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RESEARCH

Winter survival shaped by forage abundance and snow depth for a long-distance migratory ungulate

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Abstract

Adult survival is a crucial factor influencing the population dynamics of caribou (*Rangifer tarandus*), yet its relationship with environmental variables remains poorly understood. We explored linkages among lichen abundance (the primary winter forage), snow depth, and overwinter survival of adult female caribou in the Western Arctic Herd (WAH), a large population of barren-ground caribou (*R. t. granti*) in northwest Alaska. We hypothesized that caribou wintering in areas with greater lichen cover would experience higher survival rates, and that snow depth would moderate this relationship. Using GPS telemetry data from 1,067 caribou winters between 2009 and 2024, we investigated overwinter survival as a function of lichen cover and snow depth. Higher lichen cover was significantly associated with reduced overwinter mortality hazard, but this relationship was strongly and non-linearly affected by snow depth. At intermediate snow depths, caribou in low-lichen habitats experienced 9.1 times higher mortality risk compared to high-lichen areas. However, in deep snow conditions the survival benefits of lichen diminished substantially, suggesting that deep snow may limit forage accessibility. Our results underscore the importance of lichen-rich habitats for barren-ground caribou winter survival and highlight the complex interplay between forage accessibility and snow conditions. Arctic-wide declines in lichen cover could pose a threat to barren-ground caribou populations, with potential long-term demographic consequences, as our study suggests that lichen abundance plays an important role in determining the overwinter survival of adult female caribou.

Keywords Caribou · Lichens · Mortality risk · *Rangifer tarandus* · Snow · Winter

Introduction

Adult survival is a key limiting factor in population demography. Linking environmental factors with survival and mortality rates has enhanced our understanding of wildlife population dynamics (Johnson et al. 2020; van de Kerk et al. 2020; Schmelzer et al. 2020). Identifying these factors often requires an understanding of periods of resource scarcity, particularly for species with life histories that are highly dynamic across seasons (Holt 2008). Winter is often a season of resource limitation for herbivores in north-temperate, sub-Arctic, and Arctic regions and is often considered a nutritional bottleneck (Kautz et al. 2020), leading to a reduction in endogenous energy reserves (Monteith et al. 2013; Cook et al. 2013). However, caribou (*Rangifer tarandus*), the most abundant large mammal in the circumpolar north (Bernes et al. 2015), exhibit unique adaptations to extreme seasonality – adult female caribou typically experience only modest declines in body condition and may maintain or, even increase, body fat over winter (Chan-McLeod et al. 1999; Couturier et al. 2009; Cook et al. 2021). Despite these adaptations, many caribou populations across the northern hemisphere are currently in decline (Gunn and Russell 2023).

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Body-condition, encompassing body mass, body fat, and body protein, reflects the balance between nutritional intake and energy expenditure, directly influencing survival and reproductive success (Parker et al. 2009). Forage quality and availability are critical to maintaining body condition, especially during periods of resource scarcity. Early winter body fat percentage has been shown to be the best predictor of whether a caribou survives the winter and successfully reproduces (Parker et al. 2009; Cook et al. 2021), with higher fall body fat also being positively associated with pregnancy (Cameron et al. 1993). Similarly, overwinter survival rates of adult females are higher following summers with greater forage biomass, likely because these conditions allow caribou to gain more mass and fat (Johnson et al. 2022). As capital breeders, caribou maximize foraging opportunities during the brief Arctic summer to replenish body stores lost during the previous winter and accumulate reserves for the upcoming winter and reproductive cycle (Parker et al. 2009; Johnson et al. 2022).

By late fall, caribou shift from nutrient-rich summer forage to a winter diet composed primarily of lichen (Joly et al. 2007a; Joly and Cameron 2018; Webber et al. 2022). Lichens are high in dietary energy but nearly devoid of protein, which is a critical nutrient for growth and reproduction (Barboza and Parker 2006). Given their relatively poor nutritional value, a key knowledge gap lies in understanding the mechanistic link between lichen consumption and caribou demographic parameters, as their overall value in caribou diets remains complex and context-dependent. For example, the population crash of feral reindeer (also *R. tarandus*) on St. Matthew Island demonstrated the critical role of lichens: the herd depleted the lichen community, and despite summer forage availability, could not survive the winter without lichens, especially under severe weather conditions (Klein 1968). Caribou efficiently use lichens when paired with moderate-nitrogen forage and low-quality dead plant material (Klein 1968). Although wintertime lichen consumption has not been strongly linked to pregnancy or parturition rates (Barboza and Parker 2006; Joly et al. 2015), it has been posited that lichens may be associated with overwinter survival of barren-ground caribou (Joly et al. 2010).

During winter, access to forage is as critical as its abundance. Since caribou often crater (dig) through snow to access lichens, changes in snow depth and quality can create barriers to forage availability. Snow is a critical, yet understudied, component of Arctic and sub-Arctic ecosystems (Boelman et al. 2019), significantly affecting wildlife, particularly caribou (Pruitt 1959). Snow can impede movement, increase energetic travel costs, and, under certain conditions, elevate vulnerability to predation (Joly and Klein 2011; Sullender et al. 2023). Snow hardened by wind or rain-on-snow events makes it more energetically demanding to dig through to reach terricolous lichens (Fancy and White 1987). In this way, snow can affect overwinter survival through its influence on forage availability and energetic trade-offs, rather than as a direct cause of mortality.

Recent work on caribou of the Western Arctic Herd (WAH), a large migratory herd in northwestern Alaska, showed that both winter habitat use and overwinter survival of caribou shifted in recent years. Gurarie et al. (2024) reported declining annual survival and a shift in the seasonal pattern of mortality toward higher winter and spring mortality over the study period (ending in 2021), coinciding with a decreasing proportion of individuals migrating to the lichen-rich Seward Peninsula and more caribou remaining in the northern wintering areas. They also found that the relationship between winter weather variables and survival differed between these regions; particularly, snow depth had a positive effect on survival in the northern ranges, but a weak, non-significant negative effect on survival for animals wintering on the Seward Peninsula, suggesting that local conditions mediate overwinter outcomes. Complementary findings by Joly et al. (2025), indicate that areas used by WAH caribou wintering on the Seward Peninsula experience more lichen cover than caribou wintering farther north. Together, these studies suggest that higher forage availability in the southern wintering areas may help offset the energetic costs of migration, supporting the idea that access to lichen-rich habitats plays a key role in maintaining overwinter survival despite variable snow conditions.

We built on these prior findings by developing a framework that considered geographic variation in snow effects while focusing on the mechanistic role of lichen in shaping overwinter survival. Broadly, we hypothesized that the overwinter survival of adult female WAH caribou would be higher in areas with greater lichen cover, and that this relationship would be modulated by snow depth. Based on the regional differences in snow-survival relationships documented by Gurarie et al. (2024) and evidence that caribou cannot effectively access ground-based food sources at higher snow depths (Thomas and Edmonds 1983; Kinley et al. 2003), we predicted that deep snow conditions would negate the importance of terricolous forage resources by reducing their accessibility. Therefore, we predicted that survival rates (hazard ratios) would be similar under deep snow conditions regardless of lichen cover. We further hypothesized that the relationship between snow depth and mortality would be nonlinear and that intermediate snow depths would be associated with the greatest variability in survivorship. In moderately deep snow, we predicted that the benefits of abundant lichen would exceed the cost of accessing it, but that this relationship would invert as lichen cover diminished.

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Study area

The range of the WAH covers approximately 363,000 km^2 of northwest Alaska (Fig. 1). While distribution is highly variable annually, caribou can be found during winter across almost all this area (Joly et al. 2007a, 2021). The diversity of habitats across this vast area includes arctic tundra, alpine tundra, shrublands, and boreal forest. Lichen cover varies across the region but tends to be greater south of the Brooks Range mountains, which run east to west across the northern third of the herd's range, than north of them (Fig. 1; Macander et al. 2022; Joly et al. 2025). Lichens can be found in nearly all habitat types but are much less abundant in recently burned habitat (Joly et al. 2010). Except for relatively small areas that are highly wind-swept, snow covers much of the region from October through April and substantially longer in places (Macander et al. 2015; Swanson 2017). Snow depths tend to be deepest in the mountains of the Brooks Range, with typically shallower snow south of the range, and the shallowest depths north of the range

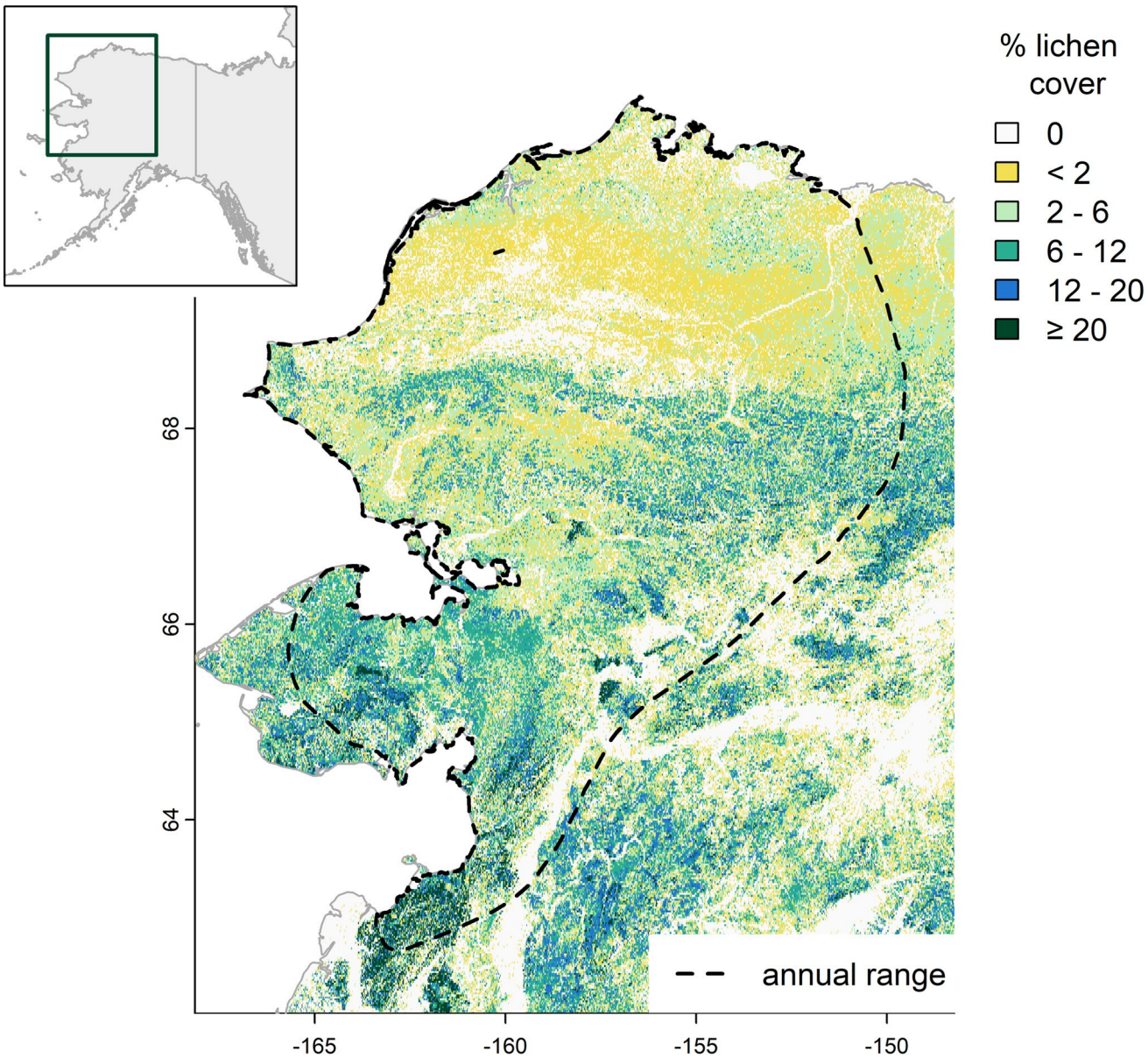


Fig. 1 Study area in northwest Alaska (2009 to 2024), showing the annual range of the Western Arctic Herd caribou (dashed polygon). Winter range is highly variable, with caribou wintering throughout much of the annual range (see Gurarie et al. 2024 for details on recent winter range use and seasonal movements). Lichen cover data are from Macander et al. (2022)

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(Bieniek et al. 2012; Gurarie et al. 2024). Temperatures can drop below −40° C during the winter months.

Methods

Movement, mortality, and environmental data

We analyzed movement data from 372 adult female WAH caribou (at least 2 years old). Caribou were captured and equipped with GPS telemetry collars (Telonics TGW-4680, Mesa, Arizona, USA and Vectronic Vertex, Berlin, Germany) between 2009 and 2023, following protocols approved by the State of Alaska's Institutional Animal Care and Use Committee (IACUC 0040–2017-40). Collars recorded locations every 2, 4, or 8 hours. We identified mortality events when collars stopped moving but continued to transmit data resulting in a cluster of positions in the same location. When possible, we visited mortality sites to recover collars and locate remains.

We subset movements and mortality events of WAH caribou to the winter season between 1 December and 31 March (Baltensperger and Joly 2019). At each location, we annotated time-varying environmental covariates related to snow and lichen. We obtained snow depth from the North American Regional Reanalysis (National Centers for Environmental Prediction, National Weather Service, NOAA, U.S. Department of Commerce 2005) at 32 km pixel resolution and 3-h temporal resolution (Mesinger et al. 2006) using the track annotation service Env-DATA (Dodge et al. 2013) on Movebank (www.movebank.org). We obtained percent lichen cover values at 30 m resolution from lichen cover rasters specific to 5-year intervals developed for Alaska and Yukon (Macander et al. 2022) using the year closest to a given caribou date (i.e., 2010 raster for years 2009–2012, 2015 raster for years 2013–2017, 2020 raster for years 2018–2024) in Program R v 4.4 (R Core Team 2024) the packages 'sf' (Pebesma and Bivand 2023) and 'raster' (Hijmans et al. 2015). Our goal was to assess overwinter survival for each individual and biological year. We determined whether the individual died during winter, the date of death (number of days since the beginning of winter) for those that died, the average snow depth, and the mean lichen cover.

Factors affecting winter survival

We tested the effect of lichen on overwinter survival using Cox proportional hazards models (Grambsch and Therneau 1994) fitted with the 'survival' package (Therneau 2022), assuming a similar underlying hazard among individuals within the winter season. We built candidate models based on our hypotheses: a lichen-only model, a model that included an interaction between lichen and snow depth, and another with an interaction between lichen and a quadratic effect of snow depth (2nd order polynomial). We compared these models to a null model using Akaike's Information Criterion (AIC; Akaike 1973).

Results

Movement, mortality, and environmental data

We analyzed a total of 1,067 caribou-winters spanning 2009–2010 through 2023–2024, during which 87 winter mortalities were recorded. Mean overwinter snow depth across all years was 35 cm (SD = 17) and did not differ significantly between caribou-winters that ended in survival versus mortality (two-sample t-test, $p = 0.66$). Median overwinter lichen cover was 8.8% (interquartile range [IQR]: 6.8–10.7). Individuals that survived experienced significantly higher lichen cover (median 8.9, IQR: 7.2–10.8, $n = 980$ caribou-winters from 351 individuals) compared to those that died (median 7.1, IQR: 5.0–9.8, $n = 87$, Wilcoxon rank-sum test, W = 53,650, $p < 0.0001$). For caribou that died, the mean number of days from the start of winter until death was 71.5 (SD = 32.9), corresponding to 9 February. This timing is significantly later than the mid-point of the winter (day 61, one-sample t-statistic = 2.98, d.f. = 86, $p = 0.004$).

Factors affecting winter survival

The model with an interaction between lichen cover and the quadratic effect of snow depth was the top performing model (ΔAIC for all competing models was > 2, Table 1). Lichen cover had a significant negative effect on the hazard rate (−0.60, $p < 0.001$), indicating a positive relationship between lichen availability and caribou survival, but both interaction terms of snow depth were significant (Supplementary Information Table S1 for coefficient estimates) indicating that the benefits of lichen varied nonlinearly with snow depth (Fig. 2). At low snow depths (0 cm), predicted

Table 1 Model results from the candidate set of Cox proportional hazards models considered for the relationship to overwinter survival (1 December – 31 March) of adult female Western Arctic Herd caribou (*Rangifer tarandus*), 2009 to 2024. Survival was modeled as a function of mean percent lichen cover ("lichen") and mean snow depth (cm) ("snow depth") encountered at each winter location

Model	AIC	ΔAIC
Lichen × Snow depth^2	1187.92	0.00
Lichen	1190.97	3.05
Lichen × Snow depth	1191.04	3.12
Null	1204.50	13.53

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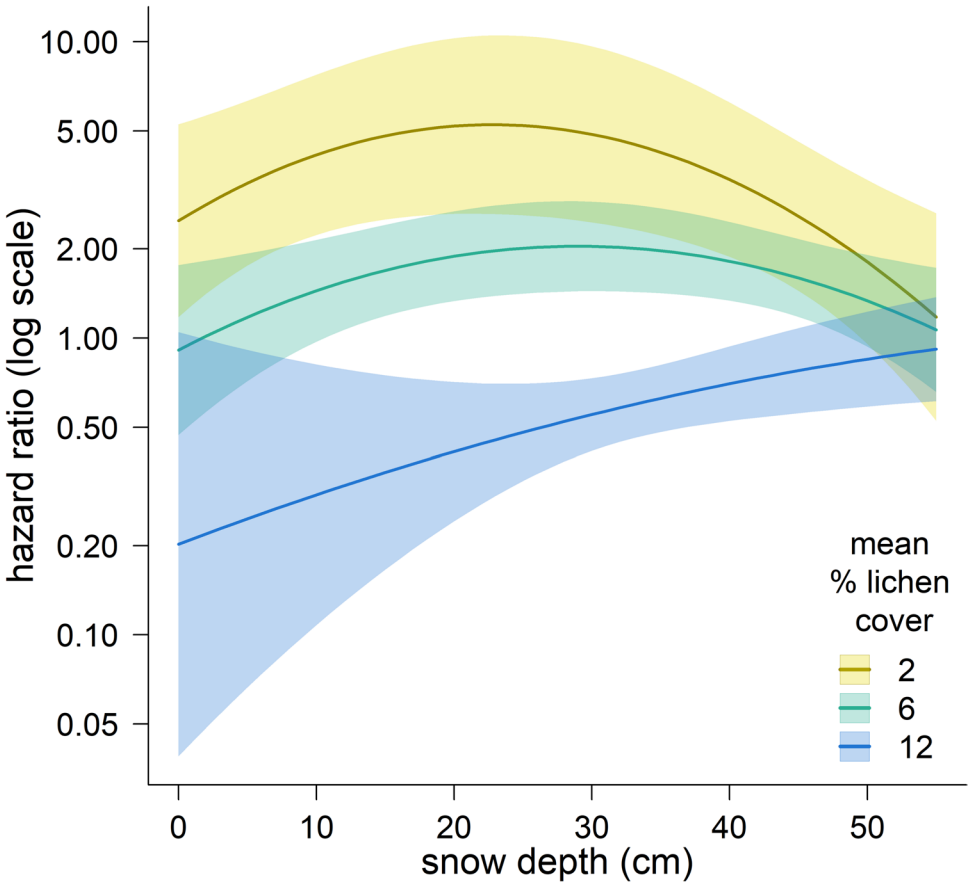


Fig. 2 Hazard ratios for adult female Western Arctic Herd caribou (*Rangifer tarandus*) predicted by the lichen × snow depth^2 model. Lines represent fitted model estimates with 95% confidence intervals. Colors (yellow, green, blue) represent mean percent lichen cover: low, medium, and high, respectively. Higher hazard ratios indicate increased risk of winter mortality

overwinter survival varied substantially with lichen cover: 98.5% [95% confidence interval: 92.6–99.7] at 12% lichen cover, 93.5% [87.9–96.6] at 6% lichen cover, and 83.3% [68.0–91.7] at 2% lichen cover. At moderate snow depths (25 cm), predicted overwinter survival exhibited the greatest range across lichen levels: 96.5% [95.0–97.6] at 12% lichen cover, 86.3% [81.1–90.1] at 6% lichen cover, and 68.2% [46.4–82.6] at 2% lichen cover (Fig. 2). However, at very deep snow (50 cm), survival rates among the varying lichen levels converged, with survival rates of 94.0% [91.4–95.8] at 12% lichen cover and 87.6% [77.8–93.2] at 2% lichen cover.

Discussion

Seasonal survival is shaped by the complex interplay of environmental conditions, forage availability, and other factors (including interactions with other species and habitat selection), particularly during periods of resource scarcity. Our results demonstrate that winter forage, quantified by an index of lichen abundance, is an important factor influencing the overwinter survival of adult female WAH caribou. Greater lichen cover was strongly associated with higher survival (i.e., reduced hazard rates). Importantly, we found evidence that the effect of lichen cover varied significantly with snow depth through a nonlinear interaction. At intermediate snow depths (20–30 cm) differences in survival between high and low-lichen areas were the most pronounced, with caribou in low-lichen areas experiencing significantly higher mortality risk. However, deeper snow reduced the positive impact of higher lichen on survival, potentially by limiting access to the terricolous lichen resource. Our findings highlight the importance of lichen-rich habitats in supporting caribou populations while revealing that snow depth mediates access to this critical winter resource in a threshold-dependent manner.

Migration, lichen, and survival

In highly seasonal environments, migration is a behavioral adaptation used, among other things, to mitigate forage scarcity (Fryxell and Sinclair 1988; Avgar et al. 2014). Caribou living in the Arctic and sub-Arctic encounter some of the most extreme seasonal environments and correspondingly exhibit the longest terrestrial migrations on the planet (Joly et al. 2019). Migration has enabled many species and populations, including herds of barren-ground caribou, to become far more abundant than would otherwise be possible (Fryxell et al. 1988; Festa-Bianchet et al. 2011). While many species must balance reducing energy expenditures with maximizing

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energy intake during harsh winter months, caribou exhibit remarkable flexibility through highly variable migration strategies, including partial migration where not all individuals are migratory (Chapman et al. 2011), and facultative migration, where individuals vary migratory tactics annually based on experienced conditions (Dingle and Drake 2007). For example, WAH caribou that migrate to southern winter ranges experience greater lichen availability compared to caribou that winter in northern ranges (Joly et al. 2025), which likely influences migratory behavior. Based on our results, we posit that caribou that move to areas with higher lichen cover may be able to maintain better body condition and improve their chances of survival by accessing more productive habitats, highlighting how greater lichen cover could drive evolutionary selection for migratory behavior. However, questions remain about why the WAH and other barren-ground caribou herds exhibit partial migration and why the proportion of nonmigratory WAH caribou has increased in recent years (Gurarie et al. 2024; Joly et al. 2025).

Snow depth and lichen

Snow depth and lichen availability interact in complex ways to influence caribou overwinter survival, as both resources and environmental conditions vary spatially and temporally across the landscape. Our results revealed a significant nonlinear interaction between snow depth and lichen cover. Previous work on the WAH showed that snow depth had differential regional effects on survival, with positive impacts north of the Kobuk River and negative impacts to the south (Gurarie et al. 2024), where lichens are more abundant (Macander et al. 2022; Joly et al. 2025). Our findings suggest that spatial variation in lichen abundance may contribute to these regional patterns, as the interaction we observed indicates that snow effects depend on local forage availability. Where caribou are less dependent on lichen for winter nutrition (such as lichen-poor areas in the north), deeper snow may provide other benefits to caribou like avoiding predation (Sharma et al. 2009; Schmelzer et al. 2020) without impeding access to critical forage. Caribou movement in response to snow and forage conditions further complicates this relationship. Caribou alter their movement in relation to snow conditions (Le Corre et al. 2017), and WAH caribou may select areas with shallower snow, potentially to mitigate movement constraints or improve forage accessibility. This highlights the need for future research on how caribou adjust movement and habitat selection in response to snow conditions and forage availability, as well as further research on how snow cover and quality are changing.

Snow conditions are highly variable and complex (Reinking et al. 2022), with depth being an imperfect proxy for other important factors such as snow hardness and crusting (Boelman et al. 2019). We found evidence supporting our prediction that a deep snowpack may negate the benefit of lichens, which we attribute to elevated energetic expenditures for caribou to dig for terricolous lichens or their ability to even detect them under deep snow (Laperriere and Lent 1977; Fancy and White 1987; Kinley et al. 2003). However, the nonlinear nature of the lichen cover and snow depth relationship – with peak mortality at intermediate rather than maximum snow depths at lesser lichen covers – suggests other factors may be involved. Lichen access could similarly be impacted by shallow snow that is hardened by wind (Collins and Smith 1991) or topographic effects. In mountainous regions, snow conditions can shift rapidly with topography and wind events, further complicating access to forage (Mahoney et al. 2018). These dynamics highlight the challenges of interpreting snow depth as a singular factor in caribou survival, and future work incorporating measures of snow hardness, crusting, and fine-scale topographic effects would further refine our understanding of how snow characteristics mediate lichen accessibility and caribou survival.

Lichen availability and caribou survival in a changing Arctic

The lichen cover product we used revealed net decreases in lichen over the mapped extent across northern and central Alaska and northwestern Canada (Macander et al. 2022). Declining lichen cover has been reported across the circumpolar Arctic generally (Fraser et al. 2014; Kennedy et al. 2020; He et al. 2024) and specifically in the winter range of barren-ground caribou in Alaska (Joly et al. 2009, 2010). These declines have been linked to several interrelated factors that predominantly contribute to lichen loss, including wildfires, overutilization by caribou, and climate-driven changes in plant communities, such as shrub expansion that outcompetes lichen (Cornelissen et al. 2001; Joly et al. 2007b, 2009; Collins et al. 2011; Chagnon and Boudreau 2019; Berner et al. 2020). Our results suggest that the widespread loss of lichen could indirectly affect caribou survival by reducing the availability of this critical winter forage. While our results indicate that lichen loss could impact caribou survival, our measure of percent lichen cover, while the best available index, remains an imperfect proxy of true lichen abundance. Ideally, biomass, which accounts for both cover and height, would better capture lichen abundance, as cover alone is a one-dimensional measure of a multidimensional resource.

The climate is rapidly changing in the Arctic, with temperatures rising two to four times as fast as the global average (Cohen et al. 2014; Rantanen et al. 2022). While experimental warming studies consistently demonstrate dramatic lichen declines (Walker et al. 2006; Elmendorf et al. 2012), long-term monitoring studies under ambient warming

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conditions have shown mixed evidence, highlighting the complex interactions among environmental drivers that are shifting under climate change (Bjorkman et al. 2020). In a warming Arctic, with less sea ice extent, more open ocean water may lead to increased snow in some regions (Park et al. 2013; Bailey et al. 2021), indirectly impacting caribou survival by dampening the value of lichen-rich habitats. Continued change is expected to increase rain on snow events in the Arctic (Bieniek et al. 2018), which can prevent caribou from accessing terricolous lichens (Joly et al. 2021). Warming during the summer months could lead to more wildfires (Hu et al. 2015; Box et al. 2019), reducing lichen cover on caribou winter ranges as well (Joly et al. 2009; Gustine et al. 2014). Our study highlights the critical role of lichen-rich habitats in caribou overwinter survival, emphasizing that understanding the interplay between forage availability and environmental factors under a changing climate will be essential for predicting long-term demographic consequences. Building on our findings, mitigating these threats will require targeted conservation efforts, including habitat management and climate adaptation strategies, to safeguard the resilience of caribou populations in the face of rapid Arctic warming.

Future directions

We recommend future work focus on understanding the potential lag effects of resource availability on population dynamics. This could include modeling how cumulative impacts of forage scarcity across seasons influence recruitment and survival over multiple years. Furthermore, our study does not account for other factors that have been shown to influence barren-ground caribou populations, such as predator-prey dynamics, summer habitat conditions, human disturbance, harvest, and insect harassment (Seip 1991; Boulanger et al. 2011; Joly et al. 2020; Johnson et al. 2022). Additional research will be essential to untangle the combined effects of these factors on caribou survival, assess their relative importance, and evaluate how they may be altered by future climate change.

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Data availability Code and data used to generate the results and figures are archived in Dryad: https://doi.org/10.5061/dryad.qbzkh18tz

Declarations

Competing interests The authors declare no competing interests.

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