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Influence of maternity penning on the success and timing of parturition by mountain caribou (*Rangifer tarandus caribou*)

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Abstract

Invasive conservation actions that require the capture and handling of individual animals are common, but the implications for both survival and reproduction are often not studied. Across North America, most populations of woodland caribou (*Rangifer tarandus caribou* Gmelin, 1788) are Threatened or Endangered. Maternity penning, where pregnant females are held in an enclosure until the calf is less vulnerable to predation, is one conservation action that is designed to increase population growth. Few studies have reported the influence of maternity penning on the occurrence or timing of parturition and the implications for reproduction. We quantified parturition success and dates of penned and free-ranging caribou within the Klinse-Za population of caribou found across east-central British Columbia, Canada. Parturition dates were identified using daily observations for penned caribou ($n=41$) and estimated dates for free-ranging caribou ($n=27$) generated using statistical modelling of GPS collar data. We related parturition outcomes to a range of ecological and environmental variables. We found that the occurrence and date of parturition did not differ between penned and free-ranging caribou. For all monitored animals there was an earlier calving date during years of higher snowfall and warmer winter weather. Our results suggested that maternity penning, a potentially invasive conservation action, did not increase or decrease the probability or date of parturition for this study population.

Keywords: caribou, captive rearing, endangered species, maternity pen, parturition, *Rangifer tarandus*

Introduction

The conservation of endangered species often requires invasive, expensive or controversial recovery actions (Pritchard et al. 2012; Russell et al. 2015). Examples of such efforts include population supplementation, captive breeding, and the lethal control of predators and competitors. The risks of these last-ditch recovery efforts are warranted for species that are close to extinction. In many cases, however, the efficacy and secondary effects of invasive conservation actions are not well tested or understood (Colman et al. 2014). There are few resources and fewer opportunities to experimentally test these activities on imperilled species that may suffer further decline from animal capture, handling, and transport (Fischer and Lindenmayer 2000; Bowkett 2009).

Caribou (*Rangifer tarandus* Linnaeus, 1758), a flagship and cultural keystone species, are Threatened or Endangered across much of Canada (Schaefer 2003; COSEWIC 2014; Gunn et al. 2011). Anthropogenic habitat alteration and the subsequent increase in predation is thought to be the proximate cause of decline for many populations of woodland caribou (*R. t. caribou* Gmelin, 1788; Festa-Bianchet et al. 2011). Known as “apparent competition”, an increase in early seral plant communities leads to larger and more widely distributed populations of moose (*Alces americanus* Clinton, 1822) and the primary predators of moose and caribou, wolves (*Canis lupus* Linnaeus, 1758; Wittmer et al. 2007). In combination with this numeric effect, the linear features associated with industrial activities increases the movement of wolves and predatory encounters with caribou (Dickie et al. 2017; Mumma et al. 2017; 2018).

Numerous conservation actions are currently being used to increase small populations of woodland caribou (Johnson et al. 2019; Serrouya et al. 2019; Heard and Zimmerman 2021). That includes captive breeding, population translocation, supplemental feeding, and actions focused

on the reduction in predation of both calf and adult caribou. Maternity penning is one approach for increasing calf survival during the neonatal period. Increased survival early in life may translate to greater calf recruitment and, ultimately, population growth (Adams et al. 2019). Although the methods of maternity penning projects differ, typically females are captured in the third trimester (e.g., mid-March), held in a fenced predator-free enclosure, fed natural or processed foods, and then released eight to ten weeks following parturition. Calves reared in maternity pens during the vulnerable neonatal period may be more physically fit and, hence, more capable of evading predators once released. Also, there may be some benefit to the adult caribou as they are temporarily free from predation and they have access to abundant and nutritious forage (Adams et al. 2019). Past applications of maternity penning of caribou have resulted in relatively few benefits to population growth. For large populations, the incremental increases in recruitment can be small and where predation of adults is limiting there is little advantage to increasing first year recruitment (Smith and Pittaway 2011; Adams et al. 2019; Johnson et al. 2019).

Nutritional condition and age can strongly influence reproductive output in ungulates (Charnov 1991; Gaillard et al. 2000; Adams 2005; Parker et al. 2009; Monteith et al. 2014; Newby and DeCesare 2020). For example, Adams and Dale (1998*a*) reported that average annual natality rates differed among age categories, with reproductive pauses of sexually mature females occurring predominantly in young (3–6 years) and old (≥ 14 years) females. Furthermore, environmental constraints can indirectly affect timing of parturition among individuals and years (Adams and Dale 1998*a; b*; Adams 2005; Paoli et al. 2018; Mallory et al. 2020). Animals with ideal weather conditions and access to high-quality forage usually attain a larger body size and better nutritional condition in comparison to animals with inadequate resources. These

differences in body condition influence the timing of parturition and lifetime reproductive output (Crête et al. 1993; Adams and Dale 1998a; Parker et al. 2009). However, relationships that link nutrition and reproductive performance are complex and can be affected by many factors such as population density, diseases, parasites, and age. Also, stress and exertion resulting from human interactions, including capture and captivity, could influence reproduction. Caribou are sensitive to harassment and disturbance during the calving period (Nellemann and Cameron 1996; Aastrup 2000; Weir et al. 2007; Lesmerises et al. 2017), but it is unknown if disturbance associated with maternity penning would have a significant influence on reproductive success. The benefits of increased nutrition associated with supplemental feeding may outweigh the costs of stress from being captured and held in captivity.

Past studies of the efficacy of maternity pens have focused on survival of dependent calves with implications for population growth (Smith and Pittaway 2011; Adams et al. 2019). To our knowledge, there has been no evaluation of how the capture, handling, and transport or supplemental feeding of adult caribou might influence reproductive outcomes. One might hypothesise a negative, stress-related effect of capture, potentially leading to pre-term abortion. Alternatively, supplemental feeding in the last trimester may result in increased maternal body condition and a greater probability of successful parturition or change in the date of parturition. Although caribou are capital breeders, primarily relying on stored reserves of energy and protein during reproduction, changes in the timing of parturition could lead to a mismatch between plant phenology and the period of peak milk production (Post et al. 2003; Taillon et al. 2013). Such an outcome could have implications for the production or recruitment of the calf (Post and Forchhammer 2008).

We quantified the occurrence and dates of parturition for caribou that were subjected to maternity penning. We define parturition as a successful birth producing a live calf. We tested a number of factors that were known to influence the occurrence or timing of parturition, such as the age of females and local climate. In particular, we tested two predictions relative to an effect of penning. First, we hypothesised that free-ranging caribou would experience a similar probability of parturition as penned cows. Such an outcome would be the result of penned and free-ranging cows originating from the same population with a similar likelihood of pregnancy. Also, we assumed that the capture, handling, and movement of caribou, although a stress-inducing activity, would not fundamentally place the fetus at risk.

Second, we hypothesised that inter-annual variation in parturition and calving dates was related to variation in climate and individual differences in fitness among female caribou. We predicted that in years with ideal climatic conditions there would be an increase in parturition events and earlier calving dates. Ideal weather conditions include a longer, more productive growing season and less severe winters. Also, we predicted that age of the cow would influence parturition success, with prime aged individuals (4–7 years of age) being the most successful. Lastly, we predicted that penned cows would have earlier calving dates in comparison to free-ranging cows. Penned caribou have access to unlimited feed and nutrition during the last trimester of pregnancy when 90% of the energy for fetal growth is required (Parker et al. 2009).

Materials and methods

Study area and population

The study was on the Klinse-Za population, a component of the Central Mountain Designatable Unit (DU 8) of caribou (COSEWIC 2011). Following from Canada's Species at

Risk Act, a DU was a unique component of biodiversity that was eligible for individual assessment and protection. Central Mountain caribou, one of 12 identified DUs for *R. tarandus* in Canada, occurred in east-central British Columbia (BC) and west-central Alberta. Populations of Central Mountain caribou experienced a rapid decline in abundance of at least 64% in the past three decades and were assessed as Endangered by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2014; Ray et al. 2015).

The Klinse-Za population ranged across an area of 5501 km² in the Rocky Mountains of northern BC (McNay et al. 2020). The habitat consisted of four biogeoclimatic zones: Sub-Boreal Spruce (SBS), Boreal White and Black Spruce (BWBS), Engelmann Spruce Subalpine Fir (ESSF) and Boreal Altai Fescue Alpine (BAFA) (Meidinger et al. 2020). This habitat was characterized by rolling hills, mountains, and forest cover of lodgepole pine (*Pinus contorta* Douglas ex Loudon) and hybrid white spruce (*Picea glauca* (Moench) x *P. engelmannii* (Parry ex Engelm.) at lower elevations, subalpine fir (*Abies lasiocarpa*; Hook. Nutt) and Engelmann spruce (*P. engelmannii*) at higher elevations, and alpine summits at about 1400 to 2090m (Meidinger et al. 2020). This area had a cold and snowy continental climate with long winters and relatively short and cool summers. The BAFA zone was the most extensive of the alpine zones, with low snowfall and windswept plateaus that were important winter habitat for caribou (Meidinger et al. 2020).

Anthropogenic disturbance covered approximately 89% of the low-elevation range and 34% of the entire population area (McNay et al. 2020). Disturbance was caused by forest harvesting, road construction, wind power generation, mining, hydro-electric power generation, oil and gas pipelines, roads, recreation, and other infrastructure/facilities (McNay et al. 2020; COSEWIC 2014).

Predators in the study area included gray wolf, black bear (*Ursus americanus* Pallas, 1780), grizzly bear (*U. arctos* Linnaeus, 1758), wolverine (*Gulo gulo* Linnaeus, 1758), cougar (*Puma concolor* Linnaeus, 1771), and potentially lynx (*Lynx canadensis* Kerr, 1792). Other ungulates included moose, elk (*Cervus canadensis* Linnaeus, 1758), and deer (*Odocoileus* spp. Rafinesque, 1832; McNay et al. 2020).

The Klinse-Za population demonstrated a rapid decline in abundance resulting in a number of intensive conservation actions, including wolf removal (2013 to present) and maternity penning (2014 to present; Bridger 2019; McNay et al. 2020). Wolf removal and penning have helped the population to increase from approximately 35 animals in 2014 to 101 animals in 2021 (McNay et al. 2021). Historically, this area had an abundance of caribou, plentiful enough to be hunted by local Indigenous communities (Spalding 2000). The elders of West Moberly First Nations spoke of once viewing a “sea of caribou” (WMFN 2009).

Similar to other penning projects for caribou (e.g., Adams et al. 2019), operation of the Klinse-za maternity pen required capturing pregnant cows during their third trimester with a netgun fired from a helicopter. Caribou were selected opportunistically and were not evaluated for pregnancy before penning. Captured animals were transported by helicopter to a predator-free fenced enclosure where they were held from mid-March to late July or early August. The cow and dependent calf were released approximately 8–10 weeks after parturition. The number of cows in the pen at any year depended on the population size and capture logistics, but was typically 10–20 (McNay et al. 2020). Procedures for capturing caribou, care while in captivity, and monitoring radio-collared caribou complied with guidelines established by the Canadian Council on Animal Care (2003; 2017), with standards for live animal capture and handling and

monitoring established by the BC Government. All activities were approved under BC Wildlife Act Permits FJ14-93094 and FJ18-93094.

The maternity pen was located in subalpine habitat about 80 km northwest of Chetwynd, BC (Figure 1). This site was at 1580m elevation and was chosen for its subalpine forest/meadow habitat that was historically used by caribou (Dubman et al. 2018). The 15-ha pen was enclosed by a tall geotextile fence, and surrounded by two electric fences to deter predators (Erickson and McNay 2018; Adams et al. 2019). Pinned caribou were fed lichen and commercial pellet rations daily. The proportional mixture of lichen and pellet ration was adjusted periodically to meet the nutritional demands of the pinned caribou (McNay et al. 2020).

Sampling design

From 2018 to 2020, we monitored the parturition status and timing of pinned and free-ranging caribou. We used visual observation to monitor and record the birth date of calves born in the pen. Frequent observations of free-ranging caribou were logistically difficult. Most methods result in a biased estimate as it can be difficult to observe a calf, especially if mortality occurs quickly after parturition and the calf is consumed by a predator. We used multiple lines of evidence to detect and confirm parturition events of free-ranging caribou, including video footage from camera collars, aerial telemetry flights, and statistical modelling of movement data collected with GPS collars. Pinned and free-ranging caribou were tested for pregnancy ($n=54$). Blood samples were taken during capture, and pregnancy was assumed if blood progesterone levels were ≥ 1.5 ng/mL or if pregnancy-specific protein B (PSPB) levels were >0.21 ng/mL (McNay et al. 2020).

Quantifying parturition events of free-ranging caribou

We used the DeMars et al. (2013) movement model to infer parturition of GPS-collared female caribou within the free-ranging portion of the Klinse-Za caribou population. The model infers a parturition event according to a reduction in the GPS inter-fix step length. Caribou were located with VECTRONIC Iridium (Vectronic Survey-2D GPS Iridium; VECTRONIC Aerospace GmbH, Berlin Germany) or Lotek Iridium (Lotek LiteTrack GPS Iridium with InSight-S Camera; Lotek Engineering Inc, Newmarket, Ontario) GPS collars. Free-ranging collared cows had a GPS fix rate of 2 locations per day ($n=4$) in 2018, and in 2019 and 2020 the fix rate was 4 locations per day ($n=10$, $n=13$, respectively). DeMars et al. (2013) developed and tested the model with a greater fix rate (12 locations per day), but observed relatively little sensitivity in the predictions of parturition date or occurrence after simulating a reduced fix rate and gaps in data. As reported by DeMars et al. (2013), we constrained break points to be a minimum of 24 step lengths away from either end of the timeseries.

We used the individual-based method that was premised on three hypothetical *a priori* movement models: a female without a calf (M_0), a female with a calf surviving to four weeks (M_1), and a female losing a calf prior to four weeks of age (M_2). Constant mean step lengths over the calving period indicated no parturition event (M_0). Break points represented a sudden drop or increase in movement, indicating parturition or neonatal mortality. A single break point followed by a linear increase in step lengths to pre-parturition movement rates indicated a female with a calf that survived (M_1). Two break points indicated a female with a calf that died (M_2). We used Akaike's Information Criterion (AIC) to calculate the most parsimonious model for each individual's movement patterns over the calving season (15 April – 31 July; Figure 1).

Verifying parturition events

We used aerial surveys or video footage observations to validate the accuracy of the parturition events predicted by the movement model. For the purpose of this study, we only confirmed if predicted parturition status matched field observations. We did not validate predictions of subsequent calf mortality events. Aerial surveys were flown to determine parturition status and calf mortality of collared caribou. We completed six flight days in 2018 (17 May, 22 May, 27 May, 2 June, 11 July, 12 July), two in 2019 (4 June, 5 July), and six in 2020 (15 May, 19 May, 23 May, 27 May, 18 June, 8 July).

GPS-collar video cameras were used during the 2020 calving season to record parturition events for six of the 13 free-ranging cows (Lotek LiteTrack GPS-Iridium with InSight-S Camera Lotek Engineering Inc., Newmarket, Ontario). Collars recorded 15 second video clips every 10 minutes from May to mid-June. Five collars successfully recorded videos, but only three captured parturition events, allowing the identification of an exact parturition date.

Statistical analysis

Parturition status and calving date

We used logistic regression and negative binomial count models to test model hypotheses that explained a parturition event (1 or 0) and variation in observed or predicted parturition dates for monitored female caribou (Table 1, 2, 3). The count was the number of days following the first observed parturition event for the monitoring year. Independent explanatory variables for both models included pen or free-ranging status, age class, and weather from 2018–2020 (Table

1). We used the variance inflation factor to test for multicollinearity. No covariates within a model surpassed the variance inflation threshold of 10 (Chatterjee and Hadi 2006).

The variable for pen or free-ranging represented the inclusion of the female caribou in the penning program during that observation year. We calculated weather variables using station data from Climate Data Canada (2020), taking the average from the two weather stations closest to the maternity pen. The Mackenzie weather station was located approximately 72 km southwest and the Chetwynd station was located approximately 76 km southeast from the pen.

We used weather data to calculate the growing season pre-gestation, winter weather during gestation, and spring weather, including green up, during the calving season (Table 1). We calculated the annual growing season productivity during the previous summer (before pregnancy) as the maximum value of accumulated daily-averaged temperature values $>5^{\circ}\text{C}$ during the growing season. We determined the length of the growing season by counting the days between the estimated seeding date (10 days after the first mean daily temp of 5°C) until fall frost (first day with minimum daily temperatures of $\leq 0^{\circ}\text{C}$) (Schmelzer et al. 2020). Winter severity was represented by the average temperature as well as the total snowfall during the winter of pregnancy (1 October – 30 April). We calculated the average temperature during the peak calving season (1 May – 30 June). Lastly, we calculated a relative measure of green up as the growing season start date during the spring of calving. We determined the growing season start date as the estimated seeding date (10 days after the first mean daily temp of 5°C ; Schmelzer et al. 2020).

There is strong theoretical and empirical evidence suggesting that age is important in determining parturition (Gaillard et al. 2000; Adams 2005; DeCesare et al. 2012). Thus, we included a variable for age in all logistic regression models. Age was categorised as ≤ 3 years, 4–

7 years, and 8+ years. Age category was either actual, if parturition date was known for calves that were held previously in the maternity pen ($n=14$), or estimated by tooth wear during capture ($n=54$) (GNWT Wildlife Care Committee 2018).

We used Akaike's Information Criterion for small sample sizes (AIC_c) to rank and select the most parsimonious candidate models for both the occurrence data and the count data of time to parturition (Anderson et al. 2000). For each analysis, we used the ΔAIC to identify the 'best' model of the set. Although AIC provides a relative assessment of model parsimony, the best model may have poor predictive capacity and ecological relevance. Thus, we used a leave-one-out cross-validation method (LOOCV) to assess the predictive accuracy of the models (Fielding and Bell 1997). Each parturition event was withheld sequentially from the model fitting process, and the resulting model ($n-1$) was used to predict an independent probability of parturition or parturition date for the withheld event (Fielding and Bell 1997). For the logistic regression, we used the probabilities calculated from the LOOCV to generate the Area Under the Curve (AUC) from an independent Receiver Operating Characteristic (ROC) test. The AUC represented the predictive accuracy of the model. Models that displayed an AUC score of 0.7 or greater were considered useful (Boyce et al. 2002). For the count models, we statistically compared the predicted parturition dates to the observed parturition dates using a two-sample Wilcoxon rank-sum test. We used 95% confidence intervals to assess the significance of each covariate in the top models. All statistical analyses were conducted in Stata (ver. 16; StataCorp 2016).

Results

In total, we monitored 41 penned and 27 free-ranging collared caribou. For free-ranging cows, the DeMars et al. (2013) movement model had an accuracy of 85%, determined by

dividing the total correctly predicted parturition events (true positives and true negatives) by the total sample number (Table 4). The false negative parturition events were assumed to be missed parturition events in the field, due to subsequent and unobserved calf mortality.

Parturition rate

The hormonal pregnancy rate of collared caribou from 2018–2020 was 0.80 ($n=54$), with a population-level parturition rate of 0.69 ($n=68$). Observed and modelled parturition rates of penned and free-ranging caribou were 0.76 ($n=41$) and 0.59 ($n=27$), respectively (Table 5). Parturition rates for free-ranging caribou were notably less in 2019 (0.50) when compared to penned caribou (0.81). We observed one stillbirth in the pen, which we classified as no parturition for the subsequent analysis.

None of the model hypotheses explained the variation in the occurrence of parturition. The most parsimonious model was age, with the probability of parturition increasing for age category 4–7 and decreasing for age category 8+. However, the covariates were not statistically significant, and the model was not different from the null model ($\Delta\text{AIC}=0.51$) (Tables 6, 7). All models had low predictive accuracy, with AUC values of < 0.48 (Table 6). This included the model that tested an effect of penning, suggesting that the likelihood of parturition did not differ between the penned and free-ranging caribou.

Parturition date

Of the 48 parturition events, there were 35 actual parturition dates, based on daily penning observations ($n=32$) and video collar footage ($n=3$). The remaining 13 dates were predicted using a combination of the DeMars et al. (2013) model, along with aerial telemetry

observations ($n=13$). Parturition dates ranged from 29 April to 4 July, with a median of 22 May and a mean of 26 May (Figure 2). The median parturition dates for penned and free ranging caribou were 22 May and 29 May, respectively.

The most parsimonious model for explaining calving date included a covariate for total winter snowfall ($AIC_c w=0.42$), where snowfall was negatively related to the date of parturition (Tables 7, 8). The second most parsimonious model included a covariate for temperature during the calving season ($\Delta AIC_c=0.17$), suggesting that parturition date was earlier with increasing temperature. Those models had good predictive performance as there were no significant differences between independent predicted and observed parturition dates ($Z=-1.66$, $P=0.10$; $Z=-1.547$, $P=0.12$, respectively). The covariates representing snowfall and temperature were both statistically significant (Table 7). There was very little support for the model representing the location of a caribou within or outside the maternity pen ($\Delta AIC_c=10.65$), suggesting that capturing caribou and holding them in a pen had little influence on the timing of parturition.

Discussion

Following three years of monitoring, penned caribou from the Klinse-Za population demonstrated a greater average parturition rate compared to the sample of free-ranging individuals. In contrast, and consistent with our first prediction, the statistical analyses revealed that the probability of a parturition event did not differ between penned and free-ranging cows. Furthermore, the difference in average parturition rates was largely attributed to observations of free-ranging caribou during 2019 (Table 5). Such inter-annual variation is consistent with our understanding of the reproductive ecology of woodland caribou. For example, Gustine et al. (2006) observed considerable variability in parturition for a population found in northeastern BC.

They reported a parturition rate of 55.6% (SE=17.6) in the first year of their study, followed by 76.9% (SE=12.2) for the second year of monitoring.

The pregnancy and parturition rates of caribou over the three-year monitoring period were 0.80 and 0.69, respectively. This rate of calf loss after pregnancy is similar to Walker et al. (2020) who reported a pregnancy rate of 0.87 and parturition rate of 0.76. We could find no data describing the loss of caribou calves between pregnancy and parturition. Late *in utero* reabsorption events are thought to be rare (Dauphine 1976; Ringberg and Aakvaag 1982), but calf mortality during the last trimester of pregnancy can still occur due to poor nutrition and the inability of a cow to meet the high energy demands of gestation (Roffe 1993). During the period of this study, 34 penned caribou were determined to be pregnant. We observed two apparent aborted births and one still birth.

A limitation of our methods is that the DeMars et al. (2013) movement model may not capture the birth of calves that are stillborn, non-viable (e.g., too weak to nurse), abandoned or killed immediately. Such observations may be missed if the cow maintains a normal daily step length immediately following parturition. Thus, the lower rate of parturition for free-ranging cows in our study could have been the product of undetected parturition events that were masked by early calf mortality. Calf survival can be highly variable among years, and substantial calf mortality is common during the neonatal period (Mahoney et al. 1990; Linnell et al. 1995; Gustine et al. 2006; Pinard et al. 2012).

DeMars et al. (2013) suggested using a 4-hour time interval between GPS fixes. Bonar et al. (2018) used a 2-hour time interval and found this to be even more accurate. The majority of our GPS collars had a 6-hour time interval, yet we successfully predicted the parturition event for 85% of the free-ranging caribou. A confounding factor is the realised fix rate of the collar that

can be influenced by vegetation overstory and topography (D'Eon et al. 2002; Cain et al. 2005). For the caribou we monitored, the fix rates were relatively high at 82–83% in 2018, 97–100% in 2019, and 91–99%, with one lower fix rate of 81% in 2020.

Caribou can produce offspring at two years of age, however young cows (≤ 3 years of age) have been shown to have low and variable reproductive potential (Charnov 1991; Gaillard et al. 2000; Adams 2005). Reproduction is more consistent for prime aged caribou, but is reduced again for older cows. Adams and Dale (1998a) reported that individuals from the Denali population of Grant's caribou (*R. t. groenlandicus* Borowski, 1780) had decreased natality when they were older than 14. Adams et al. (2019) reported that reproductive senescence began at the age of 8 or 9 for the Chisana population of woodland caribou, with natality rates declining from 0.95 for 4–6 year old caribou to 0.47 for 18 year old individuals. Given limitations in aging caribou from tooth wear, we adopted three broad age categories (i.e., ≤ 3 , 4–7 and 8+). Both parturition success and dates did not differ among these age categories. This was likely because none of the sampled caribou were estimated to be older than 11, and potentially did not reach reproductive senescence. Such a flattened age pyramid is consistent with small populations emerging from a demographic bottleneck, as was observed for the Klinse-Za population that had declined to approximately 35 individuals.

The effect of ungulate body condition on reproduction is well-known, with poorer female body condition leading to lower parturition rates and longer gestation periods (Skogland 1983; Cameron et al. 1993; Gerhart et al. 1997; Cook et al. 2004; Parker et al. 2009). Several studies have also related body condition and timing of parturition to climatic influences. We concluded that over the three-year study period, climate had an influence on the timing of parturition, with years of higher total snowfall and warmer winter temperatures resulting in an earlier calving

date. This finding is inconsistent with the results of other similar studies. In Ontario, Walker et al. (2020) observed the calving dates of woodland caribou in three different study regions. One region experienced significantly later birth dates relative to the other two, which was thought to be related to the 1.5–2.0 times greater snow in that region. Skogland (1983) observed that later calving dates were common for wild reindeer following winters of deep snowfall, when females were in poor body condition, suggesting that parturition was postponed until the fetus attained a critical size.

Several other authors reported that the time of calving was related to local climate and vegetation growth during spring. Paoli et al (2018) documented earlier reindeer calving dates in response to reduced April snow cover. Chen et al. (2018) found that peak calving dates of the Bathurst barren-ground caribou (*R. t. groenlandicus*) population were altered by both the previous year's conditions and the start of the growing season in the current year. Mallory et al. (2020) found that snow cover influenced the migration of barren-ground caribou to their calving grounds. They found that as the start of green-up advanced, so did migration and the date of peak calving. Plasticity in the length of gestation might allow for changes in the time of parturition in response to variation in annual winter conditions. However, this plasticity would likely not fully compensate for poor body condition resulting from undernutrition experienced during the previous summer or the winter of gestation (Mallory et al. 2020).

We suspect that climate-parturition relationships are population specific and a product of a number of interacting factors. Southern Mountain caribou, for example, are dependent on a deep snowpack to access arboreal lichen (Terry et al. 2000). Thus, one might hypothesise that deeper snow would result in greater access to forage, greater body condition, and an earlier not later calving date. Central Mountain caribou of the Klinse-Za population are less dependent on

arboreal lichen, but deep snow may facilitate access to that forage type. Alternatively, a deep snow pack that persists into spring may limit access to emergent vascular plants. Also, we expect some covariation between winter temperature and snow depth. Years with warmer temperatures may be associated with greater precipitation and snow with concurrent changes in access to terrestrial and arboreal lichen. Also, those warmer winters may provide earlier annual green up. Thus, it can be challenging to attribute one broadly measured climactic variable to an inherently variable biological phenomenon, such as the timing of parturition.

Parturition success and date has been related to maternal nutrition both late in gestation and as a product of dietary quality in the previous summer. Espmark (1980) noted that female reindeer held at a low nutritional level calved, on average, 4 days earlier when compared to well-nourished controls. Similarly, Crête et al. (1993) reported that with two years of *ad libitum* feeding, captive female caribou increased body mass, and calving dates advanced by two weeks. Escaping the high nutritional demands of lactation earlier enhances fat accretion and increases the chance that a cow will reach a condition where it can successfully breed and reach parturition the following year (Cook et al. 2004). Thus, where nutrition is limiting, the calving success and foraging ecology of the previous year may have an effect on body condition and a female's ability to reproduce in successive years. For the Klinse-Za population, the growing season for plants during the previous summer and the effect of penning during the last two months of pregnancy had no effect on parturition success or date. We did not have data describing the calving history of all study animals, thus, we could not test for an effect of reproductive history.

Observed variation in parturition success and date for the Klinse-Za population was not fully explained by our results. In particular, we had little success in modelling the probability of parturition. That lack of explanatory power may be related to a failure to test key hypotheses,

such as an individual cow's calving history, and a relatively small number of observed caribou within each year. Although on an annual basis, that sample represented a large proportion of the female caribou in the Klinse-Za population (~47 to 90%). Where other studies represented variation in climate across portions of caribou range (e.g., Walker et al. 2020) the data we applied were constant across space and only differed by year ($n=3$). Further, the data were taken from two weather stations adjacent to, but not directly within the study area. Those data represented the conditions of valley bottom not alpine areas where caribou spent the majority of their time.

The variation in parturition occurrence and dates could potentially be explained by a more sensitive measure of climate. Several other studies have used remotely sensed data to represent climate across a herd range. The CircumArctic Rangifer Monitoring and Assessment (CARMA) network has used NASA's Modern Era Retrospective Analysis for Research and Applications (MERRA) satellite data to create caribou-relevant climatic datasets across broad regional areas (Schmelzer et al. 2020). Mallory et al. (2020) used the Moderate Resolution Imaging Spectroradiometer (MODIS) imagery to derive snow cover and the normalized difference vegetation index values (NDVI) to assess migration timing and calving dates for barren-ground caribou. Our study area was small when compared to other caribou ranges. Also, we applied actual measures of climate not remotely sensed data that were extrapolated across relatively large cell-sizes (e.g., MERRA=50-km distance along latitudinal axis) and would be sensitive to the topographic variability found across the high-elevation ranges of the Klinse-Za population.

Parturition date could also be related to the estrous cycle and the spatial location of males and females during the breeding season. If females fail to conceive, they may go into a second or

third estrous (Bergerud 1975). The timing of the rut and the ability of a female to conceive may influence the parturition date. If rut timing is fairly stable across years, the effect of body condition on gestation time may be a more important driver of parturition date (Gurarie et al. 2019).

Conclusion

We found that the probability of parturition did not differ between penned and free-ranging cows. Parturition is not a constant for woodland caribou, but the statistical models that we tested did not explain the observed variation among caribou within the Klinse-Za population. In contrast, the statistical models represented observed variation in the timing of parturition. Penning did not have a statistical effect, but years of higher total snowfall and warmer winter temperatures resulted in an earlier calving date. There was likely some covariation between temperature and snowfall and the analysis was limited to only three years of climate data. Thus, we caution against using these findings to infer a mechanistic relationship between parturition and seasonal climate patterns.

Maternity penning is an invasive conservation action designed to avert population decline by increasing the survival of caribou calves and reproductively active females. However, there are few studies reporting the influences of maternity penning on parturition. Our data suggest that the effect of capture, feeding or care within a maternity pen does not influence the annual reproductive performance or timing of parturition for caribou from the Klinse-Za population. The lack of an apparent effect of maternity pens is an important conclusion as it is plausible that capture-related stress could lead to pre-term abortion and reduced reproductive productivity. Further, changes in parturition date associated with stress or supplemental feeding could lead to a

mismatch between peak lactation and plant phenology. Neither of those potential risks were apparent in our data. Likewise, there appeared to be little short-term reproductive advantage to penning caribou. Similar to the outcomes of our study, Adams et al. (2019) reported that annual natality rates did not differ significantly between captured and free-ranging radio collared females in any year that penning occurred, and that penned females produced calves that were of comparable mass to those born in the wild. Given our conclusion that maternity penning does not have a negative or positive effect on the underlying reproductive state within the year of capture, conservation advantages would need to be realised through a multi-year effect of feeding and reproductive success or more directly, decreased calf mortality and increased recruitment rates.

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Table 1. Independent variables for logistic regression and count models designed to quantify variation in parturition event and date of the Klinse-Za caribou (*Rangifer tarandus caribou*) population from 2018–2020. Weather data from Mackenzie and Chetwynd stations were from Climate Data Canada (2020).

Variable	Description
Age category	Age grouped into three categories: ≤ 3 years, 4–7 years, and 8+ years.
Pen or free-ranging	Caribou in the maternity pen (0) or free-ranging (1).
Year	Year of parturition observed during 2018, 2019 and 2020.
Winter temperature	Average temperature during winter of pregnancy (1 Oct–30 April).
Winter snowfall	Total snowfall during winter of pregnancy (1 Oct–30 April).
Previous summer growing season	Annual growing season productivity during the previous summer.
Calving temperature	Average temperature during the peak calving season (1 May–30 June).
Grow season start	Start of the growing season during the spring of calving calculated as estimated seeding date.

Table 2. Logistic regression models designed to test a range of factors hypothesized to influence the parturition success of female caribou (*Rangifer tarandus caribou*) from the Klinse-Za caribou population, 2018–2020.

Model name	Hypothesis	Model structure
Age	Caribou age affects parturition.	age category
AgeXLocation	Penning makes a difference in parturition for younger cows but not ‘prime aged’ caribou.	age category * pen or free-ranging
Year	Parturition varies among year.	age category + year
LocationXWinter	Penning of caribou during harsh winters affects parturition.	age category + pen or free-ranging * winter temperature * winter snowfall
WinterTemp	Temperature during the winter of pregnancy affects parturition.	age category + winter temperature
WinterSnow	Total snowfall during the winter of pregnancy affects parturition.	age category + winter snowfall
PrevSummerGrow	Growing season productivity during the previous summer influences body condition and therefore affects parturition.	age category + previous summer growing season

* Indicates an interaction term.

Table 3. Negative binomial regression models designed to test a range of factors hypothesized to influence parturition dates for the Klinse-Za caribou (*Rangifer tarandus caribou*) population, 2018–2020.

Model name	Hypothesis	Model structure
Age	Caribou age affects parturition date.	age category
Location	Parturition date differs between penned and free-ranging caribou.	pen or free-ranging
Year	Parturition date varies among year.	year
AgeXLocation	Penning affects parturition date for younger caribou but not ‘prime aged’ caribou.	age category * pen or free-ranging
LocationXWinter	Penning affects parturition date during harsh winters.	pen or free-ranging * winter temperature * winter snowfall
AgeXWinter	Caribou age affects parturition date during harsh winters.	age category * winter temperature * winter snowfall
WinterTemp	Temperature during the winter of pregnancy affects parturition date.	winter temperature
WinterSnow	Total snowfall during the winter of pregnancy affects parturition date.	winter snowfall
PrevSummerGrow	Growing season productivity during the previous summer affects the parturition date.	previous summer growing season

CalvingTemp	Temperature during the calving season affects the parturition date.	calving temperature
GrowSeasStart	Start of the growing season (green up) affects the parturition date.	growing season start
GrowSeasStartXAge	Start of the growing season (green up) and caribou age influences the parturition date.	growing season start * age category

* Indicates an interaction term.

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Table 4. Accuracy of the DeMars et al. (2013) movement model for predicting parturition events of free-ranging cows within the Klinse-Za caribou (*Rangifer tarandus caribou*) population. The predictions were compared to the field observations (aerial telemetry flights and video collars).

		Field Observations	
		Parturition	No Parturition
Model Predictions	Parturition	True Positive 12	False Positive 2
	No Parturition	False Negative 2	True Negative 11
	Accuracy = 85.19%		

Table 5. Parturition rates of penned versus free-ranging collared caribou (*Rangifer tarandus caribou*) within the Klinse-Za population, 2018–2020. Field observations and a movement model (DeMars et al. 2013) were used to identify a parturition event for free-ranging caribou.

Year	Parturition – Pen		Parturition – Free-ranging	
	Rate	<i>n</i>	Rate	<i>n</i>
2018	0.75	12	0.75	4
2019	0.81	16	0.50	10
2020	0.69	13	0.62	13
Total	0.76	41	0.59	27

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Table 6. AIC_c scores, change in AIC_c from the best model (ΔAIC_c), and model weights (w_i) for logistic regression models used to predict parturition of female caribou (n=68) within the Klinse-Za population (*Rangifer tarandus caribou*), from 2018–2020. The predictive accuracy of each model is represented by the Area Under the Curve (AUC) calculated from the receiver operating characteristic using a leave-one-out cross-validation method.

Model	<i>K</i>	AIC_c	ΔAIC_c	w_i	AUC (SE)
Age	3	85.62	0.00	0.32	0.41 (0.08)
Null Model	1	86.13	0.51	0.24	
WinterSnow	4	87.73	2.11	0.11	0.43 (0.08)
WinterTemp	4	87.77	2.15	0.12	0.42 (0.08)
PrevSummerGrow	4	87.88	2.26	0.10	0.41 (0.08)
AgeXLocation	6	88.54	2.92	0.07	0.48 (0.10)
Year	5	90.05	4.43	0.03	0.42 (0.08)
LocationXWinter	8	93.84	8.22	0.01	0.48 (0.08)

Table 7. Coefficients, standard errors (SE), and 95% confidence intervals (CI) from the most parsimonious logistic regression and count models ($\Delta AIC_c < 2.0$) describing the occurrence and timing of parturition for female caribou (*Rangifer tarandus caribou*) (n=68) within the Klinse-Za population, from 2018–2020.

Model	Coefficient	SE	95% CI	
<i>Occurrence of Parturition - Age</i>				
Intercept	0.406	0.646	-0.860	1.671
Age - 4–7 years	1.016	0.771	-0.495	2.527
Age - 8+ years	-0.223	0.775	-1.741	1.295
<i>Date of Parturition – Winter</i>				
<i>Snow</i>				
Intercept	4.067	0.210	3.657	4.479
Winter Snow	-0.003	0.001	-0.004	-0.001
<i>Date of Parturition – Calving</i>				
<i>Temp</i>				
Intercept	7.922	1.251	5.471	10.37
				3
Calving Temperature	-0.372	0.101	-0.570	-0.174

Table 8. AIC_c scores, change in AIC_c from the best model (ΔAIC_c), and model weights (w_i) for negative binomial regression models used to predict parturition date of female caribou (*Rangifer tarandus caribou*) (n=68) from the Klinse-Za population, from 2018–2020. The predictive accuracy of the models was tested using a leave-one-out cross-validation method and the Wilcoxon rank sum test.

Model	K	AIC_c	ΔAIC_c	w_i	Wilcoxon z-score	Wilcoxon P-Value
WinterSnow	2	371.37	0.00	0.42	-1.66	0.10
CalvingTemp	2	371.54	0.17	0.39	-1.55	0.12
Year	3	373.63	2.26	0.14	-1.69	0.09
LocationXWinter	6	376.50	5.13	0.03	-1.38	0.17
WinterTemp	2	379.20	7.83	0.01	-2.25	0.02
Null Model	1	381.17	9.81	0.003		
GrowSeasStart	2	381.44	10.07	0.002	-2.96	<0.01
Location	2	382.02	10.65	0.002	-2.68	0.01
PrevSummerGrow	2	382.99	11.62	<0.001	-3.12	0.00
Age	3	383.42	12.05	0.001	-2.43	0.01
AgeXWinter	9	384.85	13.49	<0.001	-1.23	0.22
GrowSeasStartXAge	9	384.87	13.50	<0.001	-1.28	0.20
AgeXLocation	6	386.68	15.32	<0.001	-2.50	0.01

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Figure captions:

Fig. 1. Example of the DeMars et al. (2013) a priori movement models fit to movement data of the same adult female caribou (*Rangifer tarandus caribou*) from the Klinse-Za population. Model M0, M1, and M2 represent reproductive status based on the scale parameter and distribution of step lengths. In all 3 graphs, the vertical grey lines represent the step lengths inferred from GPS-collar data. Solid black lines represent the mean step length related to the scale parameter for each model, whereas the vertical dashed lines represent the predicted break points. In this example, model 2 was best fit ($\Delta AIC=0$), predicting that the caribou gave birth on May 18th and lost her calf on May 28th. The model accuracy was verified by field observations; a calf was observed alive on May 19th, then dead on May 23rd during aerial surveys.

Fig. 2. Parturition dates of caribou (*Rangifer tarandus caribou*) from the Klinse-Za population, 2018–2020. Parturition dates of penned caribou were determined by daily observations ($n=32$). Parturition dates of free-ranging caribou were determined by video-collar footage ($n=3$), or by using a predicted date of parturition from the DeMars et al. (2013) movement model combined with aerial telemetry surveys ($n=13$).

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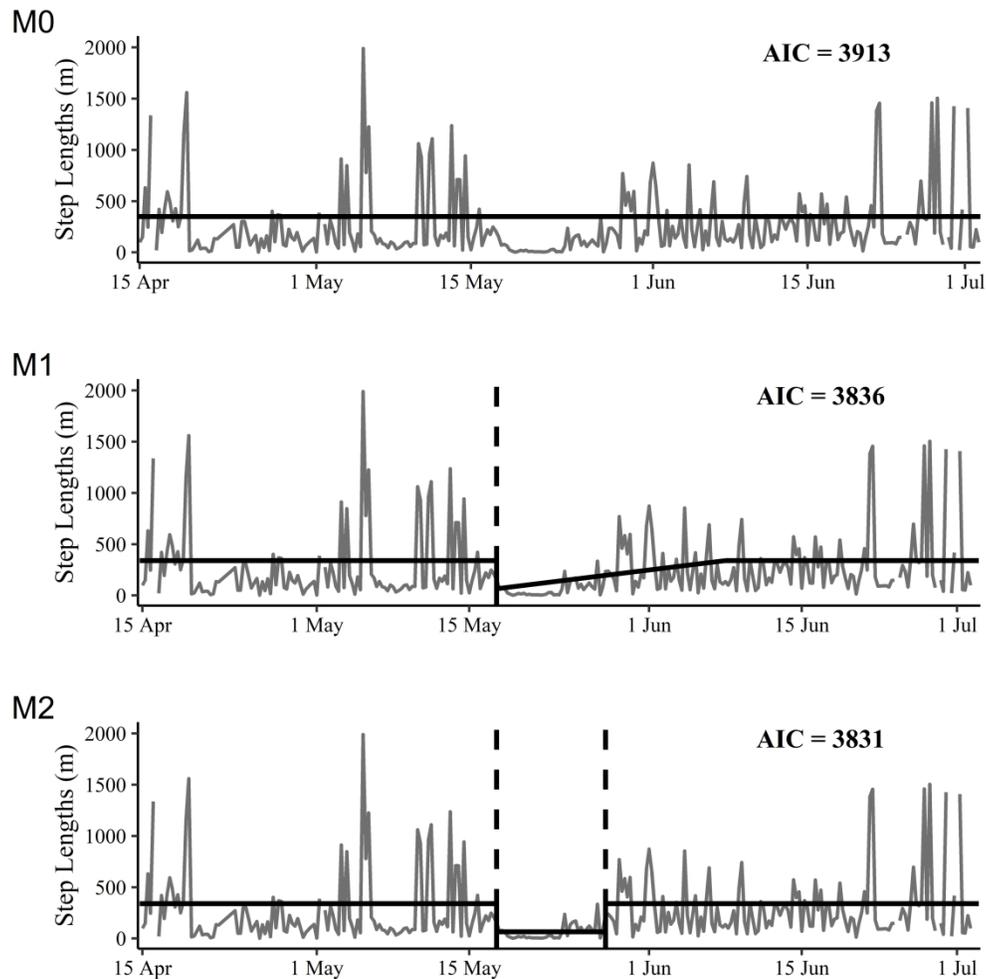


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373x386mm (300 x 300 DPI)

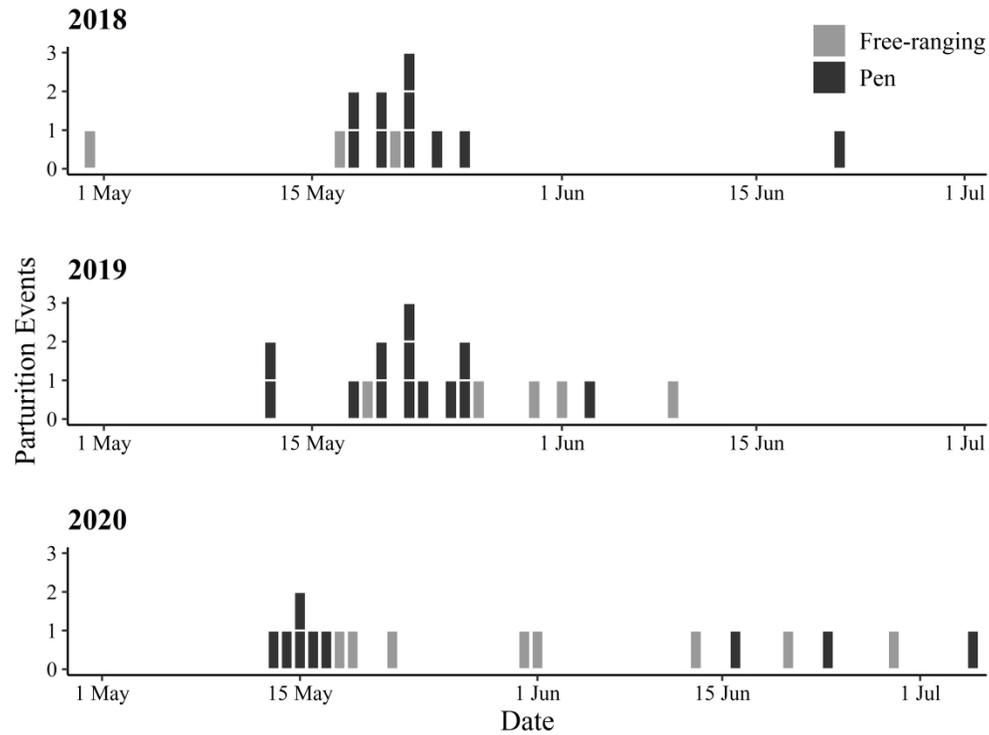


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