. & Burton, A. C. Wildlife winners and losers in an oil sands landscape. *Front. Ecol. Environ.* **16**, 323–328 (2018).
- Myers, J. H. Population cycles: generalities, exceptions and remaining mysteries. *Proc. R. Soc. B* **285**, 20172841 (2018).
- Boutin, S. et al. Population changes of the vertebrate community during a snowshoe hare cycle in Canada's boreal forest. *Oikos* **74**, 69–80 (1995).
- Murray, D. L. & Boutin, S. The influence of snow on lynx and coyote movements: does morphology affect behavior? *Oecologia* **88**, 463–469 (1991).
- Penczykowski, R. M., Connolly, B. M. & Barton, B. T. Winter is changing: trophic interactions under altered snow regimes. *Food Webs* **13**, 80–91 (2017).
- Cornulier, T. et al. Europe-wide dampening of population cycles in keystone herbivores. *Science* **340**, 63–66 (2013).
- Kausrud, K. L. et al. Linking climate change to lemming cycles. *Nature* **456**, 93–97 (2008).
- Ims, R. A., Henden, J.-A. & Killengreen, S. T. Collapsing population cycles. *Trends Ecol. Evol.* **23**, 79–86 (2008).
- Hodges, K. et al. in *Ecosystem Dynamics of the Boreal Forest* (eds Krebs, C. et al.) 141–178 (Oxford Univ. Press, 2001).
- Oli, M. K. et al. Demography of snowshoe hare population cycles. *Ecology* **101**, e02969 (2020).
- Peacock, S. Projected twenty-first-century changes in temperature, precipitation, and snow cover over North America in CCSM4. *J. Clim.* **25**, 4405–4429 (2012).
- Krebs, C. J. et al. What factors determine cyclic amplitude in the snowshoe hare (*Lepus americanus*) cycle? *Can. J. Zool.* **92**, 1039–1048 (2014).
- Yan, C., Stenseth, N. C., Krebs, C. J. & Zhang, Z. Linking climate change to population cycles of hares and lynx. *Glob. Change Biol.* **19**, 3263–3271 (2013).
- Studd, E. K. et al. Use of acceleration and acoustics to classify behavior, generate time budgets, and evaluate responses to moonlight in free-ranging snowshoe hares. *Front. Ecol. Evol.* **7**, e154 (2019).

21. Mills, L. et al. Camouflage mismatch in seasonal coat color due to decreased snow duration. *Proc. Natl Acad. Sci. USA* **110**, 7360–7365 (2013).
22. Wilson, E. C., Shipley, A. A., Zuckerman, B., Peery, M. Z. & Pauli, J. N. An experimental translocation identifies habitat features that buffer camouflage mismatch in snowshoe hares. *Conserv. Lett.* **12**, e12614 (2019).
23. Guillaumet, A., Bowman, J., Thornton, D. & Murray, D. L. The influence of coyote on Canada lynx populations assessed at two different spatial scales. *Community Ecol.* **16**, 135–146 (2015).
24. Peers, M. J. L., Thornton, D. H. & Murray, D. L. Reconsidering the specialist–generalist paradigm in niche breadth dynamics: resource gradient selection by Canada lynx and bobcat. *PLoS ONE* **7**, e51488 (2012).
25. Bowler, B., Krebs, C., O'Donoghue, M. & Hone, J. Climatic amplification of the numerical response of a predator population to its prey. *Ecology* **95**, 1153–1161 (2014).
26. Krebs, C. J., Boutin, S. & Boonstra, R. (eds) *Ecosystem Dynamics of the Boreal Forest* (Oxford Univ. Press, 2001).
27. O'Donoghue, M., Boutin, S., Krebs, C. & Hofer, E. Numerical responses of coyotes and lynx to the snowshoe hare cycle. *Oikos* **80**, 150–162 (1997).
28. Hodges, K. in *Ecology and Conservation of Lynx in the United States* (eds Ruggiero, L. F. et al.) 117–161 (Univ. Press of Colorado, 2000).
29. Brown, R. D. & Mote, P. W. The response of Northern Hemisphere snow cover to a changing climate. *J. Clim.* **22**, 2124–2145 (2009).
30. Korpela, K. et al. Nonlinear effects of climate on boreal rodent dynamics: mild winters do not negate high-amplitude cycles. *Glob. Change Biol.* **19**, 697–710 (2013).
31. Kielland, K., Olson, K. & Euskirchen, E. Demography of snowshoe hares in relation to regional climate variability during a 10-year population cycle in interior Alaska. *Can. J. Res.* **40**, 1265–1272 (2010).
32. Humphries, M. M., Studd, E. K., Menzies, A. K. & Boutin, S. To everything there is a season: summer-to-winter food webs and the functional traits of keystone species. *Integr. Comp. Biol.* **57**, 961–976 (2017).
33. Peers, M. J. L. et al. Prey availability and ambient temperature influence carrion persistence in the boreal forest. *J. Anim. Ecol.* <https://doi.org/10.1111/1365-2656.13275> (2020).

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Methods

Study area and long-term snow depth measurements. Our study was conducted in southwestern Yukon, Canada (60.9°N, -138.0°W), where snowshoe hares have been studied for the last 40 years (ref. ³⁴). The boreal forest in this region is comprised primarily of white spruce (*Picea glauca*), with smaller amounts of trembling aspen (*Populus tremuloides*) and balsam poplar (*Populus balsamifera*). The shrub layer is dominated by areas of grey willow (*Salix glauca*) and dwarf birch (*Betula glandulosa*). In addition to Canada lynx and coyote, other predators include great-horned owl (*B. virginianus*) and goshawk (*A. gentilis*), which account for a smaller percentage of hare mortalities¹⁵. During this study (2015–18), snowshoe hare populations were at their late increase, peak and entering the early decline of their cycle³⁵.

Along a 25-km transect in the study region, snow depth measurements were recorded throughout the winter (November–March) since 2001. Snow depth measurements were recorded at consistent locations every 5 km, <72 h following snowfall events. We examined the change in average January snow depth across all locations and the maximum winter snow depth from 2001 to 2019 using linear regression in the program R.

Monitoring survival and daily weather. Between January 2015 and May 2018, we captured hares in Tomahawk live-traps (Tomahawk Live Trap Co.) on three different trapping areas within an ~8-km stretch of forest (see Supplementary Fig. 1). Hares weighing >1,100 g were fitted with very high frequency (VHF) collars equipped with mortality sensors (Model SOM2380 from Wildlife Materials or Model MI-2M from Holohil; <40 g, <5% body weight). Handling and collaring procedures were approved by the University of Alberta Animal Care and Use Committee (protocol AUP00001973).

We monitored the survival of 321 individuals almost daily throughout the winter. We considered the winter season as December through March. During this time, snow cover was continuous and average monthly temperatures remained below 0 °C throughout the four winters we monitored survival. When a mortality signal was detected, we located the kill site to determine cause of death and identified the predator species responsible based primarily on the presence of predator tracks in snow, portions of the carcass remaining and other field sign such as feathers, scat and pellets¹⁵. We attempted to locate kill sites on the date the mortality signal was detected to reduce the potential for scavenging by predators to be misidentified as sign of predation. To further examine this possibility, we monitored hare carcasses in our study area using remote cameras and determined scavenging as an unlikely bias in our designation of cause of death, as predators only visited 35% of carcasses and took an average of 5.5 d to discover the carcasses³³. However, we acknowledge the possibility that some instance of mortality may represent scavenging events or individuals that died due to other ultimate factors (parasitism).

On each of the three trapping areas, we monitored snow conditions at three stations in relatively open forest: total snow depth was measured to the nearest 0.5 cm; snow hardness was determined by the sinking depth of a 250 g cylinder penetrometer dropped from 50 cm above the snow¹⁰; and daily snowfall was determined using plywood boards that were laid on the snow surface to capture snow that fell during the last 24 h. We determined daily temperature using a minimum of two Ibuttons (DS1922L, Maxim Integrated) on each grid that took at least six temperature recordings per day. Ibuttons were mounted on stakes and facing north to reduce the influence of sunshine. Locations where snow and temperature data were recorded were fixed during the study. Across the study years, hardness and depth were recorded on >60% of days and snowfall and temperature were recorded every day. Days with missing snow depth and hardness measurements were linearly interpolated using the 'zoo' package in R (ref. ³⁶).

We also measured snow depth and hardness at each kill site; and 10 m in each direction from the kill site, if we were confident the carcass remains had not been moved by predators or scavengers. Snow conditions at each kill site were considered the average of the five measurements.

Effects of environment on survival. We assessed the influence of environmental conditions on winter hare survival using semiparametric Cox-proportional hazards (CPH) models. Time intervals in our CPH models represented each telemetry check (68.8% 1 d, 97.0% within 3 d) and we excluded monitoring gaps that exceeded 7 d. Daily weather values were averaged over monitoring intervals and each hare was associated with weather conditions from its trapping area. We used a right-censored design with time-at-risk (days) based on time since the start of the season³⁷.

First, to examine the influence of weather conditions on overall hare mortality risk, we developed CPH models (hereafter referred to as all-cause model) that grouped all causes of death together (lynx, coyote, birds of prey and unknown predator). Over the 4 years, we had a total of 153 predator-caused mortalities and four mortalities that were attributed to starvation and subsequently censored. We censored 35 individuals because of either collar failure causing an unknown status ($n=28$) or the removal of their collar before the completion of the study ($n=7$). To ensure that informative censoring did not influence our results, we developed models (detailed below) on datasets that either censored missing individuals or treated them as mortality events³⁸. These models reveal qualitatively similar

results (Supplementary Table 7) implying that our results are robust to informative censoring^{38,39}.

For our all-cause CPH model, we included daily temperature, snow depth and snow hardness as explanatory variables given their suspected impact on predator-prey interactions in our system^{34,10}, as well as our interests in their influence on risk. We then used a model selection approach to test the importance of daily snowfall, days since snowfall >1 cm and an interaction between snow depth and hardness⁴⁰. This was done by including combinations of these variables with temperature, snow depth and snow hardness (the core group of variables). Exploratory analysis revealed that sex was not influential to hare survival and was not considered further ($P=0.37$). Candidate survival models also considered random effects of year and trapping area. We determined HRs for each variable in the all-cause model using our top model on the basis of lowest Akaike information criterion (AIC_c). For the top model, we assessed multicollinearity using a variance inflation factor (VIF; ref. ⁴¹) and ensured that no variables had a VIF > 2, except between main variables and those representing interactions between multiple variables. We further ensured that the top model satisfied the proportionality assumption of CPH models, that the HR of two covariates remains proportional through time³⁹. We used the predict function in R to examine the effect of prolonged weather conditions on monthly hare survival. We compared the effect of weather covariates from our top model to models built from 500 bootstrapped samples of our data to produce a measure of uncertainty on the effect of each covariate on monthly survival. Each bootstrapped dataset included resampled survival intervals, with replacement, until the number of intervals in the resample equalled the original dataset⁴².

Next, we examined how our weather variables influenced risk from lynx and coyote using a competing-risk framework based on the data augmentation approach^{39,43}. We replicated our dataset for each cause of death and a dummy variable was used to assign each risk to a specific cause⁴⁴. Within each risk set, we identified death only for the appropriate cause (lynx or coyote), with all other entries being censored. Mortalities from goshawks and great-horned owls were not considered in the cause-specific analysis due to the limited sample sizes (ten and six, respectively). Unknown causes primarily occurred due to inclement weather limiting kill site classification (snowfall after mortality) and were suspected to consist largely of predation events from either lynx or coyotes. We therefore censored unknown mortality events in the cause-specific model as opposed to including them as an 'other' classification. However, to ensure our results are not sensitive to this decision, we developed models including an 'other' classification that failed to reveal qualitatively different results (see Supplementary Table 7), implying that our designation of only two mortality events is robust to the classification of unknown mortalities³⁸. We included two-way interaction terms between causes of death in the model to allow the effects of environmental covariates to vary on the basis of predator species. We used AIC_c to identify the model that best explained variation in cause-specific mortality and included combinations of variables from the all-cause model with an interaction term for cause of death. However, given the smaller sample size of predator-caused mortalities (lynx, 63; coyote, 27) relative to the all-cause model, we included only single effect terms to reduce the number of parameters in the model⁴⁵.

Finally, we examined whether hare survival between age classes is differentially affected by winter conditions by splitting our dataset into sub-adults and adults. Adults consisted of tagged individuals known to be >1 year of age, while suspected sub-adults were individuals who were caught for the first time that autumn or summer and weighed <1,000 g if first capture occurred in June or July (as in ref. ⁴⁶). We restricted data used in age-specific models to study areas that were monitored over the previous year, which reduced our sample size to 236 individuals and 116 mortality events. Our classification of sub-adults therefore assumes that newly caught hares in the autumn represent juveniles as opposed to dispersing adults. We feel this approach is more accurate than purely body mass given: (1) most individuals in the autumn population are juveniles¹⁵ and instances of adult dispersal over summer are relatively rare⁴⁷; (2) hares have multiple litters per summer and early litter juveniles are indistinguishable from adults based on mass by autumn, therefore mass restrictions would remove early litter juveniles and potentially bias results to late litter juveniles which have relatively low survival⁴⁸. Furthermore, >96% of individuals captured in May during our study were previously tagged by us (M.J.L.P., unpublished observations), suggesting that unmarked individuals on our study grid were rare at the beginning of the breeding season. We determined the top predictors of age-specific mortality by comparing CPH models in an AIC_c framework that included all causes of mortality and variables were stratified by age-class. We further examined if cause of death between sub-adults and adults differed using a z-test of proportions.

Effects of snow and temperature on hare foraging. A subset of the individuals monitored during our study ($n=137$) were equipped with AXY-3 accelerometers (Technosmart Europe Srl.). Accelerometers measure the acceleration of the body along three axes: anterior–posterior (surge), lateral (sway), dorsal–ventral (heave), allowing for the characterization of different behavioural patterns⁴⁹. Accelerometers were attached to VHF collars on the dorsal side of the neck and recorded at 1 Hz with a resolution of $\pm 8g$ forces. Using behavioural classifications according to the decision tree developed for snowshoe hare accelerometers by Studd et al.²⁰, we

calculated the daily time spent foraging for each individual. The foraging behaviour represented feeding mixed with single hop movements and was classified over 4-s intervals with an accuracy of 93.1% (ref. 20).

We examined the influence of weather variables on daily foraging rate (h^{-1}) using a linear mixed effects model that included individual ID and year as random effects. We considered the same combination of variables as our all-cause survival models, stratified by age-class.

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.bzkh1896b>.

Code availability

The R code used to analyse the data and produce figures is available in the Dryad Digital Repository <https://doi.org/10.5061/dryad.bzkh1896b>.

References

34. Krebs, C. J., Boonstra, R. & Boutin, S. Using experimentation to understand the 10-year snowshoe hare cycle in the boreal forest of North America. *J. Anim. Ecol.* **87**, 87–100 (2018).
35. Krebs, C. J. et al. *The Community Ecological Monitoring Program Annual Data Report* (Univ. of British Columbia, 2018).
36. Zeileis, A., Grothendieck, G., Ryan, J., Ulrich, J. & Andrews, F. zoo: S3 infrastructure for regular and irregular time series (Z's ordered observations). R package version 1.8-8 (2019).
37. Fieberg, J. & Delgiudice, G. D. What time is it? Choice of time origin and scale in extended proportional hazards models. *Ecology* **90**, 1687–1697 (2009).
38. Murray, D. L. et al. Death from anthropogenic causes is partially compensatory in recovering wolf populations. *Biol. Conserv.* **143**, 2514–2524 (2010).
39. Murray, D. & Bastille-Rousseau, G. in *Population Ecology in Practice* (eds Murray, D. L. & Sandercock, B.) 123–156 (Wiley-Blackwell, 2020).
40. Burnham, K. & Anderson, D. *Model Selection and Multimodel Inference* (Springer, 2002).
41. Graham, M. H. Confronting multicollinearity in ecological multiple regression. *Ecology* **84**, 2809–2815 (2003).
42. McLellan, B. N. Some mechanisms underlying variation in vital rates of grizzly bears on a multiple use landscape. *J. Wildl. Manag.* **79**, 749–765 (2015).
43. Lunn, M. & McNeil, D. Applying Cox regression to competing risks. *Biometrics* **51**, 524–532 (1995).
44. Bastille-Rousseau, G. et al. Phase-dependent climate–predator interactions explain three decades of variation in neonatal caribou survival. *J. Anim. Ecol.* **85**, 445–456 (2016).
45. Murray, D. L., Bastille-Rousseau, G., Hornseth, M., Row, J. & Thornton, D. H. in *Population Ecology in Practice* (eds Murray, D. L. & Sandercock, B.) 17–46 (Wiley-Blackwell, 2020).
46. Hodges, K. E., Krebs, C. J. & Sinclair, A. R. E. Snowshoe hare demography during a cyclic population low. *J. Anim. Ecol.* **68**, 581–594 (1999).
47. Boutin, S., Gilbert, B. S., Krebs, C. J., Sinclair, A. R. E. & Smith, J. N. M. The role of dispersal in the population dynamics of snowshoe hares. *Can. J. Zool.* **63**, 106–115 (1984).
48. Gillis, E. A. Survival of juvenile hares during a cyclic population increase. *Can. J. Zool.* **76**, 1949–1956 (1998).
49. Graf, P. M., Wilson, R. P., Qasem, L., Hackländer, K. & Rosell, F. The use of acceleration to code for animal behaviours; a case study in free-ranging Eurasian beavers *Castor fiber*. *PLoS ONE* **10**, 1–17 (2015).

Acknowledgements

We thank the numerous field technicians who monitored hare survival and snow conditions throughout the study, as well as members of the Boutin Lab for comments on earlier versions of this manuscript. We also thank A. MacDonald and her family for long-term access to her trapline. We thank the Champagne and Aishihik, and Klwane First Nations, for supporting our work within their traditional territory. This work was supported by the Natural Sciences and Engineering Research Council of Canada, Northern Studies Training Programme, the University of Alberta Northern Research Award programme, the Association of Canadian Universities for Northern Studies, the Wildlife Conservation Society Canada, the W. Garfield Weston Foundation, the Killam Laureates programme, Government of Yukon and Earth Rangers.

Author contributions

M.J.L.P. and S.B. designed the study. M.J.L.P., Y.N.M., A.K.M. and E.K.S. led data collection. Primary logistic support was provided by S.B. with assistance by M.H., T.S.J., A.J.K., C.J.K., D.L.M. and R.B. M.J.L.P. and G.B.-R. performed the analysis. M.J.L.P. drafted the manuscript with input from all authors.

Competing interests

The authors declare no competing interests.

Additional information

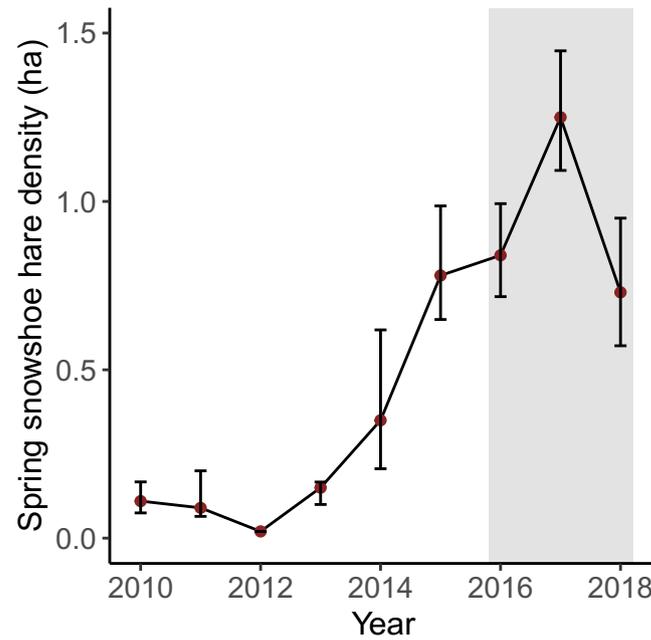
Extended data is available for this paper at <https://doi.org/10.1038/s41558-020-00908-4>.

Supplementary information is available for this paper at <https://doi.org/10.1038/s41558-020-00908-4>.

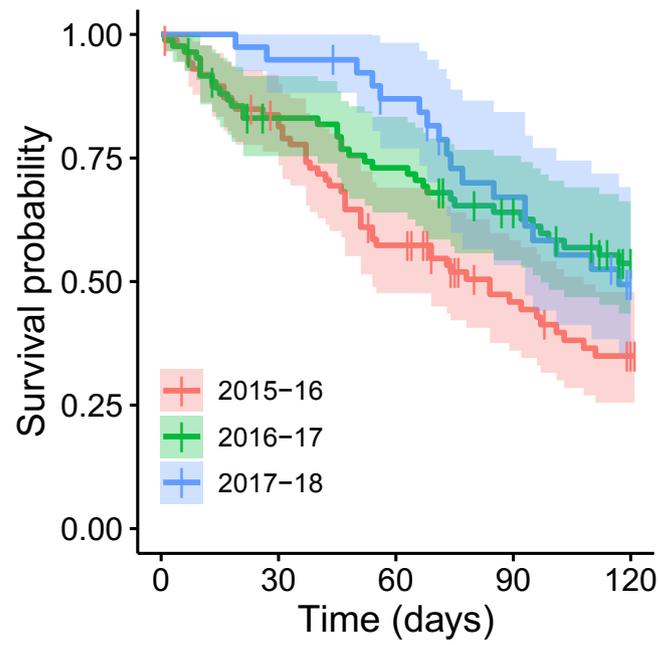
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Peer review information *Nature Climate Change* thanks Magnus Magnusson and the other, anonymous, reviewer(s) for their contribution to the peer review of this work.

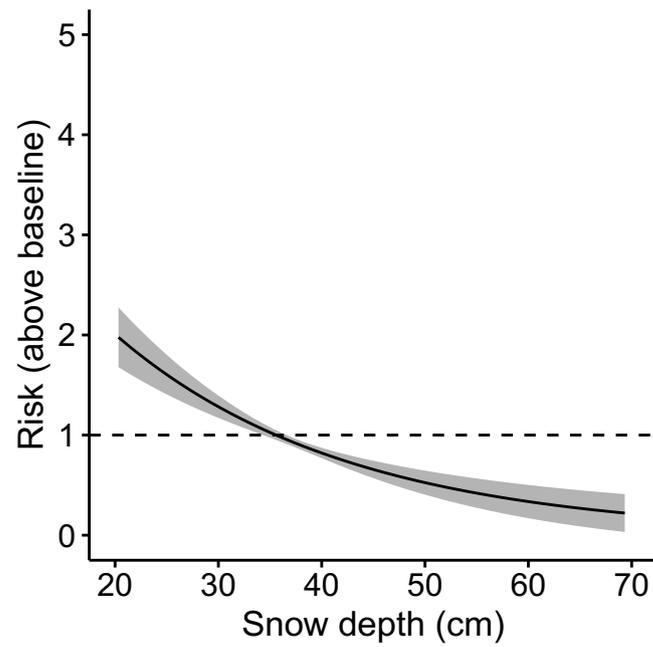
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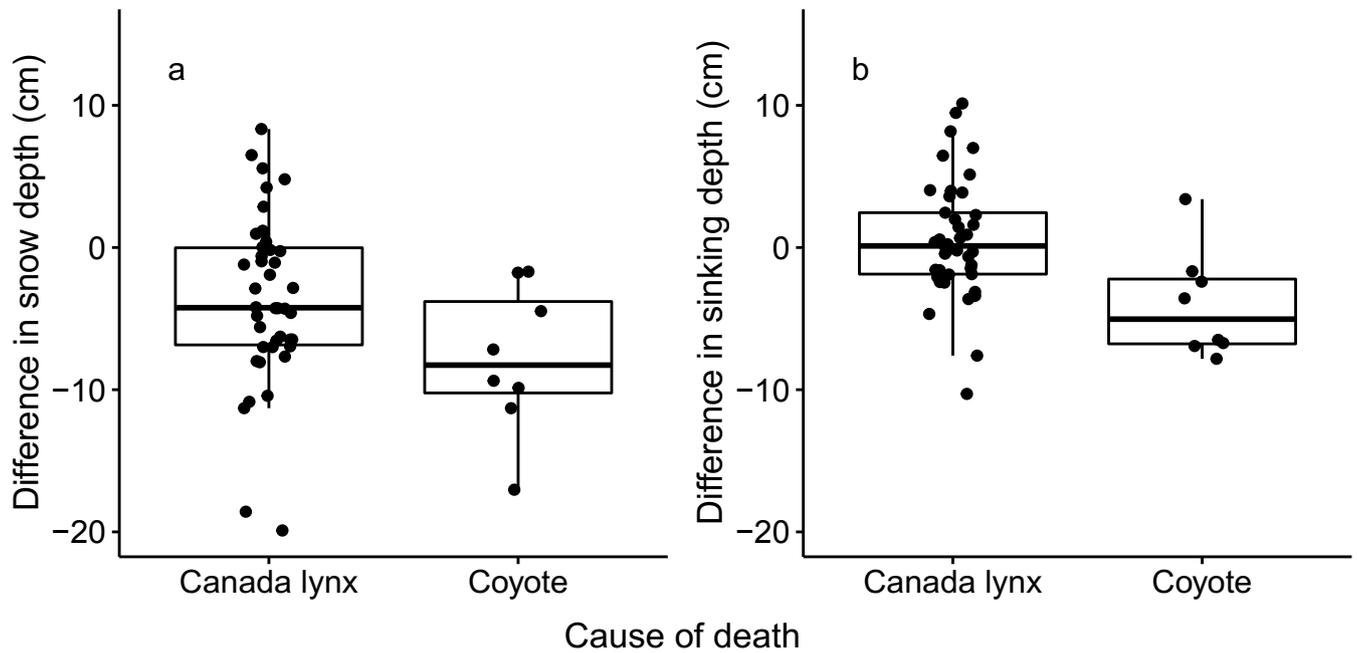
Extended Data Fig. 1 | Snowshoe hare density in our study region. Spring snowshoe hare density (\pm 95% Confidence Intervals) in the Kluane Lake region, Yukon over the last cycle. Hare density estimates are determined through mark-recapture as part of the Community Ecological Monitoring Project (CEMP; <https://www.zoology.ubc.ca/~krebs/kluane.html>), and densities displayed here come from trapping area 2 (blue) in the study area map (Supplementary Fig. 1). Shaded area represents the years where we monitored detailed survival and weather data throughout the entire winter (that is Dec-Mar).



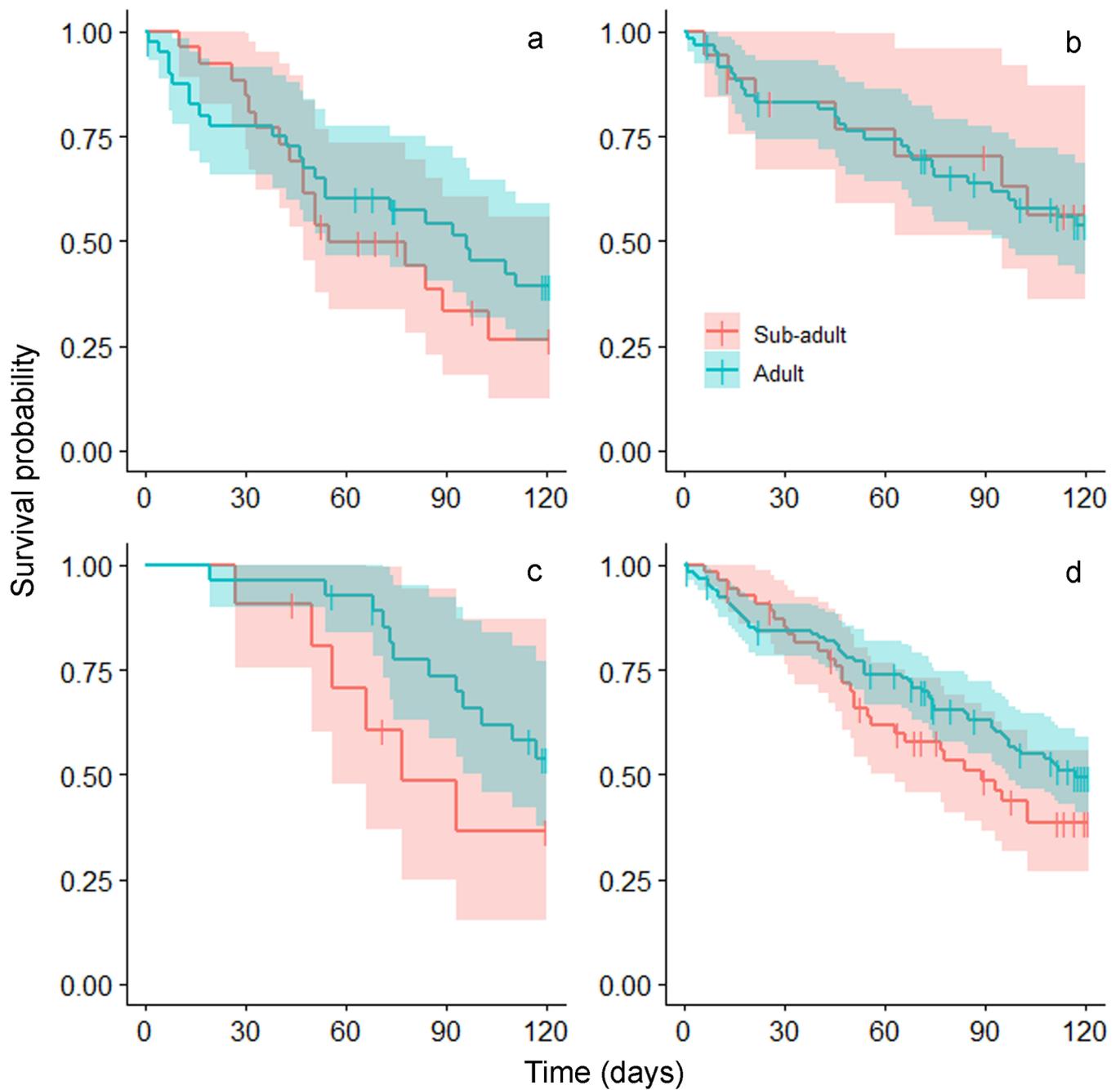
Extended Data Fig. 2 | Over-winter survival of snowshoe hares. Kaplan-Meier four-month survival curves (\pm 95% Confidence Intervals) for snowshoe hares in the Kluane Lake region, Yukon, across the three winters in which we monitored survival from December until March.



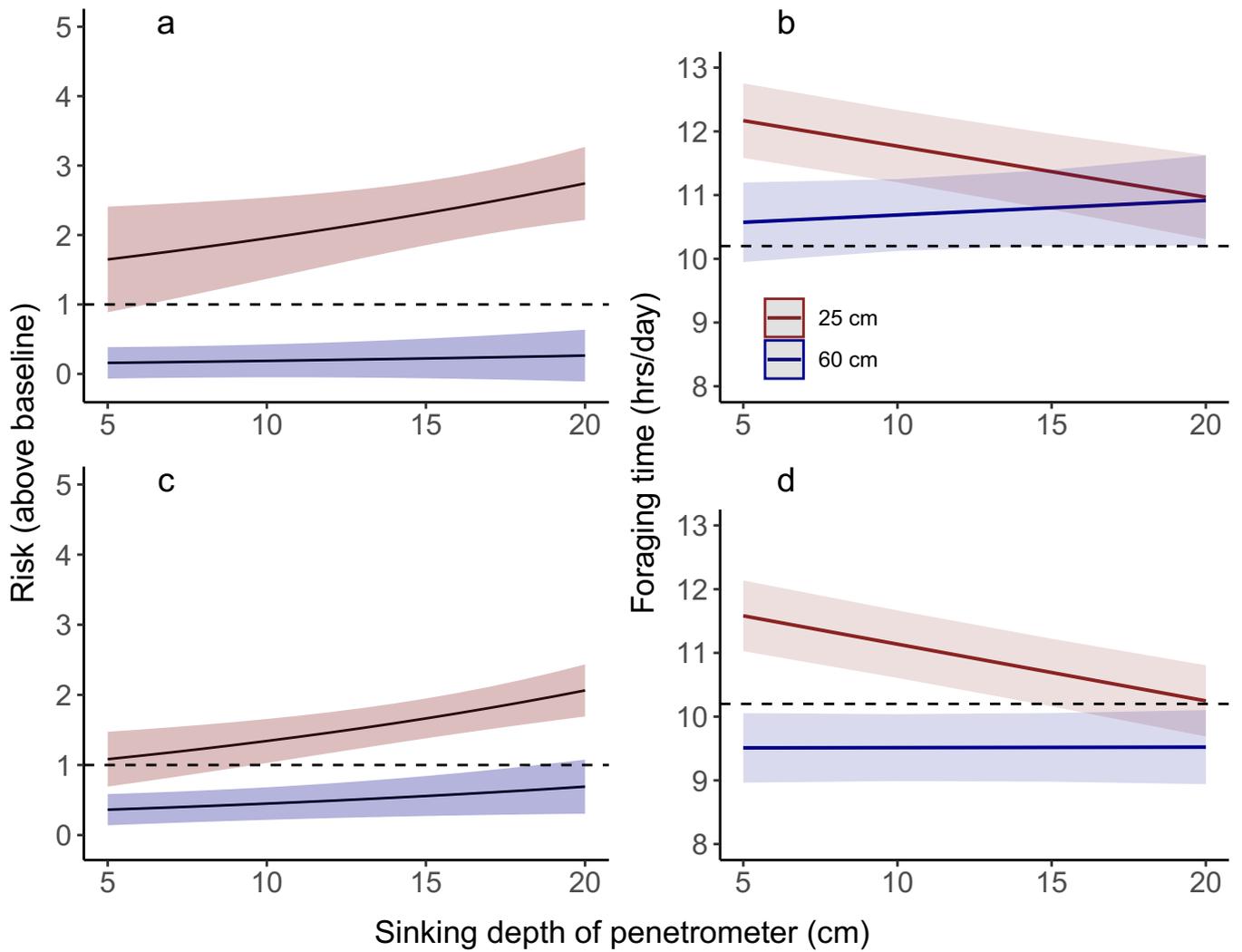
Extended Data Fig. 3 | Relationship between snow depth and mortality risk. Modelled effect of snow depth (cm) on mortality risk in snowshoe hares. Mortality risk is based on coefficients from the best supported Cox-proportional hazards model, and shaded areas represent predicted response standard errors. The dotted line represents baseline risk for hares.



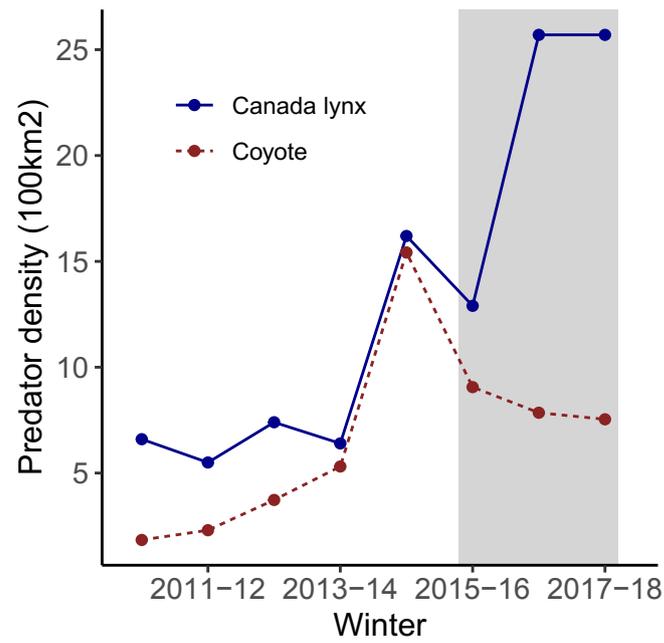
Extended Data Fig. 4 | Snow conditions at snowshoe hare kill sites. Difference in **a**) snow depth (cm), and **b**) sinking depth of the penetrometer (cm) at kill site locations for each predator species compared to the daily snow measurements taken on the date of the mortality.



Extended Data Fig 5 | Over-winter survival between age classes. Kaplan-Meier four-month survival curves (\pm 95% Confidence Intervals) for sub-adult (red) and adult (blue) snowshoe hares during the winter of **a**) 2015-16, **b**) 2016-17, **c**) 2017-18, and **d**) all years combined.



Extended Data Fig 6 | Effect of snow conditions on age-specific mortality risk and foraging behaviour. Modelled effect of the sinking depth of the penetrometer (cm) on mortality risk and daily foraging time for sub-adult (a, b) and adult (c, d) snowshoe hare at two different snow depths. Shaded areas represent predicted response standard errors and the dotted line represents baseline mortality risk (a, c) or the average time spent foraging per day in hours across the winter for sub-adults (b) and adults (d).



Extended Data Fig 7 | Predator density in our study region. Canada lynx (blue, solid) and coyote (red, dashed) density in the Kluane lake region, Yukon, for each winter over the last snowshoe hare cycle. Densities in the region are determined each year based on track transects as part of the Community Ecological Monitoring Program (CEMP; <https://www.zoology.ubc.ca/~krebs/kluane.html>), where tracks are counted along a 25-km transect that traversed our study area, on days after fresh snowfalls while tracks were distinguishable (see Krebs et al. ²⁶). Shaded area represents the years where we monitored detailed hare survival and weather data throughout the winter (that is Dec-Mar).

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Study description	Analysis examining how changes in environmental conditions (snow depth, snow hardness, temperature, daily snowfall, days since snowfall) influence the behaviour and cause-specific mortality of snowshoe hares. This study was conducted to examine whether changes in weather conditions associated with climate change may impact population cycles of hares and influence the predator-prey community of the boreal forest.
Research sample	<p>Between January 2015 and May 2018, we captured hares in Tomahawk live-traps (Tomahawk Live Trap Co. Tomahawk, WI, USA) on three different trapping areas within an ~ 8 km stretch of forest. Only hares weighing over 1100g were used in this study which represents weight restrictions approved by the University of Alberta Animal Care and Use Committee (Protocol: AUP00001973).</p> <p>Survival: 321 snowshoe hares over 4 winters, which includes 153 predator-caused mortalities. 106 mortalities were identified to a specific predator, including 65 mortalities from lynx and 27 from coyote for cause-specific analyses. For age-specific analyses, this sample size was reduced to 236 individuals and 116 mortalities.</p> <p>Behaviour: 137 individuals were equipped with accelerometers for a total of 4530 hare-days.</p>
Sampling strategy	<p>We continuously deployed VHF collars and accelerometers on hares between December-March to ensure we had an adequate sample of hares to examine how the environment correlates with survival and behaviour. Adult and sub-adult hares as well as males and females were used in our study. The temporal span of the study was large in order to capture variation in environmental conditions, and extend across the increase, peak, and decline of the snowshoe hare cycle. Locations of daily snow measurements were kept consistent throughout the four years of the study and a minimum of three sample sites at each trapping area were measured.</p> <p>Long-term monitoring of snow depth in our study region has been conducted since 2001, along a 25 km transect. Snow depth measurements were recorded throughout the winter (Nov-March) at consistent locations every 5 km, less than 72 hours following snowfall events.</p>
Data collection	VHF collars and accelerometers were deployed on hares by MJLP, YNM, AKM, EKS, or research technicians, and these individuals monitored survival and daily snow conditions over the study. Survival was checked near daily over this time. Snowfall was monitored daily at each study area between December-March, and snow depth and hardness were measured on greater than 60% of days. A minimum of two lbuttons recorded temperature 6 times per day between December-March.
Timing and spatial scale	Survival and accelerometer data used in this paper occurred between February 2015 and March 2018. This temporal scale ensured we captured variation in snow conditions and temperature. Hares were monitored from three trapping areas within an ~ 8 km stretch of forest. These study areas were chosen as they were established locations for monitoring snowshoe hares as part of the Community Ecological Monitoring Project (CEMP), a long-term project ongoing in the region (https://www.zoology.ubc.ca/~krebs/kluane.html).
Data exclusions	There were no exclusions of data in this study.
Reproducibility	The information provided above, details provided in the manuscript, and data available in a public repository gives sufficient information to repeat this study. However, aspects not controlled by the methodology such as natural temporal variation in environmental covariates cannot be repeated.
Randomization	Snowshoe hares to be collared were selected based on weight restrictions established by the University of Alberta Animal Care and Use Committee (Protocol: AUP00001973), as well as available equipment at the time of capture.
Blinding	Blinding participants was not relevant to this study.
Did the study involve field work?	<input checked="" type="checkbox"/> Yes <input type="checkbox"/> No

Field work, collection and transport

Field conditions	All field conditions relevant to this study are included in the study design and analyses and are described in detail in the manuscript.
Location	This study was conducted in southwestern Yukon, Canada (Lat: 60.9 N, Long: -138.0 W) in the Kluane Lake region which is comprised primarily of white spruce (<i>Picea glauca</i>).

Access & import/export

Working with wildlife in our study region requires a Yukon Scientists and Explorers Permit and a Wildlife Research Permit from the Yukon Government. We had the appropriate permits that were renewed each year of our study.

Disturbance

There was no perceivable disturbance caused by the study, apart from animal handling which was approved by the University of Alberta Animal Care and Use Committee (Protocol: AUP00001973).

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Laboratory animals

The study did not involve laboratory animals.

Wild animals

We captured hares in Tomahawk live-traps (Tomahawk Live Trap Co. Tomahawk, WI, USA) baited with alfalfa, rabbit pellets, and apple slices. After measurements were taken, and select animals were collared, the individual was released at the location it was trapped.

Field-collected samples

This study did not include laboratory work on field collected samples.

Ethics oversight

Ethical approval occurred through the University of Alberta Animal Care and Use Committee (Protocol: AUP00001973).

Note that full information on the approval of the study protocol must also be provided in the manuscript.