

**Seasonal patterns of mortality for boreal caribou (*Rangifer tarandus caribou*)
in an intact environment**

by
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A thesis submitted in partial fulfillment of the requirements for the degree of

Master of Science

in

Ecology

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ABSTRACT

Seasonality is an important component in shaping the dynamics that influence ecosystems, including mortality. Animals experience temporal variation in vulnerability to mortality due to interactions among environmental conditions, nutritional condition, age and life stages, and changes in their movements and behaviours as well as those of their predators. Consequently, mortalities may follow a temporal pattern that can provide insight into factors influencing the population trends or ecology of a species. We investigated patterns of mortality in the boreal ecotype of woodland caribou (*Rangifer tarandus caribou*) in the southern Northwest Territories, Canada. Survival data were collected from 423 adult female caribou tracked by radio collars, 172 of which died during the study from predation (106), non-predation (i.e., starvation), (15), harvest (11), accidents (3), or unknown causes (37). We used generalized additive mixed models to evaluate temporal patterns of mortality across the year. We found that probability of mortality followed a trimodal pattern with three peaks, one during pre-calving, one in mid-summer, and a smaller peak in late autumn, with a 6-fold difference in mortality risk between the lowest and highest periods of the year. Mortality risk was higher from late spring (pre-calving) to mid-summer than it was from late summer until the end of winter, despite decreasing for about 6 weeks post-calving. Increased encounter rates, as predicted by higher caribou movement rates, corresponded to the pre-calving and late autumn mortality peaks, but not the mid-summer mortality peak. The mid-summer mortality peak was better explained by caribou nutritional condition, as adult female caribou experience the greatest depletion of body reserves from spring to mid-summer. Predation mortalities followed the same temporal pattern as total mortalities, whereas non-predation mortalities (i.e., starvation) were clustered in the weeks between peak calving and mid-summer. Seasonal fluctuations in predator-prey encounter

probabilities, energetic demands, and nutritional condition that result in caribou being more vulnerable to predation should be considered when evaluating pressures on this species.

PREFACE

This thesis is an original work by Alicia P. Kelly. Data used in this research was collected by the Department of Environment and Natural Resources (ENR), Government of the Northwest Territories (GNWT), as part of regional monitoring programs.

The NWT Animal Care Committee approved annual wildlife handling permits for all capture work, and boreal caribou monitoring programs received annual NWT wildlife research permits from GNWT-ENR Dehcho and South Slave Regions.

As of February 1, 2020, this manuscript is in preparation for submission to a scientific journal. Co-authors include Nicolas C. Larter, Eliezer Gurarie, John G. Cook, Evelyn H. Merrill, and Andrew E. Derocher. All co-authors contributed input on analyses and manuscript content.

ACKNOWLEDGEMENTS

Many First Nations groups across the southern Northwest Territories have thoughtfully supported the research and monitoring of boreal caribou on their traditional lands, and I am appreciative of what I have learned from them directly as well as for the rich scientific data we have collected over the years. Karl Cox and the late Danny Allaire assisted with field data collection across several years, through snow, swamps, and all conditions in between. Nic Larter and Terry Armstrong have always made time for thoughtful conversations about boreal caribou, wildlife ecology, and our shared experiences of working in wildlife management.

My immense thanks to Troy Ellsworth for supporting my return to graduate school and his ongoing support to see this degree completed. Similarly, Andrew Derocher has provided support since my undergraduate days and throughout this process. I know he will be glad to see this wrapped up, and we will continue to collaborate on other projects. Thank you to Evelyn Merrill for her support and supervision, and for the excellent Landscape Ecology course which spurred ongoing friendships and collaborations.

My parents, Kyle and Cindy Kelly, exposed me to ‘the land’ early in life and I’m grateful for those experiences that grew into a love of our natural environment and its wildlife, particularly in the North. I’m also thankful for their life-long support. Finally, I am grateful to no one more than Tim Van Dam, whose steadfast support made this degree possible and who makes my life richer every day. And to our two children who did not exist when this M.Sc. program started, you have delayed its completion significantly but immeasurably increased my joy. I look forward to sharing the fun of science and an appreciation of this remarkable land with you.

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CHAPTER 1

INTRODUCTION

Most populations, particularly in temperate and polar environments, inhabit seasonal environments (Fretwell 1972). Temporal variation in the physical environment shapes community dynamics and population patterns (Chesson 2003, McMeans et al. 2015) and many aspects of ecological dynamics can be better understood when seasonality is considered (Holt 2008b, White and Hastings 2019). One such dynamic is mortality. Seasonally recurring patterns of mortality are observed across many species due to interactions among seasonal changes in reproductive state, nutritional status, energetic demands, or seasonal behaviours of predator or prey (Gaillard et al. 2000, Gonzalez and Crampe 2001, Molinari-Jobin et al. 2004, Owen-Smith 2008, Latham et al. 2013). These factors may act cumulatively in different ways to increase probability of mortality at specific times of year.

A characteristic of seasonality is variation in resource availability, which species have adapted strategies to survive during resource-limited periods, whether by physiological adaptation, internal fat stores, external storage (e.g., caches), hibernation, or migration (Holt 2008a). Energy demands also vary seasonally due to environmental conditions (e.g., temperature, precipitation), and reproductive activities (Chan-McLeod et al. 1994, Crête and Larivière 2003, Cook et al. 2004, Forsyth et al. 2005, Garroway and Broders 2005, Gardner et al. 2016). Increased mortality may result if seasonal energetic demands are not satisfied by limited nutritional resources or by other strategies such as internal fat stores (e.g., Cook et al. 2004, Kautz et al. 2020).

Nutritional resources vary interannually due to climate and weather factors that affect vegetation productivity and ultimately influence reproduction and survival (Post and Stenseth

1999, Mysterud et al. 2001). Nutritional condition also varies seasonally for many animals (Parker et al. 2009, Owen-Smith 2008, Metz et al. 2012, Cook et al. 2013). In ungulates, nutritional condition is usually measured as an individual's fat and protein stores, particular body fat (Cook et al. 2010). Greater nutritional resource availability, and consequentially good nutritional condition, positively affects demographic performance including pregnancy rates, neonate birth weight and vigour, growth rates, and juvenile and adult survival (Crête and Huot 1993, Pettorelli et al. 2003, McLoughlin et al. 2007, Parker et al. 2009, Cook et al. 2013, Proffitt et al. 2016, Douhard et al. 2018). Ungulate nutritional condition is often poorest at the end of the winter or dry season (Owen-Smith 2008, Parker et al. 2009, Metz et al. 2012, Cook et al. 2013). In predator-free environments, most adult mortality occurs in the season characterized by the lowest annual body condition (Albon et al. 2000, Coulson et al. 2001).

Where predators occur, predation rates may be higher during the time of year when prey body condition is most depleted (Peterson et al. 1984, Huggard 1993, Montgomery et al. 2014). Animals in poor body condition have reduced marrow fat content (Mech and Delgiudice 1985, Cook et al. 2001), may have higher levels of the stress hormone cortisol (Mislán et al. 2016, Ewacha et al. 2017), and may be more susceptible to predation (Peterson et al. 1984, Huggard 1993, Metz et al. 2012, Shave et al. 2019) because weaker animals are easier to capture and kill (Smith et al. 2000, Husseman et al. 2003). Predators disproportionately kill more individuals in vulnerable age and sex classes (Peterson et al. 1984, Owen-Smith 2008, Metz et al. 2012). Females are particularly vulnerable to predators during late gestation, whereas males may be more vulnerable during or following the mating season (Molinari-Jobin et al. 2004, Forsyth et al. 2005, Owen-Smith 2008). Predators often focus on neonates or juvenile ungulates when they are seasonally available (Peterson et al. 1984, Linnell et al. 1995, Molinari-Jobin et al. 2004,

Mattisson et al. 2016). Body condition may also be reduced by disease and parasites (Pérez et al. 2015, Forde et al. 2016). Decreasing survival with age is also common in many species (Loison et al. 1999, Gaillard et al. 2000).

Mortality from predation may be positively correlated to encounter rates between predators and prey (Whittington et al. 2011, Gurarie and Ovaskainen 2013). Encounter rates increase when prey are more mobile or use larger home range areas (Gilman et al. 2010), and may be influenced by changes in predator behaviour including social behaviour that affects movements (e.g., pack cohesion, mobility of young) (Fuller 1989, Latham 2009). Seasonal diet shifts (e.g., Potvin et al. 1988, McMeans et al. 2015), or migration of predators or alternate prey can also result in seasonal shifts in predation pressure (Seip 1992, Metz et al. 2012). Seasonal changes in synchrony of habitat use may affect the probability of a predator-prey encounter (Basille et al. 2013). Individual vulnerability also depends on characteristics of the physical environment (Bergman et al. 2006). Snow depth and winter severity can also influence habitat use and movements of both predator and prey (Fuller 1991, Stuart-Smith et al. 1997) and mortality may increase when prey experience deep snow or are disadvantaged by ice (Patterson and Messier 2003, Dumont et al. 2005, Penczykowski et al. 2017).

We used data on the boreal ecotype of woodland caribou (*Rangifer tarandus caribou*, hereafter boreal caribou) collected during a long-term monitoring program in the southern Northwest Territories, Canada, to assess seasonal variation in mortality and why it may be greater during some seasons than others. Boreal caribou occur at low densities in boreal forests across Canada, selecting unproductive habitats where other ungulates and predators are less abundant (James et al. 2004, McLoughlin et al. 2005). Boreal caribou have experienced population declines in many local populations and are listed as *Threatened* under Canada's

Species at Risk Act (Environment Canada 2012). Across some ranges, human habitat disturbance and a warming climate have resulted in long-term habitat changes that support increases in alternate prey species (e.g., moose (*Alces alces*), white-tailed deer (*Odocoileus virginianus*)), which in turn support higher densities of wolves (*Canis lupus*) and subsequent declines in caribou via apparent competition (Holt 1977, Seip 1992, Messier 1994, Latham et al. 2011). Roads, seismic exploration lines, and other linear features can facilitate wolf travel into boreal caribou habitat (James and Stuart-Smith 2000, Dickie et al. 2017). In addition, habitat disturbance creates functional habitat loss (Dyer et al. 2001, Sorensen et al. 2008), and industrial activity and an increased proximity of predators may elicit stress responses in caribou that reduce caribou condition and increase susceptibility to predation (Wasser et al. 2011). Under these conditions, high predation rates have contributed to population declines (Wittmer et al. 2005).

It can be difficult to separate top-down (predation) and bottom-up (nutrition and climate effects) influences on ungulate survival, in part because interactions between the two can be dynamic over species, time, and space (Hunter and Price 1992, Andrén and Liberg 2015, Proffitt et al. 2016). Where large predators and ungulates co-occur, predation is typically the cause of >50% of mortalities (reviewed in Gaillard et al. 2000). Predation is the most common cause of death in boreal caribou studies that partition cause of death, and much research has focused on understanding spatial aspects of predation (e.g., James and Stuart-Smith 2000, James et al. 2004, McLoughlin et al. 2005). Less attention has been paid to nutritional condition, which may operate independently or interactively with predation as a contributing factor to explain population declines (Brown et al. 2007, Parker et al. 2009, Thompson et al. 2015). In woodland caribou, malnutrition as a cause of death in adult females typically occurs in summer (e.g., 4-13% of total mortalities; Stuart-Smith et al. 1997, Wittmer et al. 2005, McLellan et al. 2012,

Table 1). Many ungulates lose body condition throughout winter due to negative energy balance, regaining condition in spring when more nutritious food becomes available (e.g., Peterson et al. 1984, Metz et al. 2012). In contrast, barren-ground caribou (*R. t. groenlandicus*) in many populations maintain body fat over winter, and the low point in the body condition is mid-summer (e.g., Huot 1989, Crête and Huot 1993, Gerhart et al. 1996, Chan-McLeod et al. 1999). Repeated measures of body condition of individual boreal caribou in the southern Northwest Territories showed that similar to barren-ground caribou, boreal caribou lost little body condition over winter, and may follow the same annual pattern of body condition as other caribou subspecies, with an annual minima in late spring or summer instead of late winter (J. Cook unpublished data).

Species often face differing threats and pressures across their range, and causes of local or subpopulation declines may differ correspondingly (Collins and Kays 2011, Environment Canada 2011). For boreal caribou, human habitat disturbance, defined as the percent of range within 500 m of an anthropogenic habitat disturbance, is highly variable across the entire range but is generally high in northeast British Columbia (BC) and Alberta, $\bar{x} = 61.4\%$ disturbed (range 22-95%, n=19), and low (10%) in the southern Northwest Territories (NT) (Environment Canada 2012). Bergerud and Elliot (1986) suggested that caribou populations would be stable at wolf densities < 6.5 per 1000 km². Wolf densities are 6.4 – 15.6 wolves/1000 km² in northeast BC (Serrouya 2016), and 0.6-1.4 wolves/ 1000 km² in boreal caribou ranges in the NT where bison (*Bison bison*) are absent (Alberta Biodiversity Monitoring Institute 2017, 2018). In northeast Alberta, the wolf density supported by increased abundance of non-caribou ungulates doubled (6 to 11.5 wolves/1,000 km²) since the onset of development concurrent with a 10-fold increase of caribou in the diet of wolves (Latham et al. 2011). Seasonal mortality patterns can provide insight

into factors that contribute to population growth rate, and help with directing conservation actions towards those factors, especially for threatened or endangered species. We studied boreal caribou ranges that were characterized by low anthropogenic disturbance and low densities of predators and alternate prey. This dataset was collected throughout the year over several years (2003-2018), which is critical to understand the role of seasonality (White and Hastings 2019).

Our objectives were to assess seasonal variation in boreal caribou mortality and to examine whether periods of differing mortality risk were more variable intra-annually or interannually. We then evaluated the ecological processes or conditions that may underlie temporally different periods of mortality risk. We expected that seasonal periods characterized by increased caribou movement rates would be associated with increased mortality risk due to increased caribou-wolf encounters. We expected adult female mortality would be higher during life cycle periods of greater vulnerability, particularly during later stages of gestation (April) and lactation (May-July). In addition, we expected that during the calving season (peak May 15) predators would focus on neonates and young calves, decreasing predation on adults. Finally, we expected that mortality risk would be increased during the seasonal period of lowest body condition (mid-summer, for lactating females).

METHODS

Study area

The study area (Fig. 1) is in the Taiga Plains Mid-Boreal ecological region of the southern Northwest Territories, and extends into northeastern BC and northwestern Alberta (Calendar and Bistcho caribou ranges defined by Environment Canada (2011). The area is approximately 75,000 km² and vegetation is dominated by open black spruce (*Picea mariana*)

forests interspersed with patches of mixed forests including deciduous (*Populus* spp.), white spruce (*P. glauca*), and jack pine (*Pinus banksiana*). Peatlands (30-40%) and discontinuous permafrost result from extensive low-lying areas, a cold climate, and poor drainage, and support treed fens and black spruce-lichen peat plateaus. Productive mixed-wood and upland deciduous forests occur where drainage and soil conditions permit, particularly along major rivers and hill slopes (Ecosystem Classification Group 2009). Approximately 33% of the study area has been burned by wildfire in the past 40 years, resulting in a mosaic of early, mid- and late-seral forests. Predators in the area include wolves, black bears (*Ursus americanus*), lynx (*Lynx canadensis*), and wolverine (*Gulo gulo*). Alternate prey species include moose, beaver (*Castor canadensis*), white-tailed deer, and bison; bison are restricted to the northwestern and far western portion of the study area, and white-tailed deer are uncommon. Grizzly bears (*U. arctos*) and elk (*Cervus canadensis*) occur in the far western portion of the area. Densities of wolves (0.6 – 5.3 wolves/1000 km²) and moose (1.3 – 7.2 moose/100 km²) are low. Densities of black bears and beavers are unknown. Bison density, where they occur, is about 5 bison/100 km². There is low anthropogenic disturbance (mean linear feature density 0.34 km/km²); the anthropogenic disturbance footprint measured was estimated to be 10% (Environment Canada 2011). Most anthropogenic disturbance is from old exploratory seismic lines. Roads occur at low density and there are few communities (n=8). Except for a few localized industrial sites, human access is usually limited to areas near roads and communities, where trails used by snowmobiles and all-terrain vehicles are common. All species including boreal caribou are harvested by local people.

Capture and telemetry data

Between 2003 and 2018, adult boreal caribou were captured with a net fired from a helicopter as part of regional monitoring programs. Capture crews fitted each animal with a collar equipped with a mortality sensor (Telonics, Mesa, Arizona). Collared animals were monitored until the collar failed, released, or the animal died. Doppler-shift and GPS collars were monitored remotely for reduced movements and mortality sensors that provided a warning when a collar had been stationary for > 6 hours. Mortality dates were assigned to GPS collars at the time of the mortality warning or the time of the first location at the site where the mortality occurred. We visited the locations of stationary collars to determine cause of death. VHF-only collars were relocated periodically using fixed-wing aircraft. VHF-collared caribou contributed to annual survival estimates and total known mortalities including cause of death; however, some known-mortality dates of VHF-collared caribou were not specific enough to include in our analysis of temporal mortality patterns.

All capture and handling occurred under annual Wildlife Care Committee permits for each region, and followed Government of the Northwest Territories animal care protocols consistent with the Canadian Council on Animal Care (ccac.ca).

Causes of mortality

Cause of death was assigned based on evidence at the mortality site and classified as predation (i.e., wolf, bear, or unknown), non-predation (i.e., caribou carcass intact), harvest, accidental (e.g., entrapment, vehicle collision), or unknown. Evidence of predation included signs of struggle (e.g., broken branches, blood, vegetation, tracks), bite marks, and state of carcass (e.g., disarticulated, consumed). Predator species was determined from predator hair, tracks, scat, and bedding sites at the site and carcass remains. Some mortality sites could be

attributed to predation but predator species was inconclusive. Non-predation events were determined by the carcass position and absence of predation signs, with additional data from the environment immediately around the carcass, and data from field necropsies. Harvest was determined by evidence of humans at the site or when the collar was returned by the hunter. Mortality was classified as unknown if there was insufficient evidence to determine a cause of death, or if mortality sites were not visited.

Teeth, bones, and other available tissues were retrieved from mortality sites when possible. Age at death was determined by analysis of cementum annuli of teeth (Matson's Lab, Manhattan, Montana). Bones were submitted for bacterial culture and marrow fat assessment (Prairie Diagnostic Services, Saskatoon, SK, and University of Calgary Faculty of Veterinary Medicine, Calgary, AB), and a pathologist assessed cause of death for animals when case histories and samples were provided (Prairie Diagnostic Services, Saskatoon, SK). We restricted marrow fat data to bones that were retrieved ≤ 10 days to prevent biases from degradation, and deducted 0.54% per day between death and field necropsy to account for dehydration (Kie 1978).

Timing of caribou mortalities

We used generalized additive mixed models (GAMMs) to identify temporal patterns of boreal caribou mortality and to identify periods with higher and lower probability of mortality. We excluded VHF-only collared animals from the temporal models because the relocation interval was too long to determine date of death. To model the distribution of mortalities in time across seasons, we subset the year into 5-day intervals and counted the proportion of dead in each interval: $p.died = n.died / (n.died + n.survived)$, where $n.survived$ includes animals present both at the beginning and end of each period. The 5-day interval minimized data censoring (i.e.,

collars that went off-line without a mortality) but was large enough that the probabilities were not dominated by zeroes.

We then fit the 5-day mortality probability against ordinal date (i.e., 1 to 365; date) using the *gam4* package (Wood and Scheipl 2017). We weighted the GAMMs (i.e., the contribution of the 5-day period to the log likelihood) using *n.total* (the total number of collared animals alive at the beginning of each 5-day interval) and used a circularly wrapped spline that matched the modeled probability on December 31 (date 365) with January 1 (date 1) as the smooth term, and included year as a random effect. The number of knots, k (corresponding to the number of cubic polynomials that are joined together to obtain the smoothed additive fit) of the GAMM was initially determined by the default algorithm, which selects a parsimonious level of complexity by minimizing a generalized cross validation criterion (Wood 2017). If k is large enough so the basis is more flexible than needed to represent the function, then the exact choice of k does not have a large influence on model fit; rather, the smoothing parameter controls the behaviour of the fitted model (Wood 2017).

We fit models to the complete set of mortalities (I) a model with date only, and (II) a model with date and year as random effect, and used Akaike's information criterion (AIC) to compare these (Burnham and Anderson 2002). We also fit individual models to the subsets of predation mortalities and non-predation mortalities. To divide periods identified in the top model into "mortality seasons", we used the estimated inflection points between each local minimum and the subsequent local maximum of the fitted GAMM values, defining the interval around the maxima as "high mortality", and the interval around the minima as "lower mortality" seasons, and evaluated *post hoc* the rates and causes of mortality across these seasons.

Timing of caribou movements

We calculated mean movement rates (km/h) for individual caribou included in the temporal mortality models by measuring the distance travelled between consecutive GPS locations, summing distances for each date and dividing by 24. We then used a generalized additive model (GAM) to fit the mean movement rate against ordinal date (i.e., 1 to 365; date) using the *mgcv* package (Wood 2019). We plotted the fitted GAM of movement rates with the fitted GAMM of mortality patterns and overlaid the ‘high mortality’ seasons defined in the top GAMM model. All analyses were done in R (R Core Team 2019).

RESULTS

Causes of mortality

One hundred and seventy-two of 423 collared adult females (73 Argos Doppler-shift, 286 GPS, 64 VHF) died in the southern NT between 2003 and 2018. Predation was the proximate cause of 106 mortalities (93 wolf, 6 black bear, and 7 unknown predator). We documented 15 non-predation “carcass intact” mortalities, 11 mortalities due to harvest, and 3 accidental deaths (i.e., vehicle collision, caught in wolf snare, entrapment). The cause of mortality was classified as unknown for 37 mortalities (of these, 27 mortality sites were inaccessible and 10 mortality sites were visited but cause of death was inconclusive).

Age at death

We determined age at death for 61 caribou ($\bar{x} = 9.7$ years, range 2 to 22 years) that died of predation (44), non-predation (15), harvest (1) and accident (1) (Fig. 2). There was no significant difference in the mean age distribution of predation ($\bar{x} = 10.0$ years, $SD = 4.1$, $n=44$)

and non-predation mortalities ($\bar{x} = 9.0$ years, $SD = 4.1$, $n=15$); $t(24) = 0.8$, $p=0.42$). Following the review in Gaillard et al. (2000), we considered caribou 3-9 years old to be of prime age and caribou ≥ 10 years to be old. More mortalities were of older caribou (54% ≥ 10 years, $n=33$) than prime age adults (44%, 2-9 years, $n=27$), $Z = 4.36$, $p < 0.001$). One 2-year old caribou died of a non-predation cause.

Marrow fat

We obtained marrow fat from bones collected from 6 mortality sites ≤ 10 days of death. Of these, 3 bones were collected from intact carcasses in July 2013 and had 0% marrow fat, indicating starvation, which was confirmed by pathology reports. The other bones were collected from predation sites and had 24% (July 2013), 61% (April 2017), and 71% marrow fat (July 2018).

Mortality patterns

The temporal analyses (i.e., the GAMMs) included 359 adult females with known fate, 139 of which died during monitoring; 64 VHF-collared animals were excluded. The number of knots in fitted models using all mortality data was $k = 8$, which corresponds to three modes of mortality. Including year as a random effect improved the model fit (AIC of 933 versus 956). Although there was significant variation across years, the fixed component (date, i.e., intra-annual seasonality) was significant ($p < 0.001$). The fitted values for the GAMM of all adult female mortalities indicated three seasonal mortality peaks, one during pre-calving (May 5, 5-day probability of mortality (hereafter, *p. mort*), 0.0049) one mid-summer (July 26, *p. mort* 0.0045), and a smaller peak in late autumn (November 13, *p. mort* 0.0027) (Fig. 3). The highest

probability of mortality during the year (pre-calving peak, May 5) was 6.1 times greater than the lowest point (late winter, February 10, p. mort 0.0008). Although mortality risk for adult females decreased for about 7 weeks post-calving (May 24-July 8) before increasing again in mid-summer (July 9-August 17), it was still higher during the post-calving period than during late summer, autumn, and winter (August 18- April 10) (Fig. 3).

We delineated (using inflection points) 3 higher-mortality and 3 lower-mortality seasons: winter (low; December 5-April 9, p.mort at minimum: 0.0008), pre-calving (high, April 10-May 23, p.mort at maximum 0.0049), post-calving (lower, but part of the elevated late spring to mid-summer mortality period that was higher than the autumn ‘peak’, May 24-July 8, p.mort at minimum 0.0036), mid-summer (high; July 9-August 16, p.mort at maximum 0.0045); late summer/rut (low; August 17-October 24, p.mort at minimum 0.0015), and late autumn (peak, but lower than the elevated mortality period from late spring to late summer, October 25 – December 4, p.mort at maximum 0.0027).

Cause of death in high-and low-mortality ‘seasons’ were identified (Table 2, Fig 4). Cause of death differed significantly among seasons (Pearson’s Chi-squared test: $\chi^2=67.152$, $df = 20$, $p\text{-value} < 0.001$). *Post hoc* analysis based on residuals of Pearson’s Chi-squared test using the Bonferroni method indicated that the only significant difference was that non-predation mortalities occurred more in the post-calving season ($p < 0.001$).

The fitted GAMM of known-predation mortalities followed the same trimodal pattern as the GAMM of all mortalities. (Fig. 3a, b). Non-predation mortalities included in the GAMM were documented in 2005 (n=1), 2006 (n=1), 2013 (n=8), 2015(n=2) and 2017 (n=2). A GAMM of the non-predation mortalities (n=14) shows one significant peak (July 2) (Fig. 3c).

Movement patterns

Mean movement rates were highest during the pre-calving dispersal period, and lowest during late winter, peak calving and mid-summer (about 6 weeks after peak calving). Mean movement rates increased steadily from mid-summer until after the rut in late autumn, and then decreased during the winter (Fig. 6).

DISCUSSION

We found that boreal caribou had seasonal patterns of mortality throughout the year with a 6-fold difference between the lowest and highest periods of mortality risk. The annual mortality pattern had three periods of higher mortality risk (hereafter, “peaks”) separated by lower-risk periods, with the first (late spring; pre-calving) and second (mid-summer) peaks representing the periods of highest mortality risk. Although these two higher peaks were separated by a lower mortality period, the lower post-calving mortality period still represented a period of elevated mortality risk relative to late summer, autumn and winter. Few caribou died of any cause during late winter (mid-December to mid-March). Temporal patterns of mortality in our study were similar to the pattern of mortalities by month observed in north-eastern Alberta before the onset of disturbance (Figure 2 in McLoughlin et al. 2003). In our study, adult female mortality varied annually, but intra-annual (i.e., seasonal) variation was even greater than the interannual differences, indicating that some fundamental principles may be influencing these intra-annual patterns.

Caribou – predator encounter rates should increase when individual caribou movements increase (Gurarie and Ovaskainen 2013, Mumma et al. 2017). Our study found higher caribou movement rates corresponded to higher mortality risk during the late spring and autumn

mortality peaks, but not during the mid-summer mortality peak or the period of elevated mortality during post-calving. Higher mortality risk in late spring corresponds to the spring dispersal period, when annual movement rates of adult females are highest. Adult females travel long distances to seek out solitary calving sites (Bergerud et al. 1990) and this is the likely reason for movements in our study. The smaller peak in mortality risk in late autumn also coincides with progressively higher movement rates by females through the rut and late autumn. Caribou movements are lowest in winter, perhaps due to reduced mobility in deep snow (Stuart-Smith et al. 1997), which corresponds to the season with lowest mortality risk. However, we found caribou movement rates were also low during post-calving and in mid-summer, when mortality risk was high. We suggest that encounter rates as a result of prey movements provide some explanatory power for the seasonal timing of increased mortality risk in late spring (pre-calving) and autumn, but not post-calving or in mid-summer.

Caribou-wolf encounter rates also depend on the movement rates of wolves. In northern Alberta, moose kill rate was related to movements of both moose and wolves, but most variation in kill rates was attributed to wolf movement rates (Vander Vennen et al. 2016). Movement rates of boreal wolves in Saskatchewan were higher during the snow free season (May to October; (McLoughlin et al. 2019). Wolf packs are less cohesive during summer, which may lead to more individual predator paths increasing random encounters with prey (Peterson et al. 1984, Fuller 1989, Latham 2009). Other studies have documented more predation mortalities during the summer or snow-free period than in the winter or snow period (Rettie and Messier 2000, McLoughlin et al. 2003, Whittington et al. 2011). Overall, predation in our study was higher from May until mid-August, but then it declined for the remainder of the snow-free period (i.e., May to October in our area, Government of Canada 2019). Although higher wolf movement

rates throughout the summer may increase encounter rates with caribou, the 3-fold variation (from mid-summer peak (0.0045) to late summer/autumn (and snow-free) low period (0.0015)) was still large and suggests there was more to the mortality dynamic than just summer and winter (or snow and snow-free) seasons (Metz et al. 2012). Seasonal changes in wolf behaviour may be a factor in seasonal boreal caribou mortality risk but more data are needed to evaluate this.

We observed seasonal changes in mortality risk consistent with differing vulnerability at different life stages. Mortality risk increased in spring during late gestation, which may have contributed to mortality as the outcome of a predator encounter during this period (Molinari-Jobin et al. 2004). Boreal caribou calving is synchronous in time but not in space (Bergerud et al. 1990, DeMars 2015). Peak calving (mid-May; Nagy 2011) coincided with a modest decline in adult female mortality risk. We hypothesize the lower adult female mortality risk was due to a transfer of predation pressure from adults to more vulnerable neonates, as observed in other species (Peterson et al. 1984, Linnell et al. 1995, Molinari-Jobin et al. 2004, Metz et al. 2012, Mattisson et al. 2016).

In our study, most non-predation mortalities occurred after peak calving until mid-summer. Mortalities when starvation was the most likely proximate cause of death were strongly temporally clustered in early July, about 6 weeks post-calving. Marrow fat data from a predation kill site during this period indicated severe malnourishment at time of death (24% marrow fat; (Mech and Delgiudice 1985) and marrow fat (all with 0% fat) from 3 non-predation mortalities during this season indicated starvation. Energy and protein demands are highest during early lactation which doubles the energy requirements compared to non-lactating females (Parker et al. 2009), can reduce energy reserves (i.e., body condition), and can reduce subsequent survival and reproduction compared to non-lactating females (Clutton-Brock et al. 1989, Cook et al. 2004,

Bender et al. 2008). Adult female caribou lose body mass for about 3 weeks following calving due to lactation (Parker et al. 2009), and this typically occurs at a time just before growth initiation of vascular plants, a source of food high in energy and protein (Cook et al. in review). Concurrent with high energetic demands of lactation, insect harassment likely increases energy expenditure and impedes efficient foraging, particularly in late spring and early summer (Helle and Tarvainen 1984, Weladji et al. 2003).

Compared to ungulates that typically are in poorest condition in late winter (e.g., moose, elk, white-tailed deer (Peterson et al. 1984, DelGiudice et al. 2002)), the decline in body condition of boreal caribou is delayed to late spring through mid-summer. Body condition loss through spring and early summer with the low point in mid-summer was documented in barren-ground caribou (Fig. 6, raw data from Huot 1989, Adamczewski et al. 1993, Crête and Huot 1993, Gerhart et al. 1996, Chan-McLeod et al. 1999). When over-winter body reserves gained during the previous summer and autumn are insufficient to meet the combined energetic demands of winter (with variable annual severity), gestation, and especially lactation, caribou vulnerability to mortality is likely elevated in late spring through midsummer, possibly contributing to a significant proportion of the annual mortality of boreal caribou: 40% (55 of 139) of annual mortality occurs in the post-calving and mid-summer mortality periods (1/4 of the year). In predator-rich areas, researchers may be less likely to detect early- and mid-summer malnutrition if tagged animals are more likely to encounter predators and die regardless of their nutritional status.

The proximate cause of mortality in our study was predominantly predation, consistent with other boreal caribou studies (e.g., McLoughlin et al. 2003, Wittmer et al. 2005). We found that predation was a component of mortality throughout the year, following the same trimodal

pattern as that of total mortalities. Thus the predation patterns we observed may reflect the seasonal vulnerability of prey because predators may select prey in poorer body condition than the overall population (Peterson et al. 1984, Huggard 1993, Metz et al. 2012, Shave et al. 2019); but see (McLellan et al. 2012). Predator-killed ungulates often have lower marrow fat reserves than their conspecifics that died of random causes (e.g., road or railway collisions (Huggard 1993); accidental deaths (Mech 2007); hunter harvest (Sand et al. 2012)).

We detected more mortalities of older adult female caribou (≥ 10 years old) than prime-aged caribou, consistent with increased probability of mortality of older ungulates in other studies (Loison et al. 1999, Gaillard et al. 2000, DelGiudice et al. 2002). Yet, we also documented long-lived caribou (up to 22 years old) that exceeded ages expected for wild ungulates (Loison et al. 1999, Larter and Allaire 2016). Low wolf densities on our study area may contribute to longevity of caribou regardless of increased vulnerability due to advanced age.

Recently, Gurarie et al. (2019) developed a parametric approach to detecting and quantifying temporal variation in mortality. Using boreal caribou data from our study, the *cyclomort* package (Gurarie et al. 2019) also selected a three-season mortality model as the best fit to the data. It identifies comparable high-mortality peaks: April 21 (vs. May 2), July 13 (vs. July 28), and November; the earlier dates are likely influenced by a slightly different subset of animals included in the models. A benefit of this parametric approach is precise estimates of the hazard function (i.e., probability of mortality at different times of year). However, the non-parametric GAMM is a more flexible and perhaps accurate characterization of the seasonal hazard, despite requiring *post hoc* decisions to define seasonal periods as we did using inflection points (Gurarie et al. 2019). The GAMM also allowed us to account for variability among years with a mixed-effects model, which *cyclomort* is unable to do. The consistency of both analyses

supports the conclusion that a trimodal annual pattern accurately described the mortality risk to boreal caribou in our study area.

Summary

We suggest that a variety of factors interacted synergistically to result in seasonal periods of higher and lower mortality risk for boreal caribou during the year. First, predator-prey encounter rates likely varied throughout the year and high caribou movements in spring and autumn were related to proportionately higher mortality risk at those times (though mis-matches occur at other times of year). Secondly, our results are consistent with other studies documenting seasonal variation in predation associated with changes in prey vulnerability, specifically prey reproductive state, nutritional condition, and prey size (Owen-Smith 2008, Metz et al. 2012). Mortality risk was highest during demanding life history stages (late gestation and lactation), and adult mortality risk declined when neonates were available as prey. Nutritional condition of females was lowest in mid-summer and coincided with the period when most non-predation mortalities occurred (i.e., starvation), and a period of high overall mortality risk. These seasonal patterns in mortality provide insight into potential mechanisms contributing to caribou vulnerability. Although wolf predation was the main, proximate cause of boreal caribou mortality in our study, other non-predator-related factors mediate predation and contribute to it. Predator-prey encounter probabilities, energetic demands, and prey nutritional condition are factors that may contribute to seasonal variation in mortality of boreal caribou, and can be considered hypotheses for further research to better understand seasonal pressures on this species.

TABLES

Table 1. Non-predation or malnutrition mortalities in published studies of woodland caribou (boreal and mountain ecotypes) in western Canada, recorded as the number and percentage of total documented mortalities.

Reference	No. non-predation (carcass intact)	Total mortalities	No. assigned cause of death	Non-predation as percent of total mortalities
(McLoughlin et al. 2003)	5	112	80	4
(Seip 1992)	2		18	11
(Wittmer et al. 2005)	10	155	95	6
(Stuart-Smith et al. 1997)	2	16	16	13
(McLellan et al. 2012): Females only	7	61	61	11*

* does not include 5 “unknown-not predation” (7 were described as “malnutrition”). Including both would result in non-predation mortalities increasing to 20% of total mortalities.

Table 2. Cause of mortalities in each mortality period identified in a mixed generalized additive model (GAMM) of boreal caribou mortality risk across the calendar year. The GAMM fit data from 359 adult female boreal caribou monitored in the southern Northwest Territories (2003-2018), with known date of death for 139 total mortalities. Mortality periods were identified using inflection points from the fitted model.

Cause	Winter	Pre-calving	Post-calving	Mid-summer	Late		Totals
					summer / rut	Late autumn	
Accident	2	0	0	0	0	1	3
Harvest	0	5	0	2	0	1	8
Non-predation	0	1	10	3	0	0	14
Predation	4	32	10	20	6	9	82
Unknown	1	9	5	5	5	7	32
Totals	7	47	25	30	11	18	139

FIGURES

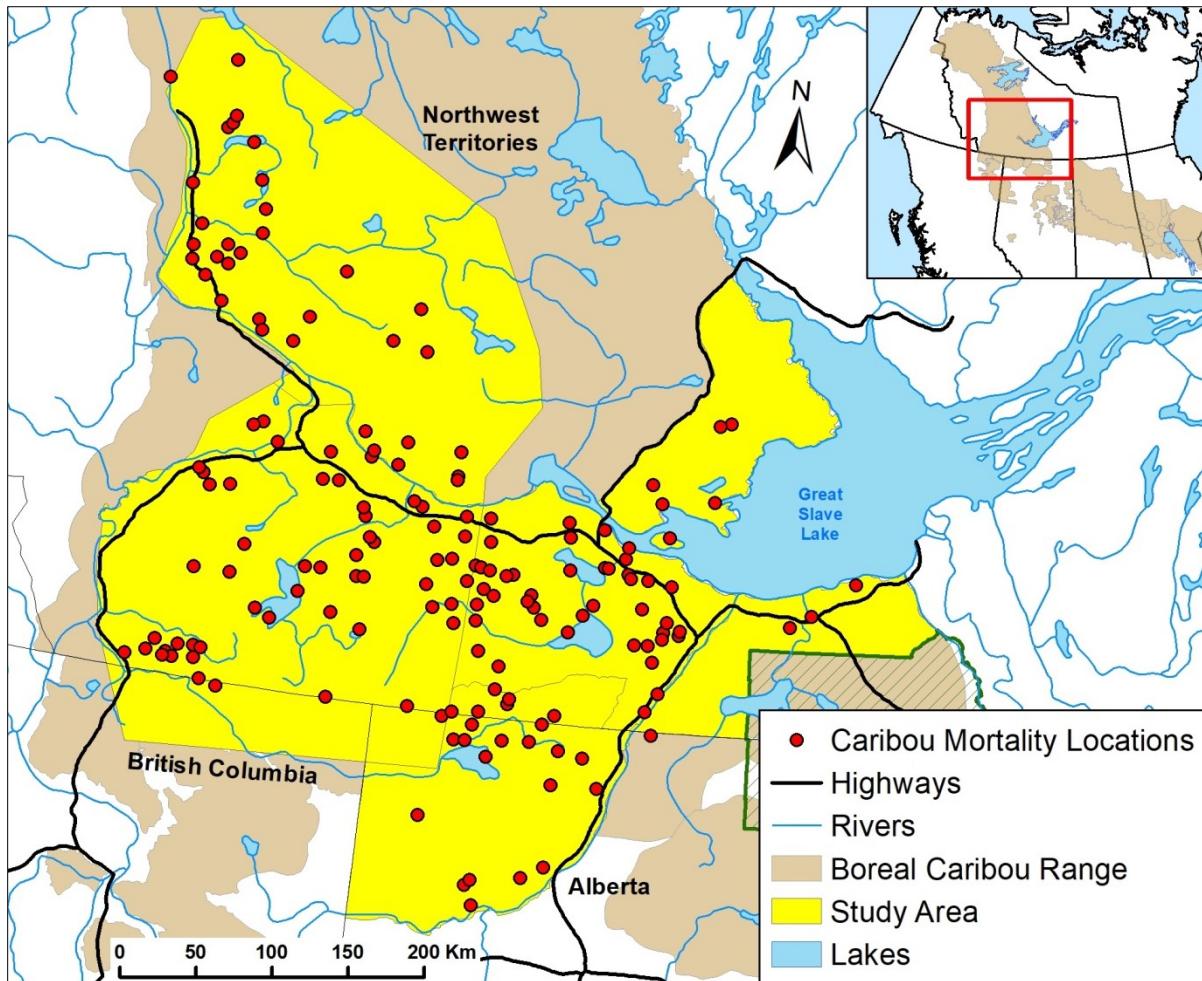


Figure 1. Study area primarily located in the southern Northwest Territories, Canada, with locations of adult female boreal caribou mortalities.

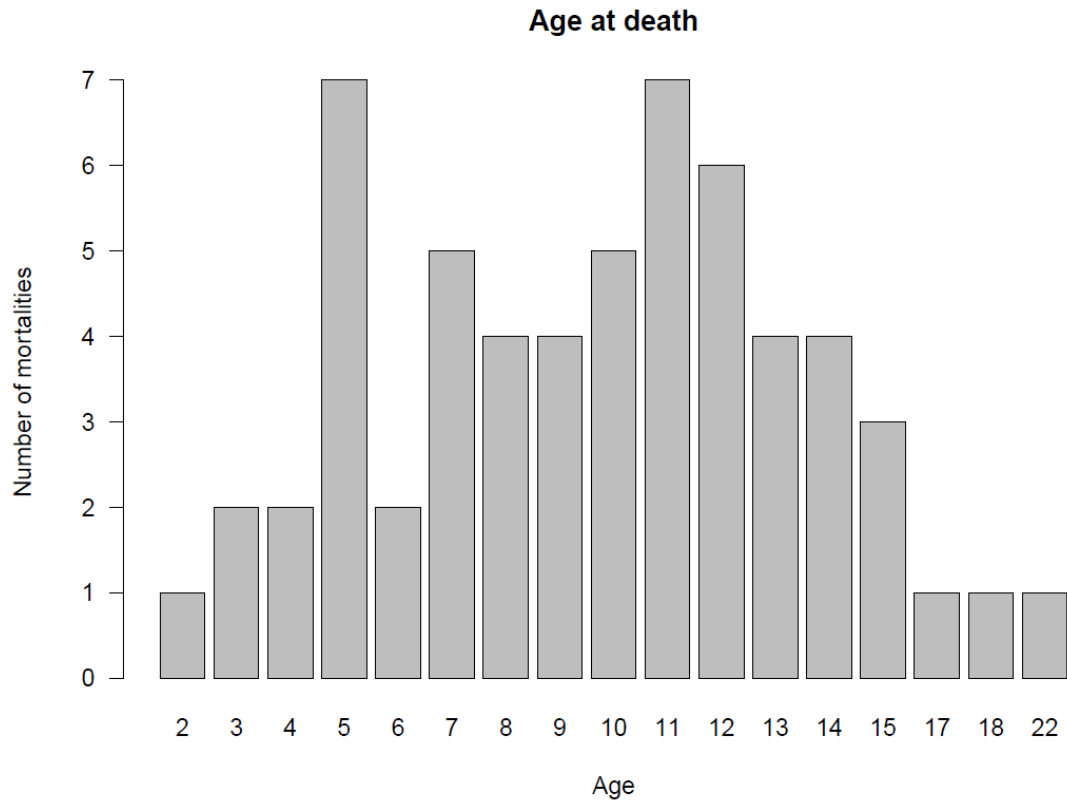


Figure 2. Age distribution at death for known-age predation mortalities of adult (2+ years) female boreal caribou (n=61) in the southern Northwest Territories, as determined by analysis of cementum annuli of teeth collected at mortality sites (2003-2017).

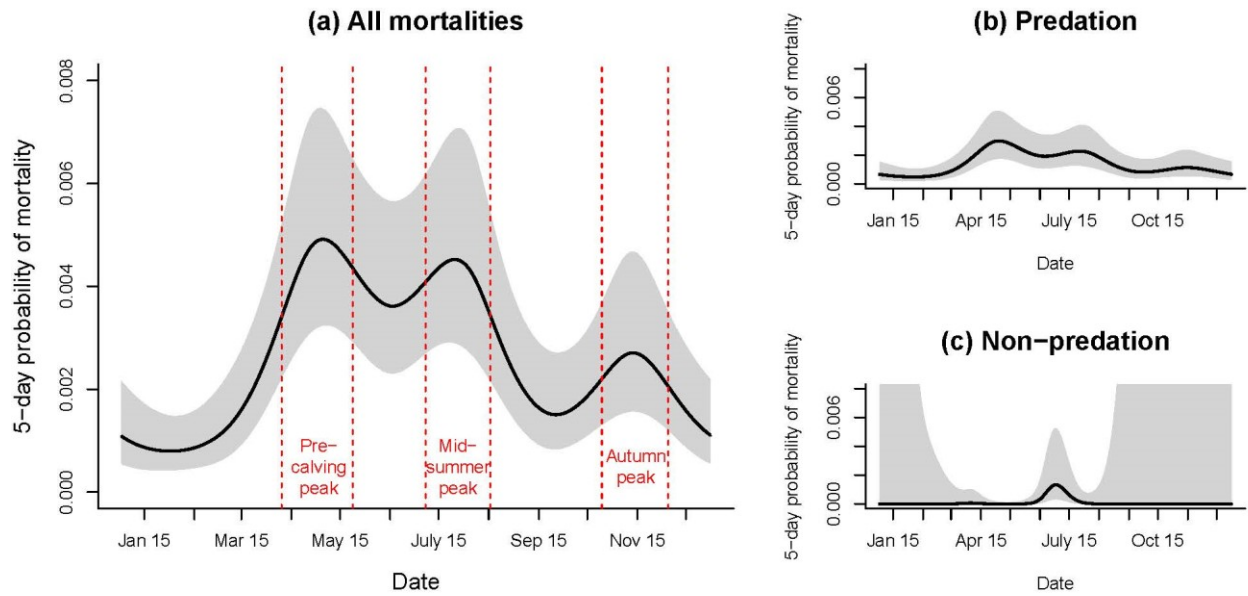


Figure 3. Mixed generalized additive models (GAMMs) of boreal caribou mortality risk across the calendar year: (a) all mortalities; (b) predation mortalities; (c) non-predation mortalities. The shaded areas represents the 95% confidence intervals. Vertical dashed lines in (a) indicate the inflection or ‘change’ points used to delineate periods identified by the GAMM, and subsequently evaluate cause of death by those periods. The GAMMs fit data from 359 adult female boreal caribou monitored in the southern Northwest Territories (2003-2018), with known date of death for 139 total mortalities, 82 predation mortalities, and 14 non-predation mortalities.

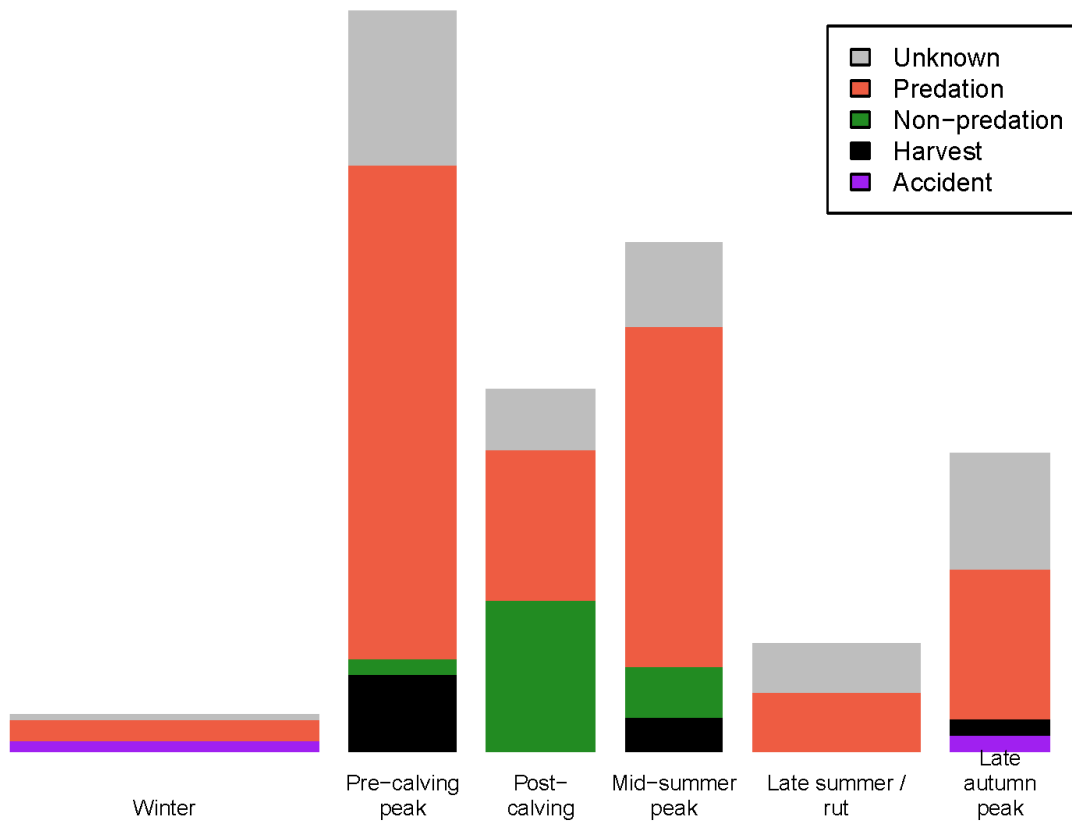


Figure 4. Cause of mortalities in each mortality period identified in a mixed generalized additive model (GAMM) of boreal caribou mortality risk across the calendar year. The GAMM fit data from 359 adult female boreal caribou monitored in the southern Northwest Territories (2003-2018), with known date of death for 139 total mortalities. Mortality periods were identified using inflection points from the fitted model. Width of bars corresponds to number days in period.

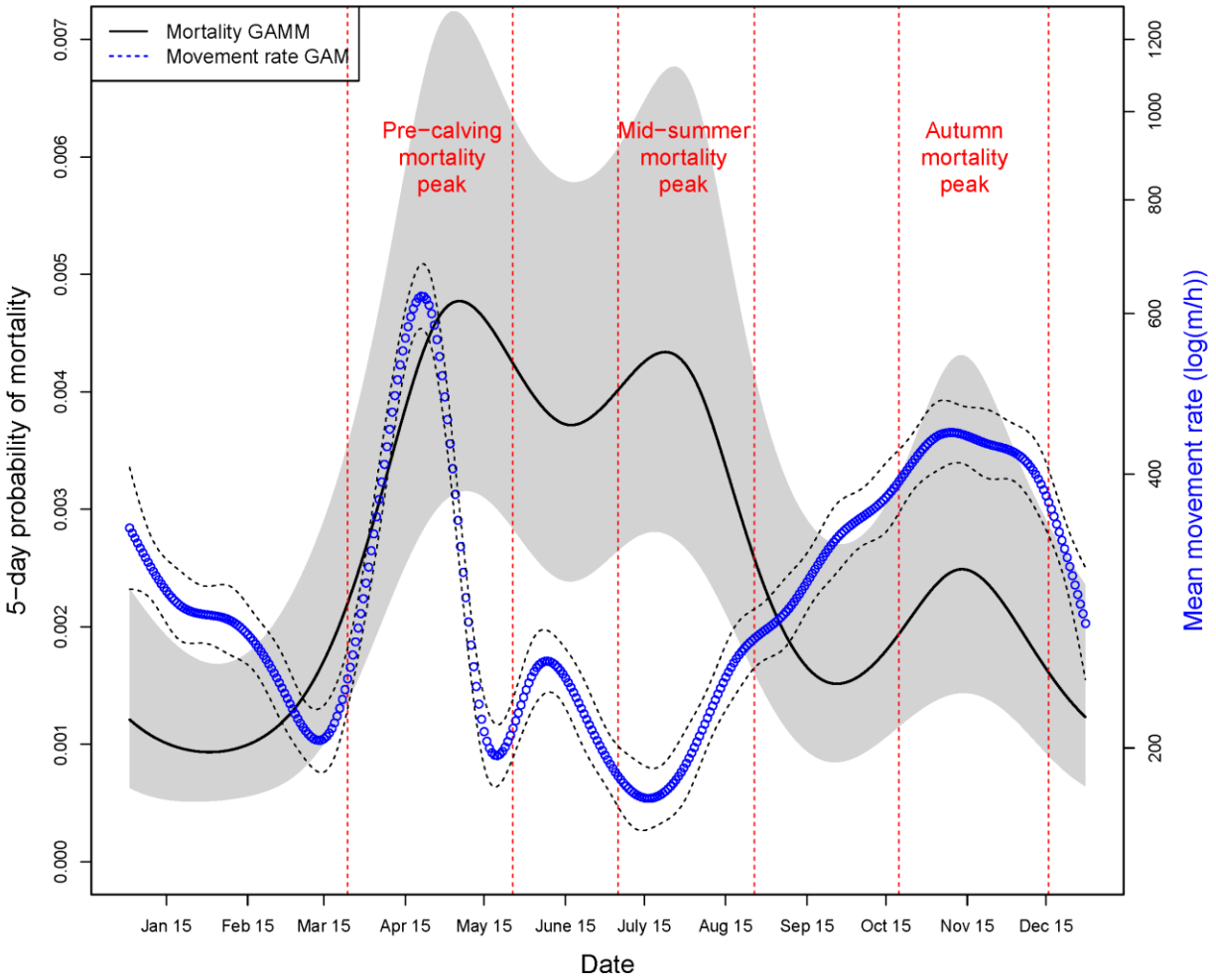


Figure 5. Generalized additive model (GAM) of adult female boreal caribou mean movement rates in the southern Northwest Territories, 2003-2018 (blue dotted line). Dashed lines show 95% confidence intervals. This GAM is overlaid on the generalized additive mixed model (GAMM) of boreal caribou mortality risk shown in Fig. 3a. Vertical dashed lines indicate the three ‘high mortality’ seasons identified in the GAMM using inflection points to delineate periods.

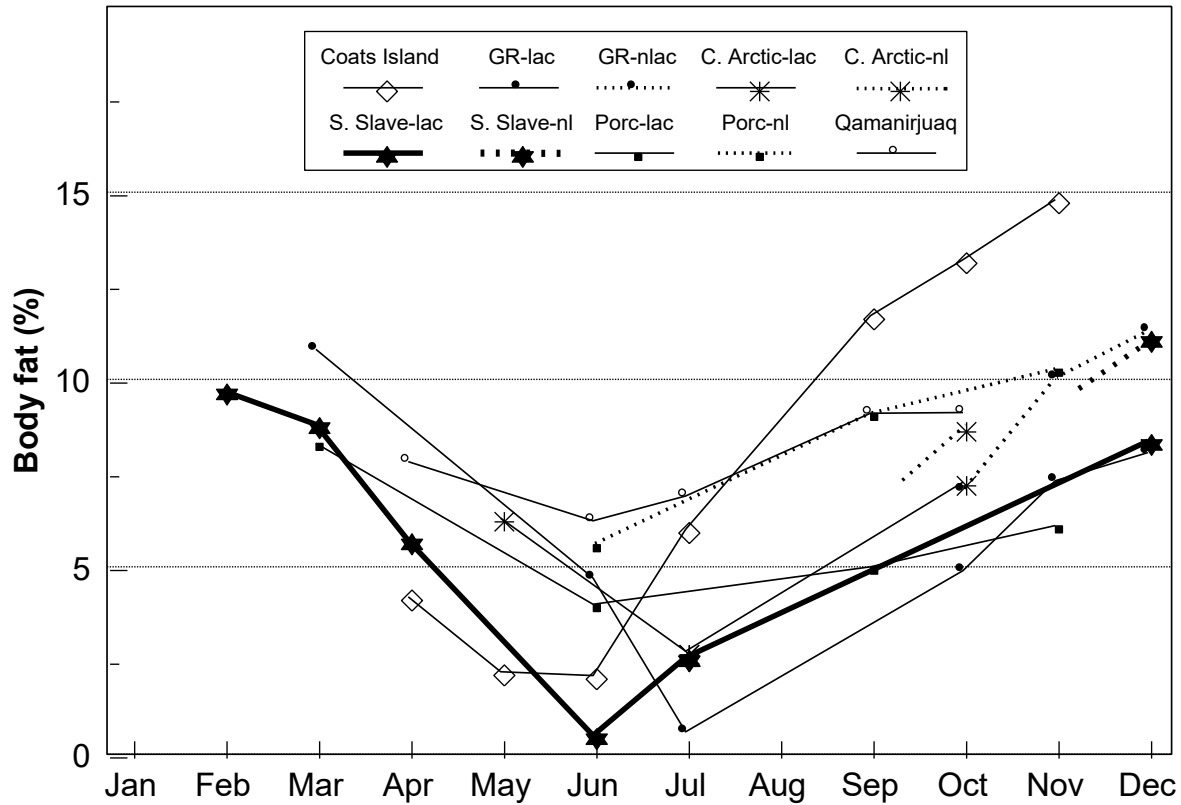


Figure 6. Annual patterns of percent fat of the ingesta-free body of adult females (i.e., body condition) for barren-ground caribou, graphed by J. Cook using published data: barren-ground caribou for the Coats Island population in northern Hudson Bay (Adamczewski et al. 1987); George River population (GR) mainly in northern Quebec (Huot 1989, Crête and Huot 1993); the Central Arctic population (C. Arctic) in Alaska (Table 2 in Gerhart et al. 1996); the Porcupine (Porc) population in eastern Alaska and western Canada (Table 1 in Chan-McLeod et al. 1999); and the Qamanirjuaq population in eastern NT and northern Manitoba to Hudson Bay (from Fig. 15 [prime age caribou] in Dauphiné 1976). All data sets except South Slave were from harvested caribou. South Slave data are from body condition measurements of live caribou during captures in December, February and March, and from marrow fat estimates from bones retrieved at mortality sites in April, June and July. Where available, data for lactating (lac) and non-lactating (nl) females in summer and autumn within herds are presented.

REFERENCES

- Adamczewski, J. Z., C. C. Gates, R. J. Hudson, and M. A. Price. 1987. Seasonal changes in body composition of mature female caribou and calves (*Rangifer tarandus groenlandicus*) on an arctic island with limited winter resources. *Canadian Journal of Zoology* **65**:1149-1157.
- Adamczewski, J. Z., R. J. Hudson, and C. C. Gates. 1993. Winter energy balance and activity of female caribou on Coats Island, Northwest Territories: the relative importance of foraging and body reserves. *Canadian Journal of Zoology* **71**:1221-1229.
- Alberta Biodiversity Monitoring Institute. 2017. Censusing wolves to determine associations between human footprint, habitat, and boreal caribou population growth rates: summary of field activities for the 2017 Fort Providence wolf censuses. Edmonton, Alberta, Canada.
- Alberta Biodiversity Monitoring Institute. 2018. Counting wolves to determine associations between human footprint, habitat, and boreal caribou population growth rates: interim report for the 2018 Fort Resolution wolf surveys. Edmonton, Alberta, Canada.
- Albon, S. D., T. N. Coulson, D. Brown, F. E. Guinness, J. M. Pemberton, and T. H. Clutton-Brock. 2000. Temporal changes in key factors and key age groups influencing the population dynamics of female red deer. *Journal of Animal Ecology* **69**:1099-1110.
- Andrén, H., and O. Liberg. 2015. Large impact of Eurasian lynx predation on roe deer population dynamics. *PloS one* **10**:e0120570-e0120570.
- Basille, M., D. Fortin, C. Dussault, J.-P. Ouellet, and R. Courtois. 2013. Ecologically based definition of seasons clarifies predator–prey interactions. *Ecography* **36**:220-229.

- Bender, L. C., J. G. Cook, R. C. Cook, and P. B. Hall. 2008. Relations between nutritional condition and survival of North American elk (*Cervus elaphus*). *Wildlife Biology* **14**:70-80.
- Bergerud, A. T., and J. P. Elliot. 1986. Dynamics of caribou and wolves in northern British Columbia. *Canadian Journal of Zoology* **64**:1515-1529.
- Bergerud, A. T., R. Ferguson, and H. E. Butler. 1990. Spring migration and dispersion of woodland caribou at calving. *Animal Behaviour* **39**:360-368.
- Bergman, E. J., R. A. Garrott, S. Creel, J. J. Borkowski, R. Jaffe, and F. G. R. Watson. 2006. Assessment of prey vulnerability through analysis of wolf movements and kill sites. *Ecological Applications* **16**:273-284.
- Brown, G., L. Landriault, D. H. Sleep, and F. Mallory. 2007. Comment arising from a paper by Wittmer et al.: hypothesis testing for top-down and bottom-up effects in woodland caribou population dynamics. *Oecologia* **154**:485-492.
- Burnham, K. & Anderson, D. (2002) *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach, 2nd edn. Springer, New York, New York, USA.*
- Chan-McLeod, A. C. A., R. G. White, and D. F. Holleman. 1994. Effects of protein and energy intake, body condition, and season on nutrient partitioning and milk production in caribou and reindeer. *Canadian Journal of Zoology* **72**:938-947.
- Chan-McLeod, A. C. A., R. G. White, and D. E. Russell. 1999. Comparative body composition strategies of breeding and nonbreeding female caribou. *Canadian Journal of Zoology* **77**:1901-1907.
- Chesson, P. 2003. Understanding the role of environmental variation in population and community dynamics. *Theoretical Population Biology* **64**:253-254.

- Clutton-Brock, T. H., S. D. Albon, and F. E. Guinness. 1989. Fitness costs of gestation and lactation in wild mammals. *Nature* **337**:260-262.
- Collins, C., and R. Kays. 2011. Causes of mortality in North American populations of large and medium-sized mammals. *Animal Conservation* **14**:474-483.
- Cook, J. G., B. K. Johnson, R. C. Cook, R. A. Riggs, T. Delcurto, L. D. Bryant, and L. L. Irwin. 2004. Effects of summer-autumn nutrition and parturition date on reproduction and survival of elk. *Wildlife Monographs* **155**:1-61.
- Cook, R. C., J. G. Cook, D. L. Murray, P. Zager, B. K. Johnson, and M. W. Gratson. 2001. Development of predictive models of nutritional condition for Rocky Mountain elk. *The Journal of Wildlife Management* **65**:973-987.
- Cook, R. C., J. G. Cook, T. R. Stephenson, W. L. Myers, S. M. McCorquodale, D. J. Vales, L. L. Irwin, P. B. Hall, R. D. Spencer, S. L. Murphie, K. A. Schoenecker, and P. J. Miller. 2010. Revisions of rump fat and body scoring indices for deer, elk, and moose. *Journal of Wildlife Management* **74**:880-896.
- Cook, R. C., J. G. Cook, D. J. Vales, B. K. Johnson, S. M. Mccorquodale, L. A. Shipley, R. A. Riggs, L. L. Irwin, S. L. Murphie, B. L. Murphie, K. A. Schoenecker, F. Geyer, P. B. Hall, R. D. Spencer, D. A. Immell, D. H. Jackson, B. L. Tiller, P. J. Miller, and L. Schmitz. 2013. Regional and seasonal patterns of nutritional condition and reproduction in elk. *Wildlife Monographs* **184**:1-45.
- Coulson, T., E. A. Catchpole, S. D. Albon, B. J. T. Morgan, J. M. Pemberton, T. H. Clutton-Brock, M. J. Crawley, and B. T. Grenfell. 2001. Age, sex, density, winter weather, and population crashes in Soay sheep. *Science* **292**:1528-1531.

- Crête, M., and J. Huot. 1993. Regulation of a large herd of migratory caribou: summer nutrition affects calf growth and body reserves of dams. *Canadian Journal of Zoology* **71**:2291-2296.
- Crête, M., and S. Larivière. 2003. Estimating the costs of locomotion in snow for coyotes. *Canadian Journal of Zoology* **81**:1808-1814.
- Dauphiné, T. C. 1976. Biology of the Kaminiriak population of barren-ground caribou. Part 4: Growth, reproduction and energy reserves. *Canadian Wildlife Service Report Series* **38**: 1-71.
- DelGiudice, G. D., M. R. Riggs, P. Joly, and W. Pan. 2002. Winter severity, survival, and cause-specific mortality of female white-tailed deer in north-central Minnesota. *The Journal of Wildlife Management* **66**:698-717.
- DeMars, C. A. 2015. Calving behavior of boreal caribou in a multi-predator, multi-use landscape. University of Alberta, Edmonton, Alberta, Canada.
- Dickie, M., R. Serrouya, R. S. McNay, and S. Boutin. 2017. Faster and farther: wolf movement on linear features and implications for hunting behaviour. *Journal of Applied Ecology* **54**:253-263.
- Douhard, M., S. Guillemette, M. Festa-Bianchet, and F. Pelletier. 2018. Drivers and demographic consequences of seasonal mass changes in an alpine ungulate. *Ecology* **99**:724-734.
- Dumont, A., J.-P. Ouellet, M. Crête, and J. Huot. 2005. Winter foraging strategy of white-tailed deer at the northern limit of its range. *Écoscience* **12**:4:476-484.
- Dyer, S. J., J. P. O'Neill, S. M. Wasel, and S. Boutin. 2001. Avoidance of industrial development by woodland caribou. *The Journal of Wildlife Management* **65**:531-542.

- Ecosystem Classification Group. 2009. Ecological Regions of the Northwest Territories -Taiga Plains. Government of the Northwest Territories, Yellowknife, NT, Canada.
- Environment Canada. 2011. Scientific Assessment to Inform the Identification of Critical Habitat for Woodland Caribou (*Rangifer tarandus caribou*), Boreal Population, in Canada: 2011 update. Page 102 pp plus appendices, Ottawa, Ontario, Canada.
- Environment Canada. 2012. Recovery Strategy for the Woodland Caribou (*Rangifer tarandus caribou*), Boreal population, in Canada. Environment Canada, Ottawa.
- Ewacha, M. V. A., J. D. Roth, W. G. Anderson, D. C. Brannen, and D. L. J. Dupont. 2017. Disturbance and chronic levels of cortisol in boreal woodland caribou. **81**:1266-1275.
- Forde, T. L., K. Orsel, R. N. Zadoks, R. Biek, L. G. Adams, S. L. Checkley, T. Davison, J. De Buck, M. Dumond, B. T. Elkin, L. Finnegan, B. J. Macbeth, C. Nelson, A. Niptanatiak, S. Sather, H. M. Schwantje, F. van der Meer, and S. J. Kutz. 2016. Bacterial Genomics Reveal the Complex Epidemiology of an Emerging Pathogen in Arctic and Boreal Ungulates. *Frontiers in Microbiology* **7**.
- Forsyth, D. M., R. P. Duncan, K. G. Tustin, and J.-M. Gaillard. 2005. A substantial energetic cost to male reproduction in a sexually dimorphic ungulate. *Ecology* **86**:2154-2163.
- Fretwell, S. D. 1972. *Populations in a Seasonal Environment*. Princeton University Press, Princeton, New Jersey.
- Fuller, T. K. 1989. Denning behavior of wolves in north-central Minnesota. *The American Midland Naturalist* **121**:184-188.
- Fuller, T. K. 1991. Effect of snow depth on wolf activity and prey selection in north central Minnesota. *Canadian Journal of Zoology* **69**:283-287.

- Gaillard, J.-M., M. Festa-Bianchet, N. G. Yoccoz, A. Loison, and C. Toïgo. 2000. Temporal variation in fitness components and population dynamics of large herbivores. *Annual Review of Ecology and Systematics* **31**:367-393.
- Gardner, J. L., T. Amano, W. J. Sutherland, M. Clayton, and A. Peters. 2016. Individual and demographic consequences of reduced body condition following repeated exposure to high temperatures. *Ecology* **97**:786-795.
- Garroway, C. J., and H. G. Broders. 2005. The quantitative effects of population density and winter weather on the body condition of white-tailed deer (*Odocoileus virginianus*) in Nova Scotia, Canada. *Canadian Journal of Zoology* **83**:1246-1256.
- Gerhart, K. L., R. G. White, R. D. Cameron, and D. E. Russell. 1996. Body composition and nutrient reserves of arctic caribou. *Canadian Journal of Zoology* **74**:136-146.
- Gilman, R. T., N. E. Mathews, B. G. Skinner, V. L. Julis, E. S. Frank, and J. Paul-Murphy. 2010. Effects of maternal status on the movement and mortality of sterilized female white-tailed deer. *The Journal of Wildlife Management* **74**:1484-1491.
- Gonzalez, G., and J.-P. Crampe. 2001. Mortality patterns in a protected population of isards (*Rupicapra pyrenaica*). *Canadian Journal of Zoology* **79**:2072-2079.
- Government of Canada. 2019. Monthly summaries of snow on ground, Hay River weather station. Available http://climate.weather.gc.ca/prods_servs/cdn_climate_summary_e.html [accessed on 10 Dec 2019].
- Gurarie, E., and O. Ovaskainen. 2013. Towards a general formalization of encounter rates in ecology. *Theoretical Ecology* **6**:189-202.

- Gurarie, E., P. R. Thompson, A. P. Kelly, N. C. Larter, W. F. Fagan, and K. Joly. 2019. For everything there is a season: Analysing periodic mortality patterns with the cyclomort r package. *Methods in Ecology and Evolution* **11**:129-138.
- Helle, T., and L. Tarvainen. 1984. Effects of insect harassment on weight gain and survival in reindeer calves. *Rangifer* **4**:24-27.
- Holt, R. D. 1977. Predation, apparent competition, and the structure of prey communities. *Theoretical Population Biology* **12**:197-229.
- Holt, R. D. 2008a. IJEE soapbox: Habitats and seasons. *Israel Journal of Ecology and Evolution* **54**:279-285.
- Holt, R. D. 2008b. Theoretical perspectives on resource pulses. *Ecology* **89**:671-681.
- Huggard, D. J. 1993. Prey selectivity of wolves in Banff National Park. II. Age, sex, and condition of elk. *Canadian Journal of Zoology* **71**:140-147.
- Hunter, M. D., and P. W. Price. 1992. Playing chutes and ladders: Heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology* **73**:724-732.
- Huot, J. 1989. Body composition of the George River caribou (*Rangifer tarandus caribou*) in fall and late winter. *Canadian Journal of Zoology* **67**:103-107.
- Husseman, J. S., D. L. Murray, G. Power, C. Mack, C. R. Wenger, and H. Quigley. 2003. Assessing differential prey selection patterns between two sympatric large carnivores. *Oikos* **101**:591-601.
- James, A. R., S. Boutin, D. M. Hebert, A. B. Rippin, and J. White. 2004. Spatial separation of caribou from moose and its relation to predation by wolves. *Journal of Wildlife Management* **68**:799-809.

- James, A. R., and A. K. Stuart-Smith. 2000. Distribution of caribou and wolves in relation to linear corridors. *The Journal of Wildlife Management* **64**:154-159.
- Kautz, T. M., J. L. Belant, D. E. Beyer Jr., B. K. Strickland, and J. F. Duquette. 2020. Influence of body mass and environmental conditions on winter mortality risk of a northern ungulate: Evidence for a late-winter survival bottleneck. *Ecology and Evolution* **n/a**.
- Kie, J. G. 1978. Femur marrow fat in white-tailed deer carcasses. *The Journal of Wildlife Management* **42**:661-663.
- Larter, N. C., and D. G. Allaire. 2016. Longevity and mortality of boreal woodland caribou (*Rangifer tarandus caribou*) of the Dehcho Region, Northwest Territories. *Canadian Field-Naturalist* **130**:222-223.
- Latham, A. D. M. 2009. Wolf ecology and caribou-primary prey-wolf spatial relationships in low productivity peatland complexes in northeastern Alberta. University of Alberta, Edmonton, Alberta.
- Latham, A. D. M., M. C. Latham, K. H. Knopff, M. Hebblewhite, and S. Boutin. 2013. Wolves, white-tailed deer, and beaver: implications of seasonal prey switching for woodland caribou declines. *Ecography* **36**:1276-1290.
- Latham, A. D. M., M. C. Latham, N. A. McCutchen, and S. Boutin. 2011. Invading white-tailed deer change wolf-caribou dynamics in northeastern Alberta. *The Journal of Wildlife Management* **75**:204-212.
- Linnell, J. D. C., R. Aanes, and R. Andersen. 1995. Who killed Bambi? The role of predation in the neonatal mortality of temperate ungulates. *Wildlife Biology* **1**:209-223.

- Loison, A., M. Festa-Bianchet, J.-M. Gaillard, J. T. Jorgenson, and J.-M. Jullien. 1999. Age-specific survival in five populations of ungulates: Evidence of senescence. *Ecology* **80**:2539-2554.
- Mattisson, J., G. R. Rauset, J. Odden, H. Andréén, J. D. C. Linnell, and J. Persson. 2016. Predation or scavenging? Prey body condition influences decision-making in a facultative predator, the wolverine. *Ecosphere* **7**:e01407.
- McLellan, M. L., R. Serrouya, B. N. McLellan, K. Furk, D. C. Heard, and H. U. J. O. Wittmer. 2012. Implications of body condition on the unsustainable predation rates of endangered mountain caribou. *Oecologia* **169**:853-860.
- McLoughlin, P. D., J. S. Dunford, and S. Boutin. 2005. Relating predation mortality to broad-scale habitat selection. *Journal of Animal Ecology* **74**:701-707.
- McLoughlin, P. D., E. Dzus, B. Wynes, and S. Boutin. 2003. Declines in populations of woodland caribou. *The Journal of Wildlife Management*:755-761.
- McLoughlin, P. D., J. M. Gaillard, M. S. Boyce, C. Bonenfant, F. Messier, P. Duncan, D. Delorme, B. V. Moorter, S. Saïd, and F. Klein. 2007. Lifetime reproductive success and composition of the home range in a large herbivore. *Ecology* **88**:3192-3201.
- McLoughlin, P. D., C. Superbie, K. Stewart, P. Tomchuk, B. Neufeld, D. Barks, T. Perry, R. Greuel, C. Regan, A. Truchon-Savard, S. Hart, J. Henkelman, and J. F. Johnstone. 2019. Population and habitat ecology of boreal caribou and their predators in the Saskatchewan Boreal Shield. University of Saskatchewan, Department of Biology, University of Saskatchewan, Saskatoon.
- McMeans, B. C., K. S. McCann, M. Humphries, N. Rooney, and A. T. Fisk. 2015. Food web structure in temporally-forced ecosystems. *Trends in Ecology & Evolution* **30**:662-672.

- Mech, L. D. 2007. Femur-marrow fat of white-tailed deer fawns killed by wolves. *The Journal of Wildlife Management* **71**:920-923.
- Mech, L. D., and G. D. Delgiudice. 1985. Limitations of the marrow-fat technique as an indicator of body condition. *Wildlife Society Bulletin* **13**:204-206.
- Messier, F. 1994. Ungulate population models with predation: A case study with the North American moose. *Ecology* **75**:478-488.
- Metz, M. C., D. W. Smith, J. A. Vucetich, D. R. Stahler, and R. O. Peterson. 2012. Seasonal patterns of predation for gray wolves in the multi-prey system of Yellowstone National Park. *Journal of Animal Ecology* **81**:553-563.
- Mislan, P., A. E. Derocher, V. L. St. Louis, E. Richardson, N. J. Lunn, and D. M. Janz. 2016. Assessing stress in Western Hudson Bay polar bears using hair cortisol concentration as a biomarker. *Ecological Indicators* **71**:47-54.
- Molinari-Jobin, A., P. Molinari, A. Loison, J.-M. Gaillard, and U. Breitenmoser. 2004. Life cycle period and activity of prey influence their susceptibility to predators. *Ecography* **27**:323-329.
- Montgomery, R. A., J. A. Vucetich, G. J. Roloff, J. K. Bump, and R. O. Peterson. 2014. Where wolves kill moose: The influence of prey life history dynamics on the landscape ecology of predation. *PloS one* **9**:1-7.
- Mumma, M. A., M. P. Gillingham, C. J. Johnson, and K. L. Parker. 2017. Understanding predation risk and individual variation in risk avoidance for threatened boreal caribou. *Ecology and Evolution* **7**:10266-10277.

- Mysterud, A., N. C. Stenseth, N. G. Yoccoz, R. Langvatn, and G. Steinheim. 2001. Nonlinear effects of large-scale climatic variability on wild and domestic herbivores. *Nature* **410**:1096-1099.
- Nagy, J. A. S. 2011. Use of space by caribou in northern Canada. University of Alberta.
- Owen-Smith, N. 2008. Changing vulnerability to predation related to season and sex in an African ungulate assemblage. *Oikos* **117**:602-610.
- Parker, K. L., P. S. Barboza, and M. P. Gillingham. 2009. Nutrition integrates environmental responses of ungulates. *Functional Ecology* **23**:57-69.
- Patterson, B. R., and F. Messier. 2003. Age and condition of deer killed by coyotes in Nova Scotia. *Canadian Journal of Zoology* **81**:1894-1898.
- Pérez, J. M., E. Serrano, R. C. Soriguer, F. J. González, M. Sarasa, J. E. Granados, F. J. Cano-Manuel, R. Cuenca, and P. Fandos. 2015. Distinguishing disease effects from environmental effects in a mountain ungulate: seasonal variation by body weight, hematology, and serum chemistry among iberian ibex (*Capra Pyrenaica*) affected by sarcoptic mange. *Journal of Wildlife Diseases* **51**:148-156.
- Peterson, R. O., J. D. Woolington, and T. N. Bailey. 1984. Wolves of the Kenai Peninsula, Alaska. *Wildlife Monographs* **88**:3-52.
- Pettorelli, N., S. Dray, J.-M. Gaillard, D. Chessel, P. Duncan, A. Illius, N. Guillon, F. Klein, and G. Van Laere. 2003. Spatial variation in springtime food resources influences the winter body mass of roe deer fawns. *Oecologia* **137**:363-369.
- Post, E., and N. C. Stenseth. 1999. Climatic variability, plant phenology, and northern ungulates. *Ecology* **80**:1322-1339.

- Potvin, F., H. Jolicoeur, and J. Huot. 1988. Wolf diet and prey selectivity during two periods for deer in Quebec: decline versus expansion. *Canadian Journal of Zoology* **66**:1274-1279.
- Proffitt, K. M., M. Hebblewhite, W. Peters, N. Hupp, and J. Shamhart. 2016. Linking landscape-scale differences in forage to ungulate nutritional ecology. *Ecological Applications* **26**:2156-2174.
- R Core Team (2019). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
- Rettie, W. J., and F. Messier. 2000. Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. *Ecography* **23**:466-478.
- Sand, H., C. Wikenros, P. Ahlqvist, T. H. Strømseth, and P. Wabakken. 2012. Comparing body condition of moose (*Alces alces*) selected by wolves (*Canis lupus*) and human hunters: consequences for the extent of compensatory mortality. *Canadian Journal of Zoology* **90**:403-412.
- Seip, D. R. 1992. Factors limiting woodland caribou populations and their interrelationships with wolves and moose in southeastern British Columbia. *Canadian Journal of Zoology* **70**:1494-1503.
- Serrouya, R., van Oort, H., DeMars, C., and S. Boutin. 2016. Human footprint, habitat, wolves and boreal caribou population growth rates. Report prepared by the Alberta Biodiversity Monitoring Institute, Edmonton, Alberta, Canada.
- Shave, J. R., A. E. Derocher, S. G. Cherry, and G. W. Thiemann. 2019. Chronic stress and body condition of wolf-killed prey in Prince Albert National Park, Saskatchewan. *Conservation Physiology* **7**:coz037.

- Smith, D. W., L. D. Mech, M. Meagher, W. E. Clark, R. Jaffe, M. K. Phillips, and J. A. Mack. 2000. Wolf–bison interactions in Yellowstone National Park. *Journal of Mammalogy* **81**:1128-1135.
- Sorensen, T., P. D. McLoughlin, D. Hervieux, E. Dzus, J. Nolan, B. O. B. Wynes, and S. Boutin. 2008. Determining sustainable levels of cumulative effects for boreal caribou. *The Journal of Wildlife Management* **72**:900-905.
- Stuart-Smith, A. K., C. J. Bradshaw, S. Boutin, D. M. Hebert, and A. B. Rippin. 1997. Woodland caribou relative to landscape patterns in northeastern Alberta. *The Journal of Wildlife Management* **61**:622-633.
- Thompson, I. D., P. A. Wiebe, E. Mallon, A. R. Rodgers, J. M. Fryxell, J. A. Baker, and D. Reid. 2015. Factors influencing the seasonal diet selection by woodland caribou (*Rangifer tarandus tarandus*) in boreal forests in Ontario. *Canadian Journal of Zoology* **93**:87-98.
- Vander Vennen, L. M., B. R. Patterson, A. R. Rodgers, S. Moffatt, M. L. Anderson, and J. M. Fryxell. 2016. Diel movement patterns influence daily variation in wolf kill rates on moose. *Functional Ecology* **30**:1568-1573.
- Wasser, S. K., J. L. Keim, M. L. Taper, and S. R. Lele. 2011. The influences of wolf predation, habitat loss, and human activity on caribou and moose in the Alberta oil sands. *Frontiers in Ecology and the Environment* **9**:546-551.
- Weladji, R. B., Ø. Holand, and T. Almøy. 2003. Use of climatic data to assess the effect of insect harassment on the autumn weight of reindeer (*Rangifer tarandus*) calves. *Journal of Zoology* **260**:79-85.
- White, E. R., and A. Hastings. 2019. Seasonality in ecology: Progress and prospects in theory. *PeerJ Preprints* **7**:e27235v2.

- Whittington, J., M. Hebblewhite, N. J. DeCesare, L. Neufeld, M. Bradley, J. Wilmshurst, and M. Musiani. 2011. Caribou encounters with wolves increase near roads and trails: a time-to-event approach. *Journal of Applied Ecology* **48**:1535-1542.
- Wittmer, H., A. E. Sinclair, and B. McLellan. 2005. The role of predation in the decline and extirpation of woodland caribou. *Oecologia* **144**:257-267.
- Wood, S. N. 2017. *Generalized Additive Models: An introduction with R* (2nd edition). CRC Press, University of Bristol, UK.
- Wood, S. N. 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)* **73**:3-36.
- Wood, S. N. and F. Scheipl. 2017. *gamm4: Generalized Additive Mixed Models using 'mgcv' and 'lme4'*. R package version 0.2-5. <https://CRAN.R-project.org/package=gamm4>.