INDICATORS OF NUTRITION AND REPRODUCTION IN FEMALE WOODLAND CARIBOU RECEIVING SUPPLEMENTAL FEED IN BRITISH COLUMBIA

by

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B.Sc., University of Northern British Columbia, 2021

THESIS SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF
MASTER OF SCIENCE
IN
NATURAL RESOURCES AND ENVIRONMENTAL STUDIES
(BIOLOGY)

UNIVERSITY OF NORTHERN BRITISH COLUMBIA

September 2025

Abstract

Adequate nutrition is closely associated with animal survival, reproduction, and population growth. Supplementary feeding, the provisioning of food to offset reduced availability of natural food and / or improve individual and population attributes, is often used as a conservation tool to reverse the decline of threatened populations. Most woodland caribou (*Rangifer tarandus caribou*) populations in British Columbia are declining throughout their range due to habitat alterations caused by human activities. In response to these declines, various management strategies have been employed to halt population declines and increase the number of caribou in BC. Supplemental feeding for caribou conservation began in 2014, with high-quality food pellets provided to free-ranging caribou in the Kennedy Siding herd each fall. The goal of this program is to improve body condition, increase winter survival, and improve reproductive outcomes. Feeding combined with predator reduction appears to have had a positive effect on caribou, with the herd growing by approximately 16% per year.

I used multiple indicators of nutritional condition and reproduction to investigate the effects of supplemental feeding on body condition and population growth among female caribou in the Kennedy Siding herd. I used body mass, visual body condition scores, fecal and hair cortisol, fecal triiodothyronine, and hair $\delta^{15}N$ to evaluate the changes in physiological and nutritional condition over the feeding period and to assess interannual variation in condition. I compared indicators measured in female caribou with a weaned calf in the fall to those without a calf to assess the effects of lactation and calf rearing on condition. I used a combination of fecal progesterone measurements and GPS collar movement data to assess the potential effects of fall supplemental feeding on ovulation, parturition, and calf survival.

My results suggest that females with calves may be more vulnerable to nutritional limitation compared to females without calves due to the nutritional costs of lactation and calf rearing. Furthermore, I found differences in indicators of condition between years, highlighting the need to account for environmental conditions when considering nutrition. Indicators of nutrition suggested that all caribou had the capacity to become pregnant, regardless of age, body condition, or whether they had a calf at heel or not. Total parturition rate was 87.5% and calf survival was 74.3% in the Kennedy Siding herd, which are at the high end of comparable rates reported in unfed caribou herds in BC. Combined, my findings suggest the mechanism that in which supplemental feeding contributes to population growth is by supporting the deposition of body fat and protein reserves, thus increasing the proportion of females that have successful pregnancies and potentially also the proportion of calves that survive until the fall. My research represents some of the first longitudinal monitoring of endocrine activity in woodland caribou and contributes to understanding the role of nutrition in caribou conservation.

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Acknowledgments

This thesis was a collaborative effort that would not have been possible without the considerable help and support from multiple organizations and people along the way. Funding for my research was provided by the Fish and Wildlife Compensation Program (FWCP). The Kennedy Siding project is located on the traditional territory of the McLeod Lake Indian Band and operates with their vital support and participation.

I am grateful for the guidance and support of my supervisory committee. Thank you to my supervisor Heather for your unwavering support, guidance, and kindness throughout the ups and downs of this thesis. I am forever grateful to have had you as a mentor. Thank you to Doug for sharing your enthusiasm and expertise. I appreciate thoughtful comments along with our many discussions on the road to Kennedy Siding that encouraged me to always think deeply and critically. Thank you to Laura for all your support and mentorship in the lab and for sharing all your knowledge on hormones. Without you I'd probably still be running assays. Thank you to Scott for sharing your expertise on caribou ecology and for all your thoughtful comments throughout the writing process.

Thank you to my field assistants Merisa and Des for all your hard work and for enduring some pretty cold and snowy conditions to help me collect hundreds of poop samples. Thank you to Carlie, Alaysia, Andrew, and Caroline for all your help in the lab washing, weighing, and grinding all that poop and hair. Thank you to the communities of McLeod Lake and Mackenzie for being so welcoming and kind while I was there for field work. Thank you to all the many people who helped interpret the thousands of trail camera photos.

To my wonderful friends that made my personal life at UNBC and around Prince George fun, entertaining and rewarding, I will always be thankful. Special thanks go to Shaye and Madi for keeping me sane and making sure I remembered to eat and to Carlie, Ben, Andrew, and Caroline for all the essential lab treat times.

I could not have completed this study without the support of my family. To my parents, Gill and Dave, I made it to this point because of you and your constant encouragement and love.

Finally—the caribou. I feel incredibly fortunate to have had the opportunity to learn so much from these animals. This project has only increased my respect for these beautiful creatures and the landscape they call home.

Chapter One: Introduction

"*So that made it quite important to us … if they looked after us way back then now I guess it's our turn to take care of them and we always try to help out and in our own way to increase herds*."

- Alec Chingee, Elder, McLeod Lake Indian Band

Habitat alteration, including conversion, degradation, and fragmentation, is often the primary cause of species endangerment and a leading factor hindering species recovery worldwide (Myers et al. 2000, Newbold et al. 2015). Habitat alteration has been implicated in the extinction or endangerment of almost 800 terrestrial mammal species globally (IUCN 2025) and in Canada, has played a major role in declines in woodland caribou (*Rangifer tarandus caribou;* (McLoughlin et al. 2003*a*, Wittmer et al. 2007, Wasser et al. 2011).

Once abundant across Canada, woodland caribou have experienced population declines over the past 50 years and in 2019 were among the most recently extirpated large mammals in the contiguous United States (Festa-Bianchet et al. 2011, Moskovitz 2019). The decline of caribou has important ecological and cultural consequences. Caribou are part of the normal functioning of boreal and mountain ecosystems and have immense cultural and spiritual value to Indigenous people (Lamb et al. 2022). The decline of caribou presents a significant threat to a way of life, culture, and identity (Lamb et al. 2022). For example, many Indigenous nations in BC have ceased hunting caribou completely (Tŝilhqot'in National Government 2019, Nak'azdli Whut'en 2021, Lamb et al. 2022, McLeod Lake Indian Band n.d.), "making the sacrifice of sustenance for conservation" (Tŝilhqot'in National Government 2019).

Among woodland caribou, the Mountain ecotype in British Columbia (BC) has experienced declines of 50–60% (Environment Canada 2014, Environment and Climate Change

Canada 2020, McNay et al. 2022). The Mountain ecotype is divided into two populations——the Southern Mountain and Northern Mountain populations (Zimmerman et al. 2025). The Southern Mountain population is further divided into three designatable units—the Northern Group, Central Group, and Southern Group—and currently consists of 32 subpopulations or herds (Zimmerman et al. 2025). The Southern Mountain population is particularly imperiled, with nine herds fully extirpated and two functionally extirpated between 2000 and 2017 (Zimmerman et al. 2025). Many of the remaining populations are small (<100 individuals) and currently continue to decline (Johnson et al. 2015, Environment and Climate Change Canada 2018, Moskovitz 2019, Serrouya et al. 2019).

The primary cause of the decline in caribou populations has been attributed to alteration of boreal and mountain ecosystems caused by human resource extraction activities such as clearcut logging, oil and gas development, and mining (Festa-Bianchet et al. 2011, Wasser et al. 2011, Johnson et al. 2015). The proximate cause of the decline in numbers is thought to be unsustainable predation caused by habitat changes that have increased the abundance, access, and mobility of predators such as wolves (*Canis lupus*); Wasser et al. 2011, Hervieux et al. 2014, DeMars and Boutin 2018). While early seral stage forests that result from habitat disturbance tend to have higher primary productivity and higher vascular plant abundance, they also support higher predator abundances and caribou will trade off access to forage for predator avoidance (McGreer et al. 2015, Viejou et al. 2018). Caribou declines are further exacerbated by climate change and the associated changes in snowpack, fire regimes, and forage availability and quality (Festa-Bianchet et al. 2011). Caribou tend to select mature forests with high lichen abundance in winter (Fortin et al. 2008, Joly et al. 2010, McGreer et al. 2015). Variation in winter temperature and precipitation can alter the depth and hardness of snowpack and, therefore, the accessibility of both arboreal and terrestrial lichens (Kinley et al. 2007, Tyler 2010, DeMars et al. 2021). Warmer and drier conditions have led to larger wildfires and extended fire seasons over the past 30 years (Gustine et al. 2014*b*), decreasing the area of mature forests and the availability of lichens for caribou (Cichowski et al. 2022, Stanton et al. 2023, Russell et al. 2025). Climate change may shift the timing of plant emergence, reduce nutrient content, and alter species composition, cover, and growth, creating nutritional phenological mismatches between caribou and their forage resources (Zamin et al. 2017, Mallory and Boyce 2018, Twining et al. 2022, Webber et al. 2022, Stanton et al. 2023).

Habitat changes and associated changes in predator-prey dynamics are contributing to declines among the Central Group of Southern Mountain Caribou The Central Group occurs on the east side of the Rocky Mountains, north of Kakwa Provincial Park in the south, to the southern shore of the east arm of Williston Lake in the north (Environment Canada 2014, Environment and Climate Change Canada 2020). There are currently five herds defined in the Central Group, the Quintette, Narraway, Burnt Pine, Klinse-Za (also known as Moberly Scott), and Kennedy Siding herds (COSEWIC 2014, Environment and Climate Change Canada 2018, 2020). The Kennedy Siding herd declined from a high of 120 in 2007 to 41 in 2012, the Quintette herd from 265 in 2002 to 106 in 2014 and the Klinse-Za and Scott East herds combined from 191 in 1997 to 16 in 2013 (Seip and Jones 2018, Serrouya et al. 2019). The Burnt Pine subpopulation was confirmed extirpated in 2014 (COSEWIC 2014).

Various management strategies have been used to halt declines and increase the population of herds in the Central Group. Federal recovery strategies for caribou identify habitat restoration and protection as the key management actions for recovering self-sustaining populations, however, habitat restoration is expected to take decades, and with continued declines, more immediate actions are needed to keep caribou on the landscape (Environment Canada 2014, Environment and Climate Change Canada 2020, Lamb et al. 2024*b*). The Province of BC began a wolf reduction program in 2015 and, over five years, the density of wolves in the area was reduced from 12.6 wolves/1000 km^2 to less than 2 wolves/1000 km^2 (Bridger 2019). In 2014, a supplemental feeding program was initiated for the Kennedy Siding herd with the goal of improving overwinter survival and reproduction by improving nutritional condition in autumn (Heard and Zimmerman 2021). These programs have increased Central Group caribou numbers since their implementation. The Quintette herd, which only receives wolf reduction, had a population growth rate (λ) of 1.08/yr and a change in lambda ($\Delta\lambda$) of 0.13 (Heard and Zimmerman, 2021). Combining management treatments appears to have an added beneficial effect on populations. Supplemental feeding and predator control resulted in the Kennedy Siding herd having a λ of 1.16/yr and a $\Delta\lambda$ of 0.25 (Heard and Zimmerman, 2021).

Supplemental feeding is a wildlife management tool that uses nutrition to maintain or increase a population (Dunkley and Cattet 2003, Murray et al. 2016). For example, supplemental feeding has been used extensively to maintain and increase populations of endangered avian scavenger species worldwide (Wilbur et al. 1974, Gilbert et al. 2007, Cortés-Avizanda et al. 2016). Nutrition underpins essentially all life processes and plays a direct role in caribou population dynamics by influencing reproduction and survival (Chan-McLeod et al. 1994, Parker et al. 2009). As environmental conditions change, the survival of endangered species such as caribou will depend on whether habitats can meet nutritional demands while also accounting for other environmental pressures.

Most studies of nutritional ecology in northern ungulates, including caribou, have focused on winter foraging conditions, as winter is the season when food is assumed to be most limiting. There is, however, increasing evidence to suggest that late spring to early autumn may be when nutritional limitation occurs for caribou (Crête and Huot 1993, Dale et al. 2008, Couturier et al. 2009, Cook et al. 2013, 2021, Kelly 2020, Heard and Zimmerman 2021, Denryter et al. 2022). In northeastern BC, mortality of adult female Boreal caribou due to starvation is highest between June and October (Cook et al. 2021). During the summer, the energy costs of lactation plus that of recovering from previous winter weight loss can more than double daily energy requirements compared to those of non-lactating females in the summer/autumn (Barboza and Parker 2008, Parker et al. 2009). Female caribou lose body mass for approximately 3 weeks following calving because of the high costs of lactation (Parker et al. 2009). Adequate nutrition is needed for a caribou to both lactate and replenish body reserves before winter (Cook et al. 2004, 2013, Dale et al. 2008, Parker et al. 2009). The body reserves accumulated over the summer influence the probability of conceiving and carrying a fetus to term, the growth of offspring in utero and post partum, and over winter survival (Crête and Huot 1993, Cameron and Hoef 1994, Chan-McLeod et al. 1994, Adams and Dale 1998, Barboza and Parker 2006, Parker et al. 2009). Nutrition also plays a major role in determining the age of puberty in caribou and other large herbivores (Festa-Bianchet et al. 1994, Gaillard et al. 2000). Maternal condition affects neonatal birth weights, which in turn impacts calf viability and susceptibility to predation (Cameron et al. 1993, Chan-McLeod et al. 1994, Adams 2005, Taillon et al. 2012). Caribou are generally predator sensitive foragers and will trade off high quality foraging opportunities as vegetation greens up at lower elevations to reduce predation risk, especially when they have a calf (Gustine et al. 2006, Jones et al. 2007, Parker et al. 2009, Viejou et al. 2018). If caribou cannot recover body stores lost to lactation and calf rearing, they may forgo reproduction that year in favour of investing energy into self maintenance (Cameron 1994, Chan-McLeod et al.

1994, Parker et al. 2009). Widespread nutritional inadequacies will result in a gradual reduction in population productivity that increases with increasing nutritional inadequacy (Crête and Huot 1993). For an already imperilled population, any additional effect on population growth rate could compromise recovery and conservation actions.

Providing food to declining populations and/or populations that are food limited can have a positive effect on population growth via improvements in individual reproduction, survival, and body condition (Milner et al. 2014, Murray et al. 2016, Horstkotte et al. 2022). Supplemental feeding may enhance female reproductive success via improvements in body condition resulting in increased pregnancy and parturition rates, decreased age of reproductive maturity, and/or improved milk production which in turn improves calf survival (Hata et al. 2021, Horstkotte et al. 2022, Heffelfinger et al. 2023, Cao et al. 2025). The effect of supplemental feeding on body condition and reproduction can be assessed using multiple physical and chemical indices. Measurements of body mass and visual body condition scoring can be combined with chemical techniques, such as stable isotope and hormone analysis, to provide a more comprehensive assessment of nutritional condition (Delgiudice et al. 1990, Barboza et al. 2004, Parker et al. 2009, Taillon et al. 2011, Pérez-Flores et al. 2016, Schiffmann et al. 2017, Found et al. 2022).

The naturally occurring stable isotope ratios of N ($^{15}N/^{14}N$ relative to atmospheric N; $\delta^{15}N$) in tissues can provide useful insights into animal nutrition (Gustine et al. 2011, 2014*a*, Barboza et al. 2020). Nitrogen (N) is essential for the synthesis of body protein and when dietary N is inadequate, animals use N from their own body proteins and microbial protein in the rumen for the maintenance of critical tissues(Lavery and Ferris 2021). Animals using endogenous protein reserves for maintenance undergo nitrogen recycling and preferentially return ^{15}N to their

N pool. This results in tissues such as hair becoming more enriched in ^{15}N because amino acids are now being synthesized from a more ^{15}N rich source than the diet (Minagawa and Wada 1984, Kelly 2000, Fuller et al. 2005, Habran et al. 2010). Nutritional stress can thus increase δ^{15}N values in tissues when an animal is in a net catabolic state associated with lean muscle degradation (N intake < N excretion or negative N balance; Fuller et al. 2005, Parker et al. 2005, Habran et al. 2010, Gustine et al. 2011). Changes in physiological status can also influence δ^{15}N values of various tissues in herbivores. Many herbivores rely on body stores of fat and protein to meet the high N demands of fetal development and lactation (Parker et al. 2009, Taillon et al. 2013, Gustine et al. 2014*a*). The net anabolic state associated with protein synthesis (N intake > N excretion or positive N balance) during gestation and lactation causes the ^{15}N isotope ratio of the maternal body protein pool to decline (Fuller et al. 2004). The body N pool of lactating animals may be further depleted in ^{15}N as it is transferred to offspring though milk, though the level of N fractionation between mother and offspring is species specific and may be influenced by the protein quality or concentration of the mother's diet (Jenkins et al. 2001, Habran et al. 2010, Endo and Kobayashi 2022). Predation and disturbance stress is correlated with lower δ^{15}N in herbivores because stress hormones such as glucocorticoids can supress protein assimilation while promoting protein degradation and amino acid export. (De Feo 1996, Deschner et al. 2012, Found et al. 2022, Jimeno and Verhulst 2023).

Nutritional and physiological condition, as well as reproduction, can be further examined using hormones. Glucocorticoids (GCs) are a class of steroid hormones that are released as part of the stress response — physiological and behavioral coping mechanisms that help to neutralize the effects of the stressor and to reestablish homeostasis (Romero 2004, Reeder and Kramer 2005). A stressor is a noxious or unpredictable stimulus caused by any event or situation that disrupts homeostasis and poses an immediate or perceived threat to an animal (Romero 2004, Reeder and Kramer 2005). Stressors can be internal, external, or psychological (Reeder and Kramer 2005). GCs mobilize energy reserves by converting glycogen to glucose, which provides an animal with the energy to respond to immediate stressors (Reeder and Kramer 2005, Baker et al. 2013). A chronic elevation in GCs due to a persistent stressor can negatively impact an animal by supressing the immune system, depleting body reserves, and reducing reproductive success (Sapolsky et al. 2000, Romero 2004, Reeder and Kramer 2005, Karaer et al. 2023). GCs are also closely associated with metabolism. When metabolic rate is low, GCs are maintained at low levels (Sapolsky et al. 2000, Jimeno and Verhulst 2023). Increases in metabolic rate may be anticipated (i.e., normal daily/seasonal fluctuations) or unanticipated (sudden temperature changes, psychological stress, etc.; Sapolsky et al. 2000, Jimeno and Verhulst 2023). GCs will rise with both gradual and acute increases in metabolic rate, resulting in an increase in circulating glucose at a rate matching metabolic requirements (Sapolsky et al. 2000, Jimeno and Verhulst 2023).

GCs can be examined alongside thyroid hormones, such as triiodothyronine (T_3), to distinguish nutritional stress from other physiological stressors (Wasser et al. 2010, Ayres et al. 2012, Behringer et al. 2018). T_3 is a modified amino acid that regulates metabolism, allowing an animal to adapt to changes in environmental conditions and nutritional availability and requirements. T_3 levels decrease when food is scarce to decrease metabolic rate and conserve energy (Blake et al. 1991, Wasser et al. 2010, Pasciu et al. 2024). T_3 is also involved in the progression and timing of developmental processes (Todini 2007, Behringer et al. 2018) and plays an important role in thermogenesis (Todini 2007, Behringer et al. 2018, Hunninck et al. 2020). Unlike GCs, T_3 is relatively unaffected by psychological stressors such as predation, disease, disturbance, and social interactions, but is highly responsive to nutritional stress. (Kitaysky et al. 2005, Wasser et al. 2010). Both thyroid and GC systems work closely together to regulate energy availability (Wasser et al. 2011, Behringer et al. 2018, Jimeno and Verhulst 2023). Examining the relative differences between these two hormones can help understand the relative importance of nutritional and non-nutritional stressors on wildlife (Wasser et al. 2011, Behringer et al. 2018, Gort-Esteve et al. 2024).

Understanding basic reproductive processes and components of individual fitness can aid species management and conservation because they are important factors influencing population dynamics in wild animals (Schwarzenberger 2007, Sontakke 2018). The general health of a population is reflected in its capacity to reproduce, because reproduction is usually the first physiological loss resulting from severe stress (Bleke et al. 2021). Progesterone is a steroid hormone produced by the corpus luteum in the ovary after ovulation and is responsible for the maintenance of pregnancy in mammals (Smith 2009, Crowe 2016, Shrestha 2021). Caribou are seasonally polyestrous, having multiple estrous cycles during a single breeding season (McEwan and Whitehead 1972, Bergerud 1975, Ropstad et al. 1995*a*). The mammalian estrous cycle consists of a follicular and luteal phase (Crowe 2016). During the follicular phase an ovarian follicle and its enclosed oocyte mature in preparation for ovulation and fertilization (Crowe 2016). Progesterone levels are low during this phase (O'Connor et al. 2013). During the luteal phase is the corpus luteum, a transient endocrine organ formed from the remnants of a mature follicle after ovulation, is formed and secretes progesterone (Asher 2011, O'Connor et al. 2013, Shrestha 2021). If pregnancy does not occur, the corpus luteum degenerates and progesterone levels decline and a new estrous cycle begins with another opportunity to establish a pregnancy (Asher 2011, Shrestha 2021). If pregnancy is established, the luteal lifespan is prolonged and the corpus luteum continues to produce progesterone along with the placenta through the gestation period (Asher 2011). The effect of nutrition on progesterone secretion and ovulation has been extensively studied in domestic ruminants. Improved pre-ovulatory nutrition increases the size of the ovulatory follicle and the progesterone-secreting ability of the corpus luteum (Robinson et al. 2006). For cattle, post-partum nutrition plays a major role in the timing of the onset of oestrous cyclicity after calving, the normality of its expression, and conception rate (Robinson et al. 2006). Negative energy balance is associated with a delay to first ovulation, cycles which are longer than normal (prolonged corpus luteum), and failure to ovulate again at an appropriate time in dairy cattle (Wathes et al. 2007). Negative energy balance and body condition loss are related to reduced serum progesterone concentrations during the breeding period and to lower pregnancy rates in dairy cattle (Butler 2003). In beef cows, those in good body condition at calving and those receiving high food intakes after calving have shorter anoestrous periods than thinner and less well-nourished animals (Robinson et al. 2006). In sheep, undernutrition reduces the number of follicles that develop and therefore the number that are available to ovulate (Robinson et al. 2006). Measures of progesterone can be combined with analysis of movement patterns using GPS radio-telemetry data to infer parturition and survival of neonatal offspring (DeMars et al. 2013).

Traditionally, blood samples were used for the analysis of hormones and isotopes, however the stress and hazards of capture and restraint can be detrimental to an animals' health and may bias the results of hormone analysis (Schwarzenberger 2007, Morden et al. 2011). For example, GCs are especially sensitive to short term stressors such as capture (Schwarzenberger et al. 2000, Hunt et al. 2019). Fecal and hair analysis has been developed as alternative, non-invasive techniques for studies of stress and reproductive physiology in wildlife

(Schwarzenberger 2007). Stable isotopes and hormones in hair reflect physiological state over the period the hair was grown and can therefore be related to longer-term life history stages such as pregnancy and lactation (Fuller et al. 2004, Bryan et al. 2013*b*). Hormones like GCs, T_3, and progesterone are metabolized by the liver into metabolites that are excreted in feces and/or urine (Wasser et al. 2010, Brown 2018, Hunt et al. 2019). Fecal metabolites reflect the endocrine activity of an animal over the gut transit time prior to sampling (Karaer et al. 2023). Fecal sampling also enables frequent data collection without disturbing the animal, allowing for longitudinal studies that can be used to assess changes in reproductive activity and stress (Schwarzenberger 2007). Very few longitudinal studies that monitor endocrine activity exist for caribou, likely due to difficulties in obtaining repeated samples from wild populations (Messier et al., 1990a, Morden et al., 2011, Joly et al., 2015).

As environments continue to change the survival of many species will depend on whether habitats are able to provide the necessary nutritional resources. Since nutrition is fundamental to both individual performance and population productivity, it should be a key consideration for managers aiming to develop effective management policies and practices (Parker et al., 2009). The information gained from measures of physiological and nutritional stress, as well as their reproductive consequences, can inform conservation and recovery strategies for endangered populations. In this thesis, I used multiple indicators to investigate the mechanisms by which reproduction and supplemental feeding could affect female caribou and population growth of the Kennedy Siding herd. I used noninvasive methods to collect body condition measurements, fecal pellets, and hair samples from female caribou using the Kennedy Siding supplemental feeding site during autumn and winter in 2021 and 2022 (Figure 1). Following sample collection, I validated assays for fecal GC, T_3, and progesterone metabolites and applied them to my research.

Finally, I drew on data from the literature and BC Caribou Recovery Program in addition to my field-collected data to put my results in context with other herds in BC.

I predicted that indices of nutritional condition would differ among reproductive classes and age classes. I also predicted that concentrations of fecal GC and T_3 metabolites would change over time in response to supplemental feeding. Finally, I predicted that improving female body condition would increase the proportion of females that bred each year and improve parturition and calf survival rates. My specific research objectives were to:

A. Compare body mass and condition, GCs and T_3 in fecal pellets, and $\delta^{15}N$ in hair samples among reproductive age classes (yearlings, adults with calves, and adults without calves) to assess the effects of reproduction on physiological and nutritional condition;

B. Determine the effect of supplemental by comparing temporal changes in fecal glucocorticoid (GC) and triiodothyronine (T3) concentrations over the feeding period.

C. Examine progesterone in fecal pellets to assess ovarian activity and test for a relationship between progesterone measurements and body condition, age, and previous reproductive status and;

D. Use GPS location data to assess parturition and neonatal survival rates and compare these results to other populations to assess potential impacts of autumn nutrition on reproductive success.

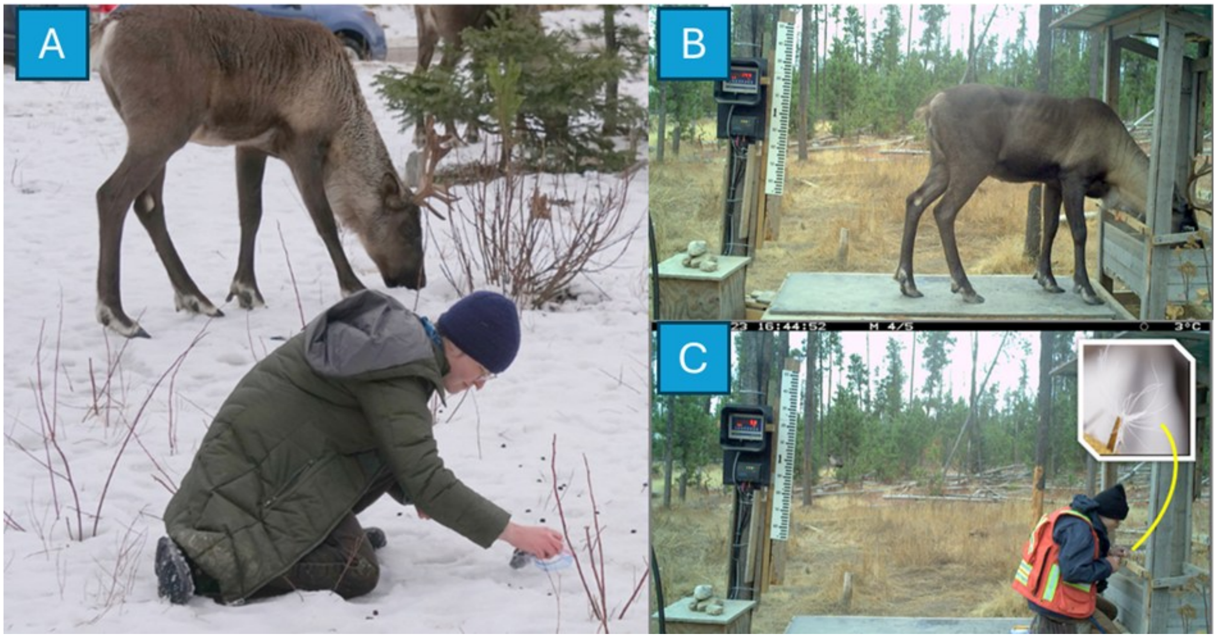


Figure 1: Fecal ample collection at the feeding site at Kennedy Siding, British Columbia, Canada, in 2021 and 2022. A) collecting fecal pellets from female caribou (*Rangifer tarandus caribou*). B) A female caribou accessing a feeder by standing on the platform. C) Hair sample collection from snares set on the feeder

In addition to this introduction (chapter 1), my thesis includes two data chapters and a research synthesis (chapter 4). I present methods and discuss results in chapters 2 (for objectives A and B) and 3 (for objectives C and D). Both chapters 2 and 3 were written as manuscripts for publication, thus there is some information repeated in both. Finally, in chapter 4, I integrate the findings of both chapters 2 and 3. To acknowledge the contributions of many to this work, chapters 2 and 3 are written in the first-person plural whereas chapters 1 and 4 are written in the first-person singular. The results of this study contribute to an increased understanding of physiology and reproduction in caribou and provide insight into the effects of nutritional resources in the summer and autumn on caribou physiology. This study demonstrates the potential for supplemental feeding to enhance caribou conservation and can be used to inform conservation strategies and land-use plans for Central Mountain caribou.

Chapter 2: Physiological bioindicators reflect nutritional differences among female caribou in an endangered herd with supplemental feeding

Introduction

Nutrition underpins essentially all animal life processes and plays a direct role in population health by influencing reproduction and survival (Chan-McLeod et al. 1994, Parker et al. 2009). As environments continue to change rapidly at both global and local scales, the survival of many species will depend on whether habitats are able to provide the necessary nutritional resources. Nutritional condition, the state of an animal's body components (i.e., fat and protein) affects many critical aspects of its life history such as juvenile growth rates, adult mass gain, body condition, probability of pregnancy, over-winter survival, timing of parturition, and neonatal birth mass and survival (Parker et al. 2009). Since nutrition is fundamental to both individual performance and population productivity, it should be a key consideration for managers aiming to develop robust and effective management policies and practices (Parker et al. 2009).

One strategy used in endangered species management to improve nutritional condition is supplemental feeding (Milner et al. 2014, Ossi et al. 2017). Supplemental feeding involves intentionally providing additional food to wild populations beyond what is naturally available (Dunkley and Cattet 2003). The practice is implemented at various scales and for multiple reasons, including enhancing individual and population health, providing emergency food when natural sources are scarce or inaccessible, and mitigating damage to crops and livestock (Dunkley and Cattet 2003). Depending on the goal, supplemental feeding can be a short (< 5years) or long-term (> 5 years) management measure (Milner et al. 2014). Feeding can lead to rapid population increases due to direct effects on survival and breeding success, which makes it an attractive management option (Robb et al. 2008, Sergio et al. 2008, Bishop et al. 2009). In addition, supplemental feeding is often more politically supported and socially acceptable compared with alternatives population recovery actions such as predator control (Robb et al. 2008). Supplemental feeding also provides an opportunity for researchers to address ecological and biological aspects of a species, such as survival, growth rates, behaviour, reproduction, and physiology by removing or mitigating the effects of food as a limiting factor and providing opportunities for data collection (Dubois and Fraser 2013).

The information gained from measures of physiological and nutritional stress, as well as their reproductive consequences, can inform strategies to conserve and recover endangered wildlife populations such as woodland caribou (*Rangifer tarandus caribou*). Once the most abundant cervid species in Canada, woodland caribou have suffered dramatic population declines over the past century, and are now among the most recently extirpated large mammals in the United States of America (Festa-Bianchet et al. 2011, Moskovitz 2019). In British Columbia (BC), caribou populations have declined by as much as 50–60% and are listed as Threatened in Canada under the Species at Risk Act (Environment Canada 2014, Environment and Climate Change Canada 2020, McNay et al. 2022). The Southern Mountain population is particularly imperiled, with ten subpopulations being extirpated between 2000 and 2017, and most remaining populations are small (<100 individuals) and continue to decline (Johnson et al. 2015, Environment and Climate Change Canada 2018, Moskovitz 2019, Serrouya et al. 2019).

The Central Group of the Southern Mountain population consists of five herds, the Quintette, Narraway, Burnt Pine, Klinse-Za, and Kennedy Siding, all of which have experienced considerable declines in recent years. The Burnt Pine population was declared extirpated in

2013. The Quintette herd declined from 265 individuals in 2002 to 106 in 2014, the Klinse-Za herd fell from approximately 250 individuals in the 1990s to 38 by 2013, and the Kennedy Siding herd declined from 120 in 2007 to 41 in 2012 (Seip and Jones 2013, 2016, 2018).

The decline of these populations is largely due to habitat disturbances caused by resource extraction such as oil, gas, coal, hydroelectricity, and wood harvesting (Wittmer et al. 2005, 2007, McNay et al. 2022). Such disturbances create favorable conditions for other herbivores, such as deer (*Odocoileus* spp.) and moose (*Alces alces*), which in turn support increased populations of predators such as wolves which increase predation on caribou (*Canis lupis*; Holt 1977, Wittmer et al., 2013, Fortin et al., 2017). Habitat loss can also reduce caribou recruitment (Johnson et al. 2020), and increase adult caribou mortality (McLoughlin et al. 2003*b*, Wittmer et al. 2007).

The influences of predation and habitat also interact with nutrition (Cook et al., 2021). Caribou are predator-sensitive foragers, and may choose to forgo high-quality foraging opportunities at lower elevations to reduce predation risk (Bergerud and Elliott 1998, James et al. 2004, Leech et al. 2017). Caribou with calves especially may use nutritionally inferior habitats to avoid predators while also sacrificing foraging time and efficiency due to increased vigilance (Gustine et al. 2006, Viejou et al. 2018).

Several strategies have been implemented to mitigate caribou population declines in BC. In 2014, a supplemental feeding program was initiated for the Kennedy Siding herd, providing caribou with food pellets each fall (Heard and Zimmerman 2021). The goal of this program is to increase survival and reproduction by improving the body condition of caribou (Heard and Zimmerman 2021). Additionally, the Province of BC began an annual program to reduce wolf density within the Kennedy Siding and adjacent herds ranges, reducing wolf densities by over 80% starting in winter 2015–16 (Bridger 2019).

Feeding appears to have an incremental effect on population growth above the effect of wolf reduction alone, as indicated by comparisons of growth rates between the Kennedy Siding and the adjacent Quintette herds, however the exact mechanism by which improved nutrition leads to a population increase is unclear (Heard and Zimmerman 2021). Accordingly, our goal was to assess the role of feeding on nutritional condition among female caribou in the Kennedy Siding Herd through two inter-related questions. First, we asked whether there is evidence of nutritional limitation within the herd, which is an important requisite for feeding to be beneficial. Second, we assessed whether there was evidence that feeding leads to improved nutrition among females that use the feeders in fall. We addressed these questions using indicators of physiological and nutritional condition including body mass, body condition scores, $\delta^{15}N$ values in guard hair, and fecal glucocorticoid and T_3 metabolites.

Indicators of nutritional condition

Multiple physical and chemical indices can be used to assess nutritional condition and the effectiveness of supplemental feeding on individuals and populations. Measurements of body mass and visual body condition scoring are commonly used to evaluate individual health. Body mass is the most frequently used index, as it integrates several components of body condition, including variations in protein and fat reserves (Parker et al. 2009, Taillon et al. 2011). Body mass is limited in that it cannot differentiate among changes in body size, fat, and protein reserves (Taillon et al. 2011). Visual scoring of body condition is a quick and non-invasive method of assessing nutritional condition and body fat reserves (Pérez-Flores et al. 2016, Schiffmann et al. 2017). It often involves assessing the visibility of skeletal structures such as the ribs, spine, and hip bones (Schiffmann et al. 2017, Zielke et al. 2018). Visual scoring can be influenced by species-specific characteristics (i.e., thick and dense hair), intestinal tract filling and hydration status, or observer variability due to the inherent subjectivity of the technique (Schiffmann et al. 2017, Smiley et al. 2020). Visual body condition also only provides information on subcutaneous fat, which may not reflect high or low nutritional condition (Smiley et al. 2020)

Body mass and condition scoring can be combined with chemical techniques, such as stable isotope and hormone analysis, to provide a more comprehensive assessment of nutritional condition. Measurements of body protein are useful for evaluating nutritional condition because nitrogen (N) is essential for the synthesis of body protein . When dietary N is inadequate, animals use N from their own body proteins for the maintenance of critical tissues and to support pregnancy and lactation. Whereas body fat is the main labile source of energy, body protein is also catabolized to provide some energy.

The naturally occurring stable isotope ratios of N ($^{15}N/^{14}N$ relative to atmospheric N; $\delta^{15}N$) in tissues can be used to describe nitrogen balance in animals (Gustine et al. 2011, 2014*a*, Barboza et al. 2020). Nitrogen balance can be used to assess the status of protein nutrition and metabolism in an individual and represents the net result of protein anabolism and catabolism in the body. The ^{14}N isotope is the most abundant form of N on Earth. Less energy is required to break bonds with ^{14}N than ^{15}N (Lavery and Ferris 2021, Fraser et al. 2025). During digestion and N metabolism in the liver and kidney, ^{14}N-containing substrates are preferentially used by enzymes over ^{15}N (Kelly 2000, Fuller et al. 2005, Lavery and Ferris 2021, Fraser et al. 2025). This results in urine being enriched in ^{14}N and body tissues such as plasma, milk, and hair being enriched in $\delta^{15}N$ than relative to dietary $\delta^{15}N$ (Kelly 2000, Fuller et al. 2005, Lavery and Ferris

2021, Fraser et al. 2025). Diet as well as physiological changes influence δ^{15}N values in hair as it is grown. Even during periods of nutritional restriction, protein synthesis must continue in vital organs such as the liver and heart (Lee et al. 2012). If animals are not consuming enough protein from their diet, they will break down their fat and muscle reserves to synthesize new protein molecules (Barboza and Parker 2006, Lee et al. 2012). Protein synthesis will result in elevated δ^{15}N values in the hair when an animal experiences a net catabolic state (negative N balance) associated with lean muscle degradation(Fuller et al., 2005, Habran et al., 2010, Lee et al., 2012, Funck et al., 2020). .Funck et al., (2020) found that wood bison (*Bison bison athabascae*) experiencing nutritional stress from harsh winter conditions or significant movement across the landscape experienced a distinct increase in ^{15}N values in hair during that period. This pattern was also observed in Western white-bearded wildebeest (*Connochaetes taurinus*) in the Serengeti, where mean δ15N value in tail hairs of starved animals was greater than that of non-starved animals (Rysava et al. 2016). Conversely, stress from predation, and disturbance may be correlated with reduced δ^{15}N levels in certain tissues such as hair because stress hormones such as glucocorticoids inhibit dietary protein assimilation (De Feo 1996, Deschner et al. 2012, Found et al. 2022). Reproductive state may also influence δ^{15}N in body tissues. Protein requirements for fetal development and lactation are high, and if forage protein is limited, maternal body stores are allocated to reproduction (Parker et al. 2009, Gustine et al. 2014*a*). During gestation and lactation the increased demand for energy and protein results in protein synthesis, or an excess of anabolism over catabolism (positive protein balance; Fuller et al., 2004, 2005, Schmidt et al., 2023)). The increased use of dietary and body N for tissue synthesis of the fetus results in a decrease in δ^{15}N values in hair during gestation (Fuller et al. 2004, 2005, Schmidt et al. 2023). The transfer of maternal body proteins to offspring in the milk can further deplete ^{15}N in nursing mothers, regardless of maternal nutritional condition (Fuller et al. 2004, Endo and Kobayashi 2022).

The effects of nutritional and physiological stress, as well as reproductive state, on nutritional condition can be further examined using indicators of endocrine activity. Glucocorticoids, a class of steroid hormones, can be used to evaluate physiological responses to a wide variety of environmental, social, and internal conditions (Karaer et al. 2023). Glucocorticoids are released in response to both acute and chronic stressors, enabling an animal to respond to a physical challenge or environmental change. The primary function of glucocorticoids is to mobilize energy reserves by converting glycogen to glucose, which provides an animal with the energy to respond to immediate environmental pressures (Reeder and Kramer 2005, Baker et al. 2013). A chronic elevation in glucocorticoids in response to a persistent stressor can, however, negatively impact an animal by supressing the immune system, depleting body reserves, and reducing reproductive success (Sapolsky et al. 2000, Romero 2004, Reeder and Kramer 2005, Karaer et al. 2023).

Variations in the release of glucocorticoids can result from numerous extrinsic and intrinsic factors including time of day, season, food availability, predation, disease, social status, habitat, body condition, reproductive status, age, and sex (Sheriff et al. 2011, Baker et al. 2013). Because glucocorticoids are released in response to a variety of stressors, they can be examined alongside other bioindicators to characterize physiological and reproductive responses to environmental stressors.

Thyroid hormones, such as triiodothyronine (T_3), can be examined with glucocorticoids to distinguish nutritional stress from other physiological stressors (Wasser et al. 2010, Ayres et al. 2012, Behringer et al. 2018). Thyroid hormones regulate energy and lipid metabolism, allowing an animal to adapt their metabolism to changes in environmental conditions and nutritional availability and requirements. T_3 levels decrease when food is scarce and increase when food is abundant. This mechanism decreases metabolic rate and conserves energy during periods of limited food availability (Blake et al. 1991, Wasser et al. 2010, Pasciu et al. 2024).

T_3 is generally unresponsive to disturbance stress but responds rapidly to nutritional stress, so combined glucocorticoid measurements, can enable environmental disturbance impacts to be separated into nutritional and non-nutritional stress (Wasser et al. 2010, 2017, Ayres et al. 2012). Thyroid hormones are also involved in the progression and timing of developmental processes such as skeletal maturation, linear growth, and brain growth (Todini 2007, Behringer et al. 2018). Young animals generally have higher thyroid hormone levels than older animals (Todini 2007, Behringer et al. 2018). Additionally, thyroid hormones play an important role in thermogenesis, as animals adjust these hormones to regulate basal metabolism and maintain a constant body temperature (Todini 2007, Behringer et al. 2018, Hunninck et al. 2020). Thyroid hormones generally decrease when temperatures rise above a species' thermal neutral zone and increase when temperatures fall below it (Silanikove 2000, Wasser et al. 2010, Behringer et al. 2018, Hunninck et al. 2020, Pasciu et al. 2024).

If nutritional quality of summer habitat is limited and/or if caribou trade off better foraging sites for safety from predators, we reasoned that females with calves would be more likely to experience nutritional stress compared with females without calves due to the nutritional and energetic costs of lactation and calf rearing. Furthermore, we expected yearling females to be more vulnerable to nutritional limitation compared with adult females because their smaller size, limited body reserves, and relatively higher metabolic demands make younger animals more sensitive to environmental and forage conditions (Parker et al. 2009). We therefore expected females with calves and yearlings to exhibit lower body condition scores, higher $\delta^{15}N$ levels in guard hair, lower fecal T_3 concentrations, and higher fecal glucocorticoid concentrations compared with adult females without calves upon arrival at the feeders. If supplemental food during the feeding period leads to improved nutritional condition, we predicted that fecal cortisol metabolites would decrease and fecal T_3 metabolite would increase over the feeding period. We tested for variation in bioindicators between years that might reflect inter-annual variation in habitat. Inter-annual variation environmental conditions such as snow depth and cover, temperature, precipitation, forage characteristics, and the start of vegetation growing season have been linked to changes in movement, recruitment, mortality, parturition date, and body condition in caribou (Adams and Dale 1998, Solberg et al. 2001, Larter et al. 2002, Chen et al. 2013, 2018, Bergerud 2014). We hypothesized that supplemental feeding would have the most beneficial effect in years when food quantity or quality was low, and that this would be reflected in higher cortisol and lower T3 and a more pronounced change in these indicators over the feeding season in years with poorer conditions. Moreover, we predicted that these changes would be more pronounced among individuals vulnerable to poor nutritional condition at the start of the feeding period (i.e., females with calves, yearlings, and individuals with smaller body mass or poor body condition scores). Overall, our study provides insight into the effects of nutritional resources in the summer and autumn on caribou physiology and demonstrates the potential for supplemental feeding to enhance caribou conservation.

Methods

Study site

The range of the Kennedy Siding caribou herd is in central British Columbia, within the traditional territory of the McLeod Lake Tse'Khene (McLeod Lake Indian Band). The habitat used by the herd is in the Sub-Boreal Spruce and Engelmann Spruce Sub-Alpine Fir biogeoclimatic zones (Meidinger and British Columbia 1991). The terrain is characterized by mountains and rolling hills ranging in elevation from 710m to 2010m above sea level (Jones et al. 2007). Caribou typically spend most of the year at high elevations dispersed in relatively undisturbed sub-alpine meadows and forests of Engelmann Spruce *(Picea engelmannii*) and Subalpline Fir (*Abies lasiocarpa*). Each fall, the population descends from summer range at high elevation to a small distinct area of lodgepole pine (*Pinus contorta*) forest at low elevation on the southwest edge of their range, which has abundant terrestrial lichen (*Cladonia* spp). Movement from high to low elevations is stimulated by the first snowfall events in the mountains. When on their fall range, caribou forage on terrestrial lichens, arboreal lichens, forbs and shrubs. Snow begins to accumulate on the ground in November and when it reaches a depth of about 1 m (usually in mid-January; (Jones et al. 2007), caribou move back to high elevations, where they feed on terrestrial lichens in wind-swept areas or arboreal lichens where snow is deep and supports their weight. Most (2894 ha) of the fall range of the Kennedy Siding herd, including the feeding site, was designated an Ungulate Winter Range under the British Columbia Forest and Range Practices Act in 2002 (Arthur 2002).

The feeding area is located approximately 30 km south-east of the community of Mackenzie. Feeding occurs in the vicinity of the Kennedy railway siding and Highway 97. The area experiences frequent vehicle traffic from forestry, railway, hydro, and other industries as well as by recreational users such as hunters. Other large mammals that inhabit the area include moose (*Alces alces*), white-tailed deer (*Odocoileus virginianus*), elk (*Cervus canadensis*), lynx (*Lynx canadensis*), wolf (*Canis lupus*), coyote (*Canis latrans*), grizzly bear (*Ursus arctos*), and black bear (*Ursus americanus*; Heard and Zimmerman 2021).

Feeding, identification of individuals, and body condition measurements

We provided food and identified individuals that used the feeders following the procedures described in Heard and Zimmerman (2021). Feeding began when caribou first arrived in late September to early October. We contracted the McLeod Lake Indian Band to build the feeders and deliver the food pellets. We initially provided small amounts of pellets in plastic livestock buckets so that any remaining feed could be removed from the site when the caribou were not present. Food removal was carried out to limit attractants to the bears that used the area. We began *ad-lib* feeding in November when the bears were assumed to be in hibernation and continued feeding until January 15th. Feeding was stopped at that date to avoid interfering with the natural movement of the herd back into their alpine habitats. Caribou consumed approximately 70 kg of food per animal over the feeding period (Heard and Zimmerman 2021).

We used 7–9 Reconyx Hyperfire motion-sensor trail cameras, focused on either a feeder, a salt block, or along a trail, to obtain a continuous photographic record of individual caribou during the feeding period. The sex, age class (calf or adult), and body condition of each caribou were recorded. Animals were considered in poor body condition if ribs were visible, and good body condition if ribs were not visible (figure 2). Individual caribou were identified from photos using the number and position of antler points, radio collars or ear tags, or unique markings (e.g. scars). Calves did not always have unique antlers, so we identified individuals based on their close association with mothers of known identity upon arrival at the feeders. The caribou were attracted onto a platform scale (using salt or pellets), with trail cameras positioned to photograph the individual caribou and record the weight (kg) on the scale's digital display. If an animal was photographed on the scale more than once, we used the average of the weights recorded as the final body mass measurement. Every animal used in the analysis was weighed one to three times.

The food pellets were produced by Hi-Pro Feeds/Trouw Nutrition Canada Inc. in Grand Prairie, Alberta. The pellets were developed at the University of Alaska Fairbanks to provide balanced and adequate levels of energy, nitrogen, and minerals for growth and reproduction of caribou (Barboza and Parker 2006) and have been used in other nutritional studies (Gustine et al. 2011) and conservation projects such as the Klinse-za herd maternity pen (McNay et al., 2022).

Figure 2*:* Examples of female caribou (*Rangifer tarandus caribou*) at the Kennedy Siding feeding site considered in poor body condition and female caribou considered in good body condition. The caribou in images A and B are considered in poor condition based on their visible ribs, spine, and hip bones in the trail camera images. The caribou in images C and D are considered in good condition based on the lack of visible ribs or other bones.

Animal care

Sample collection was conducted under research permits provided by the British Columbia Ministry of Forests as well an Animal Care and Use Protocol approved by the University of Northern British Columbia (BC Permit FJ21-618702; UNBC ACUC Protocol

Number: 2021-15). Some of the adult female caribou that used the feeding site (21 in 2021 and 19 in 2022) had collars and/or ear tags that were deployed as part of the Northern Mountain and Central Mountain Caribou Capture Program run by the BC Provincial Government (Ministry of Forests), under the BC Provincial Animal Care Protocol (Permit Number: FJ21-618702).

Sample collection

We conducted sample collection with research technicians from the McLeod Lake Indian Band. We collected fecal pellet samples opportunistically by observing female caribou around the feeders. When defecation occurred, the individual caribou was identified, and the pellets were collected in a resealable plastic bag after the caribou moved away. The pellets were stored in a cooler with an ice pack until they could be transferred to a freezer and stored at -20°C within four hours of defecation.

We collected hair samples using a noninvasive snaring method. We affixed metal alligator clips to a piece of wood which were held open using small pieces of wooden toothpicks. The piece of wood was attached to one of the feeders and when caribou put their head down to eat, their neck pressed down on the clips, knocking out the toothpick and causing them to close. When the caribou pulled away, the clip caught a sample of guard hair from the neck, at least 10 hairs/clip. This method appeared to cause very little disturbance to the caribou, as they did not avoid using the feeder where the clips were set up.

Identification of individuals and aging using DNA

We sampled feces for DNA by taking three surface rubs from each pellet sample using cotton swabs. We stored samples of guard hairs with visible root bulbs in unwaxed paper envelopes. DNA extraction, amplification, and sequencing of hair and fecal samples were conducted by Wildlife Genetics International in Nelson, BC. The DNA was extracted using

QIAGEN DNeasy Blood and Tissue kits. For hair samples, the roots clipped from a target of 10 guard hairs was used. For fecal swabs ~ 5 mm clippings from the used end of one swab per sample was used. Individual identity was established using 18 microsatellite markers established by Serrouya et al., (2012) along with a ZFX/ZFY sex marker. The success rate for producing all 19 loci was 85% for hair samples and 91% for fecal swabs. DNA results were used to identify unmarked females between years and to obtain an exact or estimated age of the animal. Yearlings were classified as animals that had been sampled for DNA the year before as calves. Adults were classified as animals that had been sampled in the year before as adults / yearlings, or as a calf more than two years previously.

Hair preparation for stable isotope analysis

We prepared samples for stable isotope analysis following procedures outlined by Hobson et al., (2000). In brief, the hair samples were washed with a solution of two parts chloroform [Thermo Fisher Scientific] and one part methanol [Thermo Fisher Scientific]. Approximately 1 mg of hair (equal to 2-3 hairs) was weighed into a tin capsule. We sent the weighed hair samples to the Stable Isotopes in Nature lab at the University of New Brunswick for analysis of $\delta\ ^{15}N$ using continuous flow isotope mass spectrometry. Instruments calibrated against international reference standards from the International Atomic Energy Agency (International Atomic Energy Agency 1995).

Fecal hormone enzyme linked immunosorbent assay (ELISA)

To extract hormones from the fecal samples we first thawed and homogenized each sample. A portion of the homogenized sample was transferred to a plastic snap cap vial which was covered with a low lint delicate task wipe secured with an elastic band. The vials were lyophilized for ~ 26 hours. The dried feces were powdered and stored in the freezer at -20˚C.

Hormone metabolites were extracted from 0.2 g of dried feces in 5 mL of HPLC grade 80% methanol [Thermo Fisher Scientific] / 20% water. Vials were sealed and rotated at 160 rpm overnight at room temperature. A portion of the methanol extract was transferred to a 2 mL centrifuge tube which had caps with o-rings to prevent evaporation, centrifuged for 30 minutes, and stored at -20˚C until analysis.

Fecal glucocorticoid metabolite (FGM) ELISA

We followed the protocol described by Graham et al., (2024) to determine concentrations of FGMs. We coated ninety-six well plates (Thermo Fisher Scientific) with affinity-purified goat anti-rabbit gamma globulin (25 µg/plate [Sigma-Aldrich]) dissolved in coating buffer (0.015 M Na_2CO_3 [VWR], 0.035 M $NaHCO_3$ [Sigma-Aldrich]; pH 9.6) and incubated them overnight at room temperature. The coated plates were washed (0.04% Tween 20 [Sigma-Aldrich]) and refilled with 200 µl Trizma assay buffer (0.02 M Trizma [Sigma-Aldrich], 0.300 M NaCl [VWR], 0.1% bovine serum albumin [VWR]; pH 7.5) and stored at room temperature for at least 1 hour to block non-specific binding. We diluted fecal extracts (1:4 to 1:32) in Trizma assay buffer prior to the assay. The wells were emptied of the Trizma buffer and 50 µl each of diluted sample and standards were dispensed. Horse-radish peroxidase-labeled cortisol was dispensed, followed by anti-cortisol antibody or (Anti-cortisol #R4866; CJM Munro, UC Davis). The plates were incubated overnight at room temperature. Following incubation, we washed the plates three times and then added 200 µl of substrate solution (0.5 mL of 0.016 M tetramethylbenzidine [VWR] in dimethylsulphoxide [Thermo Fisher Scientific], and 100 mL of 0.175 M H_2O_2 [VWR] diluted in 24 mL of 0.01 M $C_2H_3O_2Na$ [Thermo Fisher Scientific]; pH 5.0) to each well. The plates were incubated for 45 minutes at room temperature and then the enzyme reaction was stopped by adding 50 µl of stop solution to each well (3 M

H_2SO_4 [Thermo Fisher Scientific]). The optical density was measured at 450 nm. If the sample duplicates had a coefficient of variation (CV) greater than 15%, we re-assayed the sample. The cross-reactivity of the cortisol antibody was reported for the following substances, including cortisol (100%), prednisolone (9.9%), prednisone (6.3%), cortisone (5%) and <1% with corticosterone, desoxycorticosterone, 21-desoxycortisone, testosterone, androstenedione, androsterone, and 11-desoxycortisol (Young et al. 2004).

As an analytical validation, fecal extracts from different female caribou were combined and assayed with the cortisol ELISAs. To establish parallelism, we tested serial two-fold dilutions of the pooled sample for comparison displacement curves (Figure 3A). The intra-assay coefficient of variability was determined by assaying 31 replicates of the pooled sample on the same plate. The intra-assay CV was 5.36% at 73.5% binding. The inter-assay coefficient of variation was determined by running a replicate of the pooled sample at a high and low concentration as controls. The inter-assay CV was 8.21% at 55% binding and 5.21% at 87% binding for 22 plates. As a physiological validation, fecal samples were assayed before and after a known stressful event in two caribou to ensure that the cortisol ELISA could measure the increase in FGMs associated with an increase in adrenal activity. The known stressful event was the capture and transfer of two female caribou from the Klinse-Za herd to a maternal pen. Samples were collected from the rectum at capture to represent baseline FGMs and from the pen approximately 12 hours after capture to represent elevated FGMs following capture and transfer.

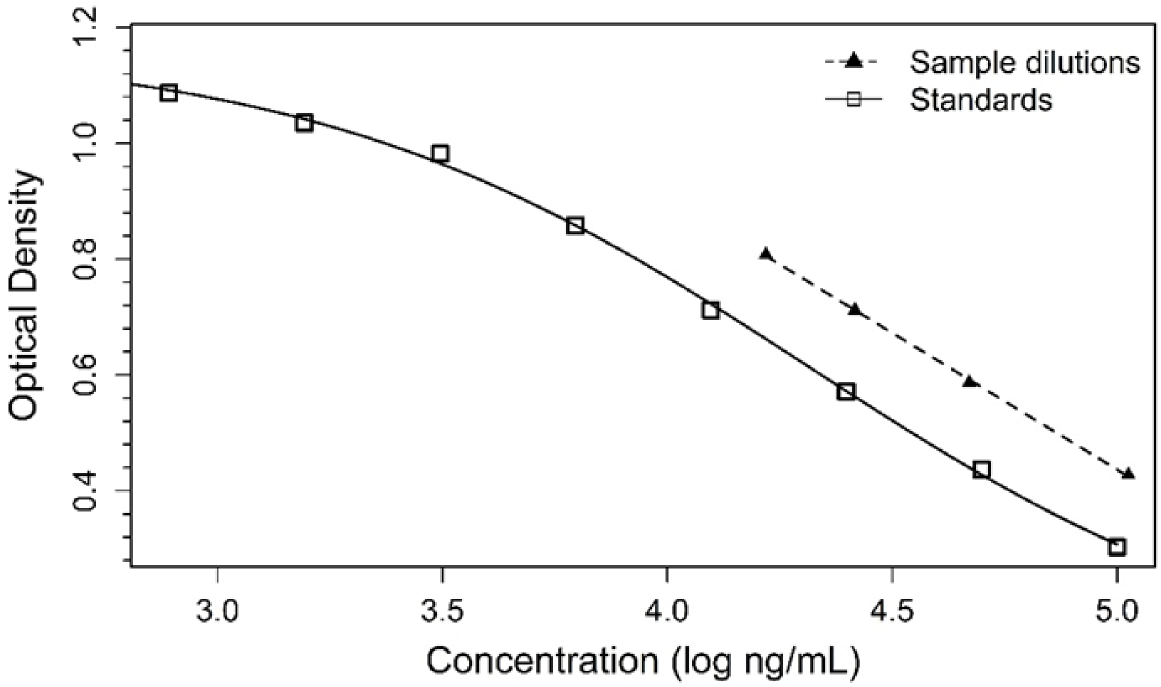
Fecal T_3 metabolite (FTM) ELISA

We measured FTM concentrations using T_3 Total ELISA kits (EIA-4569R: T3 Total ELISA, DRG Instruments GmbH, Germany). Fecal samples were evaporated to dryness under a steady stream of nitrogen. Samples were reconstituted using a solution of Trizma assay buffer

(0.02 M Trizma [Sigma-Aldrich], 0.300 M NaCl [VWR]; pH 7.5) and 100% HPLC grade methanol [Thermo Fisher Scientific]. We dispensed 50 µl of either the diluted sample, standards, or controls into each well. We added reagents and incubated plates following instructions provided by the kit manufacturer. The optical density was measured at 450 nm and if sample duplicates had a coefficient of variation (CV) greater than 15%, we reanalyzed the samples. The cross-reactivity of the FTM assay to several compounds was provided with the immunoassay kit, including I-Triiodothyronine (100%), I-Thyroxine 69 (0.37%), Reverse T3 (0.75%), D-Thyroxine (0.1%), 3,5-Diiodo-L-Thyrosine (0.2%), and 4-Phynoxyphenol (0.2%).

As an analytical validation of the FTM ELISA, pools of fecal extracts from different female caribou were combined and assayed. To establish parallelism, we tested serial two-fold dilutions of the pooled sample for comparison displacement curves (Figure 3B). The intra-assay variability was determined by assaying 15 replicates of the pooled sample. The intra-assay CV was 4.24% at 51.6% binding Inter-assay variation was determined by running a replicate of the pooled sample at a high and low concentration as controls. The inter assay CV was 10.56% at 56% binding and 8.43% at 86% binding for 10 plates.

(A) Fecal Cortisol



(B) Fecal T3

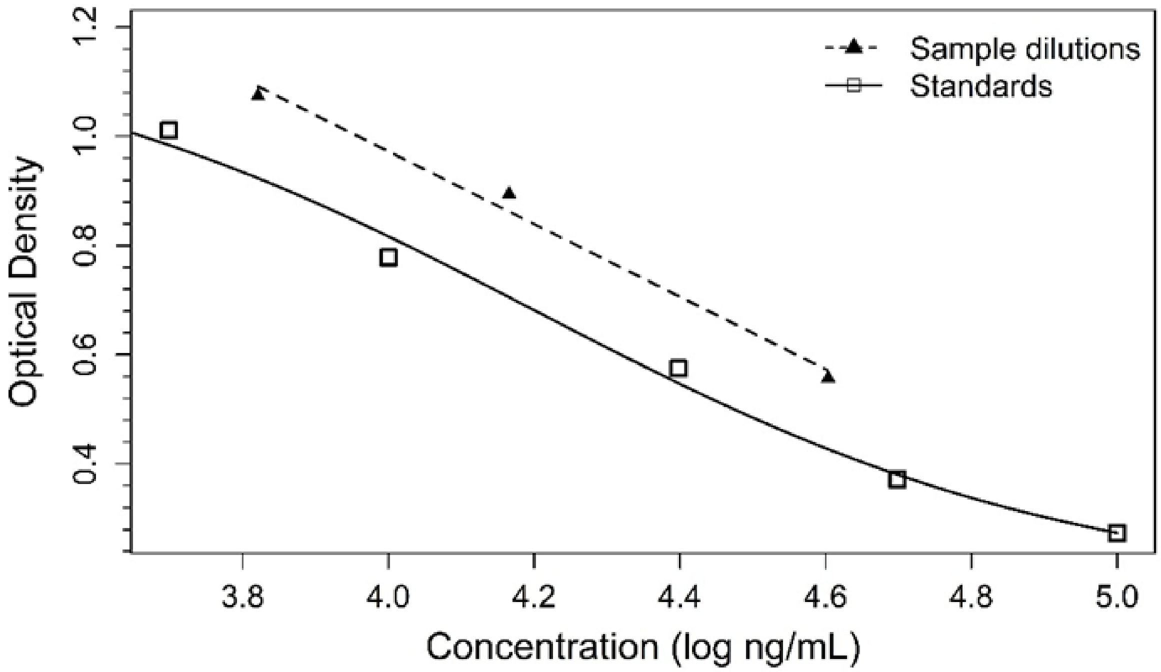


Figure 3: Parallelism of cortisol (A) and T_3 (B) standards (solid line) and a serially diluted extract from caribou (*Rangifer tarandus caribou*) fecal samples (dashed line).

Statistical analysis

All data analysis were conducted using R (R Core Team 2023). We classified each caribou sampled according to their age and reproductive status (yearlings and adults [≥ 2 years old] with and without a calf at heel).. We performed Kruskal-Wallis rank sum test to compare body mass between 1-year olds, adults with a calf, and adults without a calf, and a Wilcoxon test to compare body mass in animals in good and poor body condition (Kassambara 2019).

We used linear mixed effects regression models to assess the effects of multiple variables on hormone and isotope concentrations in hair and feces (Bates et al. 2015). We log transformed fecal cortisol and square root transformed fecal T3 to obtain normal distributions of the model residuals. We included the effects of reproductive age class, sampling day, sampling year, body mass, and body condition as fixed effects (Table 1). Individual was included as a random effect. We included reproductive age class in all the models because of the high energetic costs associated with calf rearing and lactation. Sampling day was expressed as day of the year and standardized to a mean of 0 and a standard deviation of 1 prior to analysis. Body mass was square root transformed to normalize the distribution, then standardized to a mean of 0 and a standard deviation of 1 prior to analysis. To account for the effect that sampling year, body mass, body condition, and reproductive age class might have on how fecal cortisol and T3 might change over time, we tested for a significant interaction between these variables and sampling date using Type III Analysis of Variance (ANOVAs). The only significant interaction was between sampling year and date in the cortisol models ($W(1) = 4.77$, $p = 0.03$). We tested for multicollinearity among predictor variables using pairwise correlation coefficients and variance inflation factors (Fox et al., 2001).

We selected the top model for each response variable using Akaike's Information Criterion corrected for small size (AICc; (Bartoń 2010). We used AIC scores to identify the most parsimonious (ΔAICc <2) top models within each set of candidate models. We assessed the validity of the top models based on the normality of residuals and plots of residuals versus predicted values for each response variable. We examined any models that had a ΔAICc within 0–2 units of the top model for uninformative parameters by assessing whether they differed from the best model by one parameter and had similar maximum log-likelihood values as the top model (Arnold 2010).

Table 1: Prediction category and structure of eight candidate models compared to predict fecal glucocorticoid, fecal triiodothyronine (T_3), and hair $\delta^{15}N$ in female caribou (*Rangifer tarandus caribou*) sampled in 2021and 2022 at the Kennedy Siding feeding site in British Columbia, Canada.

Prediction	**Fecal glucocorticoid metabolites**	**Fecal T_3 metabolites**	**Hair $\delta^{15}N$**
Reproduction (null)	Reproductive age class	Reproductive age class	Reproductive age class
Reproduction + time at feeders	Reproductive age class + sampling date + sampling year + sampling date*sampling year	Reproductive age class + sampling date + sampling year	Reproductive age class + sampling year
Reproduction + body condition	Reproductive age class + body condition	Reproductive age class + body condition	Reproductive age class + body condition
	Reproductive age class + body mass	Reproductive age class + body mass	Reproductive age class + body mass
	Reproductive age class + body condition + body mass	Reproductive age class + body condition + body mass	Reproductive age class + body condition + body mass
Reproduction + time at feeders + body condition	Reproductive age class + sampling date + sampling year + sampling date*sampling year + body condition	Reproductive age class + sampling date + sampling year + reproductive age + body condition	Reproductive age class + sampling year + body condition
	Reproductive age class + sampling date + sampling year + sampling date*sampling year + body mass	Reproductive age class + sampling date + sampling year + body mass	Reproductive age class + sampling year + body mass
	Reproductive age class + sampling date + sampling year + sampling date*sampling year + body condition + body mass	Reproductive age class + sampling date + sampling year + body condition + body mass	Reproductive age class + sampling year + body condition + body mass

Results

We identified and sampled 20 individual animals in both years plus 5 others unique to 2021 and 20 others unique to 2022. In 2021, we classified 14 animals as adults with a calf, five as adults without a calf, and six as yearlings. In 2022, we classified 21 animals as adults with a calf, 13 as adults without a calf, and six as yearlings. In the 2021 field season, we collected 155 pellet samples from 37 females (1-14 samples / caribou). During the 2022 field season, we collected 286 pellet samples from 43 females (1–16 samples / caribou). We collected hair samples from 27 caribou in 2021 and 33 caribou in 2022.

Body mass and condition

The body mass of caribou sampled in 2021 and 2022 ranged from 95.0 kg–153.0 kg (n=65, median = 128 kg). Body mass of adults with a calf at heel ranged from 105 kg–150.5 kg (n=35, median = 128.5 kg). For adults without a calf at heel body mass ranged from 107.0 kg–153.0 kg (n = 18, median = 138.0 kg) yearling caribou ranged in body mass from 95 kg–125.5 kg (n=12, median = 106.0 kg). A Kruskal-Wallis test showed that there was a significant difference of means between the age classes ($H = 22.87$, $df = 2$, $p <0.001$). Post hoc pairwise comparisons found that adults with a calf at heel had smaller body masses compared to adults without a calf ($p = 0.036$, Figure 4). Yearlings had smaller body masses compared to both adults with a calf ($p < 0.001$, Figure 4) and adults without a calf ($p < 0.001$). Of the caribou sampled, almost half were classified as being in poor body condition based on the visibility of ribs (Table 2, Figure 4). Most of the individuals in poor body condition were adults with a calf (Table 2); however, a Wilcoxon signed-rank test showed that the difference in body mass between caribou in good and poor body condition was not significant ($z = -0.118$, $p = 0.906$).

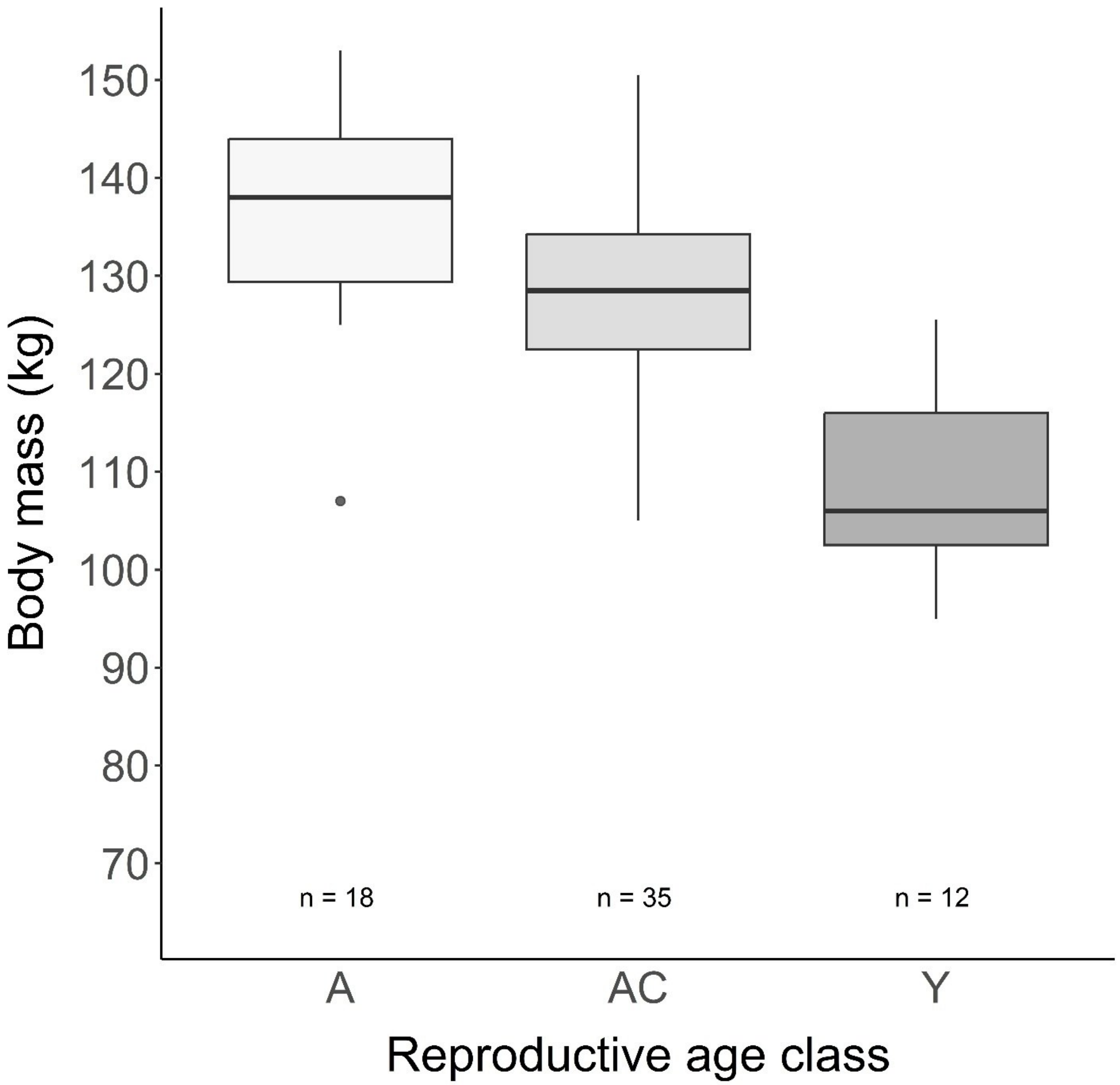


Figure 4: Body mass (kg) of adult female caribou (*Rangifer tarandus caribou*) without a calf at heel (A) and with a calf at heel (AC) compared with yearling females (Y) using the feeding site at Kennedy Siding, British Columbia, Canada, in 2021 and 2022. The centre line of each box represents the median and the outer limits represent the 25th and 75th percentiles. The lines extending below and above each box represent 1.5 times the interquartile range for each percentile.

Table 2: Number of female caribou (*Rangifer tarandus caribou*) in each reproductive age class with visible ribs at the Kennedy Siding feeding site used in our analysis. Most of the individuals with visible ribs were adults with a calf.

Age class		Adult with a calf	Adult without a calf	Yearling
Visible ribs	No	10	15	10
	Yes	25	3	2

Hair nitrogen stable isotope (δ15N)

We analyzed $\delta^{15}N$ in 52 hair samples collected from thirty-nine individual caribou using the feeding site in 2021 and 2022. Concentrations of $\delta^{15}N$ ranged from 1.712 ‰–6.921 ‰ (mean = 3.814 ‰, standard error [SE] = 0.151). The mean $\delta^{15}N$ concentration was 3.526 ‰ (n= 28, SE = 0.221) for adults with a calf, 4.095‰ (n = 15, SE = 0.255) for adults without a calf, and 4.240 ‰ (n = 9, SE = 0.257) for yearlings.

Of the 8 candidate models, 2 had a ΔAICc score <2 and carried 76.27% of the model set weight. The model that received the strongest support included an effect of reproductive age class and sampling year (ωi = 0.509, Table 3). Compared to adults with a calf, adults without a calf (Top model: β = 0.783, SE = 0.242, CI = 0.297–1.268) and yearlings (Top model: β =0.769, SE = 0.292, CI = 0.184–1.353) had higher $\delta^{15}N$ concentrations (Figure 6A). Yearling females had slightly lower $\delta^{15}N$ concentrations than adults without a calf, however, the confidence interval on the coefficient overlapped 0 (Figure 5, Figure 6A). Concentrations of $\delta^{15}N$ were lower in hair samples collected in 2022 compared to samples from 2021 (Top model: β = -0.823, SE = 0.178, CI = -1.216 – -0.465; Figure 6B).

The second ranked model also contained an effect of body condition. $\delta^{15}N$ concentration was lower in animals in good condition compared to those in poor condition, however the confidence interval overlapped 0 (Figure 4). Moreover, the model differed from the top model by only one parameter, had an AICc score that differed by 1.4 and had a similar log-likelihood value. This suggests that the top model was the most parsimonious and that the effect of body condition on $\delta^{15}N$ concentrations in the hair was negligible (Arnold 2010). The null model had a ΔAICc score of 15.34 and a model weight of 2.377×10^{-4} (Table 3).

Table 3: Top 2 of 8 linear mixed-effects models used to predict δ15N concentrations in hair samples (n=52) from female caribou (*Rangifer tarandus caribou*) sampled in fall and winter of 2021 and 2022 at the Kennedy Siding feeding site in British Columbia, Canada. Competing models within two ΔAICc are shown, as well as the null for reference.

Rank	**Candidate model**	**df**	**logLik**	**AICc**	**ΔAICc**	**ωi**
1	Reproductive age class + sampling year	6	-62.74	139.3	0	0.509
2	Reproductive age class + sampling year + body condition	7	-62.09	140.7	1.387	0.254
5	Null	5	-71.69	154.67	15.34	0

Loglik = Loglikelihood, AICc = AICc score, ΔAICc = difference in corrected AIC between model and top model; ωi = Akaike weight.

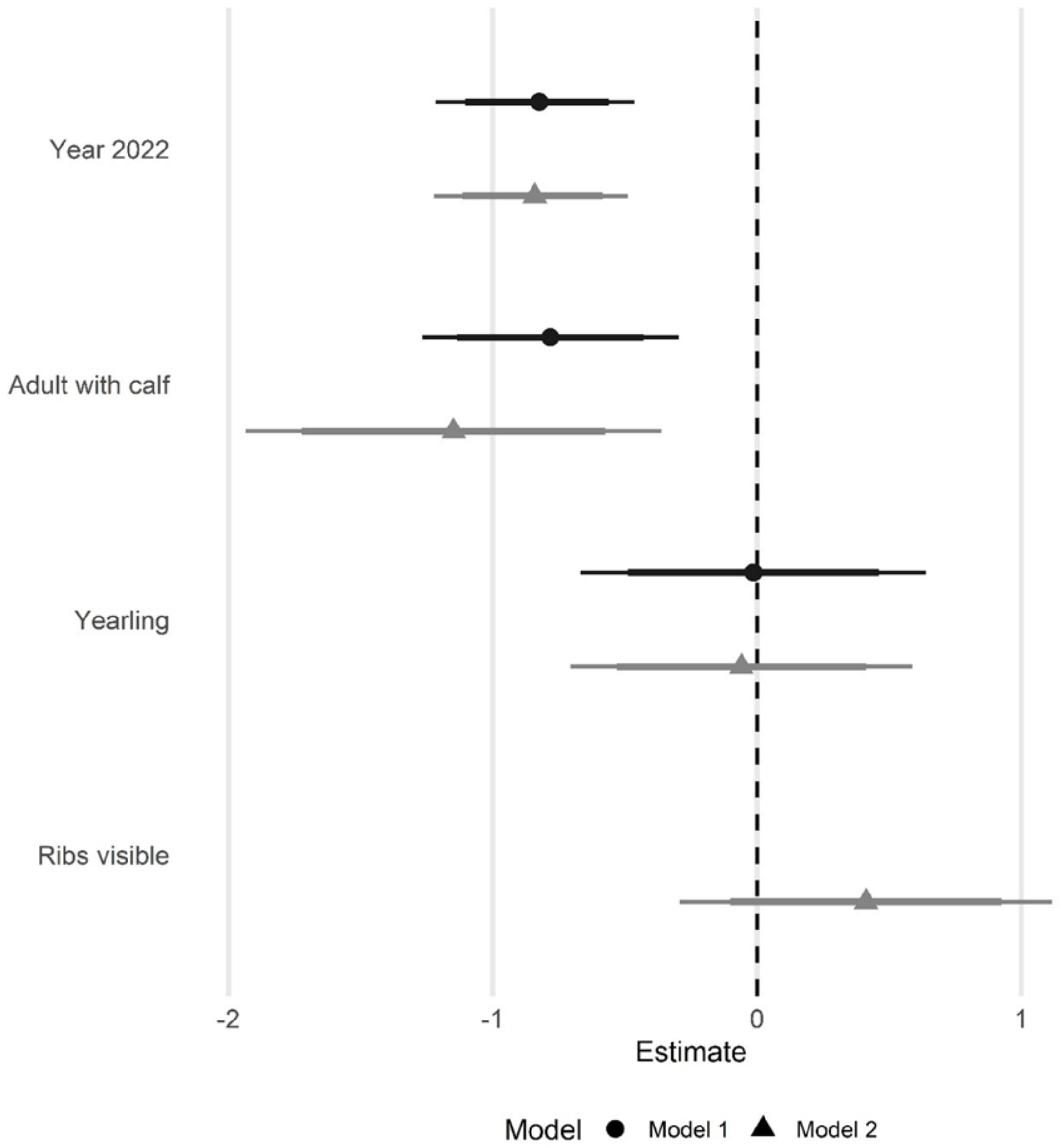


Figure 5: Coefficients and 95% and 85% confidence intervals (CI) for variables in the top three models (< 2 ∆AICc) predicting hair δ15N concentrations in female caribou (*Rangifer tarandus caribou*) sampled in fall and winter of 2021 and 2022 at the Kennedy Siding feeding site in British Columbia, Canada (n = 52). The baseline category for reproductive age class is adult without a calf at heel. The baseline category for body condition is poor (ribs visible).

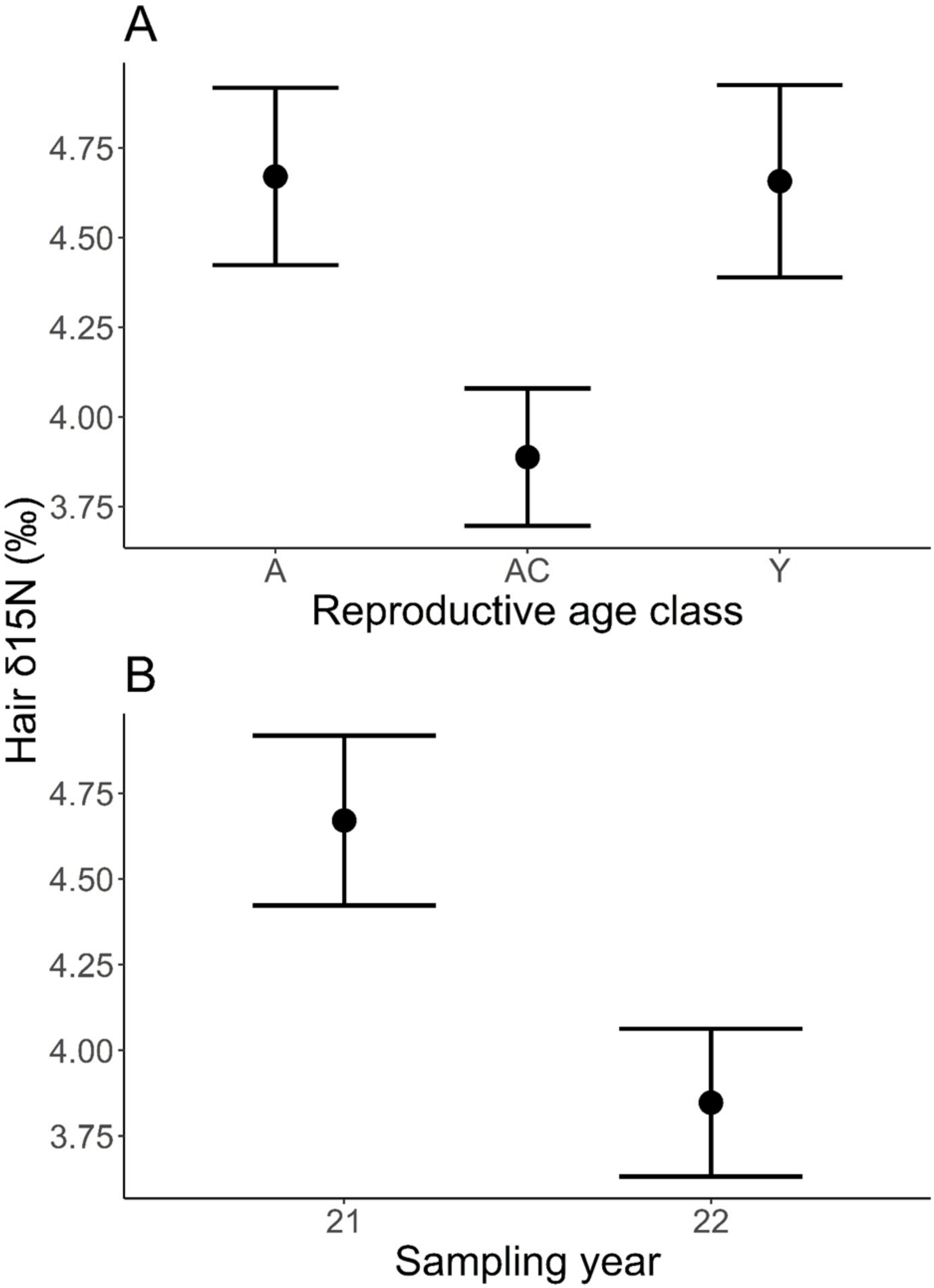

A
4.75
4.50
4.25
4.00
3.75
A
AC
Y
Reproductive age class
Hair δ15N (‰)
B
4.75
4.50
4.25
4.00
3.75
21
22
Sampling year

Figure 6: (A) The highest hair δ15N concentrations measured in caribou (*Rangifer tarandus caribou*) sampled at Kennedy Siding, BC, Canada, were found in adults without a calf (A) and 1- year olds (Y). Adults with a calf (AC) had the lowest values. The center point represents the adjusted prediction, and the error bars represent the adjusted predictions ± the standard error. (B) Hair $\delta^{15}N$ concentrations were higher in 2021 compared to 2022. The center point represents the adjusted prediction, and the error bars represent the adjusted predictions ± the standard error.

Fecal glucocorticoid metabolites (FGM)

We analyzed FGMs in 432 pellet samples from forty-five female caribou that used the feeding site in 2021 and 2022. Concentrations of FGMs ranged from 120.06 ng/g–2018.88 ng/g (median = 457.04). Concentrations of FGMs ranged from 154.78 ng/g–1367.69 ng/g (median = 456.92 ng/g) in adults with a calf at heel, 176.34 ng/g–1013.06 ng/g (median = 436.31 ng/g) in adults without a calf, and 120.06 ng/g–2018.88 ng/g (median = 489.61 ng/g) in yearlings.

Of the eight candidate models for FGMs, three had a ΔAIC_c score less than two and carried 88.01% of the model weight (Table 4). The model with reproductive age class, sampling day, and sampling year received the strongest support ($\omega_i = 0.462$, Table 4). There was an interaction between sampling day and sampling year ($F_{(1, 431.5)} = 4.811$, $p = 0.029$; Figure 7). The interaction revealed that FGM concentrations declined over time in 2021 and 2022; however, the decline was more pronounced in 2022 (Top model: $\beta = -0.074$, SE = 0.034, CI = -0.140 – -0.008; Figure 7, Figure 8A). Compared to adults without a calf at heel, adults with a calf had higher FGM concentrations however while the 85% confidence interval did not encompass zero, the 95% confidence interval did (Top model: $\beta = 0.06$, CI = -0.02–0.14, SE = 0.04, Figure 7, Figure 8B). Yearlings had greater FGM concentrations compared to adults without a calf (Top Model: $\beta = 0.12$, CI = 0.02–0.23) SE = 0.06; Figure 8B). The second ranked model contained the same variables as the top ranked model, plus an effect of body mass. FGM concentrations increased with increasing body mass, however, the confidence interval encompassed 0 (Figure 7). The third ranked model contained the same variables as the top model plus an effect of body condition. FGM concentration was greater in caribou with good body condition, however, the confidence interval on this variable also encompassed 0 (Figure 7). Both the second and third ranked models differed from the top model by only one parameter, had ΔAICc scores that differed by < 2 from the top model and had similar log-likelihood values. This suggests that the top ranked model is the most parsimonious and that body mass and body condition have little influence on the concentration of FGMs (Table 4; (Arnold 2010). The null model had a ΔAICc score of 7.911 and a model weight of 0.009 (Table 4).

Table 4: Top 3 of 8 linear mixed-effects models used to predict fecal glucocorticoid metabolites in female caribou (*Rangifer tarandus caribou*) sampled in fall and winter of 2021 and 2022 at the Kennedy Siding feeding site in British Columbia, Canada. Competing models within two ΔAICc are shown, as well as the null for reference.

Rank	**Candidate model**	**df**	**logLik**	**AIC_c**	**ΔAIC_c**	**ω_i**
1	Reproductive age class + sampling date x sampling year	8	-124.8	265.9	0	0.462
2	Reproductive age class + sampling date x sampling year + body mass	9	-124.4	267.3	1.430	0.226
3	Reproductive age class + sampling date x sampling year + body condition	9	-124.6	267.6	1.762	0.192
5	Null	5	-131.8	273.8	7.911	0.009

Loglik = Loglikelihood, AICc = AIC_c score, ΔAIC_c = difference in corrected AIC between model and top model; ω_i = Akaike weight.

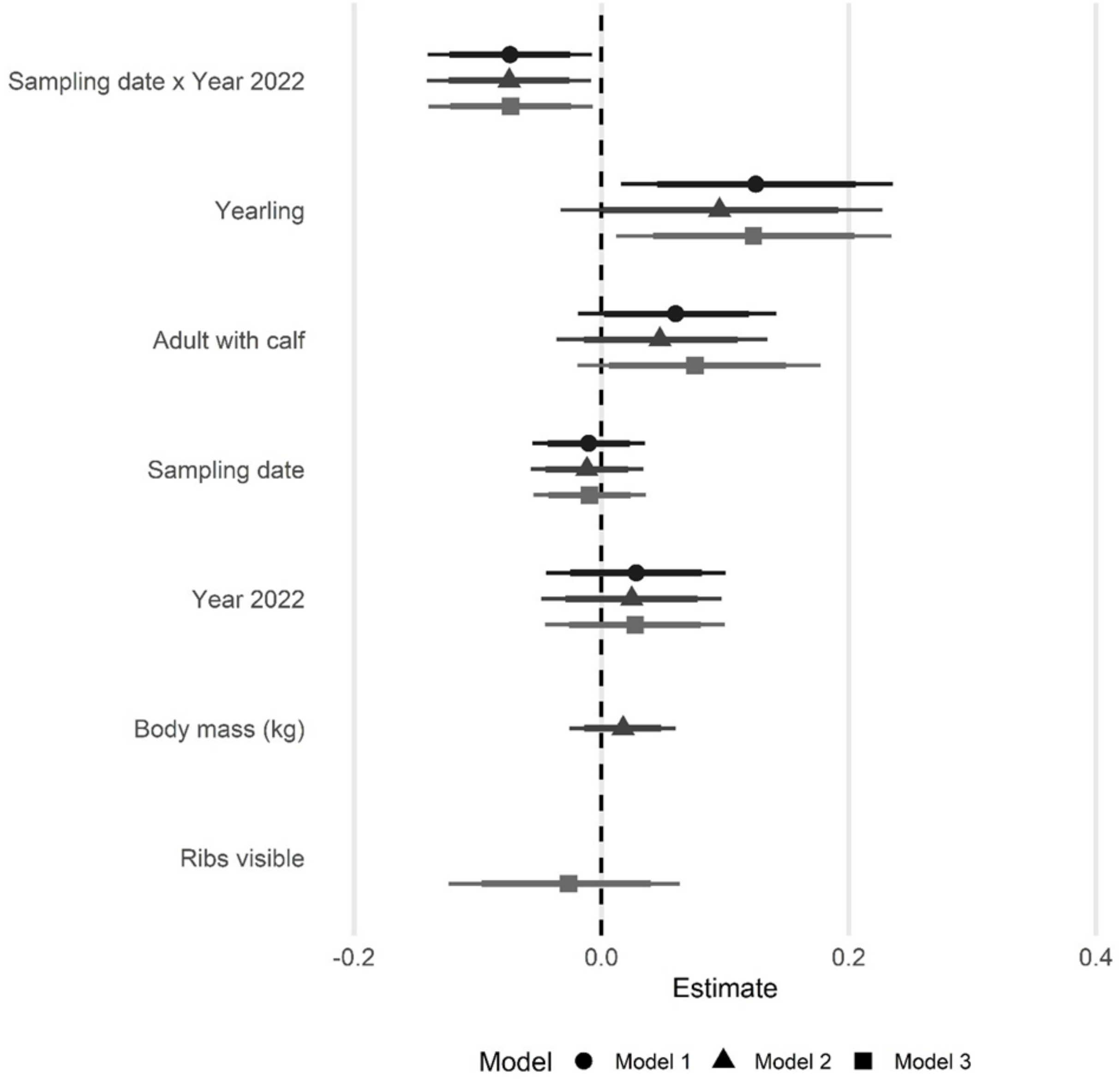


Figure 7: Coefficients and 95% and 85% confidence intervals (CI) for variables in the top three models (< 2 ΔAICc) predicting FGM concentrations in female caribou (*Rangifer tarandus caribou*) sampled in fall and winter of 2021 and 2022 at the Kennedy Siding feeding site in British Columbia, Canada (n = 432). The baseline category for reproductive age class is adult without a calf at heel. The baseline category for body condition is poor (ribs visible).

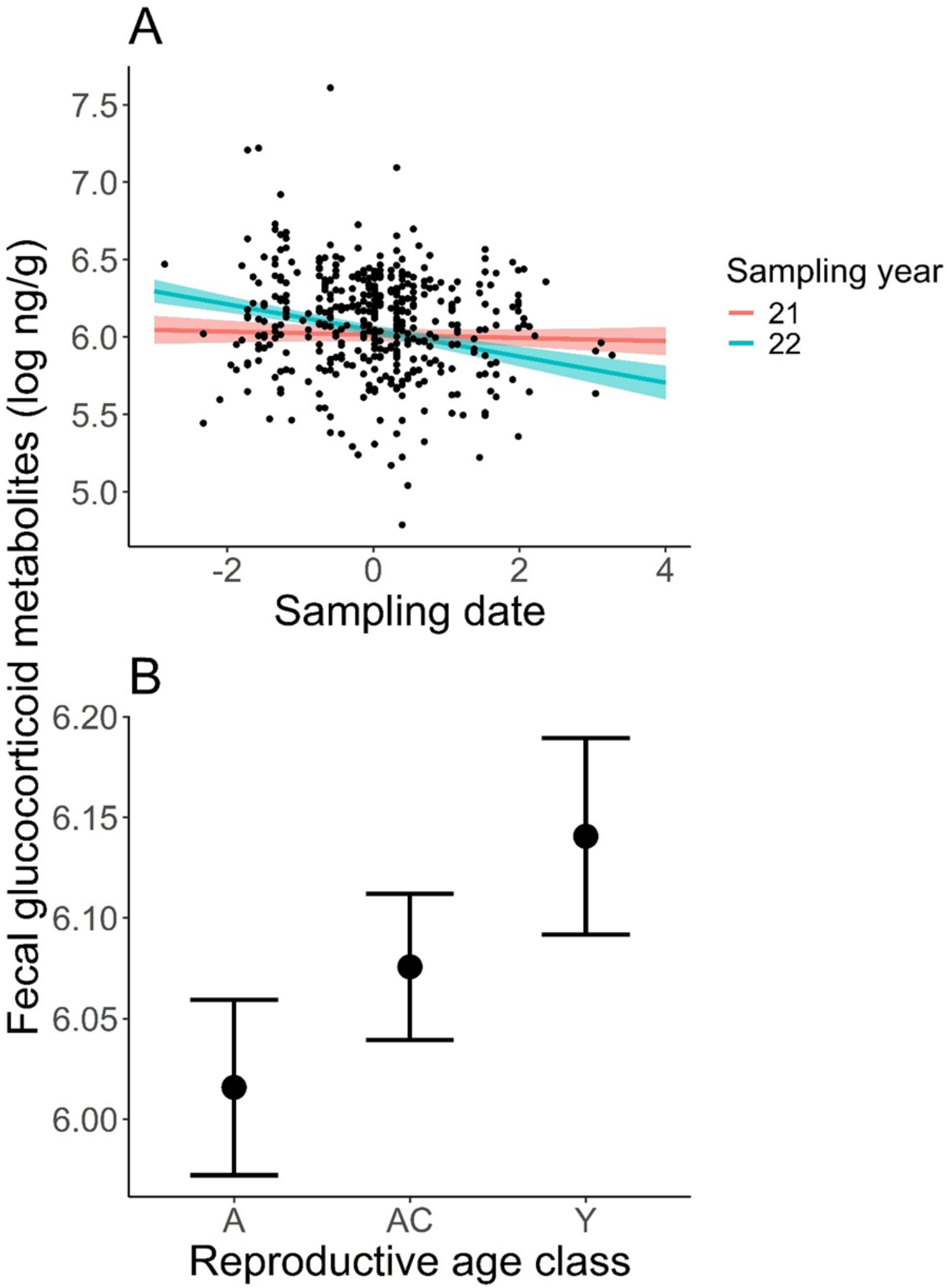

A
7.5
7.0
6.5
6.0
5.5
5.0
-2
0
2
4
Sampling date
Sampling year
21
22
Fecal glucocorticoid metabolites (log ng/g)
B
6.20
6.15
6.10
6.05
6.00
A
AC
Y
Reproductive age class

Figure 8: (A) Concentrations of FGMs decreased over time during the 2021 and 2022 feeding seasons in female caribou (*Rangifer tarandus caribou*) using the Kennedy Siding site, however the decline was more significant in 2022. The relationship between log transformed FGM concentrations and sampling date was predicted from the top model with other terms held constant at their mean value. Sampling date was standardized to a mean of zero and a standard deviation of one prior to analysis. (B) The highest FGM concentrations were found in yearlings (Y), followed by adults with calves (AC). Adults without calves (A) had the lowest values. The center point represents the adjusted prediction value, and the error bars represent the adjusted predictions ± the standard error.

Fecal T3 metabolites (FTM)

We analyzed FTMs in 385 fecal samples from forty-five female caribou that used the feeding site in 2021 and 2022. FTM concentrations ranged from 14.53 ng/g–150.73 ng/g (median = 59.47ng/g). The concentration of FTMs ranged from 25.10 ng/g–138.17 ng/g (median = 57.67 ng/g) in adults with a calf at heel, 14.53 ng/g–150.73 ng/g (median = 62.40, IQR = 25.00) in adults without a calf, and 25.33 ng/g–150.40 ng/g (median = 60.90) in yearlings.

Of the 8 candidate models for FTM concentrations, two had a ΔAICc score <2 and carried 78.35% of the model set weight (Table 5). The model containing reproductive age category, sampling day, sampling year, and body mass received the strongest support (ω_i = 0.537; Table 5; Figure 9). FTM concentrations declined over time during the feeding periods, which occurred between October and January in 2021 and 2022 (Top model: β = -0.14, CI = -0.26 – -0.01, SE = 0.06; Figure 10A). In addition, larger caribou had lower FTM concentrations (Top model: β = -0.29, CI = -0.54– -0.03, SE = 0.13; Figure 10B). The top model also included an effect of reproductive age class. The concentration of FTMs was higher in yearlings compared to adults without a calf at heel (Top model: β = 0.71, CI = 0.06–1.37, SE = 0.34; Figure 10C). FTM concentrations were similar between in adults with a calf and without (Top model: β = 0.04, CI = -0.38–0.47, SE = 0.26; Figure 9, Figure 10C). The concentration of FTMs was higher in 2022 than in 2021. This difference was significant at the 85% confidence level, but not at the 95% confidence level (Top model β = 0.28, CI = -0.01–0.58, SE = 0.15; Figure 9).

The second ranked model contained the same covariates as the top model, as well as an effect of body condition. Caribou in good body condition had lower FTM concentrations compared to those in poor body condition, however, the confidence interval on this variable overlapped with 0 (Figure 9). The second ranked model only differed from the top model by 1 parameter, had a ΔAICc score that differed by 1.6 and had a similar log-likelihood value. This suggests that the top model was the most parsimonious and that body condition has little influence on FTM concentrations (Arnold 2010). The null model had an AICc of 10.75 and a model weight of 0.002 (Table 5).

Table 5: Top 2 of 8 linear mixed-effects models used to predict female caribou (*Rangifer tarandus caribou*) FTM concentrations in caribou sampled in fall and winter of 2021 and 2022 at the Kennedy Siding feeding site in British Columbia, Canada. Competing models within two ΔAICc are shown, as well as the null for reference.

Rank	**Candidate model**	**df**	**logLik**	**AICc**	**ΔAICc**	**ωi**
1	Reproductive age class + sampling year + sampling date + body mass	8	-610.62	1237.63	0	0.537
2	Reproductive age class + sampling year + sampling date + body mass + body condition	9	-610.36	1239.19	1.56	0.253
7	Null	5	-619.11	1248.38	10.75	0.002

Loglik = Loglikelihood, AICc = AICc score, ΔAICc = difference in corrected AIC between model and top model; ωi = Akaike weight.

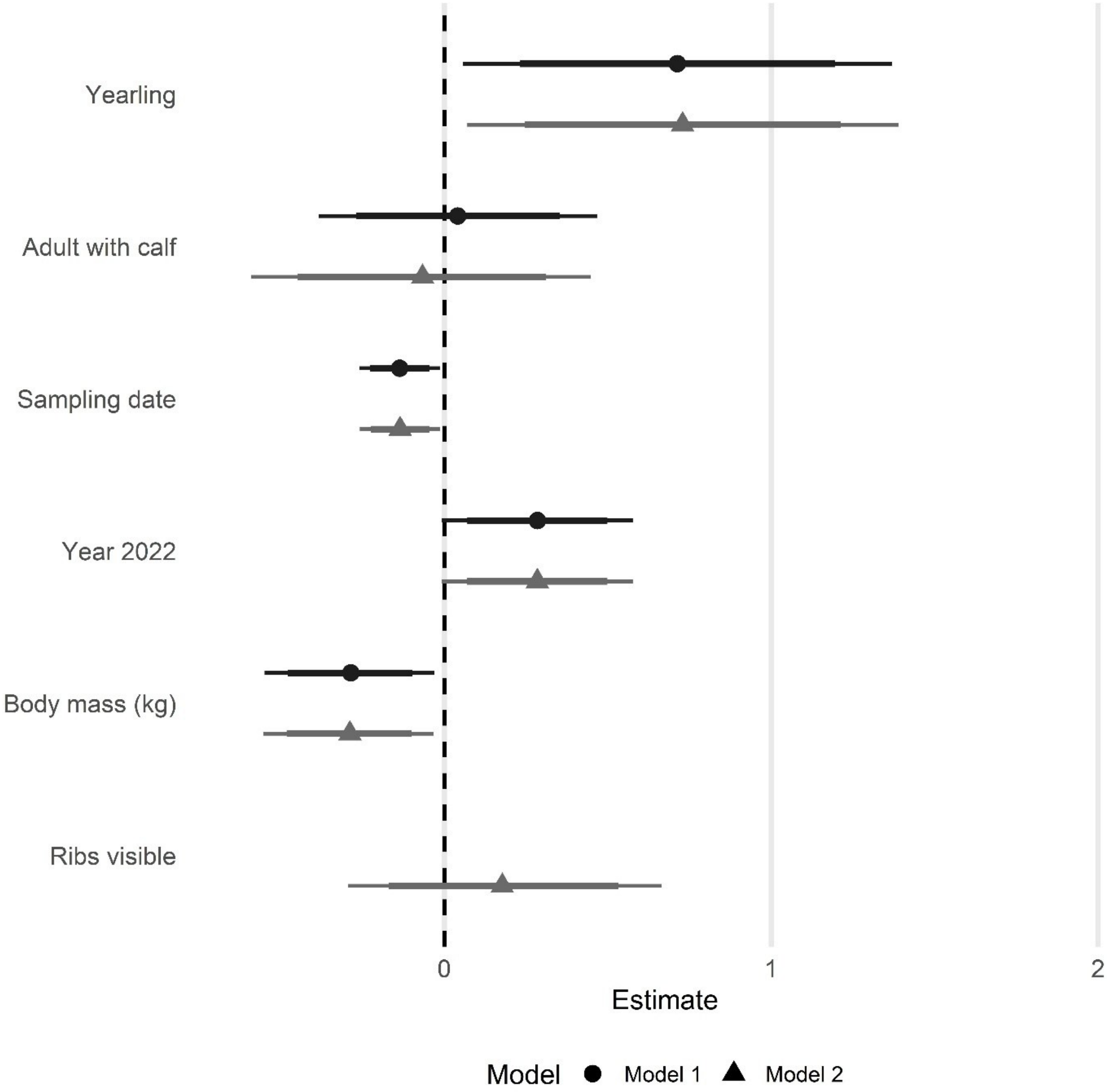


Figure 9: Coefficients and 95% and 85% confidence intervals (CI) for variables in the top three models (< 2 ΔAICc) predicting FTM concentrations in female caribou (*Rangifer tarandus caribou*) sampled in fall and winter of 2021 and 2022 at the Kennedy Siding feeding site in British Columbia, Canada (n = 385). The baseline category for reproductive age class is adult without a calf at heel. The baseline category for body condition is ribs visible.

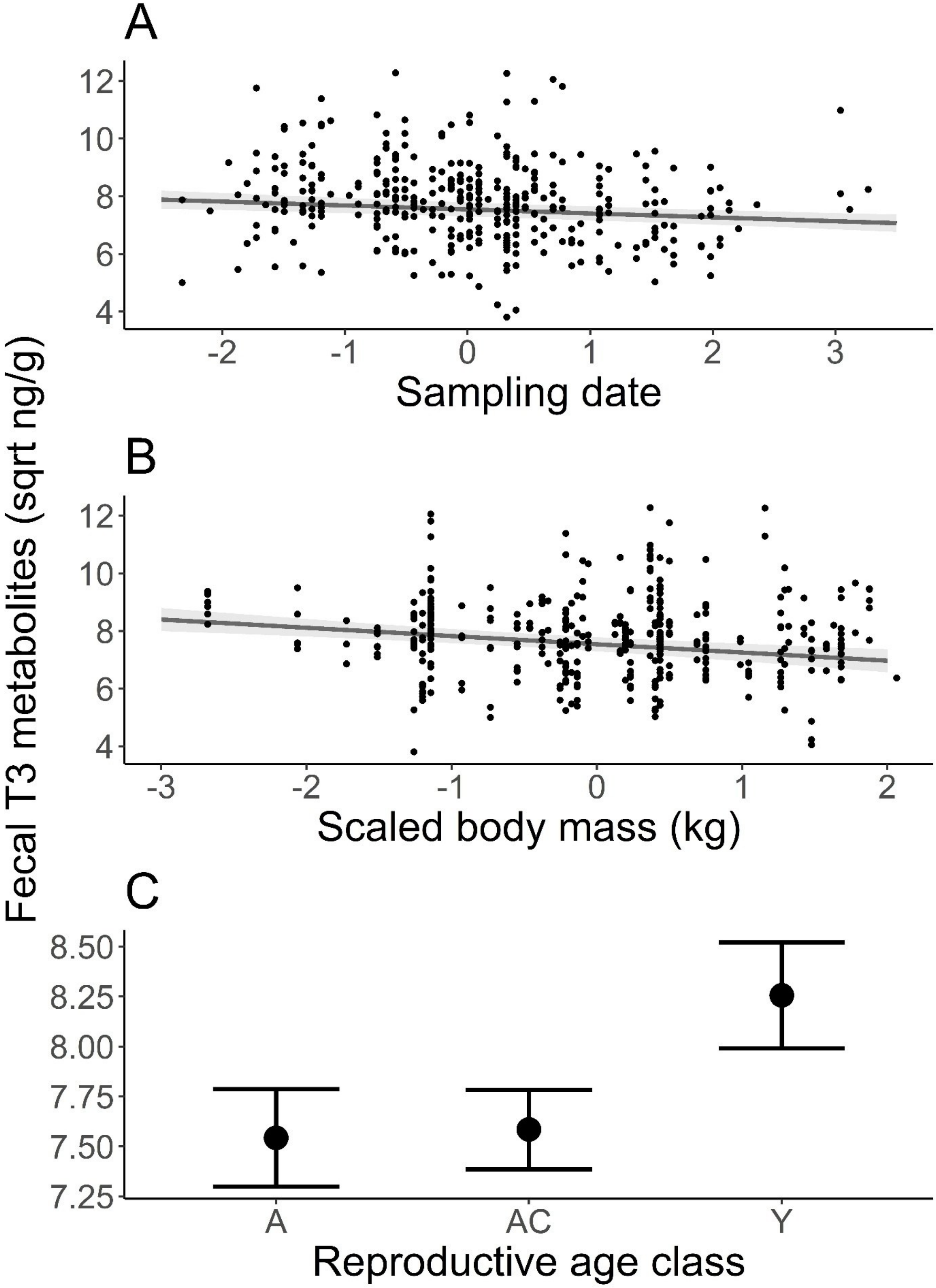

A
B
C
Fecal T3 metabolites (sqrt ng/g)
12
10
8
6
4
-2
-1
0
1
2
3
Sampling date
12
10
8
6
4
-3
-2
-1
0
1
2
Scaled body mass (kg)
8.50
8.25
8.00
7.75
7.50
7.25
A
AC
Y
Reproductive age class

Figure 10: The relationships between sampling day, body mass, and reproductive age class on the concentration of fecal triiodothyronine metabolites (FTM) in feces collected from female caribou (*Rangifer tarandus caribou*) at Kennedy Siding, British Columbia. The distribution of FTMs was normalized with a square root transformation prior to analysis. The distribution of body mass was normalized using a square root transformation and both sampling day and normalized body mass were standardized to a mean of zero and a standard deviation of one prior to analysis. The concentration of FTMs was predicted from the top model with all other terms held constant at their mean value. (A) The concentration of FTMs declined over time during both the 2021 and 2022 feeding periods. (B). The concentration of FTMs declined with increasing body mass of caribou. (C) Adults without a calf at heel had lower FTM concentrations than yearlings and similar concentrations to adults with a calf. The center point represents the adjusted prediction, and the error bars represent the adjusted predictions ± the standard error.

Discussion

Our findings provide insight into how autumn nutrition and reproduction influence body condition. Though further comparisons are required with unfed populations, these findings indicate that supplemental feeding could contribute to population recovery by facilitating rapid recovery of energy and protein stores before winter, particularly in adult females with a calf at heel. We found that adult females with calves were in poor nutritional condition compared to adults without calves and yearlings based on body mass, visual body scoring, and $\delta^{15}N$ in guard hair, suggesting that it may be difficult for caribou to fully compensate for both lactation and maintenance of body reserves during the summer. We found differences in indicators of condition between years, highlighting the need to account for environmental conditions when considering nutrition. This is the first time we are aware of that repeated sampling of fecal glucocorticoid or thyroid hormone metabolites has been conducted on woodland caribou during the autumn. Our hormone analyses are the first of their kind for this subspecies in this region and season; therefore, they should be viewed as a baseline upon which future studies can expand.

Nutritional limitation in females with calves

We predicted that if supplemental feeding has the potential to be effective in the Kennedy Siding Herd, there would be evidence of nutritional limitation in the herd. Consistent with this prediction, adult females with calves had smaller body masses and were more likely to be in poorer body condition (i.e., have ribs showing) compared with those without calves. Combined, these findings suggest that calf rearing can reduce the nutritional condition of adult females over the summer and that summer habitat may not provide adequate nutrition to compensate for the demands of lactation and calf-rearing. This finding is consistent with several studies that found substantial differences in body fat between caribou that raised a calf and those that did not (Crête and Huot 1993, Chan-McLeod et al. 1999, Cook et al. 2021). These differences are the result of increasing nutritional requirements beginning in late gestation that double during lactation compared with normal maintenance requirements (Gerhart et al. 1997*b*, *a*, Cook et al. 2004, 2021, Barboza and Parker 2006). Caribou often give birth before the onset of new vegetation growth. The lichens that are still present at that time are high in digestible energy but may may not satisfy the daily protein and dry matter needs of lactating caribou (Pulliainen 1971, Rominger and Robbins 1996, Storeheier et al. 2002). Mothers of newborn calves will also sacrifice foraging time and efficiency for increased vigilance and select habitats for predator avoidance rather than forage (Gustine et al. 2006, Viejou et al. 2018). Combined, this means that lactating females must rely on endogenous energy and protein stores from spring-early summer and experience a minimum of nutritional condition by mid-summer (Crête and Huot 1993, Chan-McLeod et al. 1999, Cook et al. 2021). Reduced body condition may affect individual performance by reducing fat accretion and ovulation in adults and survival and growth in calves and juveniles (Crête and Huot 1993, Cook et al. 2004, Albon et al. 2017). A substantial loss of condition during this time may also be life threatening by increasing susceptibility to predation, disease, extreme climactic events, and starvation (Ratcliffe 1980, Mech and Delgiudice 1985, Depperschmidt et al. 1987, Bender et al. 2008, Metz et al. 2012, Mattisson et al. 2016, Cook et al. 2021). In British Columbia, most adult female mortality occurs between May and October, with mortalities peaking in July and August (Seip 1992, Kinley and Apps 2001, McLoughlin et al. 2003*b*, Wittmer et al. 2005). The animals most vulnerable to low nutritional condition are those that have a calf or those that raised a calf the previous year, a carry over effect from one summer to another (Cook et al. 2021). The period after mid to late summer when calves are more mobile represents a critical time for caribou to recover depleted body reserves before the breeding season and winter (Chan-McLeod et al. 1999). If good quality summer forage is available and accessible, females with a calf at heel can reach a similar fatness to caribou without a calf (Adamczewski et al. 1987, Cook et al. 2004). If summer forage is not fully adequate, fall supplemental feeding could be beneficial, especially for females that raised a calf over the summer, because improved nutrition at this time can result in higher body fat levels, and overall greater survival (Crête and Huot 1993, Cook et al. 2004). Greater body fat levels would increase the chances of a female breeding and would improve calf and juvenile survival, body size, and growth rates (Crête and Huot 1993, Cameron and Hoef 1994, Cook et al. 2004, Dale et al. 2008).

In addition to lower body weights and condition, we predicted that females with calves would have higher δ^{15}N (negative nitrogen balance) compared to those without calves if dietary protein inputs were inadequate due to their use of body tissues for both maintenance and milk production in the neonatal period. In contrast with our prediction, caribou with calves had lower hair δ^{15}N than adults without a calf and yearlings. One explanation for these lower δ^{15}N values is that the synthesis of milk proteins results in a net anabolic state for the mother during lactation, which coincides with the period when hair is growing and incorporating nitrogen. Caribou are considered "capital breeders" that rely on body stores for reproduction (Taillon et al. 2013, Williams et al. 2017). The primary source of N in milk proteins is maternal body protein (Taillon et al. 2013). At calving, maternal body protein may contribute to 88–91% of milk N (Taillon et al. 2013). Maternal stores remain important throughout lactation, even when more protein becomes available in their diets (Gustine et al. 2011, Taillon et al. 2013). Nursing mothers transfer ^{15}N to their offspring when body protein reserves are used to produce milk in the neonatal period , which results in maternal tissue, including hair, being depleted in δ^{15}N, while neonate tissue becomes enriched. (Barboza and Parker 2006, 2008, Taillon et al. 2013, Endo and Kobayashi 2022).

Another possible mechanism leading to lower hair δ^{15}N in females with calves is that the demands of lactation combined with dietary restrictions during this period result in increased nitrogen-use efficiency. Before spring green up, caribou subsist primarily on lichen, which is high in digestible energy but low in N. This diet requires caribou to minimize N losses from the body by limiting the oxidation of amino acid N to urea (Barboza and Parker 2008). During periods of increased nutritional demand, such as pregnancy or lactation, the body can preferentially reroute more dietary amino acids from oxidation and excretion toward deposition at sites of tissue synthesis (Fuller et al. 2004, Taillon et al. 2013). In caribou, maternal stores are used to ensure a supply of protein for milk production, while dietary income is more likely used to rebuild maternal body stores (Taillon et al. 2013). Since dietary proteins have lower δ^{15}N than body tissues, this mechanism of protein allocation in lactating caribou could account for the lower hair δ^{15}N we observed.

Finally, female caribou with calves separate spatially from those without during parturition, seeking sites that reduce predation risk (Parker et al. 2009, Viejou et al. 2018). Caribou with calves may avoid areas of high forage quality or quantity if those areas are associated with increased predation risk, which can influence their dietary protein intake since different forage types have different δ^{15}N values (Parker et al. 2009, Drucker et al. 2010). The mass of calves at birth, which is correlated with calf survival, is impacted by maternal protein stores. In red deer (*Cervus elaphus*), calf birth weight, milk production, and milk protein content have significant allometric relationships with maternal body mass (Landete-Castillejos et al. 2003). Milk protein content is correlated with calf birth mass and calf mass gain (Landete-Castillejos et al. 2003). The relationship between maternal condition, and calf growth makes the replenishment of body protein during summer vital for future reproductive success (Landete-Castillejos et al. 2003, Adams 2005, Barboza and Parker 2008, Parker et al. 2009). Since the body mass of adults with calves was significantly lower than those without, it suggests that dietary protein and energy available in the Kennedy Siding summer range was insufficient to recover mass in caribou that successfully weaned a calf before the autumn.

Though differences between females with calves and those without were opposite to predicted, they probably reflect demands of lactation and calf-rearing. The $\delta^{15}N$ measurements represent the amount of protein that is assimilated into body tissues (Young 1991, Gustine et al. 2012). Lactation increases the protein requirements of caribou by 110–130%, and because early lactation often occurs before spring green up, meeting these demands may require the use of body protein stores. (Barboza and Parker 2008, Parker et al. 2009). Lactation may also increase the energy requirements of ungulates by 65–215% (Hardesty et al. 1988, Robbins 1993, Parker et al. 2009). In elk, fecal glucocorticoid levels have been linked to daily and seasonal energy requirements, and increase in response to the energy demands of lactation (Newediuk et al. 2024). Increased energy requirements, use of nutritionally inferior habitats, and increased vigilance and predator avoidance could account for the increased fecal glucocorticoid and hair cortisol (see supplemental material for Chapter Two) in adults with calves compared to adults without that we observed. Supplemental feeding could accelerate the recovery of body protein and energy reserves before winter, especially for caribou that lactated, thereby increasing ovulation rates and calf survival through improvements to maternal body condition (Albon et al. 2017).

Nutritional limitation in yearlings

The proportion of animals with ribs showing and the measurements of δ^{15}N were similar among yearlings compared with adult females without a calf, which suggests yearlings are not experiencing increased nutritional stress. Results from FGM and FTM models provide further support that yearlings, as a group, are not nutritionally stressed. Although yearlings had greater FGM levels compared with adults without a calf, which is consistent with nutritional stress, an alternative explanation more consistent with body condition scores relates to social dynamics within the herd. Caribou, especially females, are gregarious, and coexistence in large groups requires them to use behaviours to determine and maintain social rank (Barrette and Vandal 1986, Weckerly and Ricca 2014). Aggressive behaviour in female caribou is most often associated with conflicts over food resources. Barrette and Vandal (1986) found that in a mixed sex group of woodland caribou, aggression was correlated with access to resources, amount of time spent feeding at snow craters, age, and antler size. Among females, adults initiated most aggressive interactions with one-year olds and the outcome (gaining or maintaining access to a snow crater) was most often determined by antler size. Females with larger antlers were more successful in their interactions, regardless of age (Barrette and Vandal 1986). Within the Kennedy Siding herd, antler size and number of points is positively correlated with age, and in anecdotal observations larger females act aggressively towards smaller females (unpublished data), suggesting that adult females outrank one-year olds and have better access to and spend more time at the feeders. Female caribou in mixed sex groups, like the one formed at Kennedy Siding in the autumn, also exhibit higher frequencies of aggressive behaviour than females in same sex groups (Weckerly and Ricca 2014). The relationship between social status and stress has been examined in a wide range of species. In social, non-cooperatively breeding species such as caribou subordinate animals generally exhibit higher physiological stress than dominants, though this can be complicated by environmental conditions, reproductive status, and sex (Creel 2001, Goymann and Wingfield 2004). If younger caribou are subordinate to older individuals, this could explain the elevated FGM levels we observed. Future research could combine glucocorticoid analysis with behavioural observations to determine how social rank, age, and physical characteristics (antler size, body weight, etc.) influence physiological stress in caribou.

In contrast with our prediction that yearlings would have lower FTMs compared with females without calves, we found that FTMs were greatest among yearlings, probably because they are still growing. Elevated T_3 levels in younger animals have been observed in several ungulate species because of the role thyroid hormones have in processes such as skeletal maturation, reproductive maturation, and brain development (Todini 2007, Pasciu et al. 2024). Thyroid hormone levels are also positively correlated with growth hormone levels in domestic sheep and goats (Todini 2007, Pasciu et al. 2024). T_3 levels decline as an animal ages (Todini 2007, Pasciu et al. 2024). Age related differences in T_3 could also explain the relationship between FTMs and body mass we observed. Female caribou reach mature body mass around three-years of age (Parker 1981) . We can then infer that smaller caribou are likely younger and would therefore have higher FTM levels than larger (older) animals.

Combined, these findings suggest that yearlings are not nutritionally stressed relative to older females without calves. Improved nutritional condition in yearlings may be the result of improved nutrition in both the current year as well as the previous year, when they were calves. Calves that develop with abundant resources will be physically larger and more fecund as adults

(Pigeon et al. 2017, 2019). Evidence of an effect of feeding on body condition is suggested by the fact that yearlings have fecal progesterone values indicating ovulatory activity, and some returned to Kennedy Siding the following year having produced a calf(see chapter 3 for more detail).

Inter-annual variation in nutritional condition

Pronounced differences in physiological bioindicators between years suggest that environmental stochasticity could lead to inter-annual variation in nutritional value of habitat that could make supplemental feeding particularly important in some years relative to others. Hair $\delta^{15}N$ measurements were lower in 2022 than in 2021, while fecal glucocorticoid and T3 metabolites were higher across all reproductive age classes, which may reflect interannual variation in summer environmental conditions that affected nutritional condition for all animals. Climatic factors such as air temperature, precipitation, and sunlight can affect the quality and quantity of summer forage available to caribou (Lenart et al. 2002, Albon et al. 2017). Climate change is expected to alter precipitation and temperature patterns that are critical for plant survival and growth, thereby affecting forage composition and quality (Lenart et al. 2002, Albon et al. 2017, Zamin et al. 2017). In Svalbard reindeer (*Rangifer tarandus platyrhynchus*), changes in winter and summer weather patterns were linked to seasonal fluctuations in body mass and vital rates (Albon et al. 2017). Higher temperatures and low levels of soil moisture have been linked to decreased nitrogen content of forage (Lenart et al. 2002, Zamin et al. 2017). Additionally, changes in climate that affect snow cover can alter both the timing of spring green-up and forage nutrient content, potentially resulting in a trophic mismatch if peak nutrient availability does not coincide with the period of greatest nutritional need (Cebrian et al. 2008, Zamin et al. 2017). Caribou will increase digestible dry matter intake to restore tissues that were mobilized when food intakes were low. If 2022 foraging conditions were poor relative to 2021, caribou may have increased their intake at Kennedy Siding. This could account for the increased fecal T3 we observed in 2022, as T3 is associated with increased dry matter intake. If summer range quality is inadequate or reduced by ongoing climate change, supplemental feeding in the autumn could help buffer caribou against adverse nutritional effects. The BC Rocky Mountains have experienced more extreme high temperatures, such as the 2021 heat dome, and northern BC has been experiencing drier winter conditions, such as record low snowpack of 2023, conditions which are expected to impact the high elevation plant communities caribou rely on (Holmes et al. 2015, Haghshenas and Wood 2025). Further research is needed to determine the impact of climatic conditions on the protein and energy balance of caribou in British Columbia.

Changes in nutritional condition over the feeding period

We predicted that if caribou experienced nutritional deficits during the summer, FGM levels would decline over the fall feeding period as supplemental feeding would alleviate nutritional stress. Our modeling framework identified an overall decline in FGMs over the course of the feeding period from September to January, which is consistent with our prediction. This overall decline could reflect improved nutritional condition. An association between higher glucocorticoids and reduced food availability, quality, and nutrients has been found for a variety of species (Delgiudice et al. 1990, Stetz et al. 2013, Gregorio et al. 2019, Christianson et al. 2021, Touitou et al. 2021) including caribou and reindeer (Barboza et al. 2004, Wasser et al. 2011).

In contrast with our predictions, however, the magnitude of the decrease in FGMs was similar among adults with calves, adults without calves, and yearlings. Furthermore, there were no interactions between date and body condition or body mass, which we predicted would occur if supplemental feeding were particularly important for individuals in poor nutritional condition. These findings suggest that the magnitude of the change in FGMs over time was not strongly affected by differences in nutritional condition among individuals.

An alternative or complementary explanation for the observed decrease in FGMs relates to seasonal changes in photoperiod, with production of melatonin increasing with decreasing day length. Melatonin inhibits the production of glucocorticoids by inhibiting the secretion of corticotropin-releasing hormone leading to a decrease in the production of adrenocorticotropic hormone, and, consequently a reduction cortisol or corticosterone levels (Konakchieva et al. 1997, Lightman et al. 2020). In Svalbard reindeer, Nilssen et al., (1985) found that serum cortisol levels were lower in autumn and winter than summer, regardless of age or sex. Glucocorticoids increase the sensation of hunger by binding to receptor sites that promote muscle catabolism, limiting the secretion of appetite-suppressing hormones, and increasing blood glucose (Bini et al. 2022). A decrease in glucocorticoids in fall could contribute to the reduction in voluntary food intake and basal metabolic rates seen in reindeer during the winter (Ryg 1984). Since glucocorticoids are involved in glucose metabolism, a decrease in production could facilitate fat deposition in the autumn and the conservation of body stores over the winter. Although photoperiod could play a role in the decrease in FGMs we observed, the interaction between date and year indicated that the magnitude of the decrease in FGMs differed between years. This finding suggests that despite a potential seasonal effect, environmental and/or nutritional differences between years probably also influence FGMs in the Kennedy Siding herd.

Similar to FGMs, we predicted that changes in FTMs during the feeding period would reflect reduced nutritional stress (i.e., greater FTMs). In contrast with this prediction, we observed that FTMs decreased during the feeding period. One explanation for this finding is that, similarly as for glucocorticoids, seasonal changes in photoperiod may influence production of thyroid hormones. In studies on domestic ruminants, blood thyroid hormone concentrations increased with increasing daylength in spring and decreased with decreasing daylength in autumn, and that plasma T_3 can change rapidly in response to artificial photoperiodic cycles (Todini et al. 2006, Todini 2007). Yasuo et al., (2006) also found that the expression of the type II deiodinase gene, which catalyzes the conversion of thyroxine into T_3 decreases with increased photoperiod in Saanen goats (*Capra hircus*). In reindeer, serum T_3 levels vary seasonally, peaking in summer, and declining in winter (Ryg 1984, Nilssen et al. 1985). Although T_3 levels in cervids are thought to fluctuate with food intake, Ryg (1984) found that serum T_3 in semi domestic reindeer was greater in April and July than August and November, even when dry matter intake was similar. This suggests that a less pronounced effect of food intake on T_3 levels could facilitate the deposition of fat in late summer and autumn, which is needed for reproduction and over winter survival.

One limitation of our study is the lack of an unfed population for comparison. The Kennedy Siding herd is unique in that it consistently uses the same small, easily accessible area every year, making repeated sampling much easier than it would be for other Central Mountain herds. Very little fecal hormone data exists for woodland caribou in British Columbia, and the existing data is either from a single sample per individual and/or collected at a different time of year, making comparisons to our data challenging (Freeman 2008, Lamb et al. 2024*a*). Repeated sampling of an unfed population during the autumn would help to clarify our FGM and FTM results and make a more explicit link between these indicators and supplemental feeding. For example, Forristal et al., (2012) found that elk wintering on supplemental feed grounds in Wyoming had higher FGM levels then elk wintering in native habitats. Bahnak et al., (1981) found that serum T_3 in white tailed deer does was higher in winter and early spring when fed a high protein, medium energy diet compared to does fed a low protein, low energy diet. The increase in female body mass since the start of feeding in 2014 along with continued population growth suggests that supplemental feeding has a beneficial effect on population health (Heard and Zimmerman 2021). While feeding couldn't be directly linked to fecal hormone levels, the decline in FGMs over time suggests that caribou are not experiencing an increase in physiological stress from time spent at the feeders, except possibly yearlings, which may experience stress from social dynamics in the herd.

Management implications

Our research adds to a growing body of literature on the importance of summer and autumn nutrition to caribou in northeastern BC (Dale et al. 2008, Couturier et al. 2009, Kelly 2020, Cook et al. 2021, Heard and Zimmerman 2021, Denryter et al. 2022). We found that caribou that raised a calf had lower body mass, were in poorer body condition and had higher glucocorticoid measurements in hair and feces, which indicated that they arrived at Kennedy Siding from their summer ranges in reduced physiological and nutritional condition compared to those that did not have a calf. Caribou with calves had lower $\delta^{15}N$ which, combined with lower body masses, suggests that they relied on body stores of protein throughout lactation, and had not fully recovered body stores by the autumn. These findings suggests that summer habitat may be limiting for lactating caribou (Cook et al. 2004, Denryter et al. 2022). Lactating females are more sensitive to variations in forage quality and quantity than non lactating females. Non lactating females maintained on a low nutrition diet are able accrete fat and muscle tissues at nearly the same rate as lactating cows maintained on a high nutrition diet (Cook et al. 2004). It is possible for lactating females to accrete as much fat as non lactating cows if summer forage is accessible and quality is adequate (Adamczewski et al. 1987, Cook et al. 2004).

Caribou that enter winter in poor body condition experience reduced survival and reproductive success, which could have serious consequences for conservation and recovery outcomes for small populations such as the Kennedy Siding herd. Autumn supplemental feeding may help compensate for summer nutritional limitations by allowing caribou, especially those that reared a calf, to rapidly recover body stores lost before the onset of winter. We found that yearlings did not appear to be nutritionally limited, which suggests that improved nutrition in the previous year could carry over and benefit caribou in the next. Interpreting the changes in FGMs and FTMs over time requires further research, however these hormones did vary between years, suggesting that environmental conditions influence these bioindicators in addition seasonal conditions such as photoperiod. Ultimately, we could not link the bioindicators we measured directly to supplemental feeding, however, the decline in FGMs we observed suggests that feeding is minimally invasive and unlikely to have adverse health consequences, though continued monitoring is required to ensure that remains the case. Finally, we conducted some of the first longitudinal monitoring of endocrine activity in woodland caribou that reveals information about caribou physiology and highlights gaps in understanding around links between habitat and physiology. Our interpretation was limited by lack of data from other caribou populations, so more studies are needed to address some the information gaps we identified, ideally using a control population or pre or post-rut implementation of a feeding program.

Autumn supplemental feeding may be an effective management action for herds with inadequate summer range conditions, predictable movement patterns, or prior exposure to pelleted food, such as in maternity pens. The cost of supplemental feeding is around

$7000/caribou (CDN), considerably less costly than other management actions such as wolf reduction ($26,000/caribou) or maternity penning ($148,000/caribou; Johnson et al., 2019, Heard and Zimmerman 2021). More broadly, summer and autumn nutrition should be considered when developing habitat management strategies for caribou. Widespread habitat conservation and restoration is needed if caribou are to remain on the landscape in the long term. Future land use planning should account for the nutritional landscape of the environment and promote and protect diverse plant community types (Cook et al. 2021, Denryter et al. 2022). Fostering a landscape that supports caribou nutritional needs will help maintain self-sustaining populations by improving body condition, reproduction, and survival.

Chapter 3: Reproductive rates among female caribou with fall supplemental feeding

Introduction

Habitat loss from human activities is the primary cause of population decline for most threatened and endangered species worldwide (Myers et al. 2000). In North America, the once abundant woodland caribou (*Rangifer tarandus caribou*) have experienced dramatic declines throughout their range over the past few decades (Festa-Bianchet et al. 2011, Environment Canada 2014). In British Columbia (BC), the Central and Southern Mountain populations have experienced steep declines of up to 64%, and 12 of 24 subpopulations have been extirpated (Environment Canada 2014, Environment and Climate Change Canada 2018). The primary cause of these declines has been attributed to human resource extraction activities such as clearcut logging (Festa-Bianchet et al. 2011, Wasser et al. 2011, Johnson et al. 2015). The proximate cause is thought to be unsustainable predation caused by habitat changes that increase the abundance, access, and mobility of predators such as wolves (*Canis lupus*; Wasser et al., 2011, Hervieux et al., 2014, DeMars and Boutin 2018). Threats to caribou are further exacerbated by climate change and the associated changes in snowpack, fire regimes, and forage availability and quality (Kinley et al. 2007, Cebrian et al. 2008, Joly et al. 2010, Tyler 2010, Gustine et al. 2014*b*).

Forage resources influence most aspects of ungulate ecology. Body condition is the state of body components (e.g., fat and protein) which influence an animal's ability to survive and reproduce (Harder and Kirkpatrick, 1994). The deposition and mobilization of body fat and protein depends on an animal's physiological state and environmental conditions (Parker et al. 2009). Body condition is often important in determining whether or not an animal dies, lives without reproducing, or lives and reproduces (Parker et al. 2009). The maintenance and growth of a population is in part dependent on the environment having sufficient nutritional resources year-round (Crête and Huot 1993, Cook et al. 2004, Dale et al. 2008, Parker et al. 2009).

Most studies of nutritional ecology in northern ungulates, including caribou, have focused on winter foraging conditions, as winter is the season when food is assumed to be most limiting. There is, however, increasing evidence to suggest that late spring to early autumn may be when nutritional limitation occurs for caribou (Crête and Huot 1993, Dale et al. 2008, Couturier et al. 2009, Cook et al. 2013, 2021, Kelly 2020, Heard and Zimmerman 2021, Denryter et al. 2022). During the summer, the energy costs of lactation plus those required to recover from the weight loss in the previous winter can more than double daily energy requirements compared to those of non-lactating females in the summer and autumn (Barboza and Parker 2008, Parker et al. 2009). Female caribou lose body mass for approximately three weeks following calving because of the high costs of lactation (Parker et al. 2009). Adequate nutrition is needed for a caribou to both lactate and replenish body reserves before winter (Cook et al. 2004, 2013, Dale et al. 2008, Parker et al. 2009). Despite this requirement, many habitats in BC may be inadequate to support the daily energy and protein requirements needed for both lactation and replenishment of body reserves, and those that can are not highly available (Denryter et al. 2022). Widespread nutritional inadequacies in habitat may result in a gradual reduction in population productivity that varies in magnitude along with the degree of nutritional inadequacy (Crête and Huot 1993). Furthermore, changes in predation risk associated with disturbances such as linear features within caribou habitat can alter the ability of females to access high-quality forage. Caribou are generally predator-sensitive foragers and may trade off high-quality foraging opportunities as vegetation greens up at lower elevations to reduce predation risk, especially when they have a calf (Gustine et al. 2006, Jones et al. 2007, Parker et al. 2009, Viejou et al. 2018). The combined effects of poor nutritional quality and predation risk both limit potential for population growth of imperilled caribou populations in BC. For an already imperilled population, any additional limitations on population growth rate could compromise recovery and conservation actions.

The body reserves accumulated by female caribou during the summer are closely linked with reproductive rates, including the probability of an animal ovulating, carrying a fetus to term, the growth of offspring in utero and post partum, and over-winter survival (Crête and Huot 1993, Cameron and Hoef 1994, Chan-McLeod et al. 1994, Adams and Dale 1998, Barboza and Parker 2006, Parker et al. 2009, Albon et al. 2017). If caribou cannot recover body stores lost to lactation and calf rearing before the breeding season, they may forgo reproduction that year in favour of investing energy into self maintenance (Cameron 1994, Chan-McLeod et al. 1994, Parker et al. 2009). Nutrition also plays a major role in determining the age of primiparity; animals often begin reproducing at a younger age when nutritional conditions are favourable (Festa-Bianchet et al. 1994, Gaillard et al. 2000). Furthermore, mothers in good condition may invest more energy into their offspring, which can increase survival (Landete-Castillejos et al. 2003). In caribou, mothers in better body condition produce calves with greater neonatal birth weights, which in turn increases calf viability and reduces susceptibility of calves to predation (Cameron et al. 1993, Chan-McLeod et al. 1994, Adams 2005, Taillon et al. 2012).

In BC, The Central Group of Mountain caribou occur on the east side of the Rocky Mountains, north of Kakwa Provincial Park in the south, to the southern shore of the east arm of Williston Lake in the north (Environment Canada 2014, Environment and Climate Change Canada 2020). There are currently six populations defined in the Central Group, the Quintette, Narraway, Burnt Pine, Scott West, Klinse-Za (also known as Moberly Scott), and Kennedy

Siding herds (COSEWIC 2014, Environment and Climate Change Canada 2018, 2020). The Kennedy Siding herd declined from a high of 120 in 2007 to 41 in 2012, the Quintette herd from 265 in 2002 to 106 in 2014 and the Klinse-Za and Scott East herds combined from 191 in 1997 to 36 in 2013 (Seip and Jones 2018, Serrouya et al. 2019). The Burnt Pine subpopulation was confirmed extirpated in 2014 (COSEWIC 2014). In response to these declines, several management strategies have been applied to herds in the Central Group. The province of British Columbia began a wolf reduction program in the area in 2015, and over five years the density of wolves was reduced by over 80% (Bridger 2019). A maternal penning program was implemented for the Klinse-Za herd starting in 2014 with the goal of reducing predation on caribou calves (McNay et al. 2022). A supplemental feeding program was implemented for the Kennedy Siding herd beginning in 2014 (Heard and Zimmerman 2021).

Supplemental feeding is a management tool that uses nutrition to maintain or increase a population by improving body condition, reproduction and survival (Milner et al. 2014, Murray et al. 2016, Horstkotte et al. 2022). If summer nutrition is inadequate for caribou in BC, then fall supplemental feeding could compensate for that limitation and contribute to population growth. Supplemental feeding does appear to have an additional effect on population growth rate over the effect of wolf reduction alone, with the Kennedy Siding herd having a faster population growth rate ($\lambda = 1.16$) than the Quintette herd, which only received wolf reduction ($\lambda = 1.08$; Heard and Zimmerman 2021). One possible mechanism by which feeding improves population growth is by increasing the proportion of females who become pregnant each year by increasing body weight and fat reserves, factors that can impact the onset of cyclic ovarian activity and pregnancy (Cameron et al. 1993, Gerhart et al. 1997*a*). Specifically, feeding could reduce skipped years of reproduction among adult females and/or increase the proportion of yearlings that breed.

Alternatively, improved maternal body condition going into winter could enable females to invest in higher quality calves, leading to increased calf survival.

An understanding of basic reproductive processes and components of individual fitness can aid species management and conservation because they influence population dynamics in wild animals (Schwarzenberger 2007, Sontakke 2018). Common methods for assessing reproduction in caribou include analysis of hormone levels and movement patterns of GPS collared animals. Progesterone is a steroid hormone that increases after ovulation and is the principal hormone responsible for the maintenance of pregnancy in mammals (Smith 2009, Crowe 2016, Shrestha 2021). The mammalian estrous cycle consists of a follicular and luteal phase (Crowe 2016). During the follicular phase an ovarian follicle and its enclosed oocyte mature in preparation for ovulation and fertilization and progesterone levels are low (O'Connor et al. 2013, Crowe 2016). The luteal phase is the period following ovulation when the corpus luteum is formed and is associated with increased secretion of progesterone (Asher 2011, O'Connor et al. 2013, Shrestha 2021). If pregnancy does not occur, the corpus luteum degenerates and progesterone levels decline, allowing for another opportunity to establish a pregnancy (Asher 2011, Shrestha 2021). If pregnancy is established the corpus luteum continues to produce progesterone through the gestation period or until the placenta takes over progesterone production, depending on the species (Asher 2011). The effect of nutrition on progesterone secretion and ovulation has been extensively studied in domestic ruminants. Improved pre-ovulatory nutrition increases the size of the ovulatory follicle and the progesterone-secreting ability of the corpus luteum (Robinson et al. 2006). For cattle, post-partum nutrition plays a major role in the timing of the onset of oestrous cyclicity after calving, the normality of its expression, serum progesterone levels, and, conception rate (Robinson et al.

2006). Cattle in good body condition at calving and those receiving high food intakes after calving have shorter anoestrous periods than thinner and less well-nourished animals (Robinson et al. 2006). In sheep, undernutrition reduces the number of follicles that develop and therefore the number available to ovulate and may also impact the secretion of gonadotropins such as follicle-stimulating hormone and luteinizing hormone (Robinson et al. 2002, 2006). Flushing, the practice of providing improved nutrition at the beginning of the mating season, is commonly used to increase ovulation rates in domestic ewes (Robinson et al. 2002, 2006). Flushing in ewes in low body condition has a larger effect on ovulation than in ewes in higher body condition (Robinson et al. 2002, 2006).

In caribou, serum progesterone tests on blood samples taken from captured animals have commonly been used to assess pregnancy status (Rettie and Messier 1998, Wittmer et al. 2005, DeMars et al. 2013). The stress and hazards associated with capture and restraint can be detrimental to the animals' health (Schwarzenberger 2007, Morden et al. 2011). This means that repeated blood sampling on a regular basis is often not possible. Fecal hormone analysis has been developed as an alternative, non-invasive technique that is now widely employed for studies of stress and reproductive physiology in wildlife (Schwarzenberger 2007). Hormones like progesterone are metabolized by the liver into several metabolites which are excreted in feces and can then be measured using immunoassay techniques (Brown 2018). Due to the pooling of metabolites during excretion, fecal samples present cumulative hormone secretion hours or days, depending on the species (Schwarzenberger et al. 1996, Möstl and Palme 2002, Palme et al. 2005). Fecal sampling also enables frequent data collection without disturbance of the animal, allowing for longitudinal studies of hormones that can be used to assess changes in reproductive activity (Schwarzenberger 2007). The concentration of progesterone metabolites in feces has been used to study reproductive components such as seasonality, estrus and ovulation, pregnancy, and fertility status in a variety of wildlife species (Schwarzenberger 2007, Brown 2018, Sontakke 2018). In caribou, analysis of single fecal samples has been used to determine pregnancy in late winter, but repeated sampling has not been used to monitor ovarian activity, likely due to difficulties obtaining repeated samples from wild populations (Messier et al. 1990*a*, Morden et al. 2011, Joly et al. 2015).

Previous methods for assessing parturition in wild ungulates have included aerial surveys during the calving season (Whiting et al., 2012), serum progesterone tests on blood samples taken from captured animals (Wittmer et al., 2005), and vaginal implant transmitters. Rates of neonate calf survival are usually determined by late spring aerial surveys or by radio-collaring newborn calves. These methods are invasive and stressful to the animal, costly to researchers, and may miss early post natal deaths (DeMars et al. 2013). Analysis of movement patterns using GPS radio-telemetry data provides an alternative method of inferring parturition and survival of neonatal offspring (DeMars et al. 2013). Parturition in caribou corresponds with an abrupt decrease in movement rates. Over the first four to five weeks following parturition, the female's movement rate will gradually increase as the calf grows and becomes more mobile. If the female loses her calf, her movement will quickly return to pre calving rates. This change in movement pattern is detectable from GPS collar data when a location is acquired every one to three hours, though false negatives can occur if the calf is still born or dies shortly after birth (DeMars et al. 2013, Mueller et al. 2022). GPS movements can assess calf survival for the first four weeks of life, after which calf mobility begins to approach adult movement rates (DeMars et al. 2013). Understanding parturition and neonate survival will better inform conservation measures and aid recovery actions such as the conservation of specific habitat types used for calving.

We used a combination of population counts, body condition measurements, and fecal progesterone measurements collected during autumn from the Kennedy Siding supplemental feeding site and GPS-collar data from female caribou during May and June to characterize rates of ovulation, pregnancy, parturition, and calf survival in the Kennedy Siding herd. We discuss these rates in the context of reproductive parameters reported in caribou herds elsewhere. Specifically, we predicted that the Kennedy Siding herd would have greater rates of pregnancy among adults and yearlings, higher parturition rates, earlier parturition dates, and improved calf survival compared with values reported in the literature for unfed caribou herds and closer to values for herds known to have access to high amounts of summer food (Ouellet et al. 1997, Prichard et al. 1999). Further, we speculated what these comparisons indicate about potential mechanisms linking supplemental feeding and population growth. Overall, our results contribute to an increased understanding of reproduction in woodland caribou and help to inform conservation strategies and land-use plans for central mountain caribou.

Methods

Study site

The range of the Kennedy Siding caribou herd is in central British Columbia, within the traditional territory of the McLeod Lake Tse'Khene (McLeod Lake Indian Band). The habitat used by the herd is within the Sub-Boreal Spruce and Engelmann Spruce Sub-Alpine Fir biogeoclimatic zones (Meidinger and British Columbia 1991). The terrain is characterized by mountains and rolling hills ranging in elevation from 710m to 2010m above sea level (Jones et al. 2007). Caribou typically spend most of the year at high elevations dispersed in relatively undisturbed sub-alpine meadows and forests of Engelmann Spruce *(Picea engelmannii*) and Subalpline Fir (*Abies lasiocarpa*). Each fall the population descends to a small distinct area of lodgepole pine (*Pinus contorta*) forest at low elevation on the southwest edge of their range, which has abundant terrestrial lichen. Movement from high to low elevations is stimulated by the first snowfall events in the mountains. When on their fall range, caribou forage on terrestrial lichens, arboreal lichens, forbs and shrubs. Snow begins to accumulate on the ground in November and when it reaches a depth of about 1 m (usually in mid-January; (Jones et al. 2007), the herd moves back to high elevations, where they feed on terrestrial lichens in wind-swept areas or arboreal lichens where snow is deep and supports their weight. Most (2894 ha) of the fall range of the Kennedy Siding herd, including the feeding site, was designated an Ungulate Winter Range under the British Columbia Forest and Range Practices Act in 2002 (Arthur 2002).

The feeding area is located approximately 30 km south-east of the community of Mackenzie. Feeding occurs in the vicinity of the Kennedy (BCR) railway siding and Highway 97. The area experiences frequent vehicle traffic from forestry, railway, hydro, and other industries as well as by recreational users such as hunters. Other large mammals that inhabit the area include moose (*Alces alces*), white-tailed deer (*Odocoileus virginianus*), elk (*Cervus canadensis*), lynx (*Lynx canadensis*), wolf (*Canis lupus*), coyote (*Canis latrans*), grizzly bear (*Ursus arctos*), and black bear (*Ursus americanus;* (Heard and Zimmerman 2021).

Feeding, identification of individuals, and body condition measurements

We conducted supplemental feeding and identification of individuals based on the procedures described in Heard and Zimmerman (2021). The food pellets were produced by Hi-Pro Feeds/Trouw Nutrition Canada Inc. in Grand Prairie, Alberta. The formula for the pellets was developed at the University of Alaska to provide balanced and adequate levels of energy, nitrogen, and minerals for growth and reproduction of caribou (Barboza and Parker 2006) and have been used in other nutritional studies (Gustine et al. 2011) and conservation projects such as the Chisana Herd maternity pen (Adams et al., 2019).

Feeding began when caribou first arrived in late September and early October. We contracted the McLeod Lake Indian Band to build the feeders and deliver the food pellets. Initially, we provided small amounts of pellets in plastic livestock buckets so that any remaining feed could be removed from the site when the caribou were not present. Food was removed to limit attractants to the bears that used the area. We began ad-lib feeding in November when the bears were assumed to be in hibernation and continued feeding until January 15th. We stopped feeding on that date to avoid interfering with the natural movement of the herd back into their alpine habitats. Caribou consumed approximately 70kg of food per animal over the feeding period.

We used 7–9 Reconyx Hyperfire motion-sensor trail cameras, focused on either a feeder, a salt block, or along a trail, to obtain a continuous photographic record of individual caribou during the feeding period. The sex, age class (calf or adult), and the relative body condition of each caribou were recorded. Animals were considered in poor body condition if ribs were visible, and good body condition if ribs were not visible (figure 11). Individual caribou were identified from photos using the number and position of antler points, radio collars or ear tags, or unique markings (e.g., scars). Calves did not always have unique antlers, so we identified individuals based on their close association with mothers of known identity upon arrival at the feeders. The caribou were attracted onto a platform scale (using salt or pellets), with trail cameras positioned to photograph the individual caribou and record the weight (kg) on the scale's digital display. If an animal was photographed on the scale more than once, we used the average of the weights recorded as our final body mass measurement.

Figure 11: Examples of female caribou (*Rangifer tarandus caribou*) at the Kennedy Siding feeding site considered in poor body condition and female caribou considered in good body condition. The caribou in images A and B are considered in poor condition based on their visible ribs, spine, and hip bones in the trail camera images. The caribou in images C and D are considered in good condition based on the lack of visible ribs or other bones.

Animal care

Sample collection was conducted under research permits provided by the British Columbia Ministry of Forests as well an Animal Care and Use Protocol approved by the University of Northern British Columbia (ACUC Protocol Number: 2021-15). Some of the adult female caribou that used the feeding site (21 in 2021 and 19 in 2022) had collars and/or ear tags that were deployed as part of the Northern Mountain and Central Mountain Caribou Capture Program run by the BC Provincial Government, under the BC Provincial Animal Care Protocol (Permit Number: FJ21-618702).

Sample collection

We conducted sample collection with research technicians from the McLeod Lake Indian Band. We collected fecal pellet samples opportunistically by observing female caribou around the feeders. When defecation occurred, the individual caribou was identified, and the pellets were collected in a resealable plastic bag after the caribou moved away. The pellets were stored in a cooler with an ice pack until they could be transferred to a freezer and stored at -20°C within four hours of defecation. In 2021, we collected 155 pellet samples from 37 females (1-14 samples / caribou). During the 2022 field season, we collected 286 pellet samples from 43 females (1–16 samples / caribou).

We collected hair samples using a noninvasive snaring method. We affixed metal alligator clips to a piece of wood which were held open using small pieces of wooden toothpicks. The piece of wood was attached to one of the feeders and when caribou put their head down to eat, their neck pressed down on the clips, knocking out the toothpick and causing them to close. When the caribou moved away, the clip caught a sample of guard hair from the neck, typically with at least 10 hairs/clip. This method appeared to cause little disturbance to the caribou, as they did not avoid using the feeder where the clips were set up. We collected hair samples from 27 caribou in 2021 and 33 caribou in 2022, which were used for DNA analysis.

DNA analysis

We sampled feces for DNA by taking three surface rubs from each pellet sample using cotton swabs. We stored samples of guard hairs with visible root bulbs in unwaxed paper envelopes. DNA extraction, amplification, and sequencing of hair and fecal samples were conducted by Wildlife Genetics International in Nelson, BC. The DNA was extracted using QIAGEN DNeasy Blood and Tissue kits. For hair samples, the roots clipped from a target of ten guard hairs was used. For fecal swabs ~ 5 mm clippings from the used end of one swab per sample was used. Individual identity was established using 18 microsatellite markers established by Serrouya et al., (2012) along with a ZFX/ZFY sex marker. The success rate for producing all 19 loci was 85% for hair samples and 91% for fecal swabs. DNA results were used to identify unmarked females between years and to obtain an exact or estimated age of the animal.

Fecal progesterone enzyme linked immunosorbent assay (ELISA)

To extract hormones from the fecal samples, we first thawed and homogenized each sample. A portion of the homogenized sample was transferred to a plastic snap cap vial which was covered with a low lint delicate task wipe secured with an elastic band. The vials were lyophilized for ~ 26 hours. The dried feces were powdered and stored in the freezer at -20˚C. Hormone metabolites were extracted from 0.2g of dried feces in 5ml of 80% HPLC grade methanol (Thermo Fisher Scientific)/20% water. Vials were sealed and rotated at 160 rpm overnight at room temperature. A portion of the methanol extract was transferred to a 2ml centrifuge tube with a cap that included an o-ring to prevent evaporation. Extracts were centrifuged for 30 minutes, and the supernatant was removed and stored at -20˚C until analysis.

We followed a modified version of the protocol described by Graham et al. (2001) to determine concentrations of fecal progesterone metabolites. We coated ninety-six well plates with affinity-purified rabbit anti mouse gamma globulin (25 µg/plate [Sigma-Aldrich] dissolved in coating buffer (0.015 M Na_2CO_3 [VWR], 0.035 M $NaHCO_3$ [Sigma-Aldrich]; pH 9.6) and incubated them overnight at room temperature. The coated plates were washed (0.04% Tween 20 [Sigma-Aldrich]) and refilled with 200 µl Trizma assay buffer (0.02 M Trizma [Sigma-Aldrich], 0.300 M NaCl [VWR], 0.1% bovine serum albumin [VWR]; pH 7.5) and stored at room temperature for at least 1 hour to block non-specific binding. We diluted fecal extracts (1:4 to

1:32) in Trizma assay buffer prior to the assay. The wells were emptied of the Trizma buffer and 50 µl each of diluted sample and standards were dispensed. Horse-radish peroxidase-labeled cortisol was dispensed, followed by anti-cortisol antibody or (Anti-progesterone CL425; CJM Munro, UC Davis). The plates were incubated overnight at room temperature. Following incubation, we washed the plates three times and then added 200 µl of substrate solution (0.5 mL of 0.016 M tetramethylbenzidine [VWR] in dimethylsulphoxide [Thermo Fisher Scientific], and 100 mL of 0.175 M H_2O_2 [VWR] diluted in 24 mL of 0.01 M $C_2H_3O_2Na$ [Thermo Fisher Scientific]; pH 5.0) to each well. The plates were incubated for 45 minutes at room temperature and then the enzyme reaction was stopped by adding 50 µl of stop solution to each well (3 M H_2SO_4 [Thermo Fisher Scientific]). The optical density was measured at 450 nm. If the sample duplicates had a coefficient of variation (CV) greater than 15%, we re-assayed the sample. The cross-reactivity of the progesterone antibody was reported by Graham et al. (2001), including progesterone (100%), and pregnanediol, androstenedione, and corticosterone (<0.1%).

As an analytical validation, we first created a pooled sample of fecal extracts from different female caribou. To establish parallelism, we tested serial two-fold dilutions of the pooled sample for comparison displacement curves (Figure 12). The intra-assay coefficient of variability was determined by assaying replicates of the pooled sample on the same plate. The intra-assay CV for 35 samples was 6.9% at 59.3% binding. The inter-assay coefficient of variation was determined by running a replicate of the pooled sample at a high and low concentration as controls on each plate. The inter-assay CV was 16% at 21.3% binding and 10.8% at 71.8% binding over 12 plates. As a physiological validation, we compared the concentration of fecal progesterone metabolites between the pooled extracts of female caribou and a combined extract from fecal samples taken from two adult male caribou at the feeders. We used this comparison to ensure that the progesterone ELISA could measure changes in fecal progesterone metabolites associated with the female reproductive system with the assumption that fecal progesterone metabolite concentrations would be similarly low in males and anovulatory females.

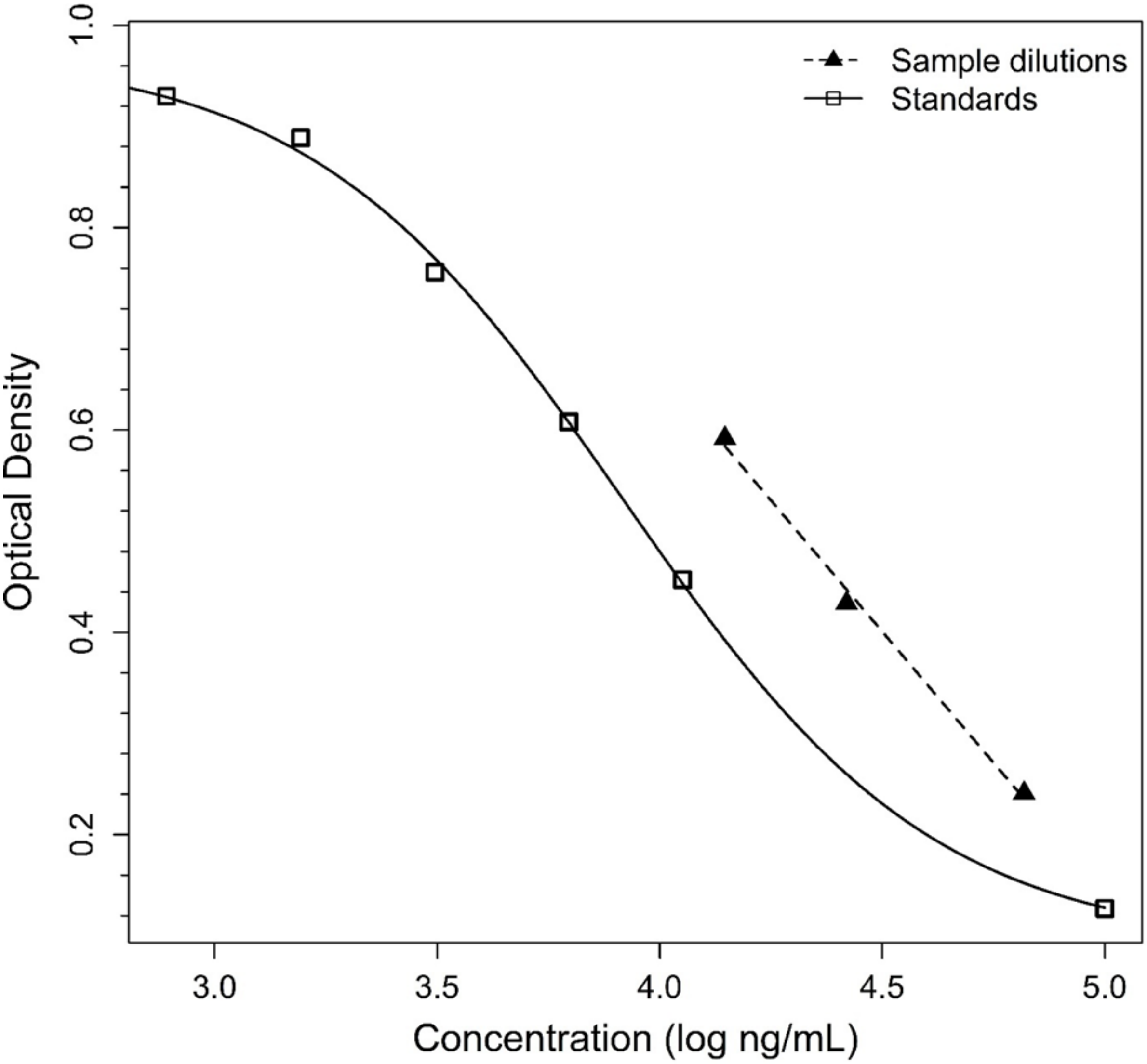


Figure 12: Parallelism of progesterone standards (solid line) and a serially diluted pooled sample extract from female caribou (*Rangifer tarandus caribou*) fecal samples (dashed line) collected in 2021 and 2022 at the Kennedy Siding feeding site in British Columbia, Canada.

Statistical analysis

All data analysis were conducted using R (R Core Team 2023). We classified each caribou sampled according to their age and reproductive status (yearlings and adults [≥ 2 years old] with and without a calf at heel). Yearlings were identified using DNA collected from calves the previous year. Adults without calves were identified using DNA collected in previous years or unique radio collars and/or ear tags. We performed Kruskal-Wallis rank sum tests followed by Wilcoxon post-hoc pairwise comparisons to compare body mass between one -year olds, adults with a calf, and adults without a calf, and a Wilcoxon test to compare body mass in animals in good and poor body condition (Kassambara 2019).

We considered an animal to be ovulatory based on whether they had at least one fecal sample with a FPM concentration above the baseline determined from male samples. We used general linear mixed effects regression models to assess the impact of age, reproductive status, and body condition on fecal progesterone concentrations (Bates et al. 2015). We applied a square-root transformation of fecal progesterone prior to analysis to obtain normal distributions of the model residuals. We included the effects of reproductive age class, body mass, and body condition body condition as fixed effects. Body mass was square root transformed to normalize the distribution, then standardized to a mean of 0 and a standard deviation of 1 prior to analysis. Individual identity was included as a random effect in all models. We examined any models that had a ΔAICc within 0–2 units of the top model for uninformative parameters by assessing whether they differed from the best model by one parameter and had similar log-likelihood values as the top model (Arnold 2010).

We estimated parturition rates based on the radio collar movements of 19 individual female caribou in the Kennedy Siding herd between 2020 and 2024 using data and analysis provided by M. Klaczek (personal communication, 2024). Parturition status was estimated using methods from DeMars et al. (2013). The movement models represent three states of females during calving season; 1) did not calve, 2) calved and the calf survived to four weeks, and 3) calved and calf was lost by four weeks of age. For the model representing females that did not calve, the movement rate remained constant over time. For the model representing females that calved, and the calf survived to four weeks, there is a single break point where movement rate abruptly drops, indicating calving, before increasing again without a clear breakpoint. For the model representing females that calved and then subsequently lost their calf, there are two break points indicating when calving and calf loss occurred. We compared the model results to observations made in the fall to confirm that females did or did not have a calf. Parturition dates and dates of calf mortality were also estimated by radio collar movement models. We estimated calf survival by comparing the estimated parturition rate to the number of adult females with a calf at heel when they arrived at the feeders.

Results

Body mass and nutritional condition

We collected body condition and hormone data from 45 individual female caribou during the 2021 and 2022 feeding seasons. We identified and sampled 20 of the total 45 animals in both years. In 2021, we classified 14 animals as adults with a calf, five as adults without a calf, and six as yearlings. In 2022, we classified 21 animals as adults with a calf, 13 as adults without a calf, and six as yearlings.

The body mass of all caribou sampled in 2021 and 2022 ranged from 95 –153 kg overall (n=65, median = 128 kg). Among reproductive age classes, body mass ranged from 105 –150.5 kg (n=35, median = 128.5 kg) for adults with a calf at heel and 107 –153 kg (n = 18, median = 138.0 kg) for adults without a calf at heel. Yearling caribou ranged in body mass from 95 –125.5 kg (n=12, median = 106 kg). The distribution of body masses differed among reproductive age classes (Kruskal-Wallis Test; H = 22.87, df = 2, $p < 0.001$). Post-hoc pairwise comparisons revealed that adults with a calf at heel had smaller body masses compared to adults without a calf ($p = 0.036$). As expected, yearlings had smaller body masses compared to adults with a calf ($p < 0.001$) and adults without a calf ($p < 0.001$). All yearling females had body mass measurements that were greater than 70% (92.75 kg) of the median adult female body mass (132.5 kg; Figure 13). Of the caribou sampled, almost half were classified as being in poor body condition based on the visibility of ribs (Table 6). Most (83%) of the individuals in poor body condition were adults with a calf (Table 6); however, a Wilcoxon signed-rank test showed that the difference in body mass between caribou in good and poor body condition was not significant ($z = -0.118$, $p = 0.906$).

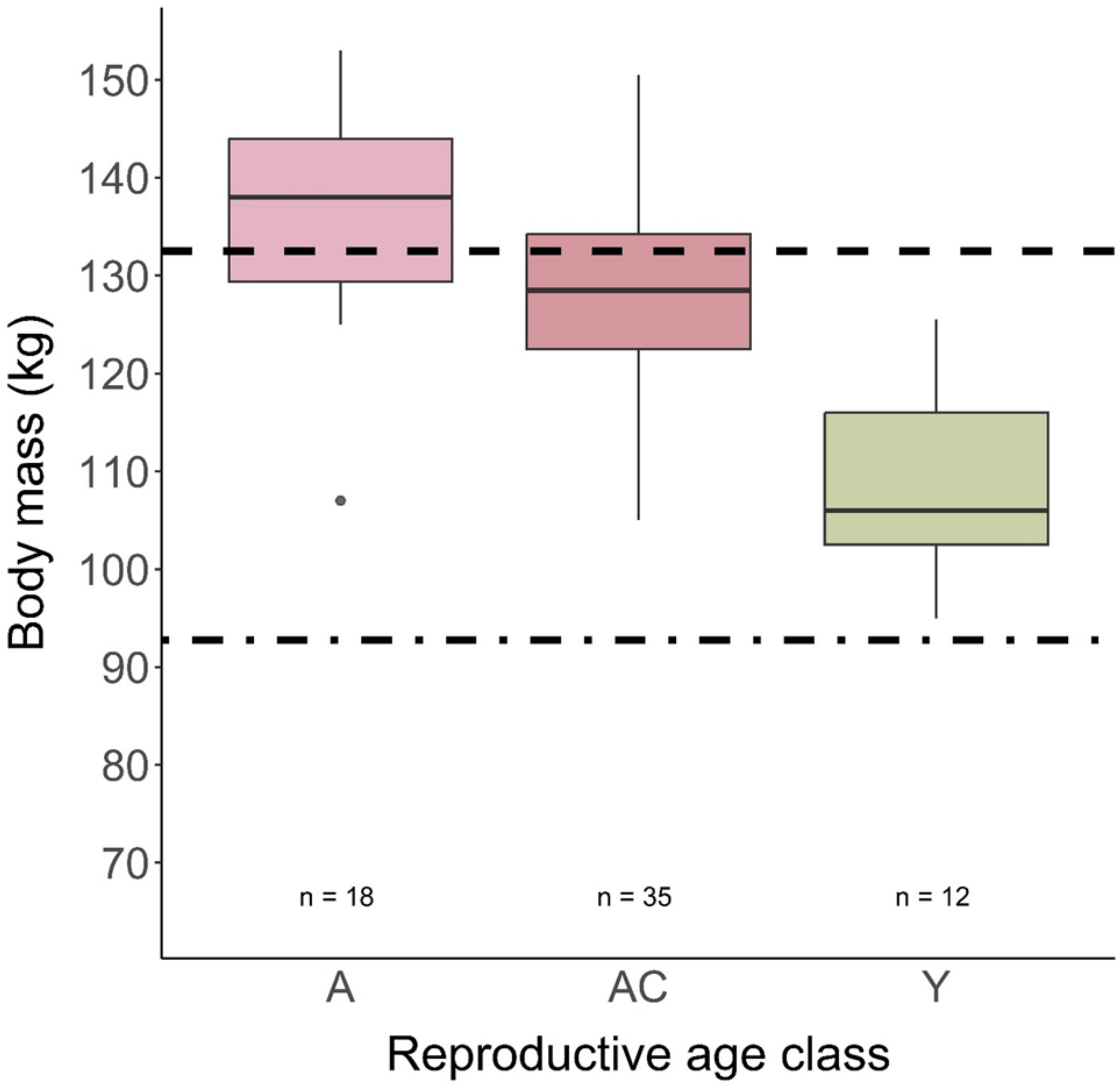


Figure 13: Body mass (kg) of adult female caribou (*Rangifer tarandus caribou*) without a calf at heel (A) and with a calf at heel (AC) compared with yearling females (Y) using the feeding site at Kennedy Siding, British Columbia, Canada, in 2021 and 2022. The centre line of each box represents the median and the outer limits represent the 25th and 75th percentiles. The lines extending below and above each box represent 1.5 times the interquartile range for each percentile. The dashed line represents the median adult female body mass (132.5 kg). The dotted line represents 70% of the median adult female body mass (92.75 kg). Sample sizes are shown at the bottom of the panel.

Table 6: Body condition (assessed as visibility of ribs) of female caribou (*Rangifer tarandus caribou*) in each reproductive age class at the Kennedy Siding feeding site in British Columbia, Canada, in 2021 and 2022.

Age class		Adult with a calf	Adult without a calf	Yearling
Ribs visible	No	10	15	10
	Yes	25	3	2

Fecal progesterone metabolites

We analyzed progesterone metabolites (FPM) in 387 fecal samples from 45 individual female caribou. The number of samples collected per individual ranged from 1 –18. Concentrations of FPMs ranged from 141– 2612.2 ng/g with an overall median of 897.35 ng/g. The median and range of FPM concentrations were very similar among age classes. Yearlings had a median FPM concentration of 942.1 ng/g (range = 169.4 –2316.7 ng/g), adults with a calf at heel had a median of 877.6 ng/g (range = 228.6 ng/g –2269.9 ng/g), and adults without a calf had a median of 925.1 ng/g (range = 141– 2612.2 ng/g; Figure 14). The baseline progesterone concentration determined by quantifying FPMs in feces from five adult male caribou was 162.8 ± 28.9 ng/g. All the female caribou sampled had at least one FPM value above the baseline value determined in males, and therefore all were considered ovulatory (Figure 14).

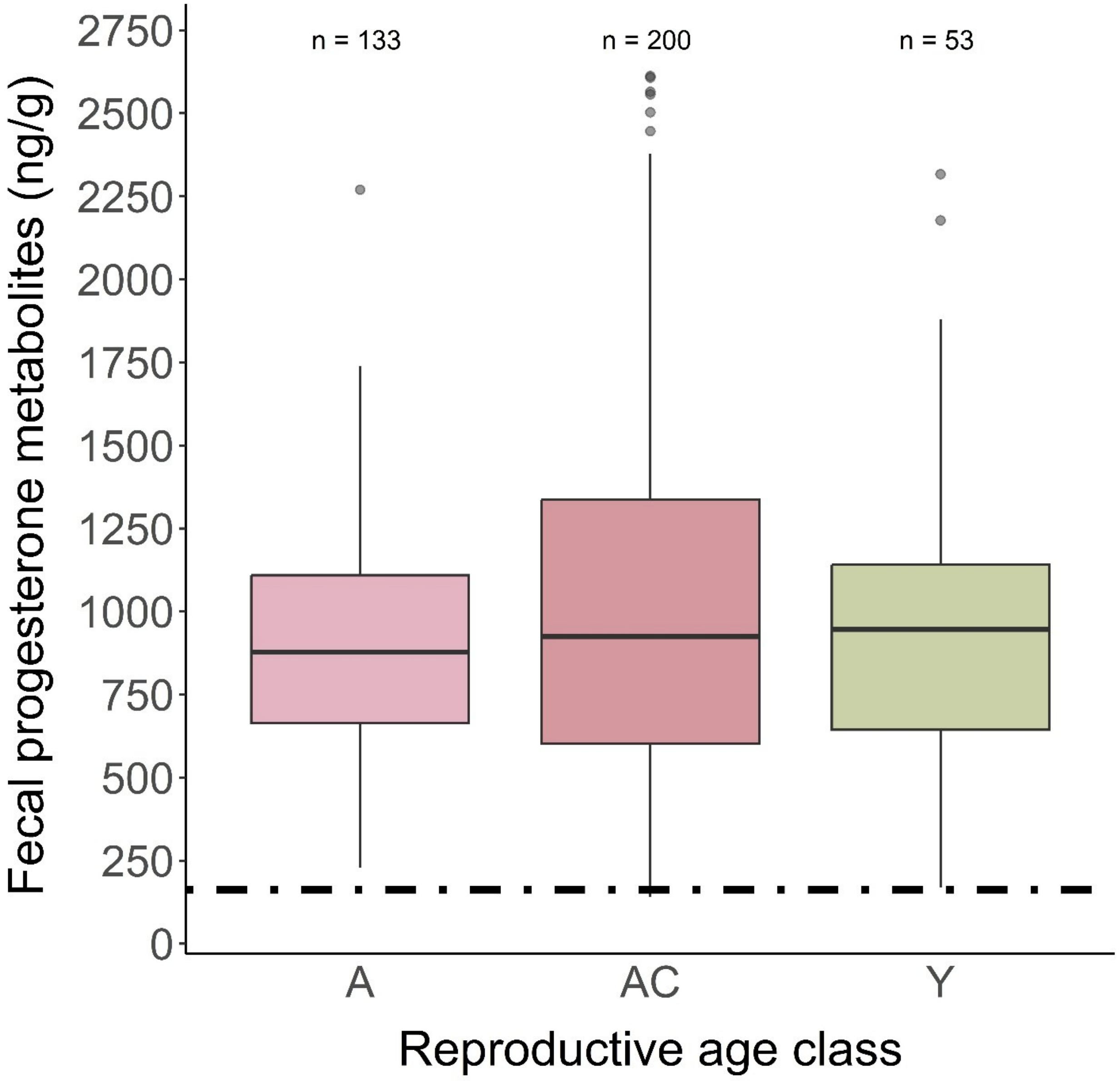


Figure 14: Fecal progesterone metabolite concentrations adult female caribou (*Rangifer tarandus caribou*) without a calf at heel (A) and with a calf at heel (AC) compared with yearling females (Y) using the feeding site at Kennedy Siding, British Columbia, Canada, in 2021 and 2022. The centre line of each box represents the median and the outer limits represent the 25th and 75th percentiles. The lines extending below and above each box represent 1.5 times the interquartile range for each percentile. The dotted line represents the baseline progesterone metabolite concentration derived from a pooled male sample mass (162.8 ng/g). Sample sizes are shown at the top of the panel.

Of four candidate models used to predict FPM concentrations, the null model ranked highest, indicating that none of the variables tested (i.e., reproductive age class, body condition, and body mass) explained more variation in FPMs than would be expected due to chance alone (Table 7).

Table 7: Ranking of four candidate general linear mixed-effects models used to predict fecal progesterone metabolite concentrations in fecal samples (n = 397) from female caribou (*Rangifer tarandus caribou*) sampled between fall and winter of 2021 and 2022 at the Kennedy Siding feeding site in British Columbia, Canada.

Rank	**Candidate model**	**df**	**logLik**	**AIC$_c$**	**ΔAIC$_c$**	**ω_i**
1	Null	3	-1313.54	2633.15	0	0.543
2	Reproductive age class	5	-1312.17	2634.51	1.355	0.276
3	Body condition + body mass	5	-1312.89	2635.93	2.779	0.135
4	Reproductive age class + body condition + body mass	7	-1311.89	2638.07	4.921	0.046

Loglik = Loglikelihood, AIC$_c$ = AIC$_c$ score, ΔAIC$_c$ = difference in corrected AIC between model and top model; ω_i = Akaike weight.

Parturition and calf survival rates

The total annual parturition rate estimated using radio collar data from 40 females monitored between 2020 – 2024 was 87.5% with 12.5% of females not producing calves (Table 3). Calving date ranged from May 11 to June 6. Of females that gave birth, 25.7% lost their calves before the fall (Table 8). Estimated parturition dates were available for 20 animals between 2021 and 2024. Parturition dates ranged from May 11th to June 7th (mean date = May 25th ± 7 days). Estimated dates of calf loss were available for five of the nine animals identified as having lost their calf. All recorded calf mortalities occurred within 30 days of parturition, between June 12th and June 21st.

Table 8: Parturition and calf survival status of 40 female caribou (*Rangifer tarandus caribou*) with radio collars in the Kennedy Siding herd, central British Columbia, Canada, between 2020 and 2024. Parturition and calf mortality was estimated using a model developed by DeMars et al. (2013).

Year	**N**	**Calved (%)**	**Did not calve (%)**	**Lost calf (%)**
2020	9	9 (100)	0 (0)	1 (11)
2021	10	8 (80)	2 (20)	2 (25)
2022	7	7 (100)	0 (0)	1 (14)
2023	10	7 (70)	3 (30)	2 (29)
2024	4	4 (100)	0 (0)	3 (75)

Total	40	35 (87.5 ± 5)	5 (12.5 ± 5)	9 (25.7 ± 7)

Discussion

We used a combination of body condition metrics, hormone analysis, and demographic rates to characterize reproductive parameters in the Kennedy Siding caribou herd. We found that all females, including yearlings, had fecal progesterone concentrations reflective of ovulation, indicating that all females had the capacity to become pregnant. In contrast, some females, especially those that produced a calf the year sampling occurred and yearlings, would be expected to exhibit suppressed ovarian activity if amount or quality of nutrition limits pregnancy rates in this population (Thomas 1982, Mani et al. 1992, Webb et al. 2004, Chaves et al. 2024). The rates of ovulation we observed could be associated at least in part to supplemental feeding, though further comparisons with unfed populations would be required to confirm the influence of supplemental feeding on ovulation. Compared with caribou herds elsewhere, caribou at Kennedy Siding had relatively high rates of parturition, pregnancy among yearlings, and calf survival. These findings provide preliminary evidence that supplemental feeding could lead to population growth in this herd via multiple mechanisms.

Body condition, ovulation, and primiparity

All females sampled had at least one FPM value above the male baseline, indicating that all females in the herd were ovulatory and therefore capable of becoming pregnant. The fecal samples, however, were collected during the breeding season and early gestation and were still fluctuating; therefore we were unable to use FPMs to determine which females became pregnant following ovulation and fertilization. Body mass, body condition, and reproductive age class were not identified by the modeling framework as strong predictors of FPM values. These findings suggest that the body mass threshold for ovulation was met, and all animals sampled had the capacity to become pregnant. By contrast, findings in caribou and other large herbivore species indicate that nutritional limitation can suppress ovulation cycles, leading to years of skipped reproduction in adult females or later age at primiparity (Thomas 1982, Festa-Bianchet et al. 1994, Cook et al. 2013, Newby and DeCesare 2020).

Our FPM results combined with the minimum body weight among females in this study (95 kg) suggest that females weighing 72% of median mature female body mass (132.5 kg) can ovulate and become pregnant. We cannot determine a lower body mass threshold for ovulation because all females in this study were ovulatory. However, a body mass threshold between 65 and 84% of the mean population body mass has been reported as the threshold for ovulation in other ungulate populations. Specifically, in woodland caribou in Labrador, Canada, Parker (1981) reported a mean (± standard deviation) spring body mass of 78.6 ± 4.5 kg in pregnant two-year olds (one-year old at breeding), 84% of the mean body mass of females older than two years. In the same population, Crête et al. (1993) suggested a live autumn body mass threshold of approximately 112 kg for parturient females, 75% of the mean body mass of all females sampled. Even lower threshold masses have been reported in elk (65–70%; Hudson et al., 1991) and domestic sheep (50–70%; Hafez 1952, Dýrmundsson, 1973). Overall, the body mass measurements of females in this study—all of which were ovulatory— fell above 70% of the body mass of the population median, which is consistent with reports of body mass thresholds for ovulation in other ungulate populations. In Svalbard reindeer, Albon et al. (2017) found that adult ovulation rate was positively related to variation in mean October adult body mass. These findings provide further support that nutritional condition does not limit ovulation rates in this population.

Nutritional conditions in early life, including maternal investment, can have a strong effect on growth and age at primiparity in many species (Festa-Bianchet et al. 1994, Gaillard et al. 2000). We found that 100% (n = 12) of yearling females at Kennedy Siding had FMP values indicating ovulation (i.e., capacity to become pregnant) and all had body mass measurements greater than 70% of median adult body mass, which is an approximate threshold for reproduction. Moreover, based on observations at the feeders in 2021 and 2022, and radio collar movements in 2023, at least four of seven yearlings re-identified the following year as two-year olds had calved, for a minimum pregnancy rate among yearlings of 57%. Combined, these findings suggest that the average age of primiparity is one year in the Kennedy Siding herd. Caribou are known to breed as one-year olds; however, the proportion varies depending on the population and environmental conditions with conception in yearling caribou occurring only when nutrition is especially good (Parker 1981, Ouellet et al. 1997, Rettie and Messier 1998). In Svalbard reindeer, the variation in yearling ovulation rates is positively correlated to their mean body mass (Albon et al. 2017). In arctic caribou populations, females generally first give birth at three years old, and the pregnancy rate of animals that were one-years old at breeding is often less than 50% (Thomas 1982, Cuyler and Østergaard 2005), however it may be as high as 100% in years with high summer and winter range quality . Rates of yearling pregnancy in wild woodland caribou populations outside of BC have been estimated at 43% (n = 21; Parker 1981), 33% (n = 3; Crête et al., 1993), and 100% (n = 5; Rettie and Messier 1998). Notably, our finding that 57% of yearling females bred is comparable to data from the Chisana herd in southern Yukon and Alaska, where 57% (n = 67) of females produced their first calf at two-years old (one-year old at conception) during 2003 to 2006 when maternal penning was applied as a management strategy (Adams et al. 2019). Caribou in maternity pens have daily access to pelleted feed and supplementary lichen that could improve nutrition and growth, resulting in earlier age of puberty (Adams et al. 2019, Lamb et al. 2024*a*). Although comparable data would be required from an unfed control population, our findings of reproductive activity in a high proportion of yearlings among females at Kennedy Siding relative to caribou elsewhere could conceivably be influenced by supplemental food. Such an effect could occur if females that use feeders invest greater energy into offspring nutrition (i.e., silver spoon effects) leading to faster growth and earlier primiparity, if feeding contributes to accelerated growth and puberty among females that use feeders as calves, or if a pulse of nutrients provided to 1.5-year-olds promotes ovulation cycles and subsequent pregnancies. We found that the median mass of adults without a calf at heel was 9.5 kg heavier than those with a calf, further demonstrating the impact that calf rearing has on body condition. The length of time that females spent nursing a calf influences their body condition in autumn. Since all females were ovulatory, most of the adults that arrived at Kennedy Siding without a calf likely had given birth but lost their calf some time before autumn. Most calf mortality occurs within summer shortly after parturition; therefore, caribou that lost a calf may have up to three extra months to regain body stores lost to lactation and would likely enter winter in better condition. In caribou, the average difference in body fat between females that raised a calf and those that didn’t is 3 percentage points (Crête and Huot 1993, Chan-McLeod et al. 1999, Cook et al. 2021). In elk, Cook et al. (2013) found that individuals that did not give birth (i.e., not pregnant the previous winter) averaged 8 percentage points more body fat than those that raised a calf. When summer conditions are inadequate females with a calf accrue smaller fat reserves than non-reproductive animals, resulting in decreased fecundity and survival (Crête and Huot 1993).

Supplemental feeding may also increase ovulation rates through the effects of nutritional flushing. Flushing is the practice of providing improved nutrition at the beginning of the mating season and is commonly used to increase ovulation rates in domestic ruminants like sheep (Robinson et al., 2002, 2006). Adequate protein and energy intake prior to breeding is essential for reproduction, as it regulates reproductive hormones and supports normal ovulation and fertility in females (Robinson et al. 2006, Ashworth et al. 2009, Assan et al. 2025). Flushing increases the release of gonadotropic hormones, including luteinizing hormone and follicle stimulating hormone, which improves the ovulation rate (Ashworth et al. 2009, Assan et al. 2025). Flushing increases the number and size of preovulatory follicles in ewes (Robinson et al. 2006, Ashworth et al. 2009). Flushing in ewes in low body condition has a larger effect on ovulation than in ewes in higher body condition (Robinson et al., 2002, 2006). Further research on the effects of nutrition on ovulation in caribou is needed to assess whether autumn supplemental feeding could have similar effects as flushing. One limitation of our study is the lack of an unfed population to which our FPM and body mass results could be compared. The Kennedy Siding herd is unique in that it consistently uses the same small, easily accessible area every year, making repeated sampling easier than it would be for other herds. Very little fecal hormone data exists for woodland caribou in British Columbia, and the existing data is either from a single sample per individual and/or collected at a different time of year, making comparisons to our data challenging (Flasko et al. 2017, Mueller et al. 2022). Body mass is also difficult to measure noninvasively in other populations. Repeated sampling of an unfed population during the autumn would help to clarify our FPM results and make a more explicit link supplemental feeding and the survival of adult females, their ability to conceive and carry a fetus to term over multiple years, and calf survival.

Demographic rates

Based on the radio collar movement data, we estimated a total parturition rate of 87.5 % for the Kennedy Siding herd. This estimate is greater than total parturition rates reported in other herds in BC (82–59%; Table 9), and the standard error for the estimates did not overlap with the standard error of our estimate. Like the other herds our estimate varied from year to year. These results support our prediction that supplemental feeding would increase parturition rates relative to other nearby herds that do not experience supplemental feeding. Parturition rates in caribou are closely tied to autumn body mass, and are sensitive to even small shifts in mass distribution (Cameron and Hoef 1994). Barboza et al., (2024) found that captive caribou fed a restricted diet during the summer then transitioned onto a high energy diet for the autumn breeding period gained approximately 0.09 kg/day, whereas caribou at Kennedy Siding may gain approximately 0.103 kg/day over the feeding period (Heard and Zimmerman 2021). Since parturition rates are positively correlated with body mass during the autumn, this rapid mass gain could improve the probability of pregnancy and parturition, especially for smaller animals (Cameron et al. 1993, Cameron and Hoef 1994, Heard and Zimmerman 2021). The effects of nutritional flushing may also influence parturition rates. Improved pre-mating body condition and diets in domestic ruminants can affect embryo survival by altering the quality of the oocyte (Abecia et al. 1999, Lozano et al. 2003, Ashworth et al. 2009). In sheep, ewes that were underfed had poorer quality oocytes, lower rates of cleavage and blastocyst formation, and lower pregnancy rates compared to ewes that received adequate or increased nutrition (Abecia et al. 1999, Lozano et al. 2003, Borowczyk et al. 2006).

Table 9: Parturition rates of caribou (*Rangifer tarandus caribou*) in five populations of woodland caribou in British Columbia and Alberta, Canada. Standard error (SE) was calculated as the standard error of the proportion.

Reference	Population / region	Years	n	Parturition (%)	SE
Gustine et al. 2006 [a]	Besa Prophet	2002	9	55.6	17.6
		2003	13	76.9	12.2
		Total	22	68.2	10.2
DeMars et al. 2013 [b]	Fort Nelson	2004	10	90	
		2011	24	79	
		2012	15	80	
		Total	49	81.6	5
Nobert et al. 2016 [b]	Narraway	1998 - 2014	48	80	6
	Redrock-Prairie Creek	1998 - 2014	35	61	8
Mueller et al. 2022 [b]	Klinse-Za (penned) [c]	2018	12	75	
		2019	16	81	
		2020	13	69	
		Total	41	76	7
	Klinse-Za (free ranging)	2018	4	75	
		2019	10	50	
		2020	13	62	
		Total	27	59	9

[a] Parturition rate determined using observations from fixed-wing aircraft twice daily

[b] Parturition rate determined using GPS movement model developed by DeMars et al. 2013

[c] Received supplemental feeding

The effect of autumn supplemental feeding did not appear to influence parturition dates for the Kennedy Siding herd as dates were similar to those reported in other herds in BC. Calving occurred between May 11th and June 7th in the Kennedy Siding herd, April 29th and July 4th in the Klinse-za herd (Mueller et al. 2022), May 18th and June 19th in the Narraway and Redrock Prairie Creek herds (Nobert et al. 2016), and May 21st and June 10th in herds in the Besa Prophet region (Gustine et al. 2006). Parturition date has been related to maternal condition in late gestation and at time of conception, with animals in better condition giving birth earlier (Cameron et al. 1993, Crête et al. 1993). An earlier calving date may enhance fat accretion and increase the chance that a female will successfully reproduce because she is able to escape the high nutritional demands of lactation earlier (Cook et al. 2004). Parturition dates may also be influenced by variables not considered in this study, such as latitude, spring and summer climatic conditions and vegetation characteristics. For example, Post et al. (2003) found that caribou calving seasons are highly synchronized to the progression of forage plant phenology.

Total calf survival, based on females with a recorded calving event returning to Kennedy Siding with a calf at heel, was 74.3%. This rate is slightly higher than previously reported total calf survival estimates for caribou that did not receive supplemental feeding, which range from 58 – 63% (Table 10). The standard error of our estimate was smaller and did not overlap with the standard errors of the other herd estimates. The higher calving rate lends support to our hypothesis that improved maternal nutrition from supplemental feeding might lead to improvements in calf survival. Calf survival can, however, be highly variable between years since it can be caused by a wide range of factors including predation, accidents, emaciation, congenital defects, disease, and stillbirths, with predation being the main cause of mortality in BC (Seip and Cichowski 1996, Gustine et al. 2006). Notably, calf survival observed in 2003 in the Besa Prophet was 79% even though the total calf survival over two years was 66% (Gustine et al., 2006). Estimates of calf mortality may also be limited by sample size. In 2024 collar locations were only available for four caribou in the Kennedy Siding herd, which may have inflated the estimates of mortality that year. All of mortalities recorded in the Kennedy Siding herd occurred within 30 days of parturition, consistent with calf mortality patterns in other herds in BC (Gustine et al. 2006, DeMars et al. 2013, Nobert et al. 2016).

Table 10: Caribou (*Rangifer tarandus caribou*) calf survival in four populations of woodland caribou in British Columbia and Alberta, Canada. Standard error (SE) was calculated as the standard error of the proportion.

Reference	Population / region	Years	n	Calf survival (%)	SE
Gustine et al. 2006 [a]	Besa Prophet	2002	25	54	11
		2003	25	79	8
		Total	50	66	7
DeMars et al. 2013 [b]	Fort Nelson	2004	9	55.6	
		2011	12	66.7	
		2012	6	66.7	
		Total	27	63	9
Nobert et al. 2016 [b]	Narraway	1998 – 2014	28	60	9
	Redrock-Prairie Creek	1998 – 2014	21	58	11
McNay et al. 2022[c]	Klinse-Za (penned)[d]	2014–2020	65	95.4	

[a] Calf survival determined using observations from aerial surveys
[b] Calf survival determined using GPS movement model developed by DeMars et al. 2013
[c] Calf survival determined from direct observations in maternal pen
[d] Received supplemental feeding

The data from the movement models suggested that approximately 10% of caribou did not calve. Since all the females we sampled had FPM values indicating they were able to become pregnant, this implies that some caribou either failed to become pregnant, despite ovulating, or lost their pregnancy before spring. Early embryonic mortality in caribou occurs close to the breeding season and is inversely correlated to maternal body fat and mass (Russell et al. 1998). Previous lactation status during the summer may impact the probability of early embryonic mortality because caribou in poor condition in autumn may sacrifice pregnancy to allocate nutrients to the growth and survival of their current calf or their own survival. All of the incidences of early embryonic mortality recorded by Russell et al. (1998) occurred in caribou that extended lactation into the fall. Late gestation in-utero reabsorption of a pregnancy is rare in caribou and reindeer but can occur when a female is in very poor condition (Ringberg and Aakvaag 1982). The prevalence of early and late term pregnancy loss in woodland caribou is not well documented, though Mueller et al. (2022) reported that out of 34 pregnant caribou held in the Klinse-Za maternity pen, two aborted births and one still birth occurred (9% of pregnancies). In Svalbard reindeer, the loss of reproductive potential between ovulation and parturition was associated with the severity of the winter and there were significantly greater losses in winters with low April body mass (Albon et al. 2017). The increase in nutritional resources provided by supplemental feeding could reduce the number of pregnancies lost due to inadequate nutritional condition. Notably, two of the females that did not give birth in 2023 were observed to be in good body condition and did not have a calf at heel at the feeders in 2022. Non nutritional causes, such as disease or congenital issues may be more likely to cause pregnancy loss. The movement model used may not detect parturition if the calf is stillborn, non-viable, abandoned, or killed immediately and the female immediately resumes a normal daily step length (DeMars et al. 2013, Mueller et al. 2022). The difference between ovulation and parturition in our study could be due to undetected parturition events that were masked by early calf mortality.

Comparison of population growth between supplemental feeding and maternal penning

Applying more than one management action simultaneously can improve population growth in caribou (Serrouya et al. 2019). Assessing the response of caribou populations to different recovery actions independently can help to identify the mechanisms by which an action influences population growth and helps inform managers on the number and intensity of recovery actions needed for population growth. We compared the demographic and population growth rates of the Kennedy Siding herd to the nearby Klinse-Za herd. The ranges of the two herds are adjacent and have similar habitat characteristics (Heard and Zimmerman 2021, McNay et al. 2022). Both herds experienced significant declines around the same time; the Klinse-Za herd declined from ~200 animals in the 1990s to 36 in 2013 and the Kennedy Siding herd declined from ~120 in 2007 to 49 in 2014 (Heard and Zimmerman 2021, McNay et al. 2022). Maternal penning began for the Klinse-Za herd in 2014, the same year supplemental feeding began for Kennedy Siding and an aerial-based program wolf removal program was initiated by the BC Government in 2015 in both ranges (Heard and Zimmerman 2021, McNay et al. 2022). Since then, both populations have increased at similar rates. The average population growth rate from 2014 to 2018 was 1.14 in the Klinse-Za herd and 1.16 in the Kennedy Siding herd. Although feeding and maternal penning appear to have had similar effects on recruitment, the mechanism underlying population growth may differ. Specifically, parturition rates were greater in the Kennedy Siding herd by 11.5–28.5 % (Table 9), whereas rates of calf survival in the 30 days following birth were greater in the Klinse-Za herd by 21 % (Table 10; McNay et al., 2022). This difference suggests that the contribution to recruitment from supplemental feeding comes mostly from an increase in the proportion of females that breed and parturition rates (Table 9), maternal penning primarily affects calf survival (Table 10).

In addition to improving calf survival, maternal penning may also benefit females through improved nutrition as Mueller et al. (2022) found that penned caribou had a higher total parturition rate (76 %) than free ranging animals 59 %; table 9). One explanation for this effect is that improved nutrition during late gestation influences parturition rates. While in the pen, caribou are supplemented with lichen and the same pelleted food used at Kennedy Siding (McNay et al. 2022). The pelleted food contains essential micronutrients such as iodine and selenium, which are critical to fetal development and survival at birth. The production of the hormones T_3 and Thyroxine (T_4) by pregnant animals are dependent on adequate selenium and iodine intake (Robinson et al. 2001). The thyroid hormones T_3 and T_4 play important roles in fetal cell and tissue differentiation, lung maturation, and development of brown adipose tissue, which are important to neonatal thermogenesis and survival (Robinson et al. 2001). Selenium and iodine deficiencies are often a cause of abortions in domestic sheep and goats. Deficencies in copper and zinc have also been implicated in abortions in domestic livestock. Caribou in the Klinse-Za herd have lower selenium, copper, and zinc compared to nearby Northern Mountain caribou and boreal caribou subpopulations (Lamb et al. 2024*a*). Selenium levels were greater in penned animals compared to free ranging animals (Lamb et al. 2024*a*). The increase in micronutrients provided by feed during penning may help caribou overcome any deficiencies later in gestation, thereby reducing pregnancy loss. Further comparison of trace nutrients in Kennedy Siding and Klinse-Za caribou could help to delineate the effect of nutrient supplementation in early or late gestation on parturition and calf survival.

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Management implications

The successful management of wildlife requires an understanding of species' reproductive biology. Information about reproductive physiology (ovulation, estrous-cycle length, pregnancy, lactational anovulation, age at the onset of puberty, birth rates etc.) can provide useful insights into the influence of factors such as population density, nutrition, genetics, climate, and anthropogenic disturbances on animal health and reproduction

(Schwarzenberger 2007, Ghosal et al. 2023). Fecal hormone sampling allows for frequent sampling needed for longitudinal studies of wildlife without subjecting animals to undue stress (Holt 2003). That all animals, regardless of age, body condition, or reproductive status, had FPM values indicating reproductive activity suggests that caribou may use the nutritional increase provided by feeding to compensate for lactation costs and insufficient summer forage that would otherwise limit reproduction. This result is similar to the effects of flushing in domestic sheep, where improved nutrition increases ovulation rates during the breeding season, especially for ewes with low body condition scores (Robinson et al. 2002, 2006). Improved body condition in the autumn could increase the probability of caribou carrying a fetus to term and decrease age at first reproduction. Although our results are consistent with an increase in reproductive success via improved nutritional condition, a control population for comparison is needed to definitively link supplemental feeding to improved pregnancy, parturition, and calf survival.

Supplemental feeding could be applied in other small, declining herds or herds with low pregnancy rates to improve female body condition and increase calf production. At the landscape scale, summer and autumn nutrition should be considered when developing management strategies for caribou. Protection and restoration of quality summer habitats would promote population growth and support caribou populations that are self-sustaining via effects on body condition, reproduction, and survival (Cook et al., 2021, Denryter et al., 2022).

Chapter 4: Conclusion

Research summary

Averting the extirpation and increasing the abundance of woodland caribou in BC represents a significant conservation challenge that intersects with multiple ecological, cultural, and economic values (Bixler 2013, Serrouya et al. 2019, Lamb et al. 2022). Caribou are a key umbrella species for boreal biodiversity due to their selection for intact, mature forest habitats forests (Serrouya et al. 2019, Campbell et al. 2020, Falconer and Ford 2020). Indigenous Peoples throughout the northern hemisphere have long relied on caribou for subsistence, ceremonial, and community purposes (Muir and Booth 2012, Lamb et al. 2022). In BC, declining caribou populations threaten fundamental cultural connections to the land (Muir and Booth 2012, Lamb et al. 2022). Activities related to the exploration and extraction of natural resources have degraded the quantity and quality of habitat for a large proportion of woodland caribou (Vors et al. 2007, Wasser et al. 2011, Johnson et al. 2015). The cumulative effects of multiple disturbance types have resulted in increased predation, altered movement patterns, which has affected the availability and quality of forage resources for caribou (Wasser et al. 2011, Johnson et al. 2015, McGreer et al. 2015, Dickie et al. 2020).

The conservation of caribou requires a combination of both short and long-term measures and has been most successful where more than one recovery action has been implemented (Serrouya et al. 2019, Heard and Zimmerman 2021, McNay et al. 2022, Lamb et al. 2024*b*). Understanding the role that nutrition plays in individual survival and reproduction and overall population dynamics can be used to enhance conservation efforts for caribou. Improved nutrition, through short term strategies such as supplemental feeding and long term habitat management, can result in increased juvenile growth rates, adult mass gain, body condition, probability of pregnancy, over-winter survival, and calf survival (Gerhart et al. 1997*b*, Parker et al. 2009, Cook et al. 2021, Heard and Zimmerman 2021, Denryter et al. 2022).

I used multiple indicators of physiological, nutritional, and reproductive condition to examine the effect that nutrition and supplemental feeding could have on female caribou in the Kennedy Siding herd. Specifically, I used fecal hormone metabolites to evaluate changes in nutritional condition over the course of the feeding period. I used a combination of fecal hormone metabolites and GPS collar data to assess rates of pregnancy, parturition, and calf survival in the Kennedy Siding herd and compared them with measures of demographic rates reported in the literature for other herds.

Age and reproductive status had the largest effect on measurements of body condition. I found that adult females that arrived at Kennedy Siding with a calf at heel were more likely to been in poor body condition based on visual scoring and had lower body masses than adults without a calf at heel. Adults with a calf had significantly lower $\delta^{15}N$ values in guard hair than both adults without a calf and yearlings. These results indicate the profound effect of lactation and calf rearing on body condition and protein / fat reserves (Chan-McLeod et al. 1994, Gerhart et al. 1997*b*, *a*, Taillon et al. 2013). My results corroborate past findings that while the nutritional landscape available to caribou in BC may be adequate to support pregnancy, it appears to be inadequate to support both lactation and the recovery and maintenance of body reserves (Dale et al. 2008, Cook et al. 2021, Denryter et al. 2022).

I found that fecal glucocorticoid metabolites (FGM) differed between reproductive age classes. Yearlings had the greatest FGM concentrations, perhaps reflecting the effects of social dynamics in a group with mixed sexes and ages (Barrette and Vandal 1986, Creel 2001, Weckerly and Ricca 2014). Adults with a calf at heel had slightly greater FGM measurements than adults without a calf, possibly representing the increased energetic demands of calf rearing (Cook et al. 2021, Newediuk et al. 2024). Fecal T_3 metabolites (FTM) also differed between age classes, with yearlings having much higher concentrations than the adults in general. This difference likely reflects the role that T_3 plays in growth and development, as caribou are still growing and have not yet reached adult size at one-years old (Todini 2007, Behringer et al. 2018).

I found differences in $\delta^{15}N$, FGMs and FTMs between the two study years. $\delta^{15}N$ was lower whereas FGMs and FTMs were higher in samples collected in 2022 compared to samples from 2021. These differences could be attributed to the difference in environmental conditions between the two years. Variables such as the timing of vegetation emergence, temperature, precipitation, wildfires, and snowpack can all influence the availability and quality of the forage available for caribou (Zamin et al. 2017, Mallory and Boyce 2018, DeMars et al. 2021, Twining et al. 2022, Russell et al. 2025). The concentration of FGMs declined over the course of the feeding seasons overall, with a more pronounced decline in 2022 than 2021. This result suggests that supplemental feeding may have the most beneficial effect on physiological condition in years where environmental conditions limit the quality and quantity of forage resources. Further investigation into inter annual differences in condition indicators is needed to understand the role that environmental conditions play in the nutritional condition of caribou in the Kennedy Siding herd, especially as climate change is expected to alter boreal and mountain ecosystems. The concentration of FTMs also declined over the course of the feeding season. This was contrary to my initial prediction that FTMs would increase in response to increased food availability. The decrease in FTMs instead likely represents the metabolic changes that occur as caribou transition from summer to winter conditions (Ryg 1984, Nilssen et al. 1985). Lower T_3 could facilitate body fat gains before winter and conserve energy during the winter (Ryg 1984).

Every caribou that I sampled had fecal progesterone metabolite (FPM) values indicative of ovarian activity, regardless of age, body condition, or whether they had a calf at heel or not. This indicated that caribou in the Kennedy Siding herd were not forgoing reproduction in response to poor condition and all females had the capacity to become pregnant during the fall breeding season (Cameron and Hoef 1994, Gerhart et al. 1997*b*, *a*). Based on the FPM values, the age of puberty in Kennedy Siding caribou is one-years old, which further supports supplemental feeding having a beneficial impact on body condition, as yearlings have to accrue enough body fat and achieve approximately 70% of their mature mass in order to undergo puberty and conceive (Parker 1981, Rettie and Messier 1998, Cook et al. 2004).

Using a combination of FPMs, GPS collar data, and fall counts conducted at the feeding site, I estimated that in the Kennedy Siding herd, the rate of ovulation and potential pregnancy was 100%, the parturition rate was 87%, and the calf survival rate was 74%. Parturition rate was greater than previously reported rates in other caribou herds in BC (Gustine et al. 2006, DeMars et al. 2013, Nobert et al. 2016, Mueller et al. 2022). Calf survival was slightly higher than in other herds, but was variable between years (Gustine et al., 2006, DeMars et al., 2013, Nobert et al., 2016). These results suggest that fall supplemental feeding could contribute to population growth by both increasing the proportion of females with successful pregnancies and increasing the proportion of calves that survive until the fall.

My interpretation is limited by the lack of data from an unfed control population to which I could compare my results to. Repeated sampling of an unfed population during the autumn would help to clarify the hormonal results and make a more explicit link between these indicators and supplemental feeding. Although I was unable to make definitive links to supplemental feeding, the decline in FGMs we observed suggests that feeding is unlikely to be negatively impacting caribou physiology and the FPM and movement model results are consistent with an increase in reproductive rates expected with improved nutrition. The increases in body mass observed by Heard and Zimmerman (2021), along with the high rates of ovulation, parturition, calf survival, and yearling reproduction suggests that supplemental feeding could provide a meaningful improvement to female body condition, resulting in cascading beneficial demographic impacts such as increased parturition and calf survival rates.

Management implications

Autumn supplemental feeding appears to be improving population growth in the Kennedy Siding herd by increasing parturition and calf survival rates via improved female body condition. My research emphasizes the importance of summer and autumn nutrition on survival and reproduction of caribou in BC (Dale et al., 2008, Couturier et al., 2009, Kelly 2020, Cook et al., 2021, Heard and Zimmerman 2021, Denryter et al., 2022). In populations where summer habitat is insufficient to meet the needs of both lactation and recovery of body reserves, fall supplemental feeding could be used to facilitate the rapid recovery of body fat before winter. Improved body condition in the autumn increases the probability of caribou conceiving and carrying a fetus to term. Supplemental feeding could be applied in conjunction with other conservation measures, such as habitat restoration or predator reduction, to more rapidly enhance small populations (Lamb et al. 2024*b*).

Widespread habitat conservation and restoration is needed if caribou are to remain on the landscape in the long term, and summer and autumn nutrition should be considered when developing habitat management strategies for caribou. Protection and restoration of quality summer habitats would promote population growth and support caribou populations that are self-sustaining via effects on body condition, reproduction, and survival (Cook et al., 2021, Denryter et al., 2022).

Finally, my research represents some of the first longitudinal monitoring of endocrine activity in woodland caribou. Analysis of single fecal samples have been used to examine reproduction and physiological/nutritional stress in caribou, however repeated sampling has rarely occurred due to the difficulties obtaining repeated samples from wild populations (Messier et al. 1990*a*, Morden et al. 2011, Joly et al. 2015, Lamb et al. 2024*a*). The Kennedy Siding herd consistently uses the same small, easily accessible area every year, providing a unique opportunity to collect repeated samples from known individuals to address questions surrounding the links between habitat conditions, physiology, and reproduction. My results demonstrate the potential of fecal hormone measurement for health monitoring and provide a baseline upon which future studies can expand.

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Appendices

Supplemental material for Chapter Two

Linear mixed effects models

Table 11: The eight linear mixed-effects models used to predict fecal glucocorticoid concentrations in female caribou (*Rangifer tarandus caribou*) sampled in fall - winter of 2021 and 2022 at the Kennedy Siding feeding project site in British Columbia, Canada.

Fecal cortisol candidate model	**df**	**logLik**	**AICc**	**ΔAICc**	**ω_i**	**Min VIF**	**Max VIF**
Reproductive age class + sampling date * sampling year	8	-124.8	265.9	0	0.462	1.060	2.160
Reproductive age class + sampling date * sampling year + body mass	9	-124.4	267.3	1.430	0.226	1.220	2.170
Reproductive age class + sampling date * sampling year + body condition	9	-124.6	267.6	1.762	0.192	1.200	2.170
Reproductive age class + sampling date * sampling year + body condition + body mass	10	-124.2	268.9	3.063	0.010	1.220	2.180
Reproductive age class (null)	5	-131.8	273.8	7.911	0.009	N/A	N/A
Reproductive age class + body condition	6	-131.4	274.9	9.022	0.005	1.550	1.550
Reproductive age class + body mass	6	-131.7	275.5	9.635	0.004	1.410	1.410
Reproductive age class + body condition + body mass	7	-131.1	276.5	10.58	0.002	1.430	2.200

Loglik = Loglikelihood, AICc = AICc score, ΔAICc = difference in corrected AIC between model and top model; ωi = Akaike weight, VIF = variance inflation factor

Table 12: The eight linear mixed-effects models used to predict fecal triiodothyronine concentrations in female caribou (*Rangifer tarandus caribou*) sampled in fall - winter of 2021 and 2022 at the Kennedy Siding feeding project site in British Columbia, Canada.

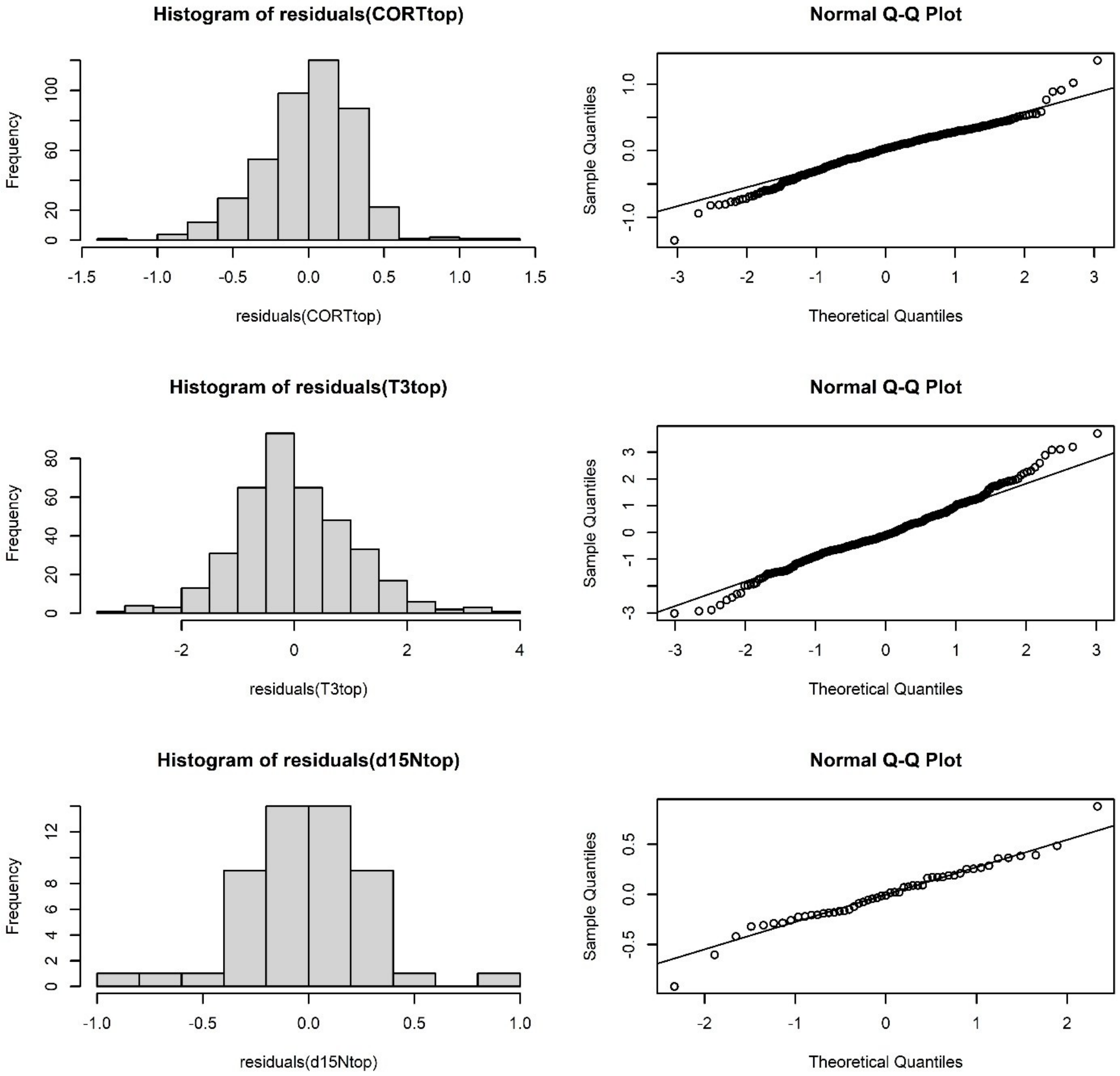
Fecal T3 candidate model	**df**	**logLik**	**AICc**	**ΔAICc**	**ω_i**	**Min VIF**	**Max VIF**
Reproductive age class + sampling date + sampling year + body mass	8	-610.62	1237.63	0	0.538	1.13	1.53
Reproductive age class + sampling date + sampling year + body mass + body condition	9	-610.36	1239.19	1.56	0.246	1.13	2.59
Reproductive age class + sampling day + sampling year	7	-613.04	1240.38	2.76	0.136	1.10	1.24
Reproductive age class + sampling date + sampling year + body condition	8	-612.80	1241.99	4.36	0.061	1.10	1.92
Reproductive age class + body mass	6	-616.58	1245.38	7.76	0.011	1.32	1.32
Reproductive age class + body mass + body condition	7	-616.26	1246.82	9.19	0.005	1.31	2.52
Reproductive age class (null)	5	-619.11	1248.38	10.75	0.002	N/A	N/A
Reproductive age class + body condition	6	-618. 83	1249.88	12.25	0.001	1.70	1.70

Loglik = Loglikelihood, AICc = AICc score, ΔAICc = difference in corrected AIC between model and top model; ωi = Akaike weight, VIF = variance inflation factor

Table 13: The eight linear mixed-effects models used to predict hair δ15N concentrations in female caribou (*Rangifer tarandus caribou*) sampled in fall - winter of 2021 and 2022 at the Kennedy Siding feeding project site in British Columbia, Canada.

Hair $\delta^{15}N$ candidate models	**df**	**logLik**	**AICc**	**ΔAICc**	**ωi**	**Min VIF**	**Max VIF**
Reproductive age category + sampling year	6	-62.74	139.3	0	0.509	1.060	1.060
Reproductive age class + sampling year + body condition	7	-62.09	140.7	1.387	0.254	1.080	2.980
Reproductive age class + sampling year + body mass	7	-62.61	141.8	2.422	0.152	1.140	1.510
Reproductive age class + sampling year + body condition + body mass	8	-61.78	142.9	3.570	0.085	1.200	4.500
Reproductive age class (null)	5	-71.69	154.7	15.34	2.000×10^{-4}	N/A	N/A
Reproductive age class + body mass	6	-71.48	156.8	17.48	1.000×10^{-4}	1.350	1.350
Reproductive age class + body condition	6	-71.59	157.1	17.72	1.000×10^{-4}	2.650	2.650
Reproductive age class + body condition + body mass	7	-71.42	159.4	20.05	2.000×10^{-5}	1.390	2.730

Loglik = Loglikelihood, AICc = AICc score, ΔAICc = difference in corrected AIC between model and top model; ωi = Akaike weight, VIF = variance inflation factor



Histogram of residuals(CORTtop)

Normal Q-Q Plot

Histogram of residuals(T3top)

Normal Q-Q Plot

Histogram of residuals(d15Ntop)

Normal Q-Q Plot

Figure 15: Model validations from each top model set for caribou (*Rangifer tarandus caribou fecal glucocorticoids*, fecal T3, and hair δ^{15}N. The histograms denote the frequency of residuals, and the Normal Q-Q plots denote standardized residuals against the values that would be expected under normality from each top model.

Hair cortisol

Methods

To extract hormones from hair samples, we followed the protocol described by (Bryan et al. 2013*a*). The hair was washed twice with approximately 40 mL of water for three minutes each time by rotating on a plate rotator (approx. 120 rpm). This washing step was repeated using 100% isopropanol [Sigma - Aldrich] for three minutes on a plate rotator. Samples were thoroughly dried between the water and isopropanol washes. The hair was powdered in a ball mill (Retch Mixer Mill 200) at 25 Hz and ~30 mg was weighed into a 20 ml glass scintillation vial. We added 100µl of 100% % HPLC methanol (Thermo Fisher Scientific) /mg of hair powder and sealed the lids of the scintillation vials with parafilm to prevent evaporation. The samples were sonicated for 30 minutes then placed in an incubator at 50˚C and rotated at 160 rpm overnight. The methanol was then centrifuged for 30 minutes to separate the hair particles from the extract. The supernatant was stored at -20 ˚C until analysis.

We used an Arbour Assays DetectX® Cortisol ELISA Kit to analyse hair cortisol concentrations. Hair samples were evaporated to dryness under a steady stream of nitrogen. Samples were reconstituted using a solution of assay buffer provided by the kit and 100% HPLC methanol [Thermo Fisher Scientific]. We dispensed 50 µl of either the diluted sample, standards, or controls into each well. Assay reagents were added, and the plate was incubated following instructions provided by the kit manufacturer. The optical density was measured at 450 nm. The cross reactivity of the cortisol assay to several compounds was provided with the immunoassay kit, including cortisol (100%), dexamethasone (18.8%), prednisolone (7.8%), corticosterone (1.2%), cortisone (1.2%), and progesterone, estradiol, cortisol 21-glucuronide, 1α-hydroxycorticosterone, and testosterone (< 0.1%).

As an analytical validation, a pooled hair extract from different female caribou was assayed with the hair cortisol ELISA. To establish parallelism, we tested serial two-fold dilutions of the pooled sample for comparison displacement curves (Figure 16). The intra assay variability was determined by assaying replicates of the pooled sample. The intra assay CV was <15% for the hair cortisol ELISA. Because we only ran one plate for hair cortisol, inter assay variation was not calculated.

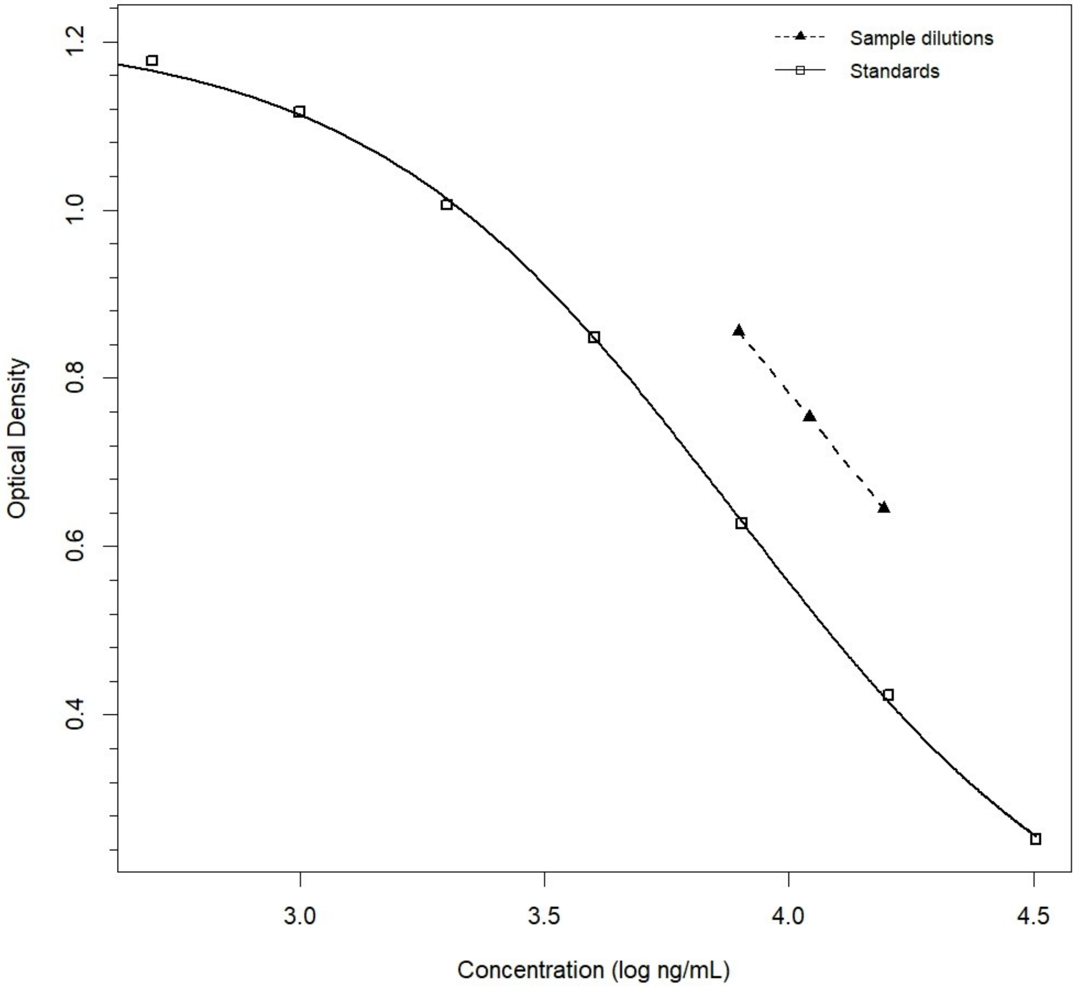


Figure 16: Parallelism of cortisol standards with a serially diluted extract from caribou (*Rangifer tarandus caribou*) guard hair (dashed line).

Results

We analyzed hair cortisol concentrations in twenty-three samples from eighteen individual caribou sampled in 2021 and 2022. Hair cortisol concentrations ranged from 2.145 pg/mg–8.570 pg/mg (mean = 4.887 pg/mg, SE = 0.377). The mean hair cortisol concentration for adults with a calf was 5.010 pg/mg (n= 14, SE = 0.505), 4.321 pg/mg (n = 6, SE = 0.696) for adults without a calf, and 5.027 pg/mg (n=3, SE = 1.179) for one-year olds. Student's t-Tests revealed that hair cortisol concentrations were higher in adults with a calf compared to adults without a calf, however this difference was not significant ($t_{(10.52)} = -0.905$, $p = 0.386$; Figure 17). Hair cortisol was also higher in adults without a calf compared to one-year olds, however the difference was also not significant ($t_{(3.468)} = -0.515$, $p = 0.638$; Figure 17). Adults with a calf and yearlings had similar hair cortisol concentrations ($t_{(2.785)} = 0.057$, $p = 0.959$; Figure 17).

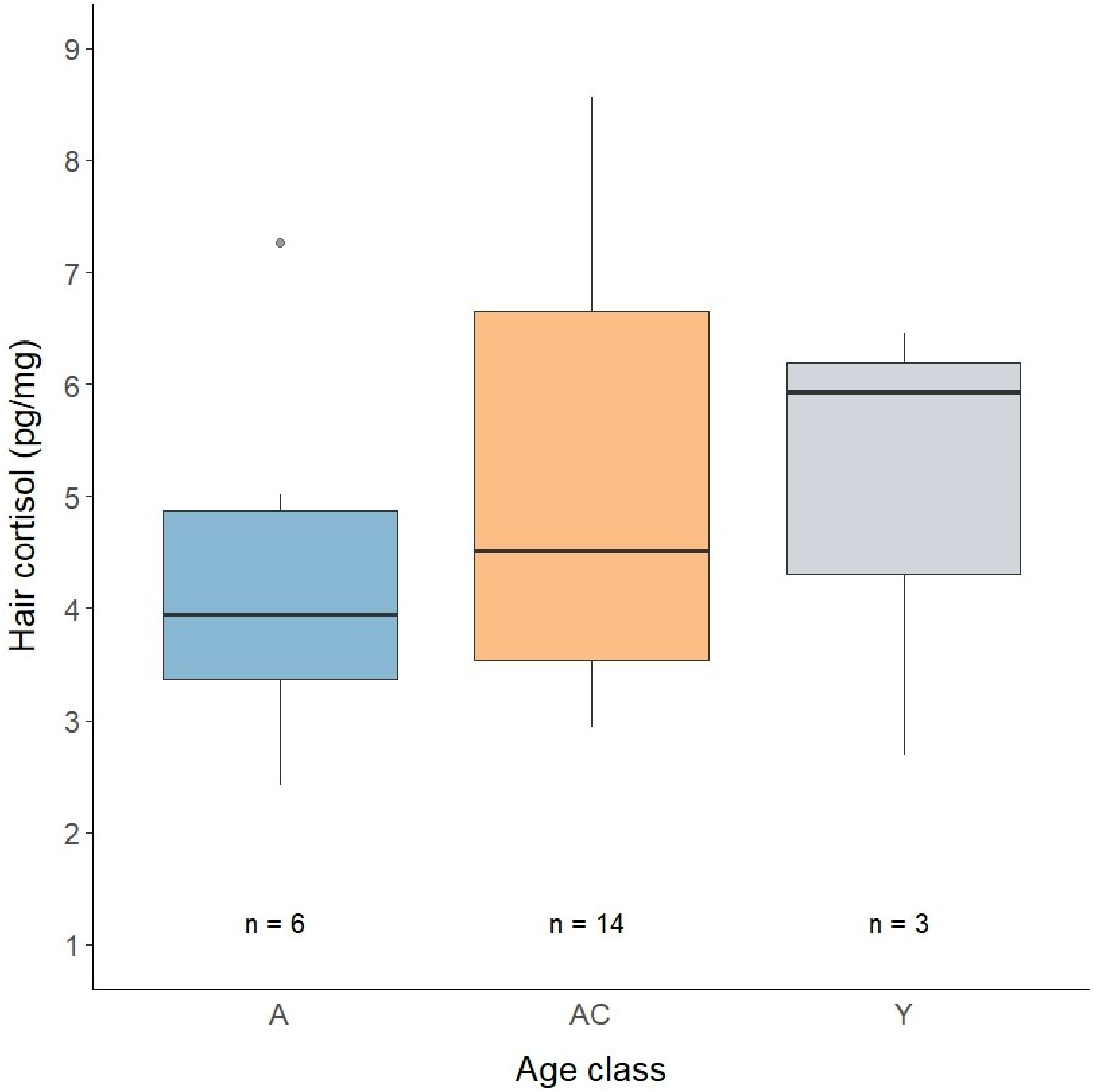


Figure 17: Cortisol concentrations in hair samples collected from female caribou (*Rangifer tarandus caribou*) at Kennedy Siding in 2021 and 2022 (n = 23). The boxes represent the median value (center line) and the 25th and 75th percentiles. The highest hair cortisol concentrations were found in yearlings (Y) and adults with calves (AC). Adults without calves (A) had the lowest values. The lines represent 1.5 times the interquartile range for each percentile. Sample sizes are shown at the bottom of the panel.

Supplemental material for Chapter Three

Linear mixed effects models

Table 14: The eight linear mixed-effects models used to predict fecal progesterone metabolite concentrations in female caribou (*Rangifer tarandus caribou*) sampled in fall - winter of 2021 and 2022 at the Kennedy Siding feeding project site in British Columbia, Canada.

Candidate model	**df**	**logLik**	**AICc**	**ΔAICc**	**ω_i**	**Min VIF**	**Max VIF**
Null	3	-1308.4	2622.8	0	0.531	N/A	N/A
Reproductive age class	5	-1306.9	2624.0	1.209	0.290	N/A	N/A
Body condition	5	-1307.7	2625.6	2.799	0.131	1.002	1.002
Reproductive age class + body condition	7	-1306.6	2627.6	4.772	0.049	1.336	2.192

Loglik = Loglikelihood, AICc = AICc score, ΔAICc = difference in corrected AIC between model and top model; ωi = Akaike weight, VIF = variance inflation factor

Individual fecal progesterone profiles

As an extension of the fecal hormone analysis, we also wanted to characterize changes in progesterone concentrations during the breeding season for woodland caribou. An understanding of basic reproductive processes and components of individual fitness can aid species management and conservation because they are drivers of population dynamics in wild animals (Schwarzenberger 2007, Sontakke 2018). Common methods for assessing reproduction in caribou include analysis of hormone levels and movement patterns of GPS collared animals. Progesterone is a steroid hormone that regulates the estrous cycle and is the principal hormone responsible for the maintenance of pregnancy in mammals (Smith 2009, Crowe 2016, Shrestha 2021). Caribou are seasonally polyestrous and will experience recurring estrous cycles during the breeding season (McEwan and Whitehead 1972, Bergerud 1975, Ropstad et al., 1995a). The mammalian estrous cycle consists of a follicular and luteal phase (Crowe 2016). During the follicular phase an ovarian follicle and its enclosed oocyte mature in preparation for ovulation and fertilization (Crowe 2016). Progesterone levels are low during this phase (O'Connor et al., 2013). The luteal phase is the period following ovulation when the corpus luteum; a transient endocrine organ formed from the remnants of a mature follicle after ovulation; is formed and is associated with increased secretion of progesterone (Asher 2011, O’Connor et al., 2013, Shrestha 2021). If pregnancy does not occur, the corpus luteum degenerates and progesterone levels decline, allowing for maturation and ovulation of a new follicle and another opportunity to establish a pregnancy (Asher 2011, Shrestha 2021). If pregnancy is established, the luteal lifespan is prolonged and the corpus luteum continues to produce progesterone through the gestation period (Asher 2011). In caribou, serum progesterone tests on blood samples taken from captured animals have commonly been used to assess pregnancy status (Rettie and Messier 1998, Wittmer et al., 2005, DeMars et al. 2013). The stress and hazards associated with capture and restraint can be detrimental to the animals' health and may bias the results of hormone analysis (Schwarzenberger 2007, Morden et al. 2011). This means that repeated blood sampling on a regular basis is often not possible. Fecal hormone analysis has been developed as an alternative, non-invasive technique that is now widely employed for studies of stress and reproductive physiology in wildlife (Schwarzenberger 2007). Hormones like progesterone are metabolized by the liver into several metabolites which are excreted in feces and can then be measured using immunoassay techniques (Brown 2018). Due to the pooling of metabolites during excretion, fecal samples present cumulative hormone secretion hours or days, depending on the species, which provides a more representative measure of hormone concentrations over time (Schwarzenberger et al. 1996, Möstl and Palme 2002, Palme et al. 2005). Fecal sampling also enables frequent data collection without disturbance of the animal, allowing for longitudinal studies of hormones that can be used to assess changes in reproductive activity (Schwarzenberger 2007). The concentration of progesterone metabolites in feces has been used to study reproductive components such as seasonality, estrus and ovulation, pregnancy, and fertility status in a variety of wildlife species and has produced detailed basic information about reproductive biology such as the length of estrous cycle and ovulation pattern in many wild ungulates (Schwarzenberger 2007, Brown 2018, Sontakke 2018). In caribou, analysis of single fecal samples has been used to determine pregnancy, but repeated sampling has not been used to monitor of ovarian activity, likely due to difficulties obtaining repeated samples from wild populations (Messier et al. 1990a, Morden et al. 2011, Joly et al. 2015).

Methods

We considered an animal to be ovulatory based on whether they had at least one fecal sample with a FPM concentration above the baseline determined from male samples. We created fecal progesterone profiles for caribou that had been sampled at least 10 times during a 50-day period (October 24thtoDecember 17th) where caribou visited the feeding site daily. We determined FPM concentrations during the luteal phases for each individual using an iterative process described by Graham et al. (2002). The average concentration of all samples from an individual was calculated and the values greater than the average plus 1.75 standard deviations (SD) were considered significant elevations and temporarily removed from the data set. The average was then recalculated and the process repeated until no values exceeded the mean + 1.75 SD. Remaining fecal progesterone values were reported as baseline (follicular phase) concentrations. If the data was more than the baseline concentration, we considered it to be the luteal phase, while if the value was less than the baseline concentration, we considered it to be the follicular phase. The FPM concentrations of the luteal and follicular phases of individuals were compared with one-way ANOVA. We estimated the length of an estrous cycle based on the methods used by (Mohammed et al. 2011). One estrous cycle was defined as the period from the first increase in FPMs above baseline to the corresponding rise in the following cycle. The day of sampling before the first increase in FPMs was considered day 0.

Results

The baseline concentrations (mean ± standard error) of FPMs for individual females were 488.1 ± 27.6 - 2059.2 ± 119.5 ng/g and averaged 957.7 ± 91.3 ng/g (Table 13). Mean luteal concentrations per female, calculated as the average of all values that exceeded baseline ranged from 578.9 ± 26.8 - 2351.9 ± 100.4 ng/g and averaged 1185.1 ± 98.7 (Table 13). The FPM concentrations during the luteal phase were higher within individuals and on average ($P < 0.05$) than those observed during the follicular phase. All females showed a fluctuating pattern of FPM levels around their individual baselines, and there was great variation in the height of peaks among individuals (Figure 18).

Table 15: Mean fecal progesterone metabolite concentrations (± standard error) of the follicular (baseline) and luteal phases from 14 individual female caribou (*Rangifer tarandus caribou*) sampled between fall and winter of 2021 and 2022 at the Kennedy Siding feeding site in British Columbia, Canada. The reproductive age classes are adult without a calf at heel (A), adult with a calf at heel (AC), and yearling females (Y).

ID	**Reproductive age class**	**Baseline (ng/g) ± SE**	**Luteal (ng/g) ± SE**
21.045	AC	869.4 ± 82.2	1080.0 ± 31.9
21.047	AC	857.4 ± 84.3	1042.9 ± 71.6
21.079	AC	2059.2 ± 119.5	2351.9 ± 100.4
22.001	A	826.4 ± 49.7	994.2 ± 77.2
22.007	AC	488.1 ± 27.6	578.9 ± 26.8
22.016	A	1111.5 ± 44.9	1362.0 ± 90.1
22.017	A	832.8 ± 57.6	1133.8 ± 80.9
22.03	AC	891.8 ± 121.4	1270.3 ± 128.6
22.032	A	989.1 ± 71.1	1192.8 ± 54.8
22.038	Y	989.1 ± 59.9	1116.7 + 35.3
22.048	AC	747.9 ± 48.5	1027.8 ± 121.1
22.058	AC	1102.6 ± 91.2	1097.4 ± 84.2
22.066	A	913.6 ± 49.9	1037.8 ± 34.8
22.077	Y	728.9 ± 105.4	1304.8 ± 49.6
Mean		957.7 ± 91.3	1185.1 ± 98.7

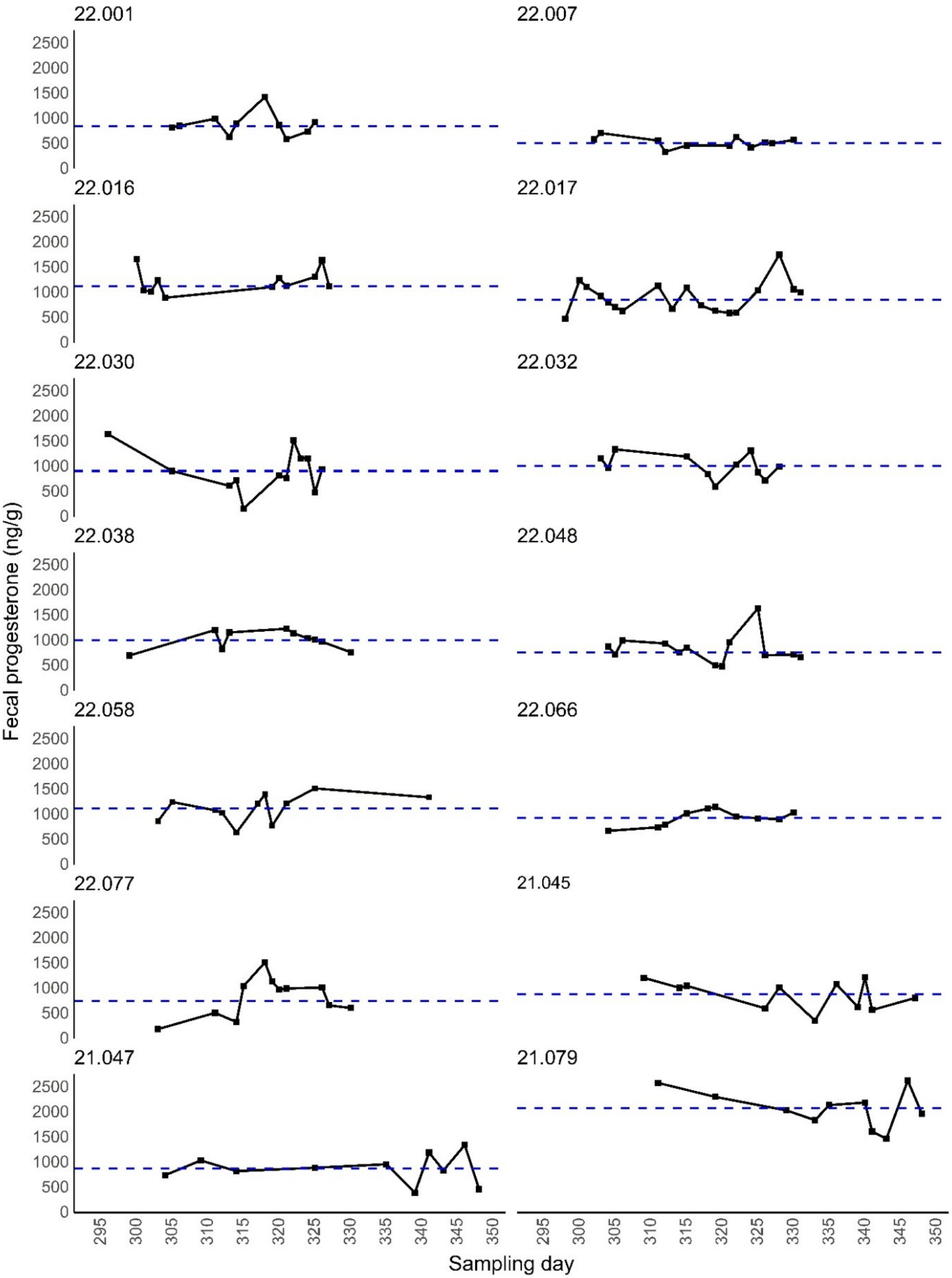

22.001
22.007
22.016
22.017
22.030
22.032
22.038
22.048
22.058
22.066
22.077
21.045
21.047
21.079
0
500
1000
1500
2000
2500
Fecal progesterone (ng/g)
295
300
305
310
315
320
325
330
335
340
345
350
Sampling day

Figure 18: Longitudinal fecal progesterone metabolite profiles for 14 female caribou (*Rangifer tarandus caribou*) sampled between fall and winter of 2021 and 2022 at the Kennedy Siding feeding site in British Columbia, Canada. Individual identities are displayed at the top of each plot. The dashed line indicates an individual's baseline value used to differentiate between the follicular and luteal phases.

Discussion

This is, to our knowledge, the first report of changes in progesterone concentrations over the breeding season for wild woodland caribou. The characteristics and endocrinology of the estrous cycle and breeding season of caribou and their interactions with external factors remains understudied and has only been described in a few reports under captive conditions. Most studies have also examined hormones in serum samples, the invasive nature of which is impractical for repeated sampling of wild populations. Previous research suggests that the reproductive season for *Rangifer* females begins in September to October, and that cyclic ovarian activity can occur until February. The length of estrous can vary greatly. Ropstad et al. (1995) reported that in Norwegian reindeer (*R.t tarandus*), estrous lasted on average (± SD) 19.4 ± 5.7 days (range = 13–33 days). McEwan and Whitehead (1972) described two types of estrous cycles in caribou and reindeer, a short 10- to 12-day, and a long 24-day cycle depending on the functional life of the corpus luteum. In woodland caribou in Newfoundland, Canada, Bergerud (1975) reported that the length of the estrous cycle was approximately 10-12 days. Because sampling was limited to the period most caribou used the feeders (mid October to mid December), we were only able to detect 1–2 possible cycles per animal and could not determine the total length of the breeding season. The mean FPM baseline of 957.7 ng/g we found was similar to the mean progestin (± SD) level of 903 ± 162 ng/g reported by Messier et al. (1990) for the early gestation period (0–50 days) of woodland caribou in Quebec, Canada. The patterns of fluctuations were variable among individual animals. Differences could be explained by individual (phenotypic, genotypic, or physiologic) and environmental attributes (Chinn et al. 2022). One female (21.079), had a baseline FPM concentration of 2059.2 ng/g, over two times the mean baseline and higher than the 2025.9 ng/g threshold used by Morden et al. (2011) to identify pregnant reindeer in February, suggesting she may already have been pregnant at the time of sampling.

Due to the opportunistic nature of our sampling design, fecal samples were collected at irregular intervals. Daily sample collections would produce more detailed profiles and allow for further analysis of estrous characteristics. Time series analyses, which becomes more powerful with increasing length of the dataset, could be used to identify cycles and determine cycle frequency with more accuracy (Fanson et al. 2014). More frequent sampling combined with a supplementary method such as behavioural observations could also help to establish more accurate estimates of when ovulation occurred. We only examined progesterone metabolites, however other indicators of reproductive activity such as estrogens, androgens, luteinizing hormone, follicle stimulating hormone, and pregnancy-associated glycoproteins could be examined to better describe the reproductive biology of woodland caribou during the breeding season and possibly detect early pregnancy (Kirkpatrick et al. 1993, Ropstad et al. 2005). An estimate of early pregnancy would provide more information on the occurrence of calf mortality between pregnancy and parturition, as there is currently very little data on this phenomenon in caribou (Ringberg and Aakvaag 1982, Russell et al. 1998, Mueller et al. 2022). Our results demonstrate the potential of fecal progesterone measurement for monitoring reproductive activity in caribou and provide a preliminary description of progesterone changes associated with estrous in free ranging woodland caribou.