



UNDERSTANDING PRODUCTIVITY OF NORTH AMERICAN MIGRATORY TUNDRA CARIBOU (*RANGIFER TARANDUS*): ROLE OF VITAL RATES AND CLIMATE

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ABSTRACT

Understanding how climate affects caribou demography is more urgent as we plan for recovery of declining migratory tundra caribou herds faced with trends toward a hotter climate. We examined relationships between climate and caribou vital rates for eight herds across western, central and eastern Arctic North America. For climate we used caribou-relevant indicators based on NASA's Modern Era Retrospective Analysis for Research and Applications (MERRA2) dataset to estimate seasonal mean values on summer, fall, winter, spring, and calving ranges. Because sample sizes for most herds was limited, we examined the relationship among vital rates and between vital rates and climate indicators using one or two-independent variable regression models.

Climate variables explained about half the variability in the vital rates which emphasizes the importance of climate in population dynamics. How individual climate variables affected vital rates varied among the herds, although some generalizations can be made across herds and across regions. A conspicuous result was that that fall (September – November) and spring (May-June) climate disproportionately impacted vital rates. During spring, 67% of the predictive climate indicators were related to rain, drought and snow depth, while in fall, snow depth accounted for 69% of the climate indicators. Fall snow depth was a predictor of spring parturition rates, June calf survival, June calves:100 cow and spring recruitment although relationships did vary with herd data. The deeper fall snow, the lower the parturition. For variables that had trends, May or June drought or freezing rain reduced adult survival in four herds while for three herds no predictive climate indicators impacted adult survival.

As we expected the linkage between climate and vital rates was complex and herd specific. Combining our results with an analysis of current and projected climate trends will help in understanding the impacts of climate change.

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INTRODUCTION

Most migratory tundra caribou herds in North America, with few exceptions, are declining or at very low numbers (Gunn et al. 2016, COSEWIC 2016). Co-management boards and governments are increasingly focused on understanding which mechanisms are influencing herd trends in the expectation that the understanding may support future recovery. Fundamental to understanding trends in abundance is monitoring of survival, productivity, and recruitment of cohorts within the herd. Although monitoring protocols and priorities vary among herds, generally managers are interested in how many calves are born and survive to be recruited in the herd at one year of age and how many adult cows annually survive. Those vital rates reflect how climate mostly works through influencing forage availability (habitat changes including human activity, predators, and parasites) which impact body condition; body condition directly links to vital rates, and vital rates collectively determine herd productivity.

In recent years, studies have linked specific climate indicators to range quality (Heggberget et al. 2002, Fauchald et al. 2017) or *Rangifer* body condition (Weladji et al. 2003, Albon et al. 2017, Mallory and Boyce 2017); and to overall herd responses for individual herds or geographic regions (Post and Forchhammer 2008, Joly et al. 2011, Tyler 2010). However, attempts to extrapolate findings from one study to *Rangifer* as a whole is simplistic (cf Post and Forchhammer 2008 with Tveraa et al. 2013, Veiberg et al. 2016, and Gustine et al. 2017). The difficulty of generalizing is partly because migratory tundra caribou have annual ranges that widely vary in landscapes and climate. For example, calving grounds of migratory tundra caribou have high landscape diversity (Russell et al. 2002) while the herd seasonal ranges have markedly varied climate trends (Russell and Gunn In Prep.).

Caribou have behavioural and physiological strategies to buffer a variable climate. Individual behavioural strategies include reducing exposure to adverse habitat conditions, for example, tracking early green-up and forage quality, exploiting north slope aspects or lte snow bed communities. Physiologically, caribou rely on trading off between energy and protein allocation to the cow's body maintenance or her calf's growth through flexible weaning strategies (Russell and White 2000, Gerhart et al. 2010; Supplement 1). At the herd scale, herds differ in the relationship between fall body condition and probability of pregnancy, a function of the evolved energy/protein dynamics of the cow and offspring during the summer (Cameron and ver Hoef 1994; Supplement 1).

The different *Rangifer* behavioural and physiological strategies are a manifestation of the trade-offs between lifetime reproductive success and survival (Gerhart et al. 1997, Weladji et al. 2008). This in turn means that any relationships between vital rates and climate are complicated by the interrelationships among vital rates which reflect trade-offs between survival and reproduction. For example, a bad insect year may have a larger impact on cow survival in a year with high parturition rates and high June calf survival compared to a year

with fewer calves and thus with fewer lactating cows entering the summer population. The availability of climate indicators across the annual ranges of 13 North American migratory tundra caribou herds (Russell et al. 2013) is an opportunity to examine whether and how the relationships of vital rates with climate indicators varied across Arctic North America. Our objective is to use the eight migratory tundra caribou herds with sufficient and available vital rate information to analyze links among vital rates and between climate and vital rates (Figure 1).

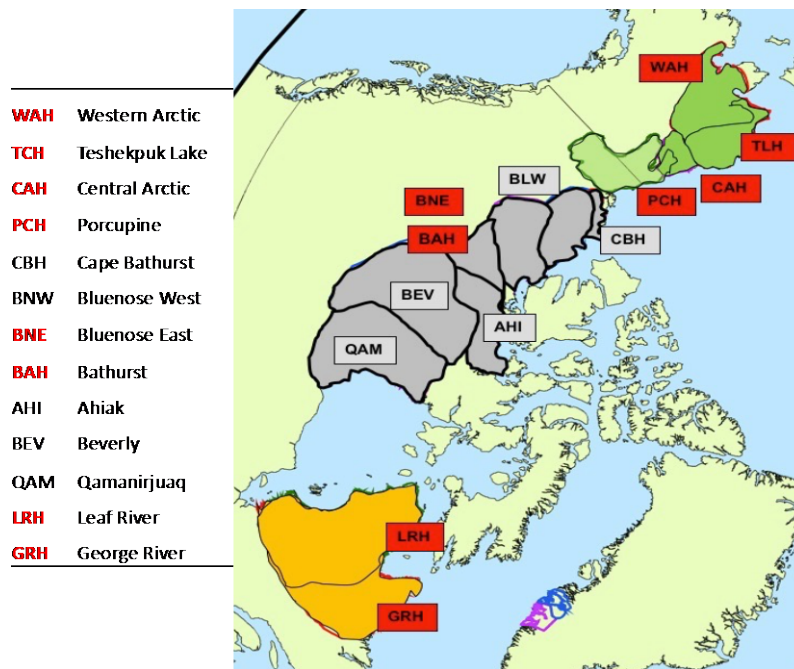


Figure 1. North American migratory tundra caribou herds: Western (green), Central (grey) and Eastern (orange). Herd labels in red are herds with sufficient vital rate information for our analysis (see Table 1).

METHODS

Vital Rates

For this analysis, we incorporated vital rates from field surveys throughout the seasonal cycle of migratory tundra caribou (Figure 2). Management agencies vary in the timing of monitoring calf survival but typically over-summer and over winter survival are monitored through calf:cow ratios in the fall and late winter, respectively. Additionally, some agencies monitor the survival of the calf to one month of age, so we treat the late June calf:cow ratios as a separate vital rate to measure calf survival for the first month of their life. Most agencies report adult survival. Adult mortality is reported for the period July 1 through the following June and thus mortality 2010, for example, represents mortality of adult cows from July 2009 to June 2010. However, for the Western Arctic herd (WAH), adult mortality is reported for the period October through the following September and thus mortality 2010, for example, represents mortality of adult cows from October 2009 to September 2010.

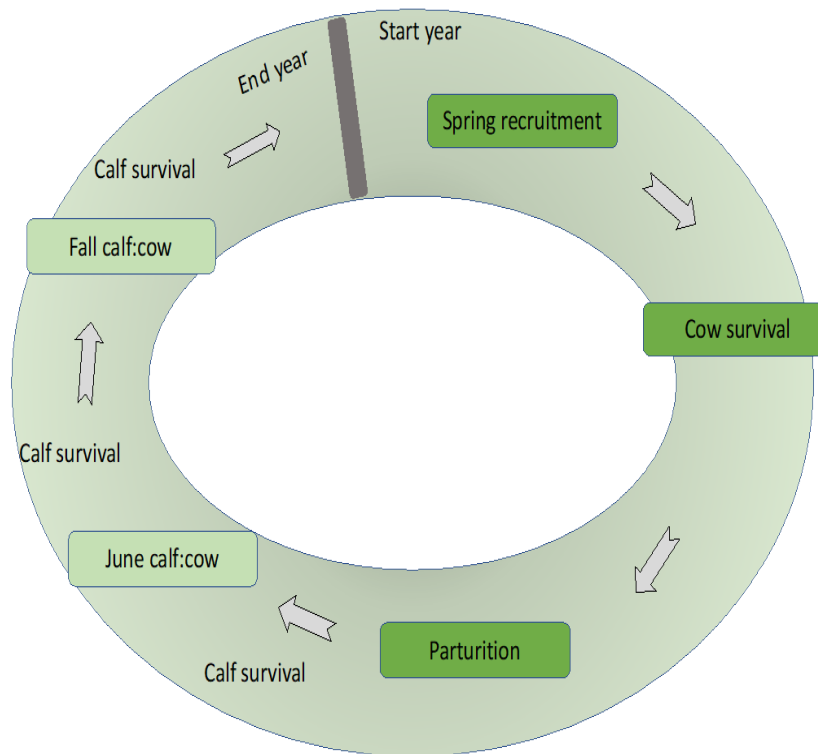


Figure 2. Field measurements from monitoring surveys conducted on migratory tundra caribou. NOTE: Cow survival is measured from July 1 of one year to June 20 of the next year except for the Western Arctic herd where cow survival is measured from October 1 to September 30.

We followed Gunn and Russell (2008) for terminology: Pregnancy rates are the percentage of pregnant females per year by age class (for example, 75% of females three years or older).

Parturition means giving birth and is the number of females about to give birth or with newborn calves; net calf production is the product of pregnancy rate and calf survival; Recruitment rate is estimated by the number of one-year-old animals (usually measured in late winter composition counts so they may be nine- to ten-month-old calves) and indexes the potential rate of increase (not the actual observed rate).

Vital rates for a number of herds were collated from government reports (Table 1) and estimates of herd size were from the CARMA database. The vital rates for the WAH (ADF&G 2015a), Porcupine (ADF&G 2015b), Teshekpuk Lake (ADF&G 2015c) and Central Arctic herds (ADF&G 2015d) were from Alaska Department of Fish and Game species management reports published online at:

www.adfg.alaska.gov/index.cfm?adfg=wildliferesearch.smr20154.

Table 1. Years of vital rate data among the eight migratory tundra caribou herds used in the analysis.

Vital rate	WAH	TCH	CAH	PCH	BNE	BAH	LRH	GRH
Spring recruitment	34	23		17	10	25		
Cow survival	28	24	22	28	10	24	19	27
Parurition	28	14	21	29	5	10		12
June calf survival	27		17	27				
June calf:cow	27	16	21	28				
Fall calf:cow	15	14	7		6	13	21	35

Vital rates for the Bluenose-East and Bathurst Herd were from J. Adamczewski (pers. comm.). Leaf River herd data were from Taillon et al. (2016) and from the George River herd from Taillon (pers. comm.) and Bergerud et al. (2008).

Study Herds: Ecology and Vital Rates

To summarize the ecological context for relationship among vital rates and between vital rates and climate, we have summarized herd-specific landscapes and climate and trends in herd abundance for the eight herds that had sufficient data available.

Western Arctic Herd

The calving and summer ranges are tussock tundra uplands extending toward the western coast. The largely clockwise movements on the summer ranges take the cows south through the Brooks Range foothills and then northwest to the coastal ranges. In the fall, migrate south to the Seward Peninsula for winter. The winter ranges are also mostly tussock tundra with lichens and shrubs (Joly et al. 2007). About 30% of the winter range is within the boreal forest.

The WAH has a maritime Arctic climate with cooler summers and warmer winters and high precipitation. Both the drought index and the oestrid index are low but winter ranges have a relatively high number of days with freezing rain and rain-on-snow days (CARMA

unpublished. data). The only significant trend (1989-2016) is an increasing October temperature. An extreme event was a midwinter thaw with rain in December 2005, by spring 2006, many caribou were in poor body condition and adult female mortality was 32%. A similar level of mortality occurred in the 2011-2012 winter which had deep snow and high levels wolf kills (Dau 2011, Dau 2013).

The vital rates cover 1987-2015 when in the 1980s, the WAH was increasing and reached a peak size of 490,000 in 2003 before declining to 164,000 by 2022. Adult mortality, calf production and recruitment, sex and age movement patterns, and distribution are annually monitored (Appendix A). Since the mid-1980s, adult survival and productivity has decreased especially since 2003. The three-year moving average for recruitment has been less than 20% since 1999 and by 2010 was 13%. June calf:cow ratios during 1982–2015 did not show a trend but fall calf:cow ratio declined during 1982–2015. Mortality increased from 13.5+1.5 SE (1987-1990) to averaged 18.8+1.3 SE (1990-2010) and was exceptionally high in 2005-2006 and 2011-12 winters (Dau 2011, Dau 2013). However, in 2015 and 2016, rates improved as overwinter survival for the calves was 82 % and calf production was high at 54 calves:100 cows in October with high 90% adult survival.

Teshkepuk Lake Herd

The Teshekpuk Lake herd (TCH) calves in the vicinity of Teshekpuk Lake on the Alaskan coastal plain. After calving and during the mosquito harassment season, the caribou move closer to the coast for insect relief (Person et al. 2007, Parrett 2013). The herd's range has a high proportion of wetlands (23%) and tussock tundra (60%) on its annual ranges. While the herd typically winters on the tundra along the coastal plain, fall and winter range are annually variable and includes, in some years the Brooks Range. The climate for the calving and summer range is influenced by the northern Alaskan coast as green-up is rapid, summer temperatures are moderated by the coast although precipitation is low which increases the drought index. Winters have higher snowfall and days with freezing rain than herds to the east. A warmer climate is driving significant trends (1989-2016) for decreasing snow depths 10 June, increased plant growing degree days (GDD) in June, an increasing mushroom index and warmer temperatures in October. Extreme events include the 2001-2002 winter with deeper snow and delayed pre-calving migration which together with a low number of plant GDD in early June reduced calf survival (Carroll et al. 2005).

The vital rates cover 1990-2014: in the early 1990s, the herd was increasing and reached a peak of 69,000 in 2008 before declining to 39,200 in 2013 and by 2017, the herd had recovered to 55,600 in 2017. Adult and calf survival and productivity are annually monitored as well as distribution and movements (Parrett 2013; Table 15). The trend for parturition is a long-term decline since 2002: parturition rates were 61%, and 28%, in 2013 and 2014, respectively compared to long-term averages for parturition (72%, 2002-2012). Recruitment (% short yearlings) has tended to decline since 2002 and averages 15%. Calf

mortality is high in late winter-spring due to predation likely interacting with malnutrition and this is especially the case for calves that winter on the coast rather than the Brooks Range (Parrett 2013). Calves are relatively small with low body weight (5.5-5.8 kg 2012-2013) compared to neighbouring herds and body weight has declined since 2006-2009 (Parrett 2013).

Up until 2010, adult mortality annually varied (14.5 ± 1.0 SE) and did not show a consistent trend although annual rates were 28-32% higher between 2012 and 2014. Unlike most reporting for caribou herds, Kaplan Meier curves are calculated which suggests caribou survival declined steadily from about one year to ten years of age and about 50% of caribou survive from one year to six years of age (Parrett 2013).

Central Arctic Herd

The Central Arctic herd (CAH) calves along the wetlands and tussock tundra of the Alaskan coastal plain and summers also on the coastal plain and the foothills and winters south into the tundra of the Brooks Range. The climate on the CAH's calving and range is more continental than the WAH and TCH to the west in Alaska. The calving and summer climate is modified by proximity to the coast and the CAH has above average number of plant GDD in June and a relatively high summer drought index as July precipitation is relatively low. The winter ranges in the Brooks Range have an average number of days with freezing rain and rain-on-snow days (CARMA unpublished data). Significant trends (1989-2016) include more plant GDD in June and July, increasing precipitation in July, an increasing mushroom index and warmer temperatures in October. Severe events include an exceptionally late spring in 2013 resulting in high mortality of adult females (33%) in May 2013.

The vital rates cover from 1994-2020: the herd increased and peaked with 72,000 caribou in 2010 before rapidly declining to a low of 22,600 in 2016 then with recovery to 30,000 in 2019. Adult and calf survival and productivity are annually monitored as well as distribution and movements (Parrett 2013, ADF&G 2015c, Lenart 2013; Appendix A). Adult survival declined between 2007 and 2010, with annual rates being 83-87% but then declined to 75% 2012-2014 (Lenart 2015). Pregnancy rates and calf survival were high 1997-2010 at >85% and >50 calves:100 cows in the fall, respectively.

In addition to those data provided in agency reports, we estimated early calf survival (June calf:cow ratio)/(parturition rate), similar to data presented for the Porcupine caribou herd (PCH; ADF&G 2015d). Our analysis regarding early calf survival ignored estimates for 1995 and 1997 which indicated over 100% survival (112 and 123 % respectively).

Porcupine Herd

The PCH usually calves on the Arctic coastal plains but summers more inland in the foothills and winters in mountainous basins. This elevation variability contributes to a climate which differs from the neighbouring herds in cooler and moister summers with a low drought

index. Snow depths are greater. Current trends (since 2000) indicate a higher late spring and summer GDD. As well, since 1979 summer precipitation has increased, summer drought decreased and fall temperatures increased.

The herd is intensively monitored with locations of calving grounds identified every year since the early 1970s. The vital rates cover from 1983-2018. The herd increased from 1972 to a peak in 1989 of 178,000 caribou, declined to 122,000 in 2001 and then recovered to 218,000 in 2017. Adult and calf survival and productivity are annually monitored as well as distribution and movements (ADF&G 2015b; Appendix A).

There are few trends in vital rates for the PCH. There was a declining trend in spring calf:cow ratios although this metric has only been measured once in the last 15 years. Adult cow survival, although showing no trend overall was higher at $87\% \pm 1.1$ SE during the increase phases (1985-1989, 2001-2017) than during the decline phase ($82\% \pm 1.2$ SE between 1989-2001).

Bluenose-East Herd

The Bluenose-East herd (BNE) has a higher percentage of its annual range (79%) within the boreal forest than neighbouring herds. The calving and summer ranges are on the tundra and mostly underlain by the Precambrian Shield which influences topography, drainage and vegetation. The winter range extensively overlaps with the neighbouring Bathurst herd in some years. The climate is similar to the Bluenose-West and Cape Bathurst with colder and drier winters but relatively warmer calving and summers due to an increasing continental effect. Warmer and drier summers increase both the drought and the oestrid index. Significant trends (1979-2016) include fewer days with freezing rain, lower snow depth in May and June, increases in June plant GDD, the drought and oestrid index and warmer fall temperatures. The drought index peaked during the late 1990s and then again in 2012 and 2014 when the index was twice the average.

The vital rates are for 2008-2020 which is the period when the herd peaked at 114,000 in 2010 then rapidly declined at a halving rate of 2.4 years and was 19,200 caribou in 2018. Data for the BNE (Adamczewski, pers. comm.; Appendix A) includes pregnancy rates from hunter-collected samples which were low in 2010 and 2012 when the pregnancy rate was likely 64%. Late winter calf-cow ratios were high 2004-2011 and <30 calves:100 cows in 2001, 2012, 2014 and 2015 (WRRB 2016).

Bathurst Herd

The calving grounds, post-calving and summer ranges of the Bathurst herd (BAH) are on the tundra over-lying the Precambrian Shield. Fall range and winter range have shifted onto the tundra with decreasing use of the boreal forests (Mennell 2021). Migration distances such as between calving and winter were twice as far in the 1990s as in the 2000s. The climate has an increasing continental influence with warmer summers and colder drier winters. July precipitation is higher than the neighbouring herds which reduces the drought index but the

oestrid index is high. Severe events include high drought indices in 2012 and 2014, and 2014 had an exceptionally severe oestrid index. Significant trends are a decrease in the number of days with freezing rain, July precipitation and the mushroom index. Increasing trends are for rain-on-snow and warmer temperatures in October.

The vital rates include spring calf survival from 1987 and adult survival from 1997-2020 which covers the time when the BAH peaked at 472,000 in 1986 and then declined to 6,200 by 2021. Data for the BAH (Adamczewski, pers. comm.; Appendix A) includes adult cow mortality, parturition, fall calves:100 cows and spring calves:100 cows. Between 1985 and 1995, late winter calf:cow ratios varied annually and averaged >30 calves:100 cows. Between 2001 and 2006, the ratio declined, and calf survival was half of previous years. Higher ratios from 2007-2011 were >30 calves:100 cows partly because adult female survival was low (Boulanger et al. 2011). In 2012, 2014 and 2015, possibly related to drought conditions, calf:cow ratios were <30. Pregnancy rates were annually variable and were also lower than average following summer droughts in 2012 and 2014 (WRRB 2016). Trends in adult survival based on modeling declined from 86% in 1985 to 76% in 2006 and 77-78% for 2009, 2012, 2015 (Boulanger et al. 2011, Adamczewski, pers. comm.).

Leaf River Herd

The Leaf River herd (LRH) calving, summer and fall ranges are on the tundra and are relatively far south, being below 60°N latitude (Taillon et al. 2016). During fall migration, the caribou move south to the tundra-forest zone which is especially extensive on the Ungava Peninsula (Payette et al. 2001). The Precambrian Shield underlies the annual ranges. The winter range is warmer than western herds with a higher frequency of rain-on-snow and days with freezing rain. Snow depths are greater in March and deeper snow persists into early June and plants GDD are low in June and July. Summers are cooler and moist so the drought and oestrid indices are exceptionally low. Trends are fewer rain-on-snow and freezing rain days while July is warmer with more GDD and a higher oestrid index.

The vital rates (Taillon et al. 2016; Appendix A) cover the period 1993-2015 when the herd had peaked about 628,000 in 2001 but then declined to 187,000 in 2018. Adult female survival averaged 89% (CV=0.078) less than 70% in 2002 and 2007 (Rasiulis et al. 2014). In 2013-2014, the survival rates of adult females decreased to 78% and adult males to 70%, before increasing for females to 83.5% in 2014-2015 although male survival remained at 66% (Taillon et al. 2016). Fall recruitment is annually variable and has averaged 33.4 (CV=0.33) calves/100 females between 1994 and 2014 and the trend is a decline. Fall calf:100 cow ratios fell to 14-17 in 2004, 2007 and 2014 (Tallon et al. 2016) and calf body mass at birth is annually variable without a clear trend. The adult sex ratio has been annually monitored in the fall since 1994. The trend in both the adult sex ratio and the percentage mature (large) bulls is a decline and were only 18% and 4%, respectively by 2015. A notable

monitoring result is that the proportion of antlerless females jumped from a 1994-2014 mean of 10.8 (± 2.04 SE) to 50% in fall 2015.

George River Herd

Most (89%) of the annual range of the George River herd (GRH) is in the forest tundra zone and the summer range is relatively far south. As numbers declined, the calving ground shifted toward eastern Labrador and the winter range contracted 78% and shifted from Ungava Peninsula east to the Labrador coast. The climate is relatively moist with high summer rainfall and winters characterized by greater snow depths days with freezing rain and exceptionally high rain-on-snow. March and early June snow is relatively deep and plant GDD are low in June and July. The cooler wetter summers reduce the drought and oestrud indices. Octobers are warm with mean monthly temperature only a few degrees below freezing and significantly increasing since 1979. Other significant trends are less rain-on-snow and days with freezing rain and warmer, wetter Julys with increases in the oestrud index.

The vital rates (Rasiulis et al. 2014, Coté 2014; Appendix A) cover the period 1980-2016 when the herd peaked at 780,000 in 1993 and then declined and collapsed to 7,200 by 2018. The data for the GRH included fall calves:100 cows (Taillon pers comm.; 1980-2016, n=35, Table A.8), adult cow mortality (Bergerud et al. 2008, Taillon pers comm.; 1985-2011, n=27; Table A.8) and parturition rate (Bergerud et al. 2008; 1980-1993, n=12; Table A.8). Average annual adult females averaged 51-59% in 2009-2011 and 68.3% in 2001-2014 with increased survival at 79% for 2013-2014 (Rasiulis et al. 2014, Coté 2014). Male survival was low 51% for 2009-2015. Fall cafl:cow ratios annually vary with low values in 2004, 2010-2013 and 2015. Body condition and reproductive performance have been extensively monitored during the herd's increase, peak and decline in abundance (Bergerud et al. 2008, Couturier et al. 2009, Pachkowski et al. 2013). Calf birth weight averages 6.1 kg and fall weaning weight increased for 2007-2011 which together with increasing adult female body mass (1985-2009) suggests summer range is not limiting. But pregnancy rates are low at 75-77% for 1989-2012.

Climate Variables

We used the National Aeronautics and Space Administration's (NASA) Modern Era Retrospective Analysis for Research and Applications (MERRA2) dataset (<https://gmao.gsfc.nasa.gov/reanalysis/MERRA-2/>). NASA's Global Modeling and Assimilation Office's MERRA project was undertaken with the objectives of placing the observations from NASA's Earth Observing System satellites in a climate context and improving upon earlier re-analyses. The resolution of the MERRA grid is 1/2 degrees latitude by 2/3 degrees longitude and data are provided daily for most variables. MERRA2 was chosen over other datasets because it covers the modern remotely sensed data (from 1980

through the present), attempts to address problems with previous re-analysis products, and is focused on the hydrological cycle. Russell et al. (2013) describe MERRA2's climate variables and how caribou-specific derived climate variables were developed from the downloaded MERRA variables. For this analysis, we chose 38 MERRA2 and derived climate indicators that represented all seasonal ranges (summer, fall, winter, spring, and calving; Table 2). We compared the seasonal mean values for selected climate variables to describe regional climate across the seasonal ranges of the 13 North American migratory tundra caribou herds.

Table 2. List of CARMA's climate variables incorporated in analysis.

Indicator description	Acronym	Units
March 31 snow depth	Mar31SnDp	meters
May 15 snow depth	May15SnDp	meters
June 10 snow depth	Jun10SnDp	meters
June 10 Growing degree days	Jun10gdd	index
June 20 Growing degree days	Jun20gdd	index
July 20 Growing degree days	Jul20gdd	index
Cumulative oestrid index to Aug5	Aug5oes	index
Cumulative oestrid index to Aug6	Aug31oes	index
Increase in oestrid index from Aug5 to Aug31	oesdiff	index
Cumulative mosquito index to July 15	July15mosq	index
Winter freeze/thaw days	WFZThaw	days
Winter Rain-on-snow days	WRoS	days
Winter Rain-on-snow	WRoSdays	kg-m-2 d-1
Winter freezing rain	WFzRain	kg-m-2 d-1
Winter freezing rain days	WFzRndays	days
Fall freeze/thaw days	FFZThaw	days
Fall Rain-on-snow days	FRoS	kg-m-2 d-1
Fall Rain-on-snow	FRoSdays	days
Fall freezing rain	FFzRain	kg-m-2 d-1
Fall freezing rain days	FFzRndays	days
January snow depth	JanSnDp	meters
February snow depth	FebSnDp	meters
March snow depth	MarSnDp	meters
April snow depth	AprSnDp	meters
May snow depth	MaySnDp	meters
June snow depth	JunSnDp	meters
September snow depth	SepSnDp	meters
October snow depth	OctSnDp	meters
November snow depth	NovSnDp	meters
December snow depth	DecSnDp	meters
January temperature	Jantmp	degree C
February temperature	Febtmp	degree C
March temperature	Martmp	degree C
April temperature	Aprtmp	degree C
May temperature	Maytmp	degree C
June temperature	Juntmp	degree C
July temperature	Julytmp	degree C
August temperature	Augtmp	degree C

Correlating Vital Rates and Climate Variables Analysis

The analysis of the climate and vital rate data was largely restricted because of the often-small sample size for vital rates (Table 1). We used a general rule of thumb that at least ten data points per explanatory variable are necessary. Given our average vital rate sample size is 21.7 years, we restricted our analysis to a maximum two-independent variable regression

model. We had three sets of vital rate data with sample sizes of <10 (lowest was eight years). For those data we did derive a simple regression, but caution is due from the low sample size. Seven data sets had between 11-19 years. As these sample sizes violate our general rule for a two-independent variable model, we present both a single and a double independent variable model.

Using Excel regression analysis tools, we correlated vital rate data to our core climate variables (Table 2). When correlates of $p < 0.10$ were determined, we tested whether two and three-year running averages of the climate variables improved the correlation to $p < 0.05$. This allowed us to explore carryover effects up to three years. After conducting the simple regression analysis with the climate variable with the highest Pearson R value, we redid the analysis using the residuals of the simple regression and determined the climate correlate that explained most of the residual variability, and thus reported the best two independent variable model.

Another issue besides sample size was when vital rates trended over the period of the data set. Thus, if a significant ($p < 0.05$) correlation was determined with a climate variable it may simply mean both variables trended over the observation period and no cause-and-effect relationship exists. Therefore, for all trending climate variables that were related to a trending vital rate we “detrended” the vital rate by determining the residuals around the vital rate trend and regressed the residuals against the climate variables. If these differences are correlated, we assumed there is a real correlation between the two variables. Thus, for trending vital rates we present the one or two-independent variable model using the climate variable with the highest r^2 with variables that were still significant after the data was detrended.

Choosing independent variables

Often multiple independent climate variables correlated to our dependent variable. We ran correlation coefficients among climate variables and a number of the variables were logically correlated. For example, temperature and rainfall are used to derive the drought index; wind and temperature are used to derive oestrid and mosquito indices. Often, we were not able to explain the linkage. For example, January temperature correlated with July drought. In those cases when both variables had a similar correlation to a vital rate, we chose the variable that, based on our collective knowledge of caribou ecology and bioenergetics, was the most logical. In other instances, if two variables were similarly correlated to vital rates and not correlated to each other, we examined the x-y plots and chose the climate-vital rate relationship that did not depend on a single influential point. If both climate variable/vital rate relationships had influential points, we chose the climate variable that retained the highest Pearson r value when the influential points were removed.

RESULTS

Climate Comparisons Among Herds

Seasonal climate varied among the 13 herds (Figure 3) and is summarized below:

- **Spring:** By May 15, about 50% of the snowpack has been reduced resulting in a similar pattern to March snow depth. The exception is on the Ahiak herd (AHI) spring range, where coldest May temperatures resulted in 80% of the snowpack remaining. The WAH experienced the warmest average May temperature.
- **Calving:** During the calving season, the four western herds are the quickest to warm up as recorded in the accumulated GDD (above 0°C) by June 10, approximately eight to ten days after the peak on calving. In contrast the AHI and the two eastern herds, LRH and GRH, had the lowest June 10 GDD. June rainfall tended to be higher in the east with the BAH, Beverly (BEV), Qamanirjuaq (QAM), GRH and LRH experiencing the highest values.
- **Summer:** Summer July drought showed no regional patterns and was highest in the CAH, Cape Bathurst (CBH), AHI and BEV and lowest in the two eastern herds. Oestrid index, a measure of warble and bot fly activity, was highest in the central herds with the highest in the BEV and QAM, herds just west of Hudson Bay and lowest in the CBH and LRH.
- **Fall:** October snow depth was similar across North America with the four western herds recorded slightly higher average snowfall. The strong maritime influence was evident in the pattern of freezing rain with the GRH, LRH and WAH receiving much higher values than the remaining herds.
- **Winter:** March snow depth on the winter range was highest in the eastern and far western herd (WAH) and lower in the central herds, a pattern also reflected in accumulated rain-on-snow levels, suggesting a result of warmer moist maritime influence.

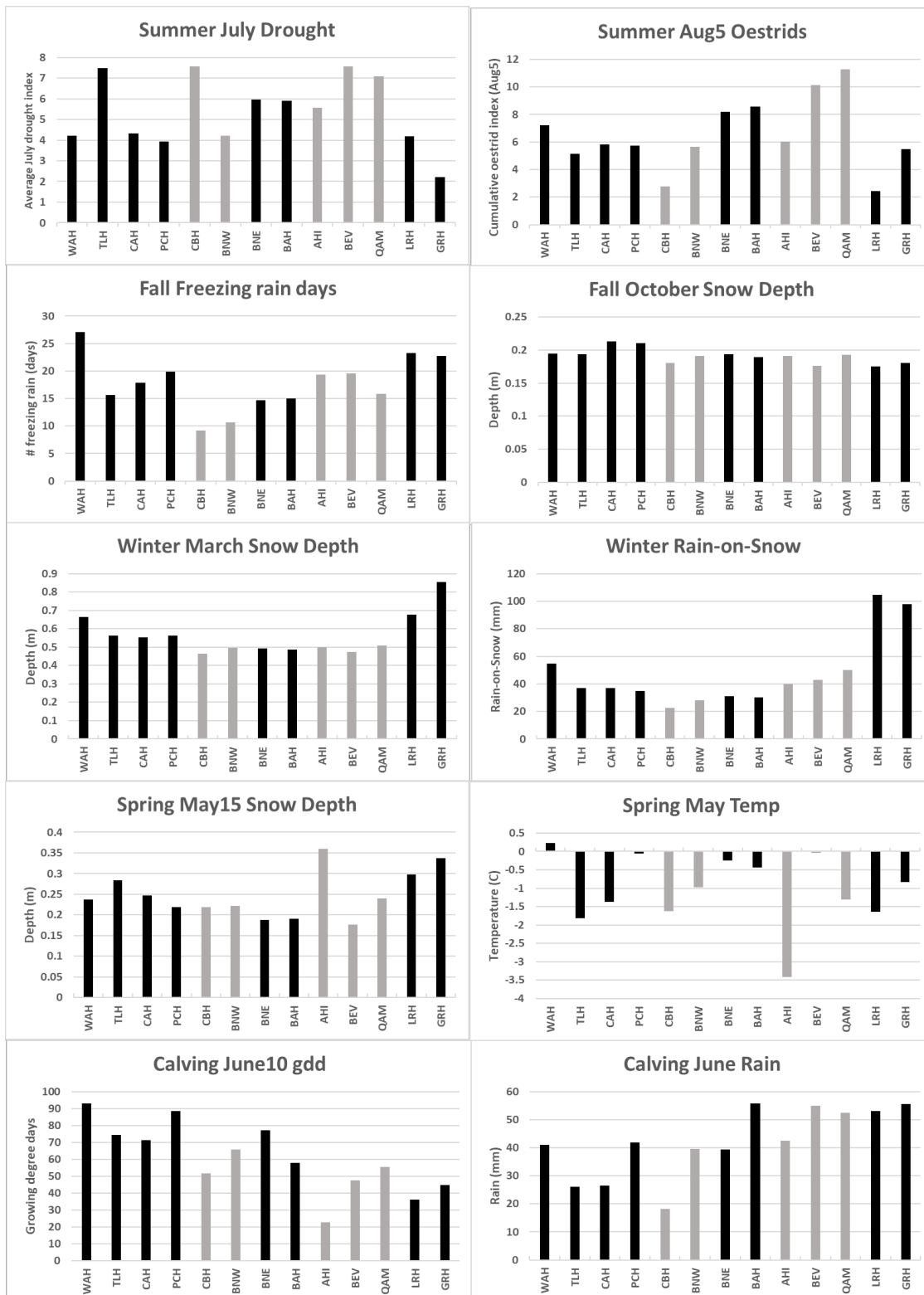


Figure 3. Examples of seasonal climate indicators (annual means) among North American migratory tundra caribou herds. Herds in black had sufficient available vital rates to be included in vital rate analysis. Herds are arranged from west to east across North America. The key for herd initials and names is in Figure 1.

Vital Rate and Climate Correlations

Western Arctic Herd

Vital rates: In the WAH, parturition exerts a greater effect on June calf:cow ratios than does June calf survival (66% versus 49%; Figure 4). High spring recruitment relates to lower fall calves:100 cows later that year. Cow survival, on the other hand, is negatively affected by the previous year's June calf:cow ratios as 14% of the variability in adult cow survival is accounted for by calf survival the previous year.

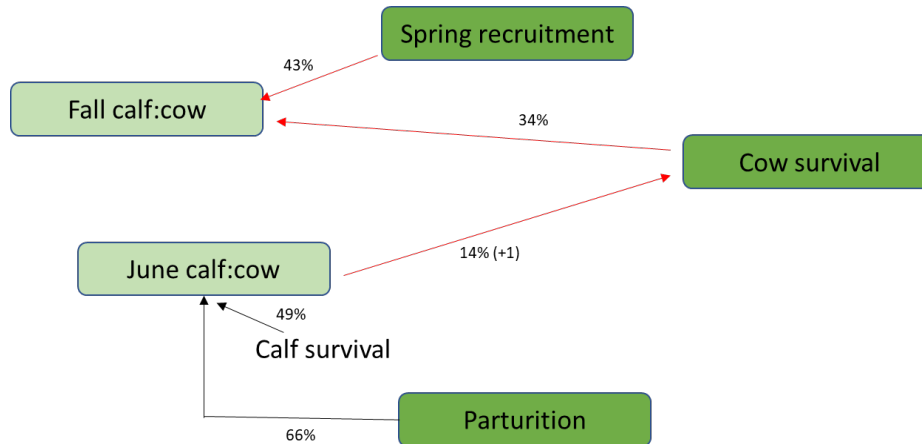


Figure 4. Linkages among vital rates for the Western Arctic herd (red – negative trend; black - positive trend; +1 is a one-year lag).

Climate versus vital rates: With only an average adjusted r^2 of 27%, WAH had the lowest percent of the variability in vital rates explained by climate indicators (Table 3). Among the regressions, May rainfall was directly or indirectly related to four vital rates (including a positive relationship between May drought and June calf survival). All May rain relationships were negative except a positive relationship between cow survival and a two-year running average of May rain. This seemingly contradictory role of May rain can be explained by the negative relationship between June calf:cow ratios and cow survival the following year (Figure 5). High rainfall in May, negatively related to June calf:cow ratios may be alleviated by warmer late springs resulting in high June 10 GDD. Fall June calf:cow ratios are negatively affected by high summer oestrid harassment.

Table 3. Vital rate and climate equations derived for the WAH.

HERD	Vital rate	N	Adj R2	F	p-value	Equation
WAH	Cow survival	28	0.41	10.22	0.001	13.3 + JanTmp * 0.746 + MayRain2yr * 0.175
WAH	Parurition	28	0.21	6.71	0.017	88.396 + MayRain * -0.382
WAH	June calf survival	27	0.29	6.31	0.006	91.071 + MayDrt * 4.469 + JulTmp * -1.412
WAH	june calf:cow	27	0.24	5.09	0.014	79.556+ Jun10gdd * -0.059 + MayRain * -0.221
WAH	fall calf:cow	15	0.24	5.05	0.044	8.851 + aug31OES * -0.867
WAH	spring calf cow	34	0.24	6.29	0.005	22.015 + AugTmp * -1.144 + SepSnD * 52.407

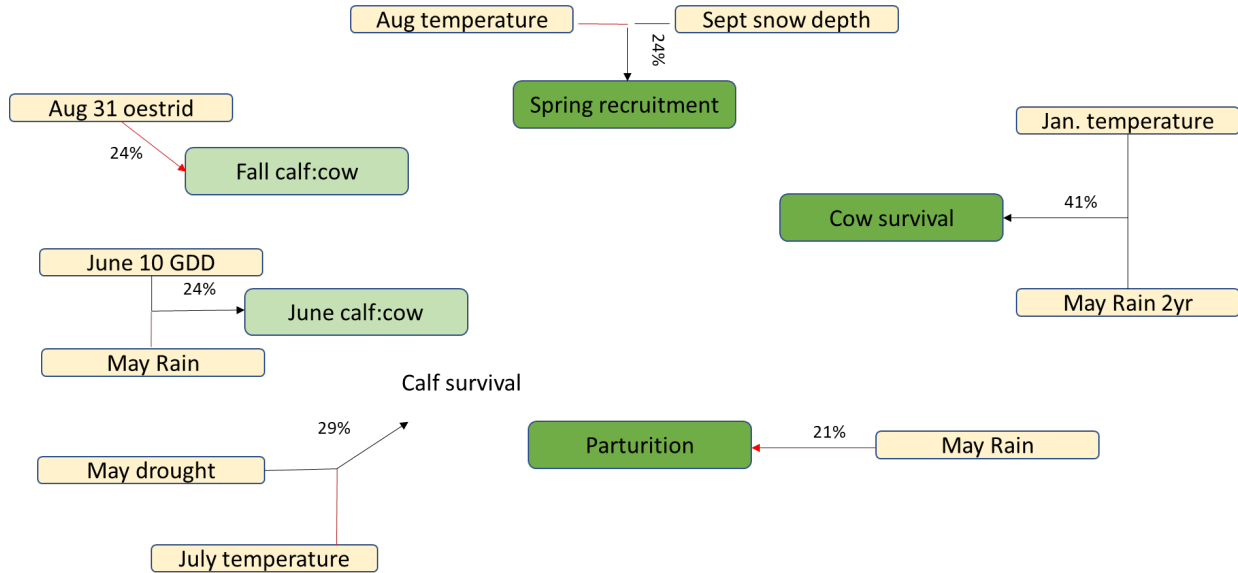


Figure 5. Climate linkages derived for WAH vital rates (red – negative trend; black - positive trend).

Teshekpuk Lake Herd

Vital rates: The among vital rate linkages for the TCH are complex (Figure 6). Similar to the WAH, parturition has a bigger effect on late June calf:cow ratios than does June calf survival (62% versus 41%). The higher the fall calf:cow ratio and the higher the spring recruitment, the lower the cow survival the following year. High June calf:cow ratio resulted in higher recruitment the next spring.

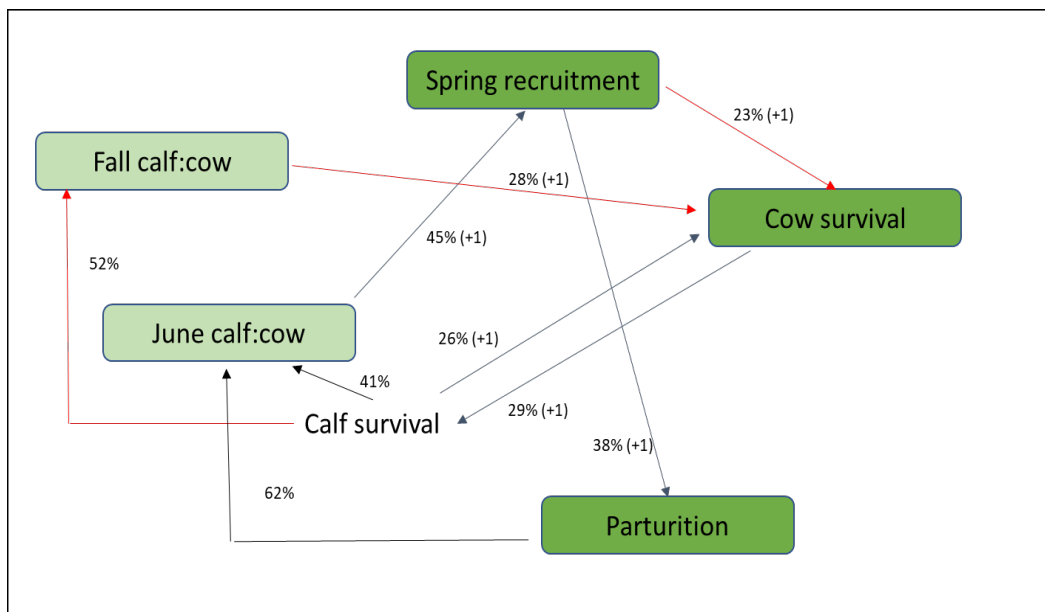


Figure 6. Linkages among vital rates for the Teshekpuk Lake herd (red – negative trend; black - positive trend; +1 is a one-year lag).

Vital rates versus climate: The relationship between November snow depth and parturition, carried through to late June calf cow ratios and the following spring recruitment rate (Figure 7, Table 4). The greater the amount of rain in June, the lower the early calf survival in the TLH. Fall calf:cow was negatively impacted by summer oestrid activity. Forty-three percent of the variation in adult cow survival was accounted for by freezing rain in the fall (negative) and March temperature (positive).

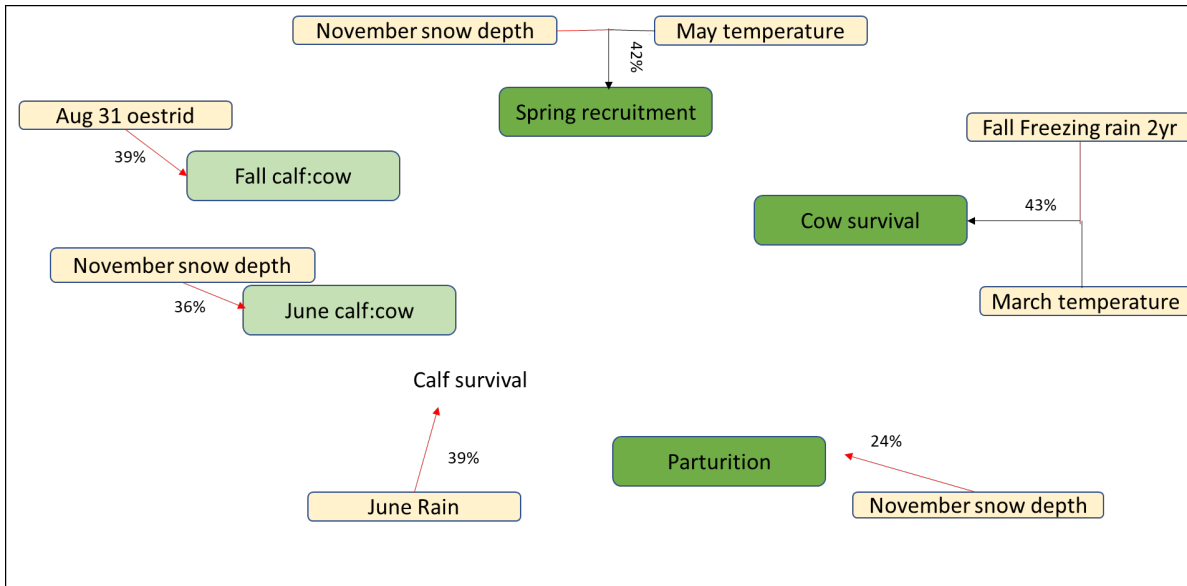


Figure 7. Climate linkages derived for Teshekpuk Lake herd vital rates (red – negative trend; black - positive trend).

Table 4. Climate equations predicting vital rates for the Teshekpuk Lake herd.

HERD	Vital rate	N	Adj R2	F	p-value	Equation
TCH	spring calf cow	23	0.42	8.81	0.002	36.732 + MayTmp * 1.92 + NovSnD * -40.699
TCH	Cow survival	24	0.43	9.83	0.001	103.568 + F FzRain2yr * -1.825 + MarTmp * 0.69
TCH	Parurition	14	0.29	5.01	0.045	117.27 - NovSnD *178.89
TCH	June calf survival	13	0.39	8.60	0.013	94.252 + JnRain * -0.756
TCH	june calf:cow	16	0.40	6.06	0.014	96.373 + NovSnD * -214.969 + JunDrt * 2.989
TCH	fall calf:cow	14	0.39	8.69	0.013	26.88 + MayDrt * -14.428

Climate and vital rates as independent variables: November snow depth explained most of the variation in the residuals from regressing recruitment with June calf:cow ratio the previous year. The multiple regression explained 55% of the variability in spring recruitment in the TCH, much higher than the 42% explained by the climate model (Table 4).

$$\text{Recruitment} = 13.628 + \text{Jncfcw} * 0.22 + \text{NovSnDp} * -55.102$$

(n=13; adj r²=0.55; F=8.3; p-value=0.007)

Central Arctic Herd

Vital rates: Cow survival as measured in late spring had a positive impact on subsequent parturition, June calf survival and late June calf:cow ratio (Figure 8). Furthermore, calf survival and June calf:cow ratio had a positive impact on next spring's cow survival. These relationships positions the CAH closer to the TCH as compared to the WAH and PCH where negative feedbacks were identified among these vital rates. Although fall calf:cow ratio was related to June calf:cow ratio, sample size was only four years and thus the equations are not reported. Parturition and early calf survival both were highly correlated to June calf:cow ratio.

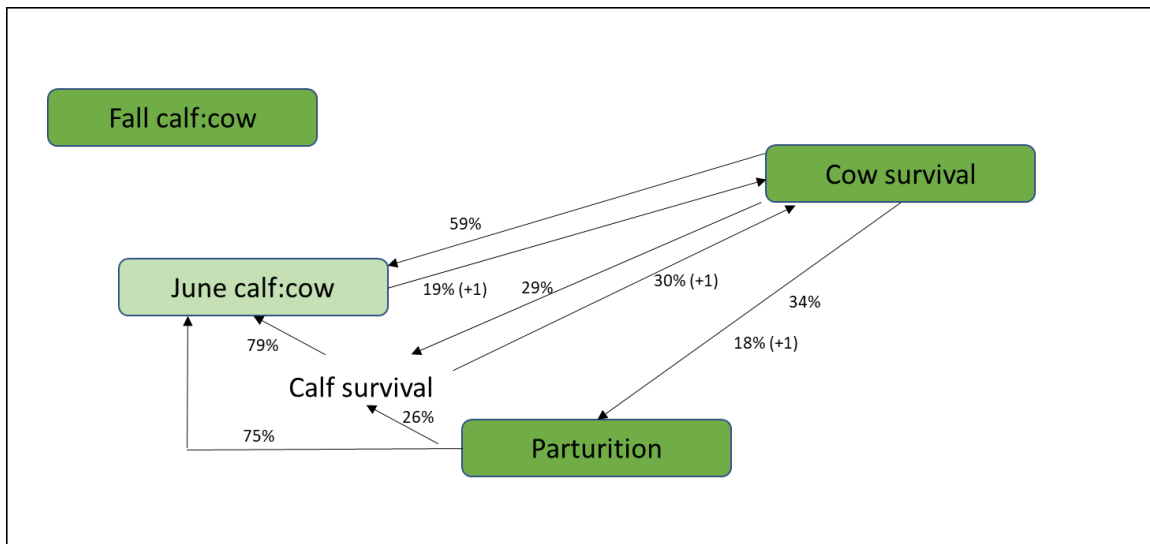


Figure 8. Linkages among vital rates for the CAH (red – negative trend; black - positive trend; +1 is a one-year lag).

Vital rates versus climate: Similar to the TCH, the relationship between November snow depth and parturition, carried through to June calf survival and late June calf cow ratios (Figure 9, Table 5). June calf:cow ratio was also impacted negatively by the previous summers July 15 cumulative mosquito index. The deeper May snow, the higher the fall calf:cow ratio. Although the r^2 is high (68%), fall surveys were only conducted in seven years.

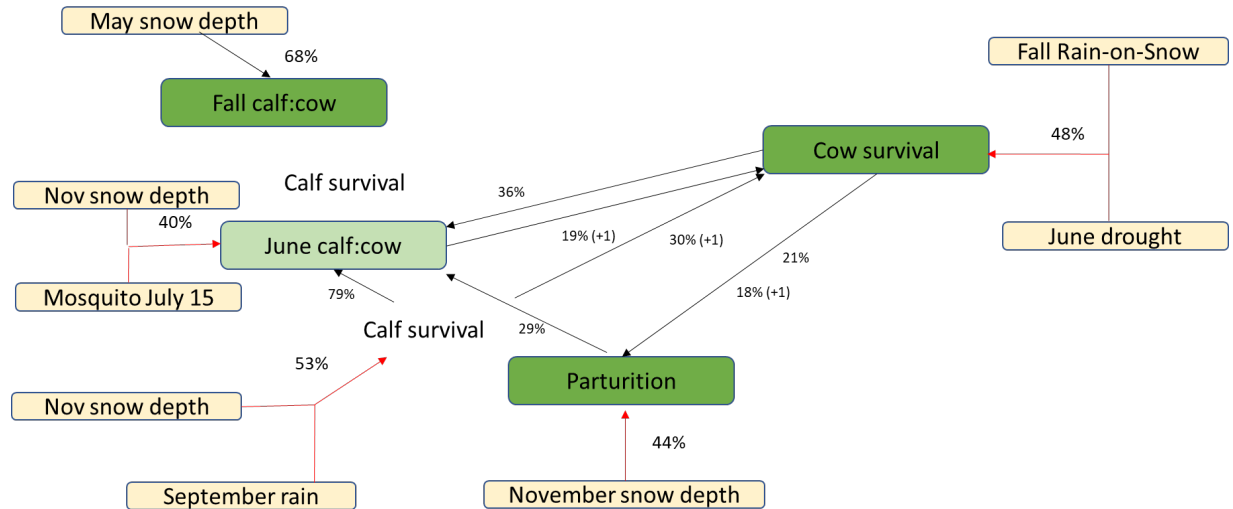


Figure 9. Linkages between climate and vital rates for the Central Arctic herd (red – negative trend; black - positive trend).

Table 5. Equations derived between climate and vital rates for the Central Arctic herd.

HERD	Vital rate	N	Adj R2	F	p-value	Equation
CAH	Cow survival	22	0.48	11.01	0.001	$10.719 + \text{JunDrt} * -1.529 + \text{F RoS} * -0.213$
CAH	Parurition	21	0.44	16.45	0.001	$118.288 + \text{NovSnD} * -102.576$
CAH	June calf survival	17	0.53	10.16	0.002	$112.524 + \text{NovSnD} * -77.767 + \text{SepRain} * -0.226$
CAH	june calf:cow	21	0.60	16.17	0.000	$120.333 + \text{Mosq Jy15} * -1.716 + \text{NovSnD} * -100.2$
CAH	fall calf:cow	7	0.68	13.65	0.014	$28.239 + \text{MaySnD} * 95.087$

Climate and vital rates as independent variables: The highest vital rate to predict cow survival was June calf survival in the previous year. Fall freeze-thaw events explained most of the residuals. The final r^2 was 54% explaining more of the variance in cow survival than the two-climate variable model (48%, Table 5). In the climate model, fall rain-on-snow, rather than fall freeze-thaw events, entered the best predictive equation. Fall freeze-thaw events, however, were also correlated to cow survival ($r=-0.43$) and rain-on-snow ($r=0.52$).

$$\text{Cow survival} = 46.682 * \text{Junecalfsurv} * 0.626 + \text{FFzThaw} * -0.783$$

($n=15$; $\text{adj } r^2= 0.54$; $f= 9$.; $p\text{-value}= 0.003$)

Porcupine Caribou Herd

Vital rates: The PCH had the most complex vital rate linkages (Figure 10) although few key results. The first key finding is that June calving success (combination of parturition rate, June calf survival and June calf:cow ratio) reflected negatively on the following spring's cow survival (keeping in mind that cow survival in the spring is based on the accumulation of cow mortalities from July of one year to June the following year). The second key finding is that high June calf survival and related high June calf:cow ratio is negatively related to calf mortality from end of June to spring composition counts. As a result, June calf:cow ratio is

not a good predictor of spring recruitment as the higher the number of calves surviving their first month, the lower their survival from June to spring surveys.

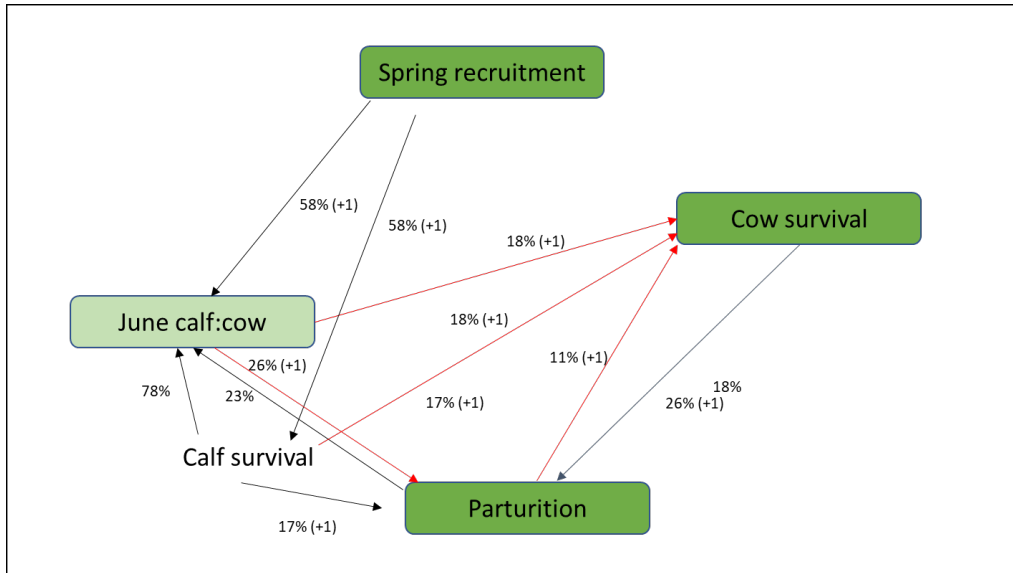


Figure 10. Linkages among vital rates for the Porcupine herd (red – negative trend; black - positive trend; +1 is a one-year lag).

Vital rate versus climate: As with the TCH and CAH, fall snow depth (October for the PCH, November for the TCH and CAH) was the climate predictor to spring parturition rate (Figure 11, Table 6). For the PCH the predominant climate condition impacting vital rates was drought. Drought entered the regression model for cow survival (August), parturition (August), June calf survival (June) and recruitment (June). In fact, June calf:cow ratio was most related to June rain (which is used to derive drought). Similar to the WAH cow survival was related to winter icing conditions which, for the PCH was freeze-thaw events.

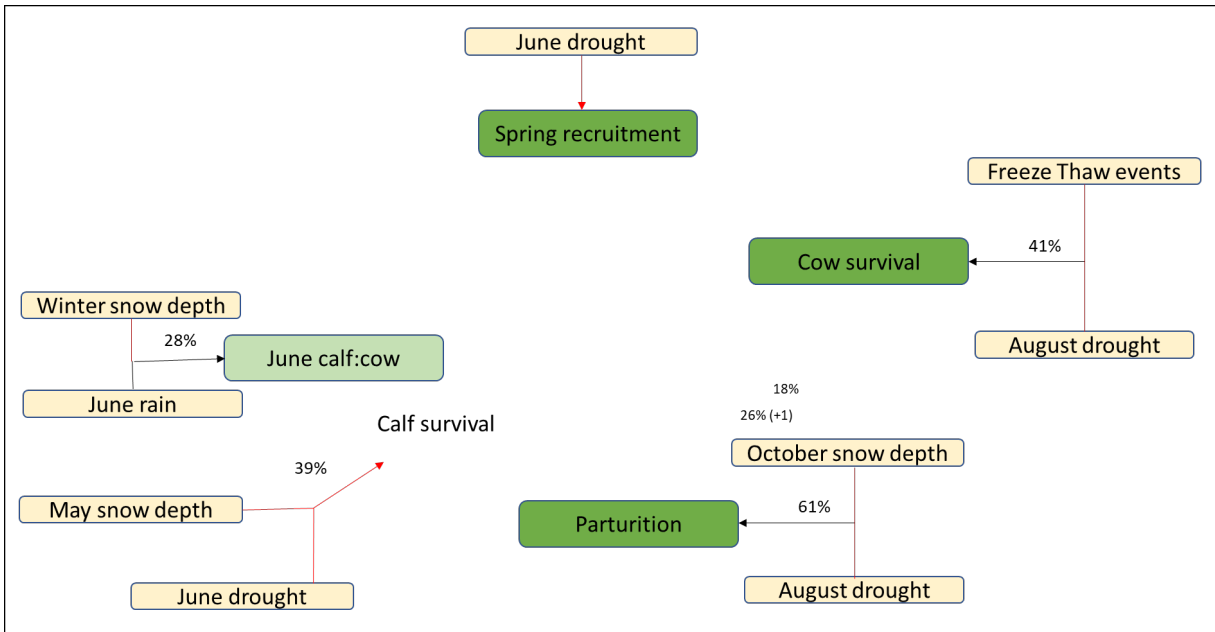


Figure 11. Linkages between vital rates and climate indicators for the Porcupine herd (red - negative trend; black - positive trend).

Table 6. Equations derived between climate and vital rates for the Porcupine herd.

HERD	Vital rate	N	Adj R2	F	p-value	Equation
PCH	Cow survival	28	0.41	9.97	0.001	$99.28 + \text{AugDrt} * -0.489 + \text{W FZThaw} * -0.279$
PCH	Parurition	29	0.61	20.70	0.000	$97.929 + \text{AugDrt} * -1.0604 + \text{OctSnD} * -63.938$
PCH	June calf survival	27	0.39	9.42	0.001	$87.993 + \text{MaySnD} * -49.116 + \text{JunDrt} * -2.228$
PCH	Post-calving survival	21	0.47	8.54	0.003	$83.121 + \text{MayRain} * 0.409 + \text{MayDrt} * -6.297$
PCH	june calf:cow	28	0.55	15.58	0.000	$96.274 + \text{Wint SnDp} * -117.574 * \text{JunRain} * 0.177$
PCH	spring calf cow	17	0.71	36.88	0.000	$42.076 + \text{JunDrt} * -3.115$

Climate and vital rates as independent variables: Because the linkages among vital rates are complicated, it is hard to identify key climate drivers that impact specific vital rates. Thus, where sample size warrants, we also derived a two independent caribou model which includes a vital rate and the climate indicator that best accounted for regression residuals.

Using June calf:cow ratios from the previous year, the best predictor of cow survival was freeze-thaw events. The resultant model explained 43% of the variability in cow survival, slightly better than the climate vital rate model (41%).

$$\text{Cow survival} = 105.871 + \text{JnCf:cow} * -0.159 + \text{WFreezeThaw} * -0.258$$

$$(n = 18; \text{adj } r^2 = 0.43; F=7.9; p\text{-value} < 0.01)$$

The best predictor of parturition rate was a negative relationship with late June calf:cow ratio the previous summer. November snow depth accounted for most of the variability of the residuals and together they accounted for 67% of the variability in parturition rate. Using

only November snow depth and August drought, the relationship accounted for 61% of parturition rate variability.

$$\text{Parturition} = 115.428 + \text{juncfcw} * -0.26 + \text{NovSnD} * -59.874$$

(n= 25; adj r² = 0.67; F=25.4; p-value <0.001)

Bluenose-East Herd

Vital rates: We found no correlation between cow survival, recruitment, parturition and fall calf:cow ratios but sample sizes are small (Table 7).

Vital rates and climate: The small sample size limited us to a simple regression linking BNE vital rates to climate (Table 7). Snow depth appeared to be a common climate indicator in three of the four vital rates. June snow depth accounted for 34% of the variability in annual cow mortality, May snow depth was related to parturition (Table 7, Figure 12; r²= 0.88) and September snow depth accounted for 61% of fall calves:100 cows.

July rain in previous summer on the fall range accounted for 88% of the variability in spring recruitment. Summer rain is correlated to mushroom production (Krebs et al. 2008) and thus more rain may indicate a protein flush in fall, affecting calf growth and weaning.

Table 7. Equations derived between climate and vital rates for the BNE herd.

HERD	Vital rate	N	Adj R2	F	p-value	Equation
BNE	Cow survival	10	0.34	5.71	0.044	68.752 + JunSnD *562.344
BNE	Parurition	5	0.88	30.49	0.012	39.758 + MaySnD * 215.231
BNE	fall calf:cow	6	0.64	5.71	0.044	50.155 + SepSnD * -147.184
BNE	spring calf cow	10	0.61	14.87	0.005	13.9978 + JulRain * 0.443

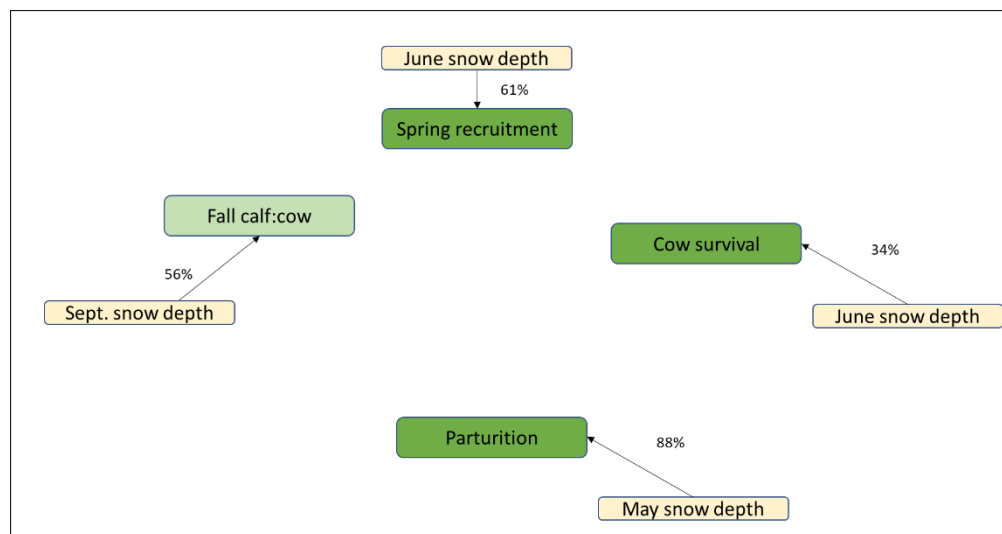


Figure 12. Linkages between climate and vital rates for the Bluenose-East herd (red – negative trend; black - positive trend).

Bathurst Caribou Herd

Vital rates: For the BAH, variability in annual spring recruitment was positively related to the previous spring’s parturition rate ($r^2 = 47\%$) and fall calves:100 cows ($r^2 = 70\%$; Figure 13). In turn, spring recruitment accounted for 22% of variability in cow survival the following year, with higher recruitment resulting in lower cow survival the next year. Spring recruitment also accounted for 33% of next year’s parturition rate variability, with higher recruitment related to higher parturition rate.

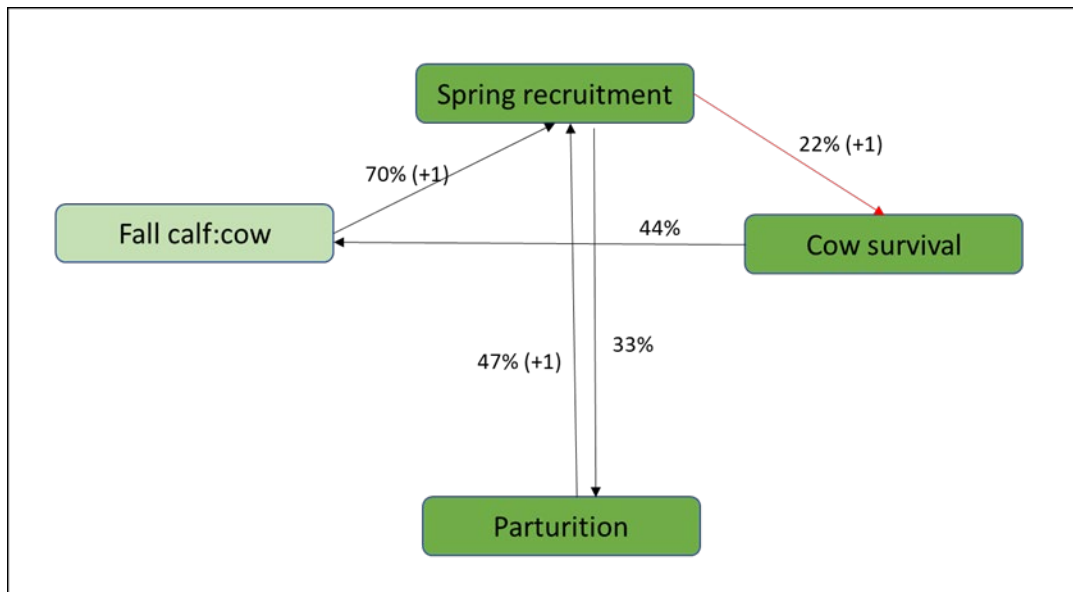


Figure 13. Linkages among vital rates for the Bathurst herd (red – negative trend; black - positive trend).

Vital rates versus climate: Similar to the western herds (PCH, TCH, and CAH), parturition rate was negatively related to the previous fall snow depth (Table 8, Figure 14). This relationship also held for the next year’s recruitment. This link between recruitment and October snow depth is strengthened by the link between parturition and spring recruitment. Cooler fall temperature (average September and October) and higher June rainfall the previous June accounted for 43% of cow mortality.

Table 8. Equations derived between climate and vital rates for the Bathurst herd.

HERD	Vital rate	N	Adj R2	F	p-value	Equation
BAH	Cow survival	24	0.43	9.56	0.001	$41.720 + \text{JunRain} * 0.271 + \text{SpOcTmp} * -5.324$
BAH	Parurition	10	0.58	13.25	0.007	$114.463 + \text{OctSnD} * -170.526$
BAH	fall calf:cow	13	0.57	16.66	0.002	$72.132 + \text{MarTmp} * 2.077$
BAH	spring calf cow	25	0.31	6.34	0.007	$67.162 + \text{OctSnD}(2) * -253.168 * \text{F FZThaw} * 0.748$

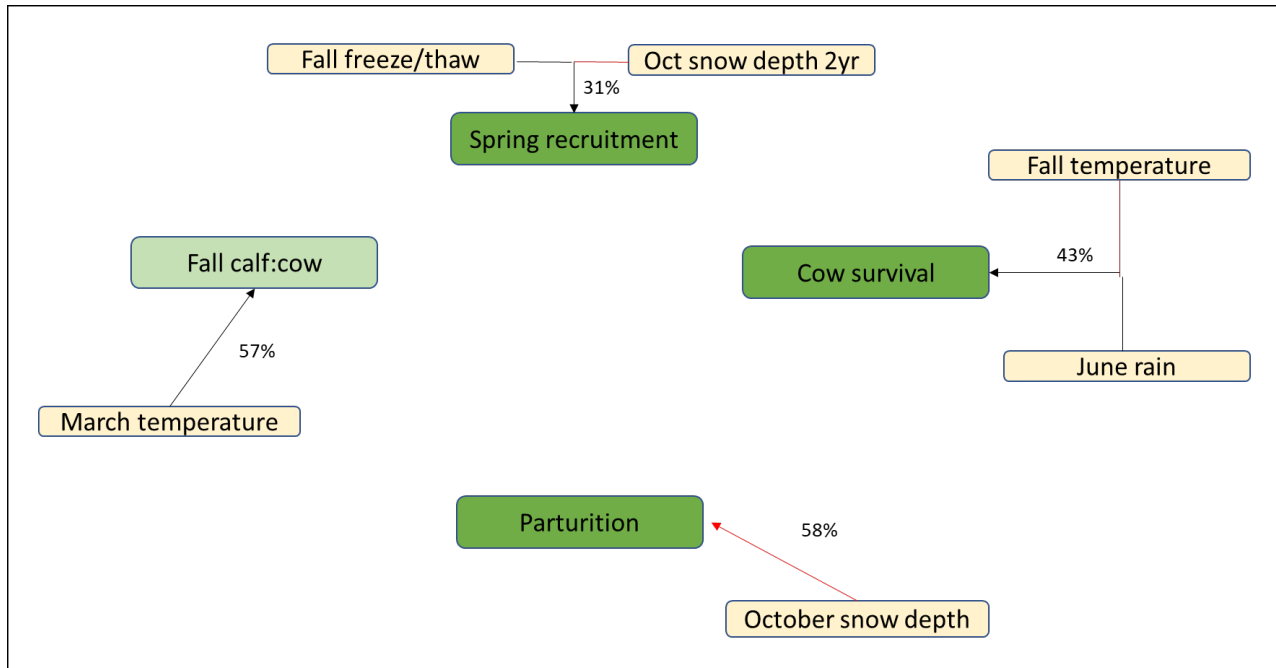


Figure 14. Linkages between climate and vital rates for the Bathurst herd (red – negative trend; black - positive trend).

Climate and Vital rates as independent variables: Last year’s spring recruitment and September temperature accounted for 48% of the variability in cow survival, an improvement from 43% for the best climate model.

$$\text{Cow survival} = 102.608 + \text{Spring recruitment} * -0.665 + \text{Septtmp} * -4.25$$

$$(\text{adj } r^2=0.48; f 7.4, p\text{-value} < 0.01)$$

Leaf River Herd

Vital rates: Calf survival, June calf:cow ratios and spring recruitment data were not available to us which is a limitation. Although Taillon et al. (2016) presents both % calves and calves:100 cows from fall composition counts, the two measures are highly correlated ($r^2=0.80$, $p<0.001$). Thirty-one percent of the variability in fall calves:100 cows was explained by cow survival that spring ($p=0.007$, $n=7$; $r^2=0.31$).

Vital rates and climate: Table 9 and Figure 15 present the predictive equations for LRH vital rates and climate indicators. As rainfall in spring and summer differentiate the LRH and GRH from other herds across North America (Figure 3), it is perhaps not surprising that too much rain appears to impact what limited productivity figures we have for the LRH. High July and May rain combined to reduce fall calf:cow ratios, accounting for 57% of the variability. In contrast, May drought the previous spring had a negative effect on subsequent cow survival, accounting for 30% of the variability. Although May drought implies more rain is positive for subsequent cow survival, we have seen for the TCH, CAH and PCH, that June calf survival has

a negative impact on cow survival the following spring. Thus, if in the LRH, higher drought (lower rain) is linked to increased June calf survival, and June calf survival has a negative impact on cow survival that could explain the apparent contradiction.

Table 9. Equations derived between climate and vital rates for the Leaf River herd.

HERD	Vital rate	N	Adj R2	F	p-value	Equation
LRH	Cow survival	19	0.30	8.55	0.009	92.515 + MayDrt * -12.411
LRH	fall calf:cow	21	0.57	14.50	0.000	66.407 + JulRain * -0.386 + MayRain * -0.393

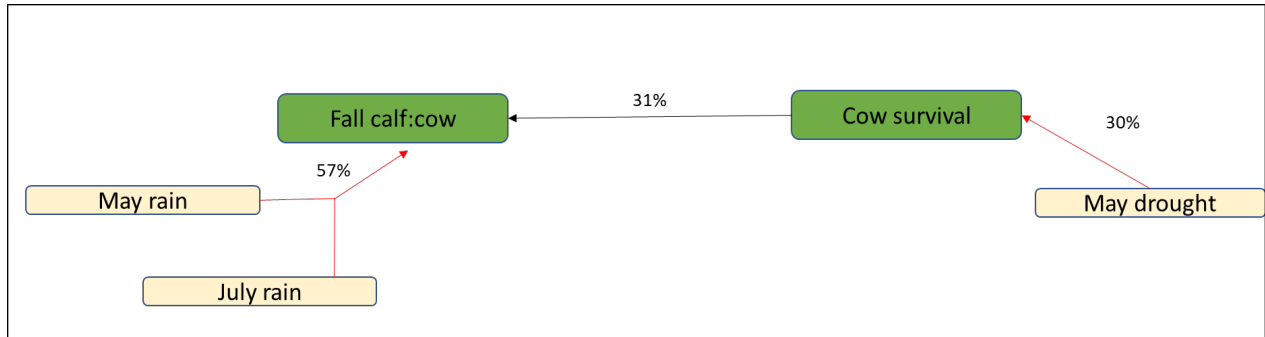


Figure 15. Climate linkages derived for the Leaf River herd vital rates (red – negative trend; black - positive trend).

Climate and vital rates as independent variables: Thirty-one percent of the variability in fall calves:100 cows was accounted for by spring cow survival. The climate indicator that accounted for most of the residuals was July drought, the higher the July drought the higher the fall calf:cow ratio. The resultant r^2 (80%) is a substantial improvement from the climate only model (57%). In this equation, the negative impact of July rain is replaced by the positive impact of July drought and the negative impact of May rain is replaced by the positive impact of cow survival.

$$\text{Fall calves:100 cows} = -28.526 + \text{CowSurvival} * 0.557 + \text{JulDrt} * 2.639$$

$$(n=17, \text{adj } r^2 = 0.80, F=32.5, p\text{-value} < 0.001).$$

George River Herd

Vital rates: We found no relationships among vital rates for the GRH but we only had available data for cow survival, parturition and fall calf:cow.

Vital rates and climate: Table 10 and Figure 16 present the results of climate-vital rate analysis for the GRH. Similar to the LRH, vital rates of the GRH are most associated with rainfall, the higher the rainfall, the lower the vital rate. June rain the previous summer and current year July rain were negatively associated with parturition and fall calf:cow ratio in the current year. Cow survival was most negatively associated with the previous fall's

freezing rain and the correlation was improved by averaging the last two year's fall freezing rain.

Table 10. Equations derived between climate and vital rates for the George River herd.

HERD	Vital rate	N	Adj R2	F	p-value	Equation
GRH	Cow survival	27	0.33	13.62	0.001	$94.875 + W FzRain2yr * -0.993$
GRH	Parurition	12	0.28	5.21	0.046	$99.823 * JunRain * -0.451$
GRH	fall calf:cow	35	0.29	7.69	0.002	$58.963 + MaySnD * -23.586 + JulRain * -0.178$

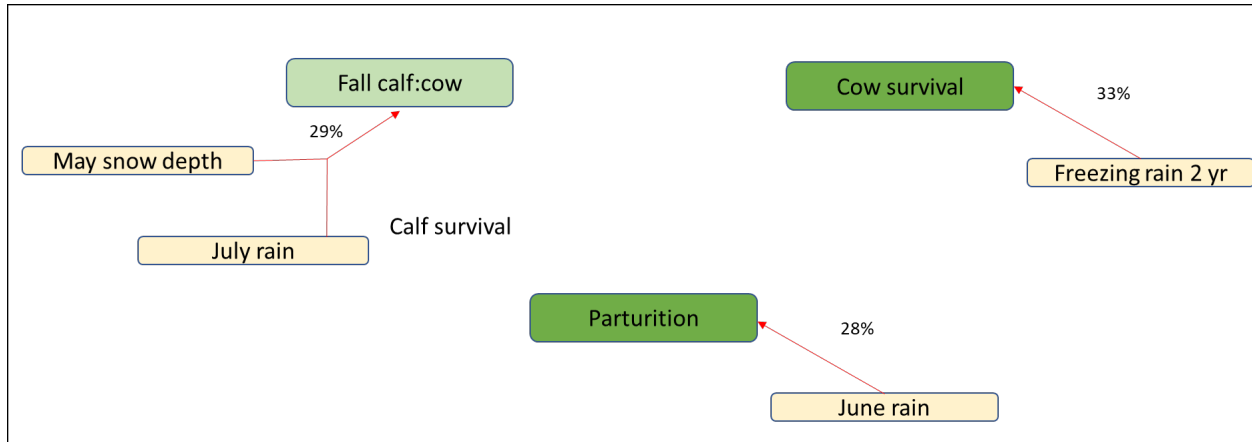


Figure 16. Climate linkages derived for the George River herd vital rates (red – negative trend; black - positive trend).

DISCUSSION

Vital Rate Linkages

Cow Survival

In general, high calf productivity by the end of June reflected negatively on that year's cow survival as measured the next spring (or in the case of the WAH, in the fall). For three of the four herds with sufficient data, June calf survival was negatively correlated with subsequent cow survival (WAH, TCH, PCH) while in the PCH, cow survival also had a negative relationship to previous parturition and June calves:100 cows (Figure 17). The only exception was the CAH, when June calf survival and June calves:100 cows both projected a positive response in subsequent cow survival. In turn, high cow survival over the year resulted in higher calf productivity in terms of parturition (PCH, CAH), June calf survival (CAH and TCH), and June calf:cow ratio (CAH).

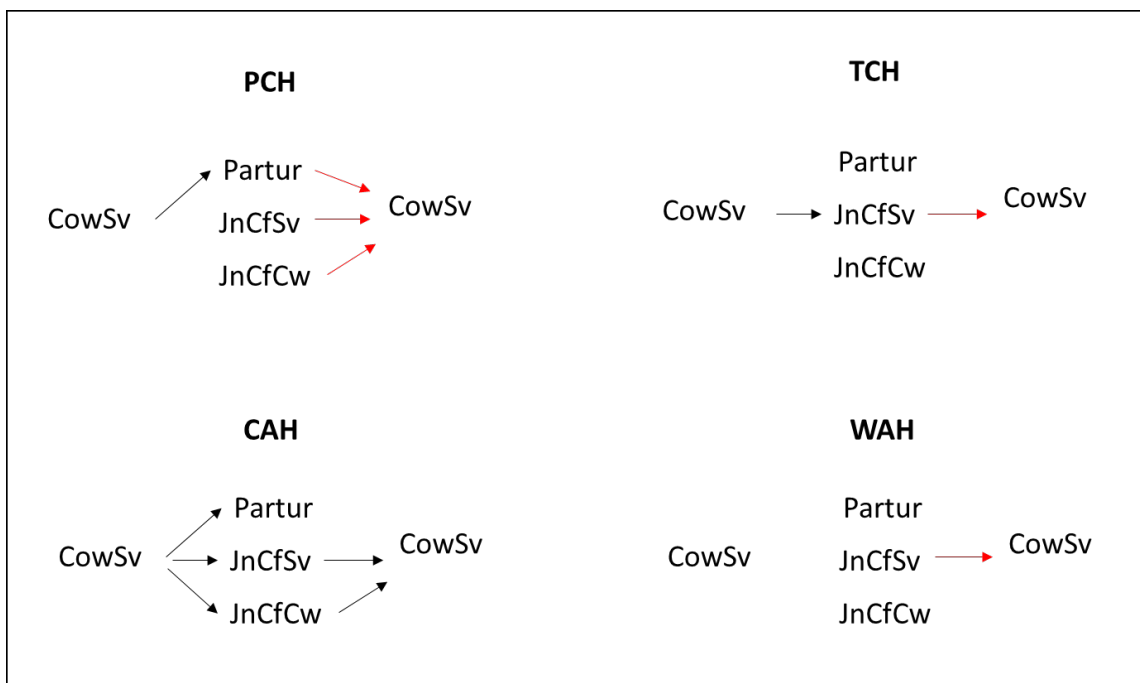


Figure 17. Summary of linkages between cow survival and other vital rates for four herds with sufficient data (red – negative trend; black - positive trend; JnCfCv is June calf survival, JnCfCw is June calf cow ratio, CowSv is cow survival).

In the CAH, Cameron (1994) reported a 24% breeding pause frequency similar to Dauphine's (1976) estimate of 20% for the Qamanirjuaq herd. Our observation that there is positive feedback between spring estimate of annual cow survival to parturition, June calf survival and June calf cow ratios is also consistent with our suggestion that a favourable year resulting in higher cow survival also benefits June calf productivity but that productivity comes with a cost the following year. It is ironic, therefore, that the only study documenting

breeding pauses among the four Alaskan herds, the CAH (Cameron 1994), is the only herd where the negative feedback of calf productivity and cow survival was not documented. However, similar analyses for breeding pauses for the WAH, TCH and PCH have not been undertaken.

Recruitment

Where data exists, three of four herds had negative feedback from recruitment to cow survival (Figure 18). These metrics are both measured in the spring and is based on, for cow survival, deaths from July to June for the TCH, BAH and PCH (WAH cow survival is measured from October to September). Recruitment is a measure of how many calves:100 cows are in the spring composition counts. We found a positive relationship with late June calves:100 cows and spring recruitment in year+1 for the TCH and WAH. This suggests that the annual recruitment is largely dependent on how many calves make it through June and we would expect that variability in climate, between June and the following spring, would play less of a role. We found no significant relationship between June calves:100 cows and subsequent recruitment in the PCH and BAH suggesting the climate may play a larger role through summer, fall and winter. In the PCH, we found a positive relationship between spring recruitment to subsequent June calf survival and late June calf:100 cows.

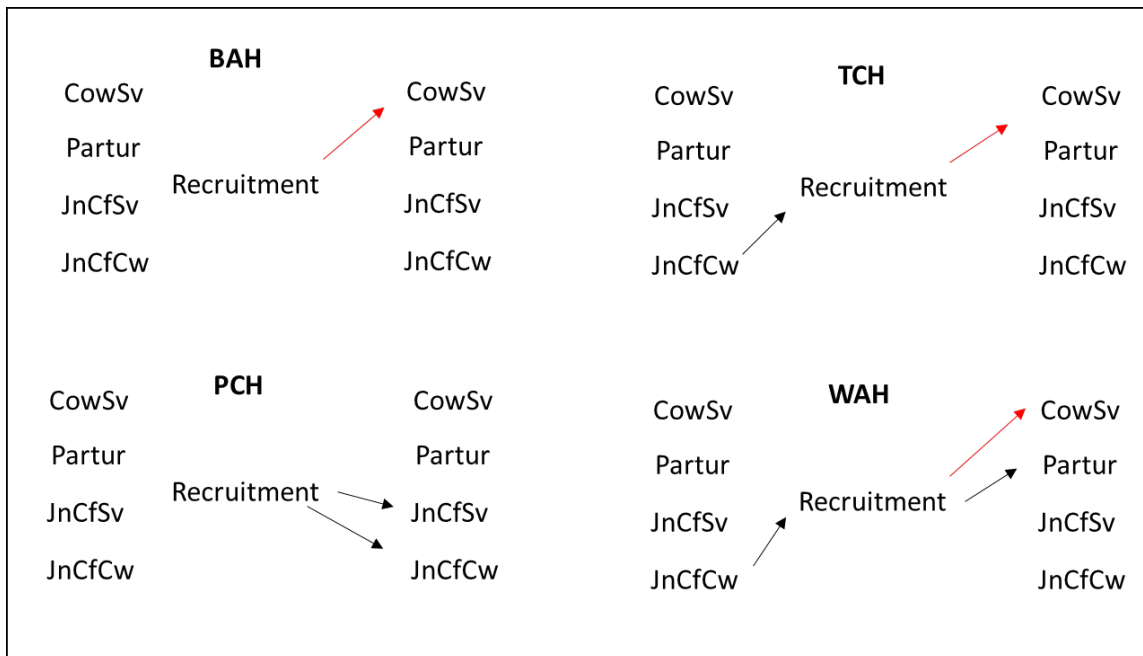


Figure 18. Summary of linkages between spring recruitment and other vital rates for herds with sufficient data (red – negative trend; black - positive trend; JnCfCv is June calf survival, JnCfCw is June calf cow ratio, CowSv is cow survival).

June Calf Productivity

For the four Alaskan herds with measured parturition and end of June calves:100 cows, we determined the pattern of June calf survival varied over the first month of life (Figure 19). The WAH and TCH had similar patterns with strong correlations between parturition and June calves:100 cows ($r^2 = 66\%$ and 62% respectively) and lower correlations between June calf survival and end of June calves:100 cows ($r^2 = 49\%$ and 41% respectively). In contrast, both the CAH and the PCH had high correlations between June calf survival and end of June calves:100 cows ($r^2 = 79\%$ and 78% respectively). Parturition in the PCH contributed the least, among the four herds, to the annual variability in calf productivity to the end of June. These results suggest that climate on the calving grounds contributed the most to end of June calf productivity for the CAH and PCH, while climate related to parturition was more important in the WAH and TCH.

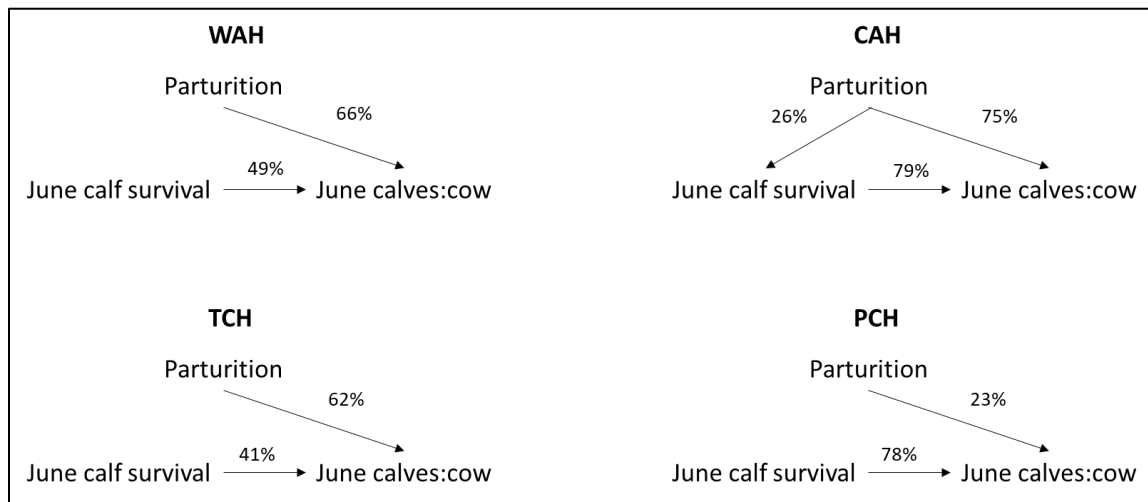


Figure 19. Summary of linkages between parturition and other vital rates for herds with sufficient data (red – negative trend; black - positive trend).

Vital Rate and Climate Indicators

Spring (44%) and fall (29%) accounted for 73% among the climate indicators related to vital rates (Figure 20) while the remaining 27% were distributed between summer (16%) and winter (11%). Reproductive and survival strategies of caribou cows apparently buffer environmental variability in summer and winter. Thus, conditions in fall (September-November) and spring (May-June) disproportionately impact vital rates. During spring, 67% of the predictive climate indicators were related to rain, drought and snow depth, while in fall snow depth accounted for 69% of the climate indicators. Only six of the 55 climate indicators (11%) were from winter climate indicators with late winter snow depth only entering the equations once.

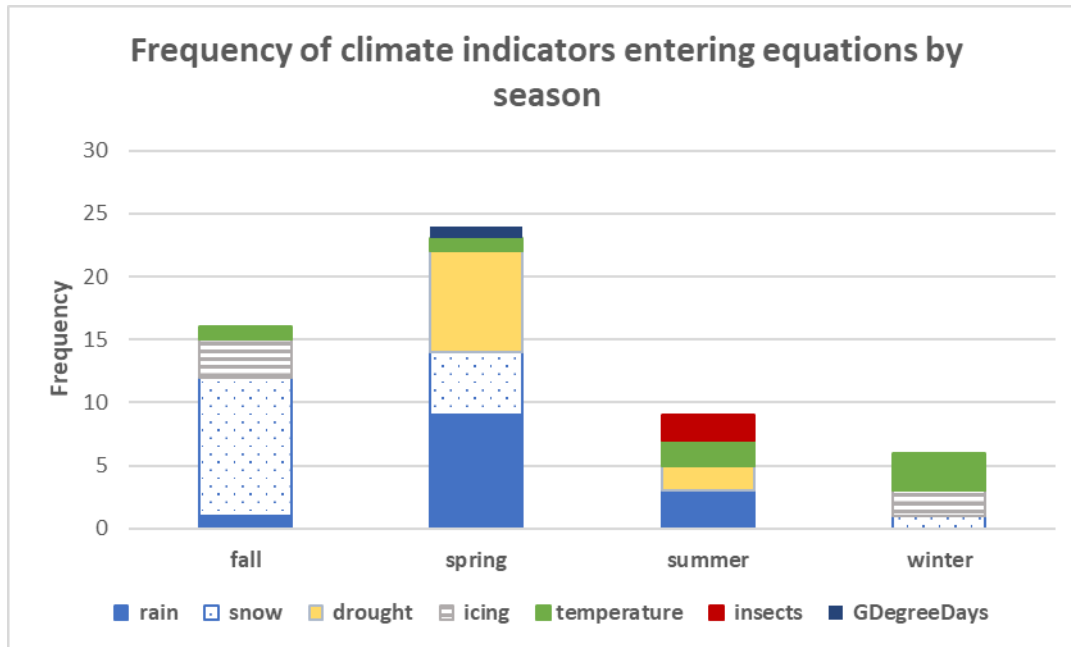


Figure 20. Frequency of seasonal climate indicators that predict vital rates for North American migratory tundra caribou herds.

Spring is an energetically stressful time for caribou. We suggest that winter conditions may result in caribou entering spring in poor condition but that, for the dataset we have, spring conditions were ultimately linked to the vital rates. We suggest a similar functional response occurs between summer and fall; conditions that result in below average cow body condition heading into fall can result in lower pregnancy rate and early embryonic loss but from our data it is fall (October-November) snow depth that is the ultimate link to the following spring parturition.

Thus, the importance of climatic conditions in summer and winter are probably underestimated in our regression equations as it is the dynamics and variability in spring and fall that ultimately dictate vital rates. Spring is the period of 1) low post-winter reserves, 2) migration energetics, 3) timing of green-up, 3) birth, 4) milk production, 5) calf viability. Similarly, cows entering fall after poor summer conditions must “decide” to 1) wean calf early, 2) wean normally during rut, 3) extend lactation into winter, 4) ovulate, 5) resorb embryo early.

Furthermore, climate variability in fall and spring is higher than winter and summer. Snow depth in fall had a coefficient of variation of 25% compared to 16% in winter and 47% in spring. Icing conditions in fall had a coefficient of variation of 55% compared to 42% in winter. Among all herds, May rain had an average coefficient of variation of 102% compared to 32% in July and August.

Parturition rate: The number of calves that are born in the spring, parturition rate, is governed by two factors: the pregnancy rate in the fall and embryonic loss *in utero*. The

probability of a female caribou becoming pregnant in the fall has been examined for a number of herds (Bergerud 2008, Cameron and Ver Hoef 1994, Thomas 1982, Russell et al. 2002, Adams and Dale 1998). In these studies, probability of pregnancy was related to body weight, body fat and body reserve index. In general probability of pregnancy follows a logistic curve with a rapid change in probability associated with moderate body weights.

Although the conception versus body mass/condition curve represents a probability for each individual in age categories, the curve can represent the population of the herd and the shape of the curve can characterize the herd. There are few data on embryonic loss in caribou. With respect to early embryonic loss, Russell et al. (1998) concluded that females with low body reserves appear to have an increased probability of terminating pregnancy shortly after breeding based on hormone assays but this has not been described for other herds. Lactation status also directly affected probability of embryonic mortality: only lactating caribou demonstrated early embryonic mortalities. Because lactating Arctic caribou continue to invest heavily in their current calf during early winter (Russell and White 2000), embryonic mortality may represent a trade-off between investment in the current calf and future offspring among females that have too few body reserves to support both further lactation and costs of pregnancy. Females could conceive a calf in October, yet "reevaluate" in November and either wean the current calf and maintain the pregnancy or allocate nutrients preferentially into either the growth and survival of their current calf (extending lactation) or into their own survival (both resorbing the fetus and weaning the current calf). The "decision" might vary according to nutrient availability during late autumn and early winter.

In our analysis, the most frequent climate indicator was October/November snow depth as a predictor of spring parturition rate (CAH, PCH, BAH). The strength of that relationship extended to June calf survival (CAH), June calves:100 cow (TCH, CAH, PCH), and spring recruitment (TCH, BAH). The deeper fall snow, the lower the parturition (Figure 21). In Figure 21 we directly plotted October snow depth regardless of the region as there was very little variability in average October snow depth across North America (Figure 3). We would suggest that the fall snow depth may be the trigger to terminate pregnancy in several North American herds while acknowledging that biologists have not sought evidence for this impact.

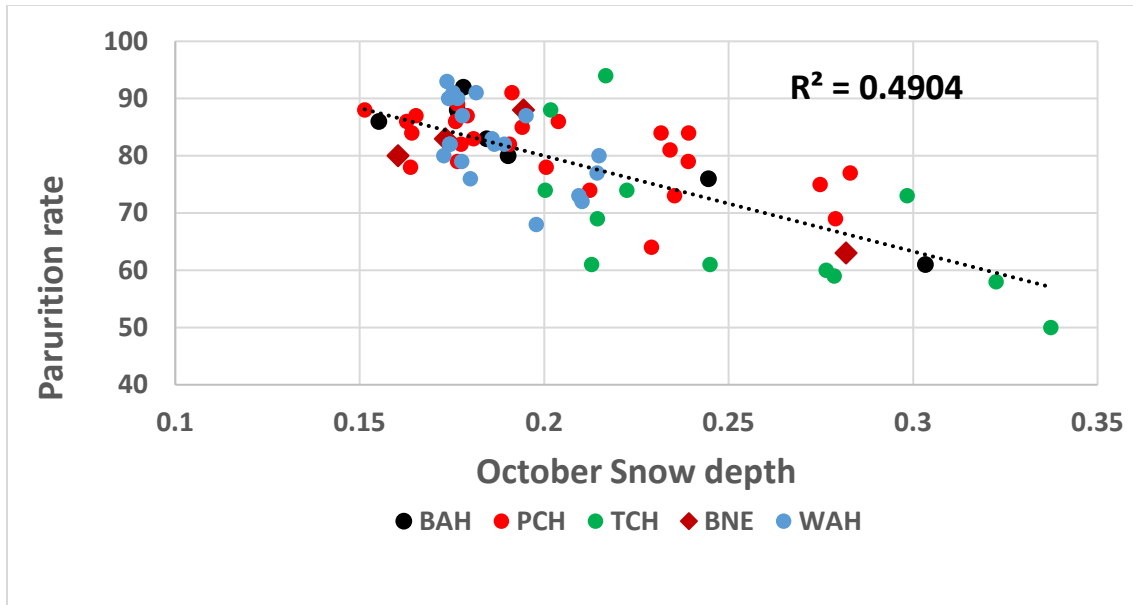


Figure 21. Relationship between October snow depth and spring parturition rate among North American migratory tundra caribou herds.

For October snow depth to be the trigger to terminate pregnancy, to be a successful evolutionary strategy, then October or November snow depth must be a reliable index of overall winter severity. Using the climate database, we ran a cross correlation among winter snow depths. Both October and November were a good predictor of overall average winter snow depth (49% and 56% respectively; n=195; Table 11).

Table 11 Cross correlation table (Pearson r) between fall snow depth (October and November) to average January to April snow depths.

	<i>Oct-SnD</i>	<i>Nov-SnD</i>	<i>Jan-SnD</i>	<i>Feb-SnD</i>	<i>Mar-SnD</i>	<i>Apr-SnD</i>	<i>average</i>
Oct-SnD	1						
Nov-SnD	0.78	1					
Jan-SnD	0.49	0.64	1				
Feb-SnD	0.49	0.60	0.91	1			
Mar-SnD	0.50	0.53	0.81	0.91	1		
Apr-SnD	0.33	0.34	0.64	0.70	0.79	1	
average SnDp	0.49	0.56	0.90	0.95	0.96	0.87	1

Early Calf Mortality to Fall Calf:Cow Ratio

In our analysis, early calf survival was annually measured in four herds (WAH, TLH, CAH, and PCH) and related to spring climate conditions except for the CAH (Figure 8). In the CAH, early calf survival was related to parturition rate, suggesting that calves from years with high parturition rates were more viable or conversely calves in years of low parturition rates, were more vulnerable to die in the first month of life. For the WAH, TLH and PCH, there was no relationship between parturition rate and June calf survival, suggesting that the climate

conditions in late spring, early summer were more important. Among those three herds, June calf survival in the WAH and TCH was negatively impacted by abundant rain (May in WAH and June in the TCH). In contrast, June calf survival in the PCH benefitted by rain. Although rain *per se* didn't enter climate/vital rate model, May snow depth and June drought did (both negatively) and both are inversely related to rainfall.

Spring Recruitment

The number of calves per 100 cows, counted during spring composition surveys, integrate climatic conditions from parturition in June. Clearly spring recruitment is related to how many are born (parturition) the previous year, how many survive their first month (June calf:cow) and how many enter winter (fall calf:cow). However only in the BAH was parturition a significant predictor of spring recruitment.

Proportional Breakdown by Region

Figure 22 depicts a seasonal proportional breakdown of climate indicators by region while Figure 23 represents the type of climate indicator by region. In the eastern herds (LRH and GRH) spring (57%) and summer (29%) were most represented in the climate independent variables. In the central herds (BAH, BNE) fall conditions dominated (44%) followed by spring (33%) while in the west (WAH, TCH, CAH, PCH) spring dominated (40%) followed by fall (31%).

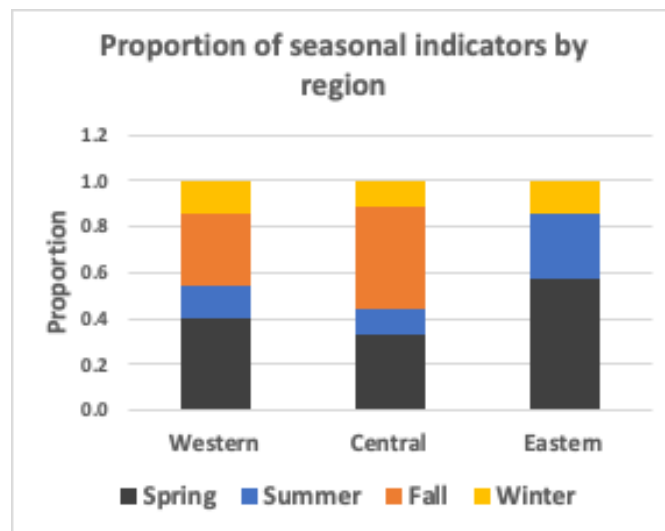


Figure 22. The proportion of climate role in predicting vital rates for western, central and eastern herds across North America.

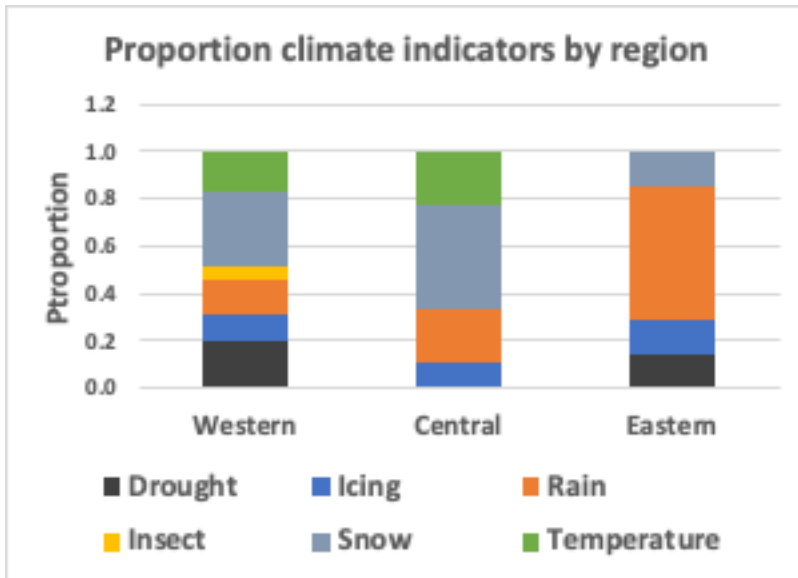


Figure 23. The proportion of climate indicators in predicting vital rates for western, central and eastern herds across North America.

From Figure 3, the GRH and LRH stand out (along with the WAH) in abundance of rain. Too much rain predominated in climate independent variables. In all eight instances, rain had a negative impact on vital rates. In six of seven instances where rain entered regression equations from the BAH to the CAH, the relationship was positive, the greater the rain the higher the vital rate. In the TCH and the WAH there was a mix of positive and negative relationships where rain was involved. It is understandable that in drier home ranges, spring rain is important for early flush of nutritious green vegetation. As well in regions of drier May and June conditions, rainfall are predictors of fall mushroom crop (Krebs et al. 2008). Conversely if May rainfall is excessive, especially in a cool climate, calves may suffer thermal heat loss (Hart et al. 1961) and negatively affect perinatal survival and June calf survival.

Snow depth entered vital rate equations 12 times with seven of those in fall, as discussed above with respect to parturition rate. Thus, only on five other occasions did snowfall appear and four of those in spring where three of four had a positive impact on a variety of vital rates. On no occasion did winter snow depth predict vital rates within those herds with the deepest snow (GRH, LRH and WAH). Winter snow negatively impacted June calves:100 cows in the PCH.

Climate Trends and Herd Vulnerabilities

Table 12 lists all climate indicators that entered the equations and identifies which have significant trends for three time periods: 1980-2020, 1980-2000 and 2001-2020. Further, we identify the direction of the trend (+ or -) and whether those trends will have a predictive positive or negative impact on vital rates. Of 28 occurrences of climate indicators exhibiting trends, 17 (64%) were predicted to have a negative impact on vital rates. Impacts varied by

herd. For example, in the PCH, all four climate indicators that trended were predicted to have a positive impact on PCH vital rates, followed by the TCH: three of six (50% positive impact). Of the remaining herds 88% of trending climate indicators had a negative impact on vital rates. We realize that not all vital rates have similar impacts on population productivity. Adult cow survival and recruitment are the two key vital rates that directly link to herd productivity. For adult cow survival, four of the eight herds were negatively impacted by trends in climate indicators (CAH, GRH, LRH, TCH), three herds had no predictive climate indicators that trended (PCH, WAH, BNE) while only the BAH herd had a trending climate indicator that had a positive impact on cow survival. Only six herds measured recruitment (CAH and GRH did not) and three had trending indicators that had a positive impact (PCH, TCH, and WAH) while three herds had trending indicators that had a negative impact (BAH, BNE, GRH).

Table 12. Trends in climate indicators that entered regressions among vital rates for seven North American migratory tundra caribou herds. Bold entries, under Vital rate column, represent vital rates where a trend in one of the independent climate variables was measured. Vital rate in **red** indicates a negative impact while black indicates a positive impact. Climate indicators in bold in the remaining columns were those where a statistical trend was measured (**red** – negative trend; **black** - positive trend). Trends were measured from “1” 1980-2020; “2” 1980-2000 or “3” 2001-2020. Trend analysis from Russell et al. (in prep).

HERD	Vital rate	1st	Trend	2nd	Trend
BAH	Cow survival	SpOctTmp		JunRain	1
BAH	Parurition	OctSnDp			
BAH	fall calf:cow	MarTmp			
BAH	spring calf cow	OctSnDp		FlFzThaw	1,2
BNE	Cow survival	JnSnDp			
BNE	Parurition	MaySnDp			
BNE	spring calf cow	JulRain	2		
CAH	Cow survival	JunDrt		FRoS	1
CAH	Parurition	NovSnDp			
CAH	June calf survival	NovSnDp		SepRain	1
CAH	june calf:cow	NovSnDp		MosqJy15	2
CAH	fall calf:cow	MaySnDp	1,2,3		
GRH	Cow survival	W FzRain2y	2		
GRH	Parurition	JunRain	2,3*		
GRH	fall calf:cow	JulRain	1	MaySnD	
LRH	Cow survival	MayDrt	2		
LRH	fall calf:cow	JulRain	2	MayRain	
PCH	Cow survival	WFrRain		WFzTw	
PCH	Parurition	OctSnD		AugDrt	
PCH	June calf survival	MaySnDp	1,2,3	JunDrt	3
PCH	june calf:cow	Wint SnDp		JunRain	2
PCH	spring calf cow	JunDrt	3		
TCH	spring calf cow	MayTmp	1,2,3	NovSnDp	3
TCH	Cow survival	FFzRain	3	MarTmp	
TCH	Parurition	MayRain	1,2,3	MosqJy15	
TCH	June calf survival	JnRain	3		
TCH	june calf:cow	NovSnD	3	JunDrt	
TCH	fall calf:cow	MayDrt			
TCH	JnFI surv	AugTmp			
WAH	Cow survival	JanTmp		MayRain	
WAH	Parurition	MayRain	1,2,3		
WAH	June calf survival	MayDrt		JulTmp	3
WAH	june calf:cow	Jun10gdd	1,3	MayRain	1,2,3
WAH	fall calf:cow	Aug31OES	1		
WAH	spring calf cow	AugTmp		SepSnD	1,2

Management Implications

Monitoring populations for their productivity involves monitoring population size and home ranges, determination of density and vital rates including conception, birth rates and cohort survival to project the intrinsic growth rate (Gaillard et al. 1998). Linking population models with data for management decisions (Nagy-Reis et al. 2021) and linking vital rates with environmental drivers to account for underlying functions of fecundity and survival is a bigger challenge because responses in population sizes are driven by individuals whose responses reflect acclimation and adaptation to influential environmental factors that may be indirectly influencing mortality and natality and thus not directly to population characteristics such as population density, migration and male-female ratios. During recent population declines in most migratory tundra caribou herds, managers are turning to computer modeling to help integrate their monitoring efforts for clues into what is driving these herds and gain insights into probable herd trends in the short term. Anticipating future declines will enable managers to better make management recommendations to reduce the probability of population declines. Thus, knowledge of the interrelationships among vital rates and the role of climate will improve model projections can aid in herd management.

We contend that the ability of caribou to buffer adverse conditions is not limitless, thus depending on the herd and the environment they evolved in, there exist bottlenecks that directly impact one or more vital rates. Further that these bottlenecks are typically unique to each herd depending on the landscape in which they evolved. Linkages between vital rates and climate are complicated by the interrelationships among vital rates. For example, a bad insect year may have a larger impact on cow survival in a year with high parturition rates and high June calf survival compared to a year with fewer calves and thus with fewer lactating cows entering the summer population.

PERSONAL COMMUNICATIONS

Jan Adamczewski, Department of Environment of Natural Resources, Government of the Northwest Territories, June 2018

Joelle Taillon, Quebec Ministère des Forêts, de la Faune et des Parcs, June 2018

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APPENDIX A. HERD VITAL RATES

Vital rate data for the WAH.

Year	Cow survival	Parturition	June calf survival	June calf:100cows	Fall calves:100cows	Spring calves:100cows
1980					53	
1981						
1982					59	29
1983						32
1984						31
1985						22
1986						23
1987		98				23
1988	91	99	82	81		22
1989	85	97	80	78		32
1990	85	92	78	72		24
1991	85					19
1992	85	100	86	86	52	22
1993	80	73	73	53		19
1994	84	99	72	71		19
1995	87	80	74	59	52	17
1996	82	82	74	61	49	22
1997	85	77	75	58	43	26
1998	92	73	73	53	45	21
1999	83	83	70	58	47	15
2000	78	93	74	69		18
2001	82	82	80	66	37	19
2002	85	87	90	78		15
2003	81	90	76	68		19
2004	86	76	78	59	35	23
2005	78	89	78	69		12
2006	71	87	75	65	40	20
2007	84	91	80	73		25
2008	69	90	78	70	48	11
2009	77	91	87	79		14
2010	72	80	91	73	35	15
2011	80	82	94	77		9
2012	67	68	91	62	38	13
2013	80	79	80	63		17
2014	85	72	96	69	42	14
2015	83	82	95	78		13
2016						
2017						
2018						
2019						
2020						

Vital rate data for the TLH.

Year	Cow survival	Parturition	June calf survival	June calves:100cows	Fall calves:100cows	Spring calves:100cows
1990						27
1991	85					31
1992	86					35
1993	87					22
1994	87				37	16
1995	83				36	18
1996	87					32
1997	76					33
1998	86				25	
1999	92			67		27
2000	86			85	13	25
2001	89			44	26	17
2002	83	94	76	71	6	10
2003	89	94	69	65	22	26
2004	75	58	83	48	32	22
2005	83	73	77	56	23	9
2006	91	88	93	82	16	20
2007	92	69	87	60		23
2008	82	74	91	67		19
2009	87	50	80	40	18	14
2010	85	74	64	47	29	15
2011	81	59	69	41		13
2012	88	60	70	42	35	
2013	68	61	72	44	34	13
2014	72	28	57	16		15
2015						
2016						
2017						
2018						
2019		61				
2020						

Vital rate data for the CAH.

Year	Cow survival	Parturition	June calf survival	June calves:100cows	Fall calves:100cows
1993					
1994				64	
1995				63	
1996				69	
1997		61		75	
1998	96	88	90	79	
1999	96	93	86	80	
2000	87	96	78	75	
2001	82	91	87	79	
2002	94	92	88	81	
2003	86	96	80	77	
2004	91	91	90	82	
2005	80	83	86	71	
2006	90	96	93	89	
2007	93	93	87	81	
2008	89	98	93	91	
2009	88	75	69	52	33
2010	86	97	88	85	46
2011	91	91	85	77	56
2012	83	92	75	69	61
2013	67	80	70	56	
2014	77	77	84	65	42
2015	80	87			
2016	81	95			47
2017	81	90			51
2018	87				
2019	82				
2020	94				

Vital rate data for the PCH.

Year	Cow survival	Parturition	June calf survival	June calves:100cows	Spring calves:100cows
1980					56
1981					
1982					
1983	90				
1984	92				
1985	78				
1986	89				
1987	75	78	71	55	
1988	93	84	65	55	
1989	78	78	74	58	43
1990	83	82	90	74	
1991	84	74	82	61	22
1992	82	86	57	49	30
1993		81	56	45	32
1994		91	77	70	40
1995		69	85	59	46
1996		89	81	72	38
1997		75	77	58	39
1998		83	82	68	28
1999		84	83	70	
2000	85	73	61	44	27
2001	90	84	61	51	31
2002	88	87	65	56	38
2003	88	87	79	69	33
2004	75	82			24
2005	81	64	77	49	
2006	86	79	73	58	39
2007	90	88	83	73	
2008	84	79	73	59	
2009	89	77	57	44	
2010	91	85	76	65	20
2011	88	86	48	41	
2012	87				
2013	87	86			
2014	88			49	
2015	80				
2016	89	75	61	46	
2017	94	90	80	72	
2018		88	73	64	
2019					
2020					

Vital rate data for the BNE.

year	Cow survival	Parturition	Fall calves:100cows	Spring calves:100cows
2007				
2008				48
2009			46	37
2010		61		46
2011	67			41
2012	96			27
2013	59	80	36	
2014	74			30
2015	76	63	35	21
2016	92		44	30
2017	87			
2018	76	83	26	38
2019	85	88	38	
2020	85			42

Vital rate data for the BAH.

year	Cow survival	Parturition	Fall calves:100cows	Spring calves:100cows
1980				
1981				
1982				
1983				
1984				
1985				34
1986		87		
1987				43
1988				
1989				39
1990		92		38
1991				49
1992				31
1993				49
1994				30
1995				50
1996		88		
1997	79			
1998	75			
1999	52			
2000	92		40	
2001	79		33	29
2002	50			21
2003	93	83		26
2004	58		18	22
2005	71			15
2006	76	76	40	9
2007	88		55	37
2008	74		32	50
2009	75	86		40
2010	61			49
2011	56		33	46
2012	52	80	23	25
2013	54			
2014	53		25	33
2015	82	61		24
2016	66			20
2017	85		43	
2018	76	70	21	
2019	91	86	32	
2020	95		39	30

Vital rate data for the LRH.

Year	Cow survival	Fall percent calves	Fall calves:100cows
1990			
1991			
1992			
1993	100		
1994	95	22	43
1995	87	11	21
1996	95	23	50
1997	96	20	40
1998	100	19	41
1999	95		
2000	96	18	36
2001	96	22	41
2002	68	16	31
2003	95	18	33
2004	81	11	17
2005	82	22	45
2006	100	20	34
2007	70	12	17
2008	87	21	32
2009	88	18	27
2010	92	18	30
2011	88	22	33
2012		23	37
2013		19	33
2014		9	14
2015		20	33
2016			
2017			
2018			
2019			

Vital rate data for the GRH.

Year	Cow survival	Parturition	Fall calves:100cows
1980		86	55
1981			57
1982		94	54
1983			50
1984		68	38
1985	95	86	
1986	92	60	46
1987	90	76	40
1988	84	63	32
1989	87	61	38
1990	88	59	28
1991	66	78	33
1992	73	76	26
1993	74	64	44
1994	74		38
1995	74		38
1996	68		38
1997	65		31
1998	77		36
1999	78		
2000	63		17
2001	91		44
2002	83		20
2003	58		32
2004	81		8
2005	80		53
2006	81		41
2007	83		30
2008	74		25
2009	73		35
2010	72		17
2011	71		17
2012			7
2013			10
2014			27
2015			35
2016			28
2017			
2018			
2019			

SUPPLEMENT 1

Optimizing lifetime reproductive success of the cow is basic to understanding productivity in migratory tundra caribou herds. Thus, in quantifying how vital rates dictate overall herd productivity, how vital rates interrelate and finally, how extrinsic factors such as climate impact vital rates, needs to be framed around the concept of lifetime reproductive success. Specific strategies include dynamics of weaning, the functional response between fitness and probability of getting pregnant, and periodic breeding pauses.

Once calves are born their survival is largely dependent on their mother's condition, the timing of nutrient forage growth, predators and the condition of the calf at birth. Maternal reserves during winter are important to the final development of the fetus, that under extreme conditions can result in birth of underdeveloped calves that cannot stand to nurse (Roffe 1993) and constitutes a measure of neonatal weaning. Birth mass, milk production and calf growth in the first three weeks postpartum are all influenced by maternal mass and body reserves at and immediately following calving.

Between four and eight weeks post-partum maintenance requirement of the calf are met by forage intake whereas calf growth is directly dependent on milk intake. Thus, the nutritional status of summer habitat directly influences the calf maintenance requirements, maternal milk production, and thereby calf growth rate. Also, maternal regain of body reserves of the lactating female is dependent on summer nutrition and thus her likelihood of conception.

Thus, early calf survival is critically linked to milk supply from the mother. In the PCH females may wean calves at five different times following pregnancy (Figure 2; Russell and White 2000). Each weaning date can potentially result in a differential pathway of maternal investment through likelihood of conception (Figure 3a).

Initial investment when terminated at or near birth (termed post-natal weaning) due to low neonate vigor and possibly underdevelopment (Roffe 1993) can result in body condition regain and increase conception likelihood. Termination of investment by weaning the juvenile due to poor summer protein availability and low gain in female body protein (termed summer weaning) can result in a variable increase in body reserves and increased conception. Later in summer weaning occurs pre-rut if the female does not make sufficient body fat gain in mid to late summer (termed early weaning) that has been attributable to insect harassment and/or dry conditions and shortened plant phenology due to drought (Gunn 2014). This strategy releases the female from lactational infertility (Gerhart et al. 1997) that can increase conception likelihood. Of these three weaning strategies this is the first for which investment in the offspring is potentially successful because calf mortality occurs for the post-natal and summer weaning strategies (Russell et al. 1991). During the normal breeding period, most offspring are weaned (termed normal weaning). However, not all offspring are weaned before or during the breeding season, maternal investment can

continue through extended lactation for females in good body condition but with calves that are low in body fat, with a possible weaning date in spring (Russell and White 2000). At weaning, such calves are large, but the cost to the female can be high. The nutritional cost of overwinter lactation results in low fat and protein reserves (Gerhart et al. 1996) and increased likelihood of mortality depending on winter conditions, at least in the PCH. An exception is for caribou in Greenland where extended lactation and moderate winter body condition occurs commonly (Cuyler et al. 2012) in this predator-free system.

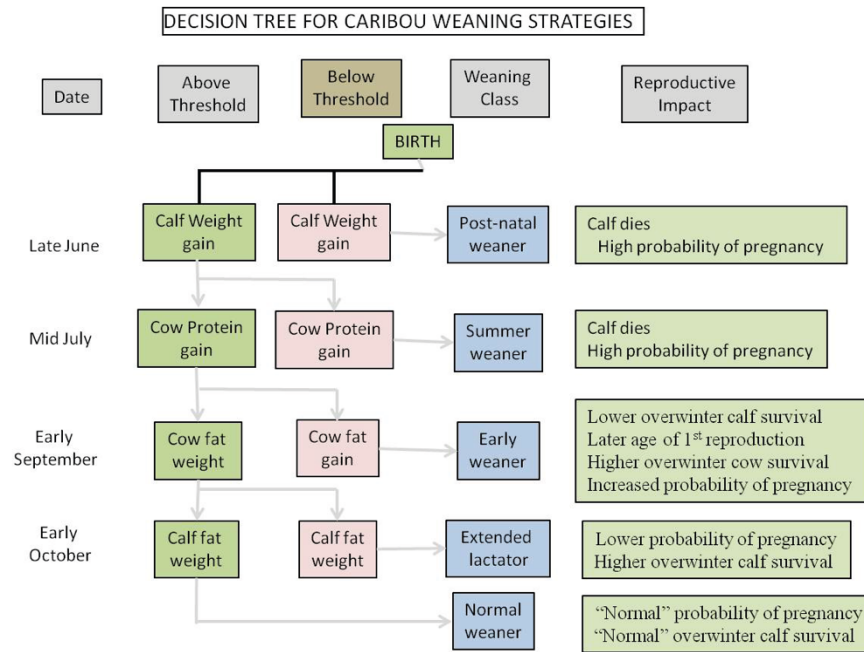


Figure 24. Steps in the weaning strategy of cows in the PCH. Figure developed from Russell and White (2000).

Thus, each weaning decision is influenced by body condition of the female at that time and the termination of investment influences body mass and body condition at the rut (breeding), and therefore it influences the individual's probability of conception (Figure 25a). Although body fat level has a stronger influence over probability of conception than body mass, and therefore of body protein, both are influential. Thus, the status of mobilizable reserves of body fat and body protein at and following breeding influence conception rate. Likewise, the level of mobilizable reserves is a potential determinant of mortality given adverse winter conditions. Determination of the relative numbers of females that adopt each weaning pathway, and its probability of conception then determines the herd conception rate; the first step in assessing herd fecundity.

Although the conception versus body mass/condition curve (Figure 25a) represents a probability for each individual in age categories, the summation curve can represent the population of the herd and the shape of the curve can characterize the population. The steepness of the summated relation between conception/pregnancy and body mass/body

condition gives a measure of productivity and resilience (Figure 25a, Russell et al. 2014). Steepness of the slope provides a measure of both productivity and resilience. The body fat/mass at which probability of conception is 0.5 gives a measure of productivity, whereas the steepness of slope gives a measure of resilience (Russell et al. 2014) and with a potential multiplicative effect (White 1983) on the population. The steeper the slope the less resilient, and the more regulated is the incidence of pregnancy based on body condition. However, a shallow slope allows for variability in pregnancy based on body fat/mass and provides a feedback of body condition on pregnancy. Caribou populations of Arctic North America show wide variation in productivity and resilience (Figure 25b). Because the population curve is the summation of individuals representing weaning pathways the relative contributions determine the herd's productivity-resilience characteristics.

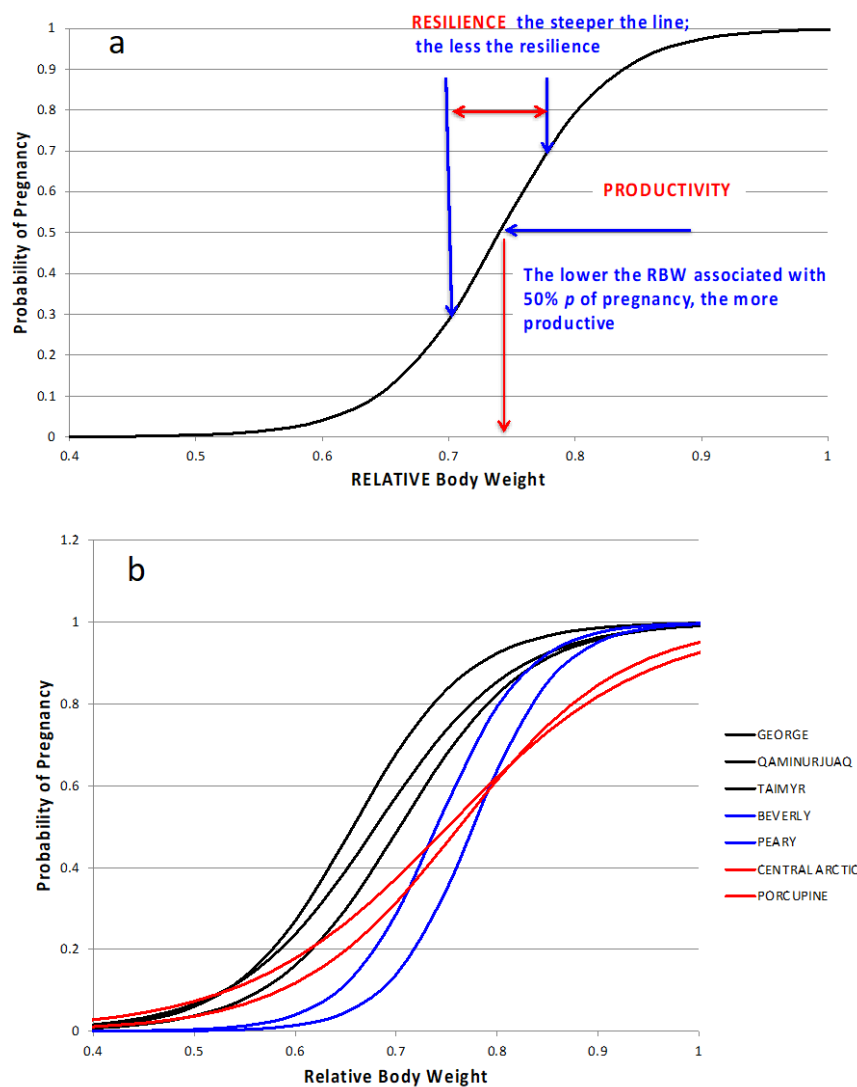


Figure 25. Logistic relationships derived from pregnancy status in relation to Relative Body Weight (RBW) among Arctic caribou populations.

A further reproductive loss can occur during and following the breeding season when shed eggs (ovules) or developing fetuses can be resorbed or shed possibly in response to adverse weather (snow, rain-on-snow) that directly affects implantation and retention or is influential due to lack of access of food (Russell et al. 1998). Accounting for this reproductive loss gives a more definitive measure of fecundity.

Maternal reserves during winter are important to the final development of the fetus, that under extreme conditions can result in birth of underdeveloped calves that cannot stand to nurse (Roffe 1993) and constitutes a measure of neonatal weaning. Birth mass, milk production and calf growth in the first three weeks postpartum are all influenced by maternal mass and body reserves at and immediately following calving. Within migratory caribou herds across Arctic North America body mass varies between 72 to 117 kg (Russell et al. 2014, unpublished observations) that has implications for both productivity and resilience (Figure 25b) and Arctic caribou appear subject to breeding pauses (Cameron 1994; Adams and Dale 1998).