ANALYSIS OF ENVIRONMENTAL, TEMPORAL AND SPATIAL FACTORS AFFECTING DEMOGRAPHY OF THE BATHURST AND BLUENOSE-EAST CARIBOU HERDS

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2024

MANUSCRIPT NUMBER 309

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Government of
Northwest Territories

ABSTRACT

One of the main conservation concerns for the Bathurst and Bluenose-East caribou herds between 2012 and 2015 were lower survival and productivity rates and rapid declines in both herds. Environmental variables may be contributing to the declines. The work described here was carried out to better understand environmental, temporal and spatial variables that may be affecting these herds and their ranges. An integrated population demographic model was used to explore associations between key demographic indicators cow survival rate, the proportion of breeding cows, and calf survival rate and environmental covariates. In addition, the locations of collared cow mortalities were compared to locations of live collared caribou to assess temporal and spatial trends. Environmental covariates included temperature, moisture, snow cover measures and a series of variables on the spring, summer and fall ranges, and combinations of variables from remote sensing and weather station data compiled by the Circum Arctic Rangifer Monitoring and Assessment Network (CARMA) as well as Pacific Decadal and Arctic Oscillation data. Analyses were conducted for the Bluenose-East herd (2008-2016) and Bathurst herd (1985-2016), which included updating these models with field measurements.

Analysis of the environmental covariates revealed correlations between many of the variables and directional trends in some. Results from the demographic model analysis suggested multiple associations of environmental covariates with demographic parameters. Most notable were positive associations between March snow-depth and adult female survival for both the Bathurst and Bluenose-East herds. In addition, the oesterid index in summer and the Pacific Decadal Oscillation were negatively associated with the proportions of females breeding in both herds. Linkages with calf survival were not as strong with none of the covariates explaining the directional trends observed in calf survival. The mushroom index was positively related and the oesterid index negatively related to calf survival in Bathurst caribou if underlying directional trends were modelled in unison with the covariates. Overall, the results demonstrated different associations for adult female pregnancy rates, calf survival, and adult survival with final models containing multiple covariates for each demographic parameter. These results demonstrate the utility of using a demographic model to explore associations with environmental variables but also demonstrate the complexity of these associations. The associations suggested in this analysis can be applied to further understand potential causes for population declines as well as refine forecasts of herd recovery.

The spatial survival analysis was conducted for the Bathurst herd cow radio collar data (1996-2016). Data screening revealed large differences in distribution of caribou in earlier (1996-2009) and later periods (2010-2016), which was potentially due to reduced population size and associated range contraction, and possible effects of recent fires on winter range areas. Mortality hotspots have shifted from a more dispersed pattern in 1996-2009 to primarily summer range areas in 2010-2016, with lower mortality on winter range areas. The summer mortalities may reflect predation by wolves and bears. Calving ranges had consistently low cow mortality rates in both periods, confirming the value of calving in remote areas removed from most predator concentrations.

Survival rates varied by season, eco-region, select northern land-cover variable, as well as with distance from roads. In addition, a linkage of temporal variation in survival rates with March 31 snow-depth was suggested. A preliminary analysis of the Bluenose-East collar data revealed a more even pattern of mortality across season (in comparison to the Bathurst herd) with a more diffuse spatial pattern of mortalities. Further refinement of a spatial mortality model is recommended including the use of updated land-cover data and more exact spatial and temporal covariates.

We note the demographic model used in this report has been updated to a Bayesian Integrated Population Model (Schaub and Kery 2022). We suggest readers review calving ground surveys for the Bathurst and Bluenose-East herds (Adamczewski et al. 2022, Boulanger et al. 2022) that contain more recent demographic analyses.

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INTRODUCTION

The main conservation concerns for the Bathurst and Bluenose-East caribou herds between 2012 and 2015 were lower survival and productivity rates and rapid declines in both herds. Most notably, demographic analyses suggested that adult female survival rates are lower in these herds than would be needed to allow population recovery and that the reduced rates cannot be explained entirely by hunting pressure (Boulanger et al. 2016, Boulanger et al. 2017). In addition, relatively low proportions of females breeding were observed on the 2015 Bluenose-East and Bathurst calving ground surveys, suggesting that environmental factors like summer drought conditions could be influencing herd demography. One possible mechanism for this would be poor summer feeding conditions and high insect harassment, resulting in cows in poor condition in the fall and a reduced pregnancy rate.

One of the challenges of researching demographic factors that influence caribou populations is the indirect nature of field demographic measurement that make it difficult to assess the mechanisms that cause variation in demographic parameters (Boulanger et al. 2011). For example, calf-cow ratios from composition surveys will be influenced by calf survival, pregnancy rates of adult females, as well as survival rates of adult females. A lower late-winter calf cow ratio in a given year could be due to low calf survival, low pregnancy rates, or both. However, pregnancy rate is determined in the year before a calf is born whereas calf survival is determined in the first year of the calf's life. Therefore, inference to determine associations between environmental factors and demography based on calf cow ratios alone can be problematic.

Another challenge with caribou demographic research is the relatively small sample size of collared caribou relative to herd size, which results in imprecise survival rates and reduced power to detect changes in survival rate and associate variation in survival rate with environmental factors. For example, the Bathurst herd declined significantly from 1985-2009, however, assessment of collar-based survival rates did not detect a change in adult female survival rate over this time period. A change in cow survival was detected when collar survival rates were combined in an integrated population model (Boulanger et al 2011). In this case, information from herd population surveys and composition surveys was used in unison with collar data to increase power to detect changes in survival rates.

To partially confront the various challenges, we modified the integrated population demographic model used in previous demographic analyses (Boulanger et al. 2011, Boulanger et al. 2016, Boulanger et al. 2017) to include assessing the influence of environmental covariates on the main demographic parameters of interest. This approach allowed separate testing of factors influencing cow survival, calf survival, and the proportion of females breeding each year. Previous analyses had used simple polynomial models to model demographic trends which provided estimates as well as assessment of change but did not provide any inference on actual mechanisms causing change. We note the demographic model used in this report has been updated to a Bayesian Integrated Population Model (Schaub and Kery 2022). We suggest readers review calving ground surveys for the Bathurst and Bluenose-East herds (Adamczewski et al. 2022, Boulanger et al. 2022) that contain more recent demographic analyses.

In addition to the demographic model analysis, collared cow survival data was scrutinized further to assess spatial and temporal factors that might influence collar survival rates. The basic premise behind this analysis was that additional information about factors influencing survival is available by assessing the geographic location patterns of mortalities relative to areas that caribou utilized as reflected by live collared caribou locations. This approach, which has been used for grizzly bears (Nielsen et al. 2004), uses a habitat selection approach where selection is replaced by mortality risk. The rationale in this case is that while collar data are imprecise estimators of cow survival rates, they still will contain useful information through a model-based assessment of individual variation in mortality risk.

METHODS

Environmental Covariates

Environmental covariates compiled by the Circum Arctic Rangifer Monitoring and Assessment Network (CARMA) were supplied by Don Russell (Yukon College, Whitehorse, Yukon; see (Russell et al. 2013)). Covariates corresponded to seasons and corresponding seasonal ranges of the Bluenose-East and Bathurst herds. In addition, Pacific Decadal Oscillation data were downloaded from the Joint Institute for the Study of the Atmosphere and Ocean at the University of Washington (Seattle: http://research.jisao.washington.edu/pdo/) and Arctic Oscillation data were downloaded from the National Ocean and Atmospheric (NOAA) climate prediction center (www.cpc.ncep.noaa.gov/products/precip/CWlink/daily_ao_index/ao.shtml). The Bathurst summer range cumulative indicator (Chen et al. 2014) was considered, however, it was only available up to 2011 and therefore could not be used in the full analysis. Climate data used for the Bathurst herd were for 1985-2016 and the Bluenose-East herd for 2008-2016. Each of the climate variables is listed in Table 1.

Table 1. Climate covariates considered in the demographic analysis.

Covariate	Description	Season
Mar31 sn	March 31 snow depth (m)	Winter
May 15 sn	May 15 snow depth (m)	Spring
Jun10sn	June10 snow depth (m)	Calving
Jun 10 gdd	June 10 growing degree days	Calving
Jun20 gdd	June 20 growing degree days	Summer
Jul20 gdd	July 20 growing degree days	Summer
aug5 oes	August 5 cumulative oestrid index	Summer
Tmp May	Average daily mean temperature-May	Spring
Tmp June	Average daily mean temperature-June	Calving
Tmp July	Average daily mean temperature -July	Summer
Drought Jn	Average daily drought index - June	Summer
Drought Jy	Average daily drought index - July	Summer
FZThaw	Average # days with freeze thaw event (Sept - May)	Spring
RoS	Average cumulative Rain-on-Snow (Sept - May)	Winter
RoS #day	Average # days Rain-on-Snow (Sept - May)	Winter
FzRain	Average cumulative freezing rain (Sept - May)	Winter
FzRn #day	Average# days Freezing rain (Sept - May)	Winter
Mushroom index	Mushroom index (Krebs et al. 2008)	Spring/summer
PDO	Pacific Decadal Oscillation	Caribou-year
AO	Arctic oscillation	Caribou-year
SRCI	Summer range cumulative indicator (Chen et al. 2014)	Summer

The climate data were organized in the context of a "caribou year" which is the yearly unit used for demographic analysis. The caribou year begins in the calving season in June and extends through the summer and fall of a given year and into the winter and spring of the following year. Of most interest will be the relationships between climate covariates and demographic indicators within each caribou year. Indicators for the calving, summer, and fall seasons of a given year were compared to indicators for the winter and spring of the following year. The covariates were also organized this way for the demographic analysis. Another potential issue with covariates was that they were on different scales which complicates comparison of covariates and can introduce issues with correlation analysis. To confront this issue all covariates were standardized by subtracting the mean value of the covariate from each observation (x_i) and dividing by the standard deviation of observations of the covariate ($x_i' = (x_i - \overline{x})/SD(x)$). Climate data were initially analyzed to determine correlations between indicators as well as to assess differences between indicators for the Bathurst and Bluenose-East herds.

Integrated Population Model Demographic Analysis

Survival Analysis

Collar data for female caribou for June 1996-December 2016 (Bathurst herd) and June 2008-December 2016 (Bluenose-East herd) were compiled by J. Williams (GNWT ENR, from the Wildlife Information Management System, WMIS). Mortality was assigned to collared caribou that became stationary, excluding cases of collar failure or device drop-off. The data were then summarized by month as live or dead caribou. Data were grouped by "caribou year" that began during calving of each year (June) and ended during the spring migration (May). A Kaplan-Meir estimator (Pollock et al. 1989) was used for estimates used in the ordinary least squares (OLS) model demographic analysis.

Demographic Model Analyses

The OLS model developed for the Bathurst herd (Boulanger et al. 2011) was used for integrated population analyses. The OLS model is a stage-based model that divides caribou into three age-classes with survival rates determining the proportion of each age class that makes it into the next age class (Figure 1). The OLS model basically generates predictions of herd trend as well as field measurements (calf-cow ratios, collar-based survival rates, bull-cow ratios, proportions of females breeding, and breeding female estimates) based upon likely levels of demographic parameters (survival rates and birth rates). The fit of the model to the data is evaluated using a penalty system; the lowest penalty terms identify the best models. An optimizer is then used to estimate the most likely demographic parameters that best fit the observed field data. The details of this model are given in Boulanger et al. (2011).

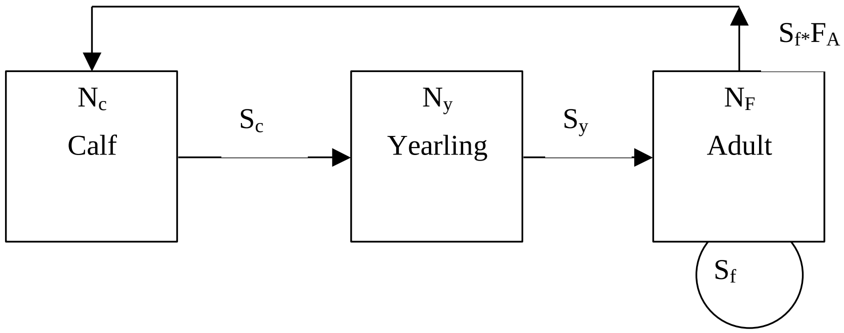

Figure 1. Underlying stage matrix life history diagram for the OLS caribou demographic model. This diagram pertains to the female segment of the population. Nodes are population sizes of calves (N_c), yearlings (N_y), and adult females (N_F). Each node is connected by survival rates of calves (S_c), yearlings (S_y) and adult females (S_f). Adult females reproduce dependent on fecundity (F_A) and whether a pregnant female survives to produce a calf (S_f). The male life history diagram is similar with no reproductive nodes.

The OLS model used for the Bathurst was based on the original version of the model which used data from 1985-2009 (Boulanger et al. 2011) and recent modeling iterations which mainly used data from 2008-2015 (Boulanger et al. 2014b, Boulanger et al. 2017). In addition, a spring calf-cow ratio estimate from 2016 was added as a field data observation. The OLS model for the Bluenose-East herd was based on previous modeling efforts for this herd (Boulanger et al. 2014a, Boulanger et al. 2016), with addition of composition surveys from the spring and fall of 2016. Assumed harvest levels were used for the analysis based on previous harvest studies for the Bathurst herd (Adamczewski et al. 2009, Boulanger et al. 2011) and reported harvest for the Bluenose-East herd (Boulanger et al 2016) to allow inference about natural survival rates which would be most likely affected by environmental variables. Harvest was assumed to be independent and additive to other mortality as developed in the original OLS model analysis with deer (White and Lubow 2002).

Exploration of factors influencing demographic parameters was challenging given the likelihood that more than one environmental factor was influencing each demographic parameter. Therefore, a sequential approach was used, as detailed below.

1. A base OLS model was initially formulated to describe longer-term directional trends in demographic parameters and associated field measurements. This model was based on linear or polynomial terms with the general objective of modelling the longer-term trends in demographic parameters.
2. Once this base model was formulated, environmental variables were individually tested as covariates to describe variation in cow survival, calf survival, and the proportion of females breeding. The support of the environmental covariate relative to the base model and its relative effect on the demographic parameter, as indexed by the slope term, was assessed.
3. Using the results from Step 2, a list of supported environmental covariates was built for each demographic parameter. The top environmental covariates were then used

to build multiple covariate models for each demographic parameter. Correlations between covariates were considered further at this step with the goal of using non-correlated covariates for each demographic parameter in the final model.

4. The top covariate models from Step 3 for each individual demographic parameter were then combined to derive an overall demographic model with environmental covariates for all parameters. This model was compared to reduced models derived in Steps 2 and 3.

Models were evaluated using the sample size-corrected Akaike Information Criterion (AIC_c) index of model fit (Burnham and Anderson 1998). The model with the lowest AIC_c score was considered the most parsimonious, thus optimizing the trade-off between bias and precision (Burnham and Anderson 1998). The difference between any given model and the most supported (ΔAIC_c) was used to evaluate the relative fit of models when their AIC_c scores were close. In general, any model with an ΔAIC_c score of ≤ 2 was considered as supported by the data.

Odds ratios were used to test the relative magnitude of the potential effect of each covariate on a given demographic parameter. The odds ratio was estimated as the exponent of the slope term for the given covariate. An odds ratio basically estimates the change in probability caused by a change of one standard deviation in the environmental covariate (since the covariate is standardized). An odds ratio of 1 indicates that there would be no change, an odds ratio of >1 indicates an increase or positive association whereas a value of <1 indicates a decrease or negative association. For example, an odds ratio estimate of 2 for an environmental covariate would indicate that a caribou would be twice as likely to survive or breed if the environmental covariate increased by a factor of one standard deviation. Conversely, an odds ratio of 0.5 would indicate that the caribou would be half as likely to survive or breed given the same change in the environmental covariate. Data were explored graphically using the *ggplot* package (Wickham 2009) in program *R* (R Development Core Team 2009).

Spatial and Temporal Collar Survival Analysis

Radio collar fate data while limited in terms of sample size at any point in time, contains information on where and when mortalities occurred. One pertinent question was whether there were some habitat types, seasons, and anthropogenic factors that might influence mortality risk and whether there were longer-term trends in how these factors influenced caribou survival. Locations of cow mortalities were plotted compared to live locations to initially assess similarities in use versus mortality patterns.

Hotspot Analyses

As an initial step, a smoothing ("hotspot") method (QGIS Foundation 2020) was used to map areas of higher use (live collar locations) or mortalities (collared cow mortality locations) for collared cows in the Bathurst and Bluenose-East herds. This approach uses a moving window approach to estimate intensity of use or mortality pressure. Conceptually this can be thought of as an estimated count of mortalities or overall use in any point on a map based on the proximity of other mortalities or collar locations as defined by a moving window radius. If mortality risk follows habitat use patterns of live collared caribou, then the same hotspot areas should occur on each map. If mortality hotspots occur in different areas, then it is likely that these areas have higher mortality risk.

Survival Analyses

The hotspot approach provided a visual aid to estimate areas of high mortality risk or use but did not provide any inference on factors influencing the mortality risk compared to use of the area. To explore this issue, monthly caribou locations were classified by geographic, seasonal, and temporal factors (Table 2). The live collar locations helped define the level of exposure of caribou to each factor and mortality locations, providing an estimate of the relative risk of each factor. This approach, which has been used previously for grizzly bears (Nielsen et al. 2004), provides a flexible approach to simultaneously consider spatial and temporal factors.

Table 2. Primary covariates used in the spatial/temporal collar survival analysis.

Covariate	Values
Period	1996-2006, 2006-2009, 2010-2016
Period2	2006-2009, 2010-2016
Caribou year	Polynomial forms to describe underlying trends
Season	Calving, Summer, Fall-rut, Winter, Spring Migration
Ecoregion	Nunavut (tundra), Southern Arctic: Tundra Plains, Taiga Plains, Taiga Shield
Northern Landcover (Olthof et al. 2009)	Deciduous, Evergreen, Herbaceous, Sparse, Lichen, Sparse Conifer, Water/ice: pooled based on previous analysis (Boulanger et al. 2012). Details are given in Appendix 2.
Distance from roads	Distance from main highways and winter ice roads (assuming they are operational for the winter season).
Distance from communities	Distance from main communities
Fire history	Years since fire occurred for each location
Environmental covariates	Most supported OLS covariates
Harvest pressure	Proportion of females harvested (from OLS model)

Logistic regression was used to model the monthly mortality risk for female caribou based upon the covariates listed in Table 2. This approach is similar to the known fate models in program MARK (White et al. 2002) and can allow both continuous and categorical predictors to build ANCOVA type models (Milliken and Johnson 2002). As with the demographic model analysis, covariates were considered individually and then combined to produce composite models. Models were compared using information theoretic methods as well as parameter significance. Model goodness of fit was also evaluated using Receiver Operating Curve scores (ROC) which provide an assessment of how well the model classifies mortalities versus non-mortality data as a function of increasing predicted scores (Fielding and Bell 1997, Boyce et al. 2002).

RESULTS

Environmental Covariates

Inspection of trends in estimates revealed that in most cases similar trends occurred for the Bathurst and Bluenose-East herds. Therefore, correlation analyses were conducted on the Bathurst environmental data assuming similarity between indicators for the two herds. In addition, some indicators, such as the growing degree indicators or drought indices, exhibited similar trends (Figure 2).

Figure 2. Trends in climate indicators for the Bathurst and Bluenose-East herds. See Table 1 for a description of each covariate.

Correlation analysis of Bathurst herd climatic indicators with indicators grouped by similar correlations indicates close correlation of the drought, temperature, growing degree day, and oesterid indices (the cluster of blue ellipses in Figure 3). Stronger correlations are indicated by darker blue (positive) or darker red(negative) ellipses. Weak correlations are indicated by lighted colored symbols that are more round than elliptical. The ellipses basically provide a general picture of what a plot of points would look like between the two covariates. Weaker correlations exist between the precipitation indicators as well as the Pacific Decadal Oscillation (PDO) and Arctic Oscillation (AO). The summer range cumulative index (Chen et al. 2014) was positively correlated with most temperature indicators and negatively correlated with many of the precipitation covariates. Most temperature covariates showed a positive correlation with year with precipitation covariates displaying negative correlations.

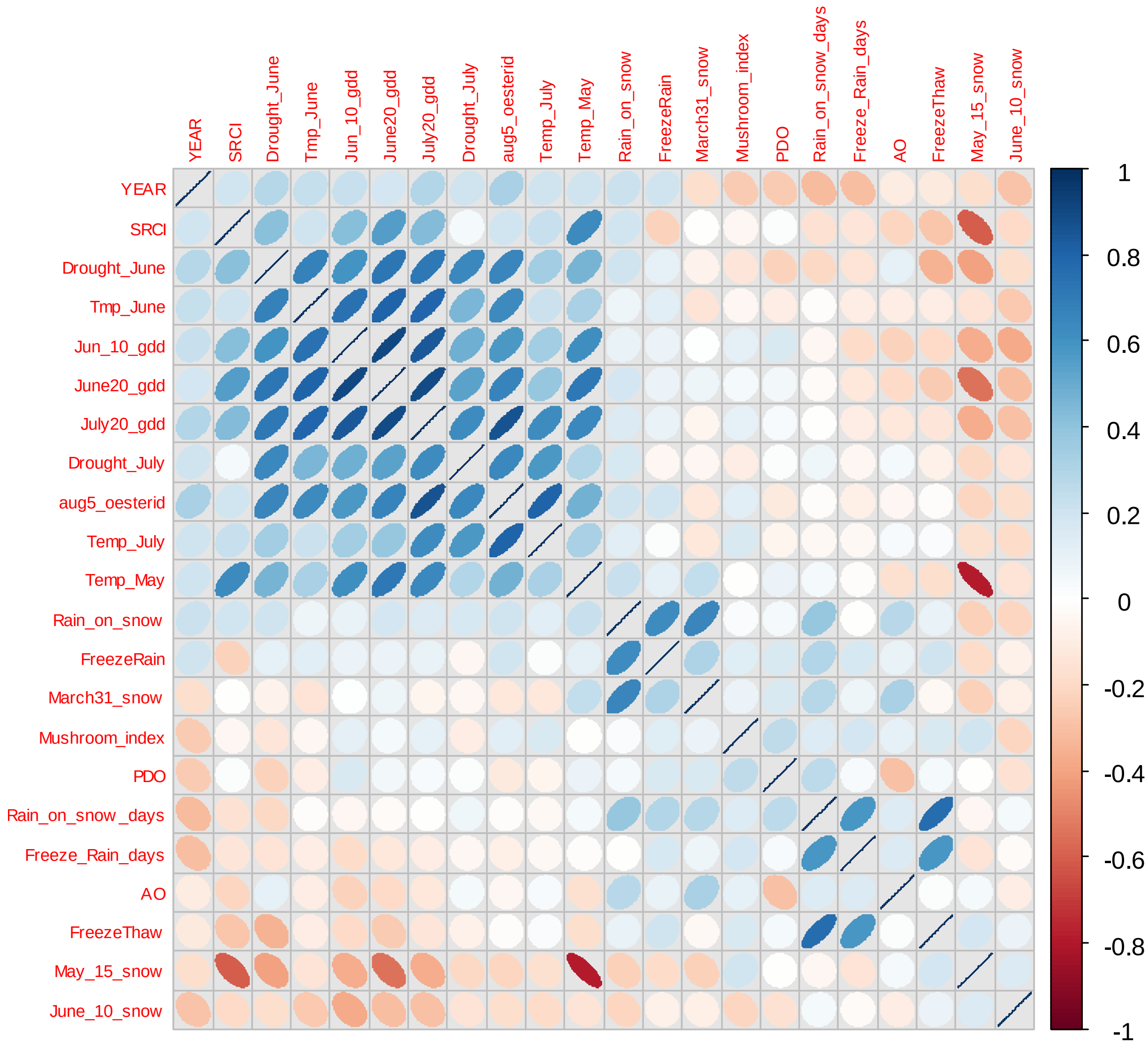

Figure 3. Correlations of Bathurst herd climatic indicators using the corrplot (Wei and Simko 2016). Stronger correlations are indicated by darker blue (positive) or darker red(negative) ellipses. Weak correlations are indicated by lighter colored symbols that are more round than elliptical. In general, a correlation of greater than 0.6 indicates a linear relationship between variables. Indicators are clustered by similarity of correlation coefficients. A version of this plot with correlation coefficients is given in Appendix 1.

Most of the climate indictors were considered in the analysis given slight difference in yearly trends (Figure 2). However, when interpreting results, it is important to note that many of the indicators are linearly related. Therefore, absolute separation of the effects of climatic indicators on demography is not possible in some cases.

Integrated Population Model (OLS) Analysis

Bathurst Herd

The base model for the Bathurst model was based on the original 2011 OLS model as detailed in Boulanger et al (2011). The main objective of the baseline model was to model general trends in demography which could be improved by the addition of environmental covariates. Using this model, a general fit to demographic data was achieved by modelling a linear trend in adult survival and polynomial trends in calf survival. For calf survival, a linear trend from 1986-2006 was modelled followed by an intercept model to meet higher calf cow estimates in 2007 followed by a linear trend from 2007-2016. This model adequately fit the general trends indicated by field estimates (Figure 4). One exception was a lower predicted breeding cow estimate in 1985 compared to the field estimate. A better model fit could be achieved with a linear trend in proportion of females breeding, however, the assumption of long-term (i.e., 1985-2016) trend in pregnancy was questionable. Therefore, a base model with constant breeding proportion was used, however, linear trends in proportion of breeding were considered when applicable.

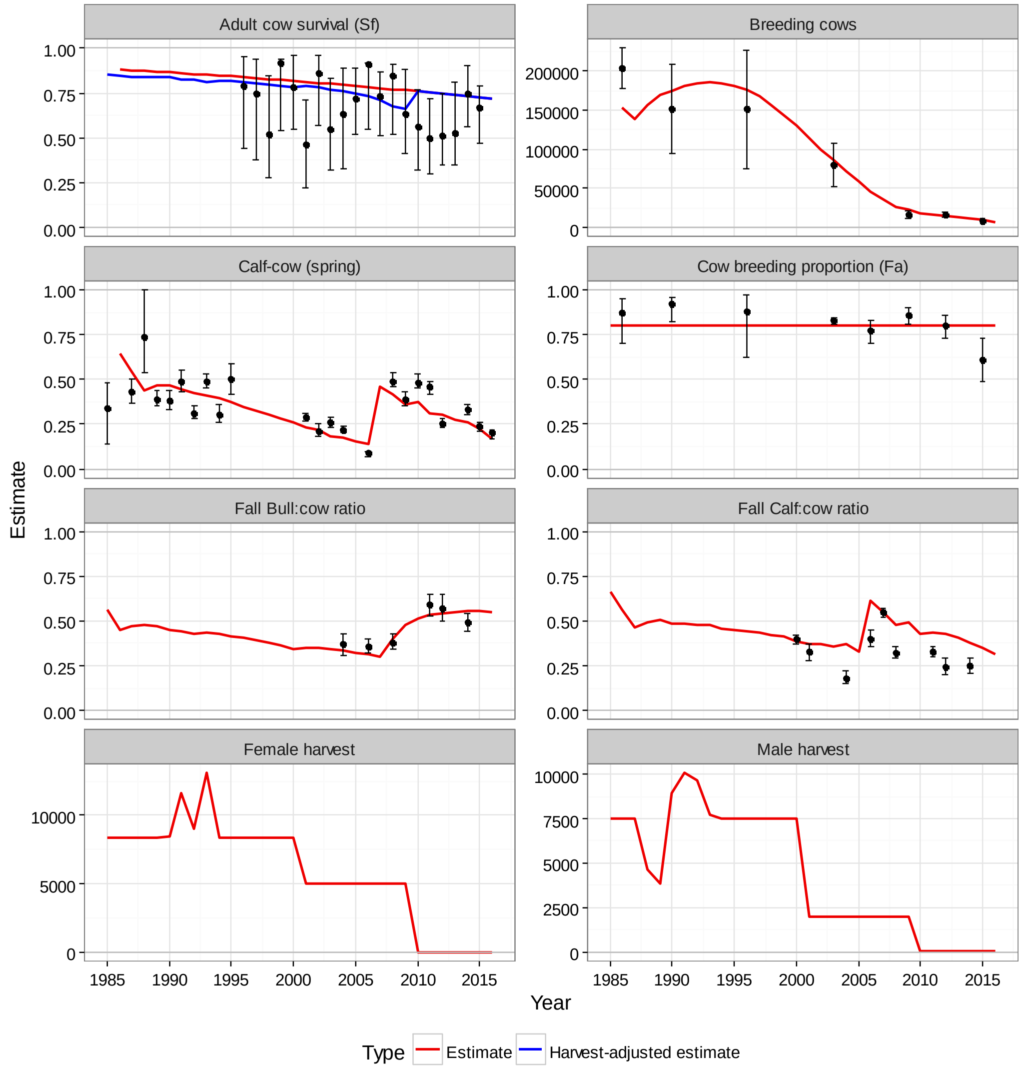

Figure 4. Base demographic model for the Bathurst herd including assumed harvest levels. The red lines are model predictions (or assumed harvest levels) with data points (with confidence limits) also shown. Adult female survival which was compared with collar-based estimates was adjusted for harvest levels (the blue line).

Univariate model runs were then conducted where single individual covariates were run with individual demographic parameters; support for each model and strength of the relationship was reflected by odds ratio scores. Univariate odds ratios for environmental covariates (Figure 5) revealed potential associations, especially for adult survival and the proportion of females breeding. The odds ratios reflected the relative strength of association under the limited assumption that the only environmental factor affecting herd demography was the single covariate being tested. This assumption was not likely to be true and therefore the next step was the building of combined models with multiple covariates.

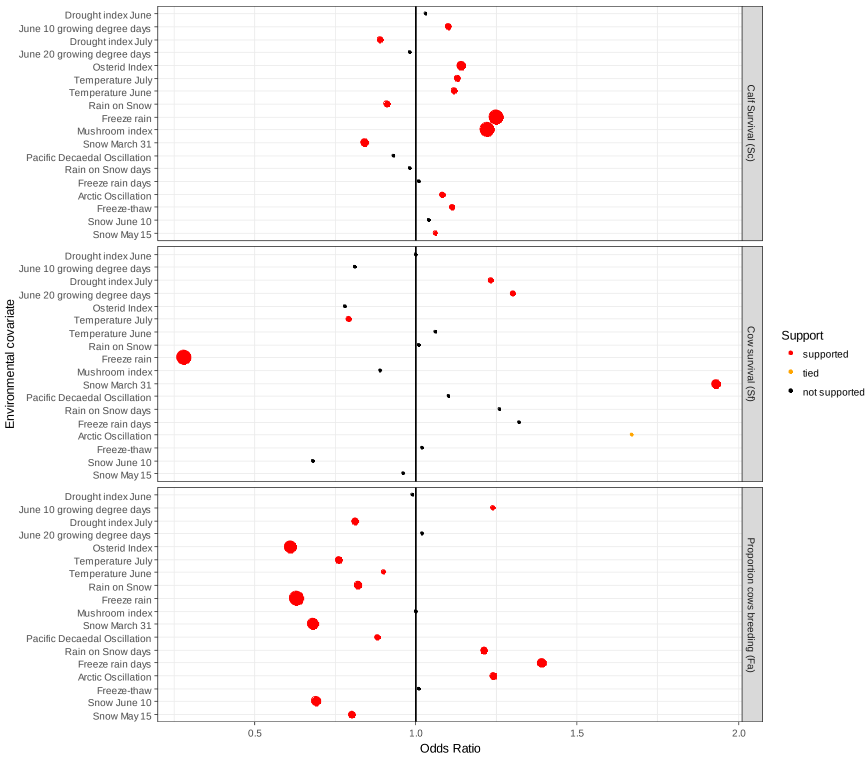

Figure 5. Results of univariate covariate tests for caribou demographic parameters. The strength of the relationship is given as the odds ratio which is the amount in which the parameter would change with one-unit standard deviation change in the climatic covariate. An odds ratio of <1 indicates a decrease in the parameter (or a negative association) whereas an odds ratio of >1 indicates an increase (or a positive association). Data points are sized and colored based on support as indicated by comparison of AICc values for a model with the covariate compared to a base model (without the covariate). Larger points had the most support and the size of the odds ratio indicates the strength of the effect.

Odds ratios for cow survival (Figure 5) suggested that freezing rain and snow depth on March 31 were strong predictors with opposite effects (positive for snow depth and negative for freezing rain). Many predictors were supported for proportions of females breeding, with the oesterid index and freezing rain showing the greatest predictive ability and negative associations. Interestingly, the PDO was supported with an odds ratio of 0.58 (negative association) if directional trends in the proportion of breeding females were assumed but with lesser support assuming a constant breeding proportion. This covariate was thus considered further in unison with other covariates. The strongest univariate predictors of calf survival were the mushroom index and freezing rain, both with positive associations. No environmental covariate was supported if the base trend model in calf survival (Figure 4) was not included.

In the next step, the top two covariates for each parameter were combined and compared to single covariate predictors for each demographic parameter. In all cases the two environment covariate models were more supported than models with single predictors.

Model predictions were then generated for the most supported predictors for each parameter (with the other parameters held at base levels) (Figure 6).

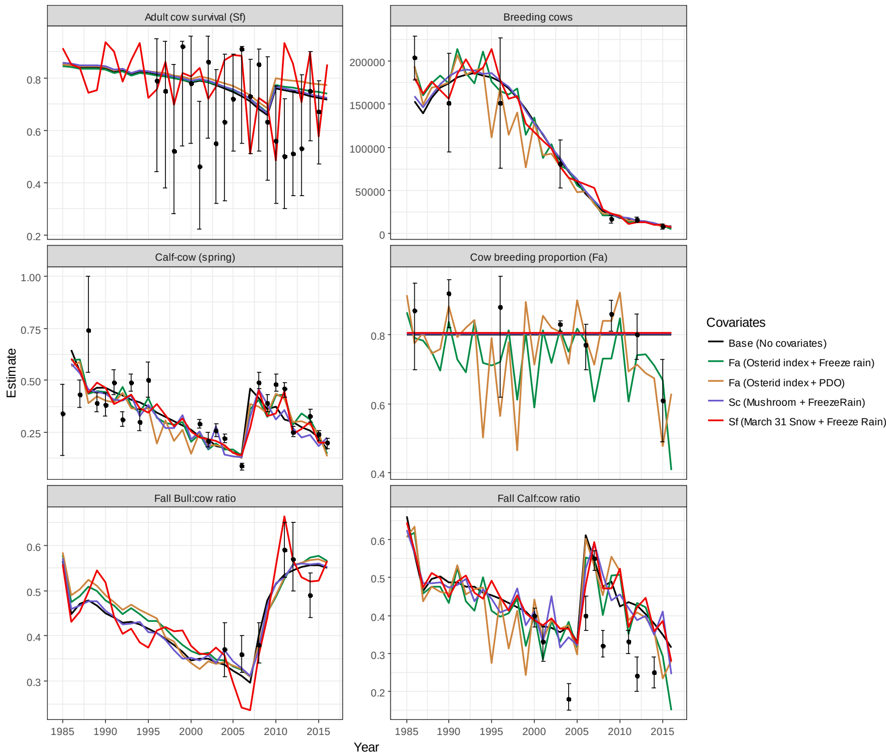

Figure 6. Comparison of predictions of covariate models for the Bathurst herd. In each model run the base model (Figure 4) was used with environmental covariates models as noted.

Of particular interest was how well the covariate predictors described variation in demographic parameters beyond those of the base model. For adult survival, the March 31 snow and freezing rain predictors created modeled calf cow ratios predictions that fit the calf-cow field data as well as breeding cow field data. The fit to the calf-cow data demonstrates how variation in cow survival alone can significantly influence calf-cow ratios. Basically, just varying adult survival (as a function of March 31 snow depth and freezing rain) created a pattern of calf cow ratio estimates similar to that observed in the field. There was a large degree of variation in adult survival predictions which also reflected the variability in collar-based estimates. The proportion of females breeding covariate models showed reasonable fit predicting recent calf-cow ratio trends as well as variation in field measurements of proportions of cows breeding. Both the PDO and freezing rain covariate models showed roughly similar fit with both predicting recent lower pregnancy rates. The calf survival covariate models showed the least amount of improvement over the base model with the adult survival and proportion of females breeding covariate models showing better predictive ability for the recent calf-cow ratio data.

The best covariate models for each parameter were then combined into a single model which showed improved fit compared to the base models or models with covariates for a single demographic parameter (Table 3, Model 2). Once the covariate model was determined (Model 2), the trend term from adult female survival was removed. Basically, this model then assumed that variation in adult female survival could be explained by environmental factors alone. The fit of the model (Model 1) was tied with the trend model, suggesting some degree of support for the assumption that variation in adult female survival is linked to environmental variation without strong directional trends. A model with linear trends in proportion of breeding females (Model 12) was much less supported than the environmental covariate models suggesting that the covariates were better descriptors of variation than the simple trend term.

Table 3. Abridged final model fitting results for the Bathurst herd demographic analysis. Environmental covariates are given for each base parameter. A "T" indicates a linear trend term for adult survival or proportion females breeding. Sample size adjusted AIC_c, the difference in AIC_c between the most supported model for each model (ΔAIC_c), AIC_c weight (w_i), number of model parameters (K) and the sum of penalties is given. Seventy-four field measurements were used to assess model fit.

No.	Covariates			Model fit			
	Adult female survival (S_f)	Calf survival (S_c)[A]	Proportion females breeding (F_a)	AIC_c	ΔAIC_c	K	ΣPenalties
1	SnowMarch + FrzRain	Mushroom +FrzRain	Oesterid+PDO	656.64	0.00	16	656.64
2	T+SnowMarch + FrzRain	Mushroom+FrzRain	Oesterid +PDO	657.89	1.25	17	612.96
3	T+SnowMarch+FrzRain	Mushroom+FrzRain	Oesterid +FrzRain	668.94	12.30	17	624.01
4	T+SnowMarch+FrzRain	Mushroom+FrzRain	Oesterid	670.11	13.47	16	628.56
5	T+SnowMarch+FrzRain	Mushroom	Oesterid +FrzRain	672.59	15.95	16	631.05
6	T+SnowMarch+FrzRain	Mushroom	Oesterid	673.84	17.20	15	635.56
7	T+SnowMarch+FrzRain		T	740.45	83.81	13	708.38
8	T+SnowMarch+FrzRain		T	748.22	91.58	14	713.10
9	T	Mushroom+FrzRain	T	764.64	108.00	14	729.52
10	T	Mushroom+FrzRain	T	826.23	169.59	13	794.17
11	T		Oesterid +FrzRain	829.06	172.42	13	796.99
12	T		Oesterid +PDO	866.22	209.58	13	834.15
13	T		T	927.38	270.74	12	898.26
14	T		Constant	997.67	341.03	11	971.41

[A] Underlying calf survival trends were modelled using the polynomial model ($T_{1985\text{-}2006}+Int_{2007}+T_{2007\text{-}16}+T^2_{2007\text{-}16}$) for all the models in the table.

If there were no calf polynomial terms model fit was reduced substantially with AIC_c of 1,410.2. This suggests that other factors, such as predation, influence calf survival. In this context the covariates aid in describing yearly variation in calf survival with an underlying deterministic trajectory as modeled by the base polynomial terms.

The fit of the final models (Models 1, 2) was then compared to field measurements (Figure 7). In general, predictions for the model with (S_f(T)) and without (S_f(.)) a linear trend in adult female survival was very similar further suggesting that the assumption of linear trends in adult survival did not substantially affect predictions.

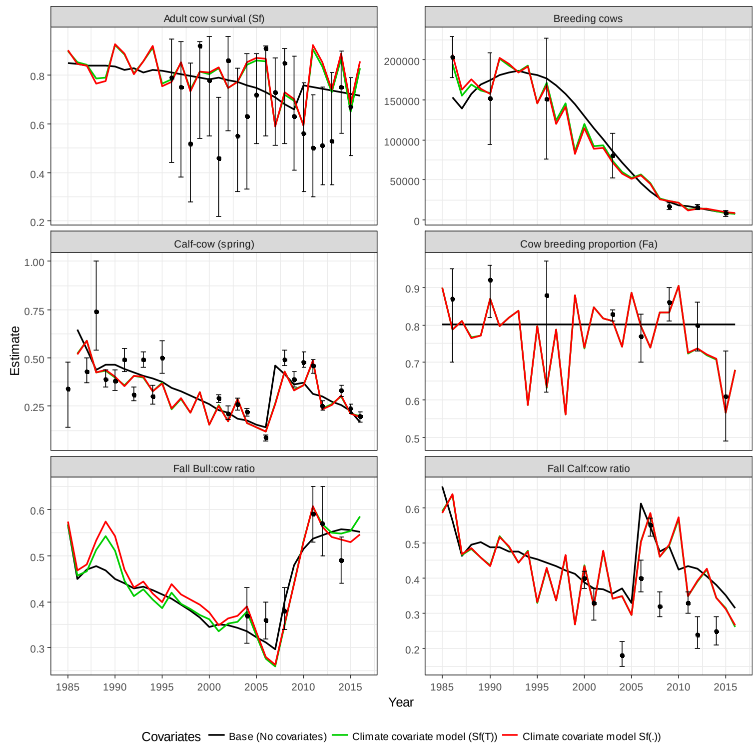

Figure 7. Comparison of predictions of the most supported environment covariate (Model 1 in Table 2) with the base demographic model for demographic indicators in the Bathurst herd. If only one line is shown (i.e., the red line) then it means that model predictions were close and therefore the prediction lines overlapped.

It is important to note that actual observed survival rates did decline from 1985-2009 due to harvest pressure (Figure 4) and therefore the model is estimating trend in natural survival trends as opposed to observed survival trends in this case. One reassuring result was that the model was able to precisely predict recent calf-cow ratio trends (2009-2016) as well as recent decreases in proportions of cows breeding, and bull-cow ratios when compared to the base model.

The actual effect of covariates on parameters can be more concisely viewed by re-plotting the estimates from Model 1 in Figure 7 as a function of standardized covariate values rather than year (Figure 8). In all cases each demographic parameter varied by two environmental covariates and therefore the plots in Figure 8 display color-coded ranges of estimates for each combination of environmental covariate. Environmental covariates are standardized with values of 0 equal to mean values. From this it can be seen that winters with greater snow on March 31 and lower levels of freezing rain are associated with higher cow survival rates. Survival rates are reduced if snowfall is low and freezing rain levels are higher than mean values. Proportions of females breeding were lower if insect levels (oesterid index) were high in the preceding summer especially when the PDO index was higher. Relationships between covariates and calf survival are less clear given that directional trends in calf survival (Figure 6) also influenced survival. Higher levels of the mushroom index and freezing rain slightly boosted calf survival levels in this case.

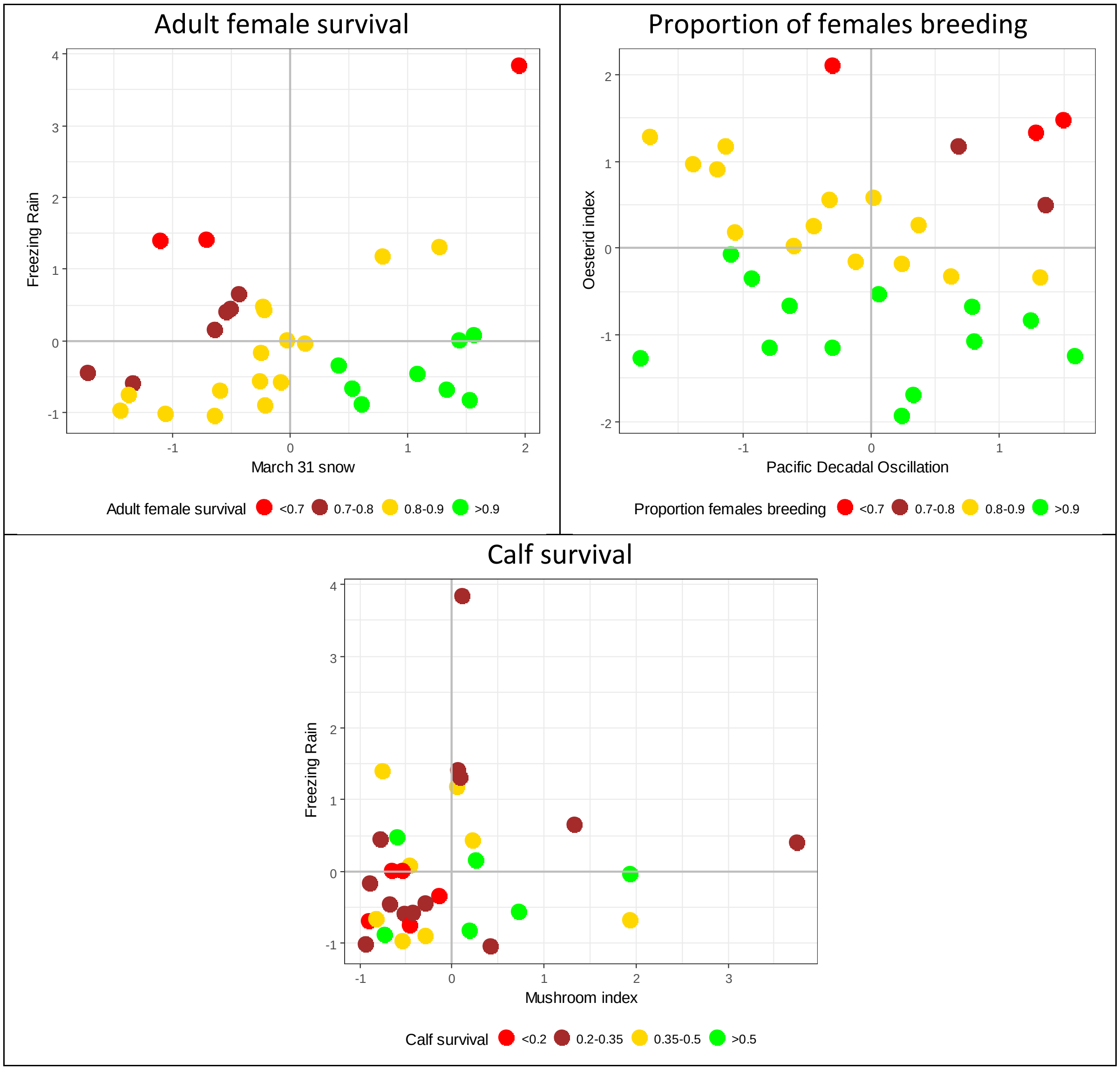

Figure 8. Individual predictions of demographic parameter values for each of the environment covariates, for the Bathurst herd. This plot basically takes the estimates from Figure 5 and plots them using the standardized value of each climatic covariate.

Bluenose-East Herd

The Bluenose-East base demographic model assumed constant values for all parameters except calf survival where a linear trend was modelled. This resulted in variable fit to field measurements with model predictions potentially describing longer term trends but not describing year to year variation in field estimates (Figure 9). The key question posed by the analysis was whether environmental covariates would better describe yearly variation in calf-cow ratios, cow survival rates, and other field measurements. Assumed harvest levels were based upon reported harvest and are likely underestimates. Only a minor difference between harvest adjusted and natural survival rate was observed. Higher harvest levels would increase the difference between natural survival and harvest adjusted survival.

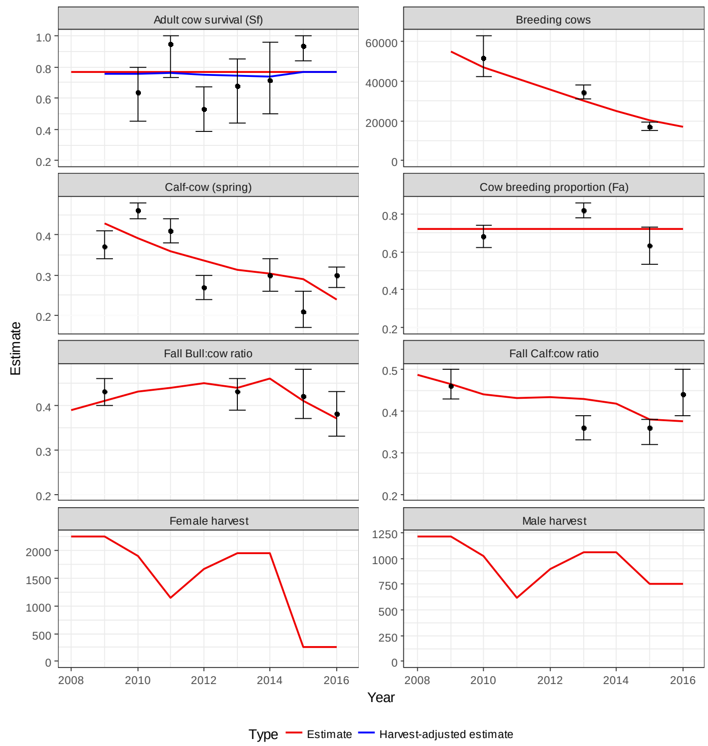

Figure 9. Base model used for the Bluenose-East demographic analysis 2008-2016 including assumed harvest levels.

Univariate tests revealed potential associations of covariates with demographic parameters (Figure 10). For calf survival, most supported associations were negative with freezing rain days, oesterid index, growing degree days, and rain on snow days all showing some support from the data. For cow survival, June 10 growing degree days and May snow depth were negatively associated and March 31 snow depth was positively associated (and supported). June temperature was negatively associated and AO positively associated with the proportion of females breeding.

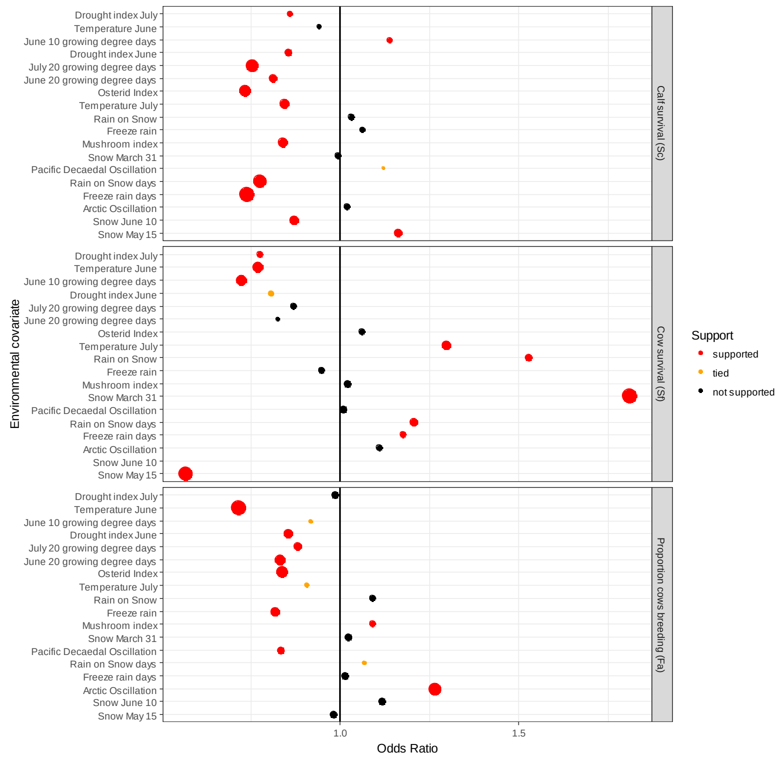

Figure 10. Results of univariate covariate tests for the effect of individual covariates on caribou demographic parameters for the Bluenose-East herd. The strength of the relationship is given as the odds ratio which is the amount in which the parameter would change with one-unit standard deviation change in the climatic covariate. An odds ratio of <1 indicates a decrease in the parameter (negative association) whereas an odds ratio of >1 indicates an increase (positive association). Data points are colored based on support as indicated by comparison of AICc values for a model with the covariate compared to a base model (without the covariate). The size of the circle shows the strength of support for the covariate and the odds ratio shows how large the effect was.

The next step of model selection involved building multiple covariate models for each of the three demographic parameters. The most supported multiple covariate models were then compared to field estimates (Figure 6) with adequate fit determined by whether estimates were within the confidence limits of field measurements (Figure 11). The cow survival covariate models (March 31 snow depth and May snow) both displayed reasonable fit to the collar-based data with predictions following the general trend indicated by collar-based survival rates. As with the Bathurst herd, predictions from cow survival covariate models also described general trends in calf-cow ratios. Predictions from the calf survival covariate model were within confidence limits of the spring calf-cow ratios for four of seven measurements suggesting moderate predictive ability of a model where only calf survival is a function of environmental covariates. The proportion of females breeding covariate model was only within field measurement confidence limits for one of three estimates but was within the confidence limits of five of seven spring calf cow estimates.

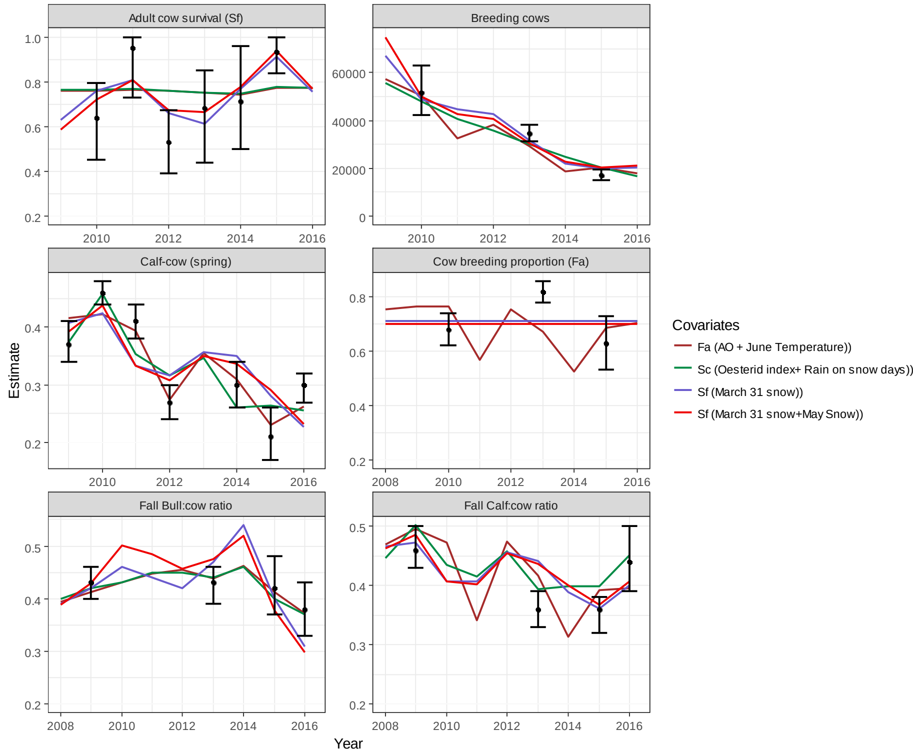

Figure 11. Comparison of predicted field indicators for component covariate models for the Bluenose-East caribou herd.

The component covariate models were then combined into a model with covariates for all target parameters (Table 4). Of the models considered, a model that combined each of the covariates (Figure 11) was most supported with a linear directional trend for calf survival (Table 4, Model 1). This model was more supported that a similar model without the directional trend term for calf survival (Model 3). The most supported Bathurst covariate model (Model 4) also displayed lower support.

Table 4. Abridged model selection results for the Bluenose-East demographic and environmental covariate analysis. Sample size adjusted AIC_c, the difference in AIC_c between the most supported model for each model (ΔAIC_c), AIC_c weight (w_i), number of model parameters (K) and the sum of penalties is given. Twenty-seven field measurements were used to assess model fit.

No	Environmental covariates		Proportion Females Breeding	Model fit			
	Adult female survival	Calf survival		AIC_c	ΔAIC_c	K	ΣPenalties
1	SnowMarch+SnowMay15	T+Oesterid+ROSdays	June Temp +AO	161.34	0.00	13	107.34
2	SnowMarch	T+Oesterid+ROSdays	June Temp +AO	172.07	10.73	12	125.78
3		T+Oesterid+ROSdays		188.76	27.42	9	160.17
4 [A]	SnowMarch+FrzRain	T+Mushroom+FrzRain	Oesterid+PDO	191.59	30.25	13	137.59
5	SnowMarch+SnowMay15	Oesterid+ROSdays	June Temp +AO	192.36	31.02	12	146.08
6		T+FzRaindays+ROSdays		199.13	37.79	9	170.54
7		FrzRaindays		205.90	44.56	8	181.90
8		T	June Temp +AO	213.15	51.81	9	184.56
9	SnowMarch+SnowMay15	T		220.75	59.41	9	192.17
10	SnowMarch	T		222.46	61.12	8	198.46
11		T	June Temp +Oesterid	224.38	63.04	9	195.79
12			June Temp	224.63	63.29	8	200.63
13	SnowMarch+TempMay	T		226.61	65.27	9	198.02
14		Oesterid		228.49	67.15	8	204.49
15			AO	237.08	75.74	8	213.08
16		T		256.13	94.79	7	236.24

[A] The most supported covariates for the Bathurst herd.

Predictions for the most supported model were then compared with field measurements along with the most supported Bathurst covariate model (Model 4) and a model without the directional calf survival term (Model 5), which are plotted in Figure 12. The Bluenose-East as well as the Bathurst herd covariate models followed general trends in collar-based cow survival rate as well as calf-cow ratio field estimates. None of the covariate models predicted the higher proportion of females breeding in 2013. Correspondence was reasonable between model predictions and field measurements for most other comparisons.

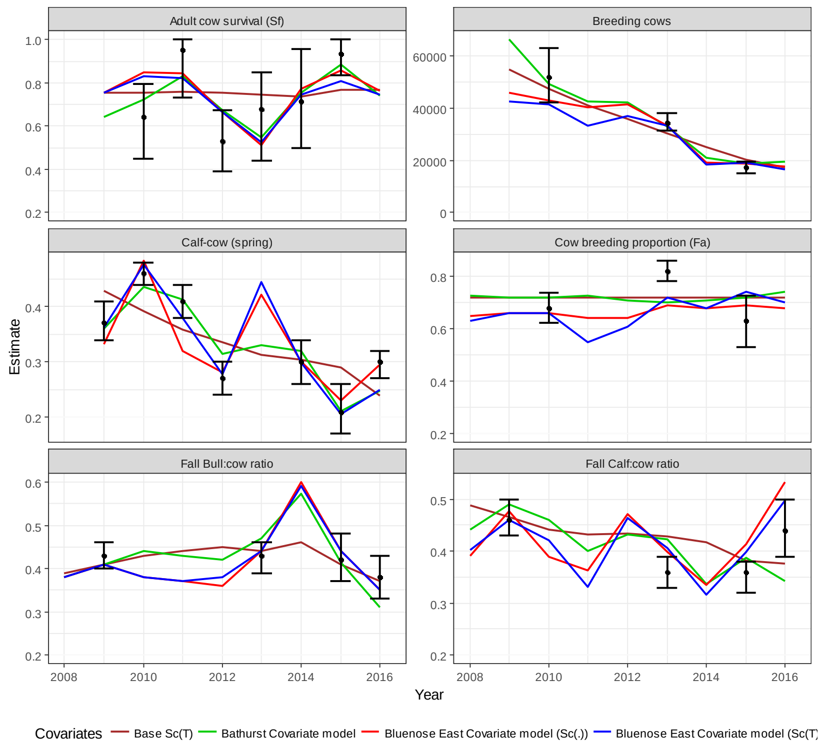

Figure 12. Comparison of the base model used for the Bluenose-East herd with the final environmental covariate model (Model 1, Table 4) and the Bluenose-East base model with the most supported Bathurst herd environmental covariate model (Model 7).

Plots of model demographic parameter estimates (Figure 13) compared to standardized environment covariate values are harder to interpret than for the Bathurst herd (Figure 8) due to sparseness of yearly data points. For adult female survival, survival was increased when March and May snow depth levels were high. The proportion of females breeding was lowest when June temperature was lower and at higher AO levels. Calf survival was lowest when the oesterid index and rain on snow levels were above mean levels.

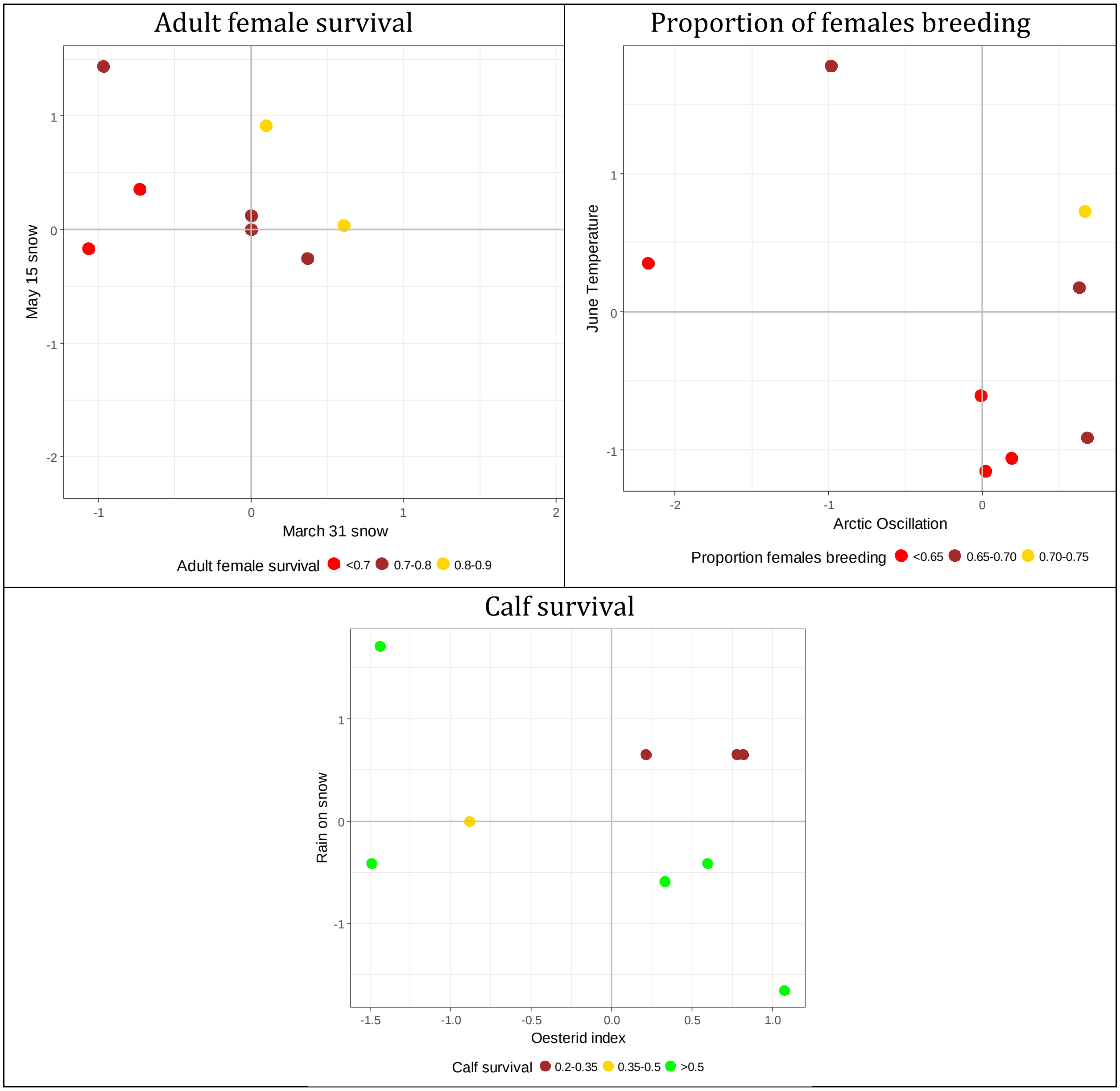

Figure 13. The effect of environmental covariates on individual demographic parameters for the Bluenose-East herd. Environmental covariates are standardized with 0 indicating mean values. Demographic parameters are color coded by estimated value. These data points were taken from Figure 12 with data re-plotted as a function of demographic covariate values rather than year.

Spatial and Temporal Collared Cow Mortality Analysis

The spatial survival analysis was conducted for the Bathurst herd given the larger time series available for the analysis. A preliminary summary analysis was conducted for the Bluenose-East herd.

Bathurst Herd

Summary of Data

Assessment of sample sizes revealed low annual numbers of collars and mortalities for the 2006-2009 interval and therefore this interval was pooled with 1996-2006 for most of the analyses (Table 5). The number of collar months, which is the cumulative number of monthly locations across all caribou was roughly similar for the 1996-2009 pooled interval (1,819) compared to the 2010-2016 interval (1,604) demonstrating the increase in collaring effort.

Table 5. Summary of sample sizes of mortalities and available female Bathurst collars for the spatial temporal survival analysis. Collar months are the cumulative number of months that collared caribou were monitored, summed over all caribou.

Period& Season	Collared Cow Mortalities	Mean # collars	Std. Dev	min	max	collar months
1996-2006						
Calving	2	11.5	3.4	6	18	126
Summer	7	10.7	3.1	5	17	235
Fall/rut	9	11.1	3.9	5	21	365
Winter	16	11.2	4.2	5	21	582
Spring Migration	3	12.0	3.5	6	19	132
	37					1,440
2006-2009						
Calving	0	15.5	4.9	12	19	31
Summer	3	14.5	4.8	9	19	58
Fall/rut	1	14.7	4.5	9	19	88
Winter	5	16.8	2.9	14	22	168
Spring Migration	0	17.0	4.2	14	20	34
	9					379
2010-2016						
Calving	2	19.8	6.7	11	31	158
Summer	26	18.6	6.2	11	31	297
Fall/rut	13	14.6	6.4	8	26	351
Winter	17	15.9	7.3	7	32	635
Spring Migration	4	20.4	6.1	14	32	163
	62					1,604

The general principle behind the mortality risk analysis is that the live collared caribou locations estimate exposure to each spatial attribute, which can then be compared to the actual mortality risk as estimated by documented mortalities. An initial assessment can therefore be obtained by comparing the proportion of collared locations in each habitat class with the proportion of mortalities in the habitat class. If mortality risk is similar across all habitat types, then the proportions of live collar locations and mortalities should be similar.

A comparison of proportions for ecoregion revealed higher relative proportions of mortalities in NU (tundra) in 2010-2016 compared to 1996-2009 (Figure 14). Relative proportions of mortalities were higher in evergreen northern land-cover in 2010-2016 compared to 1996-2009.

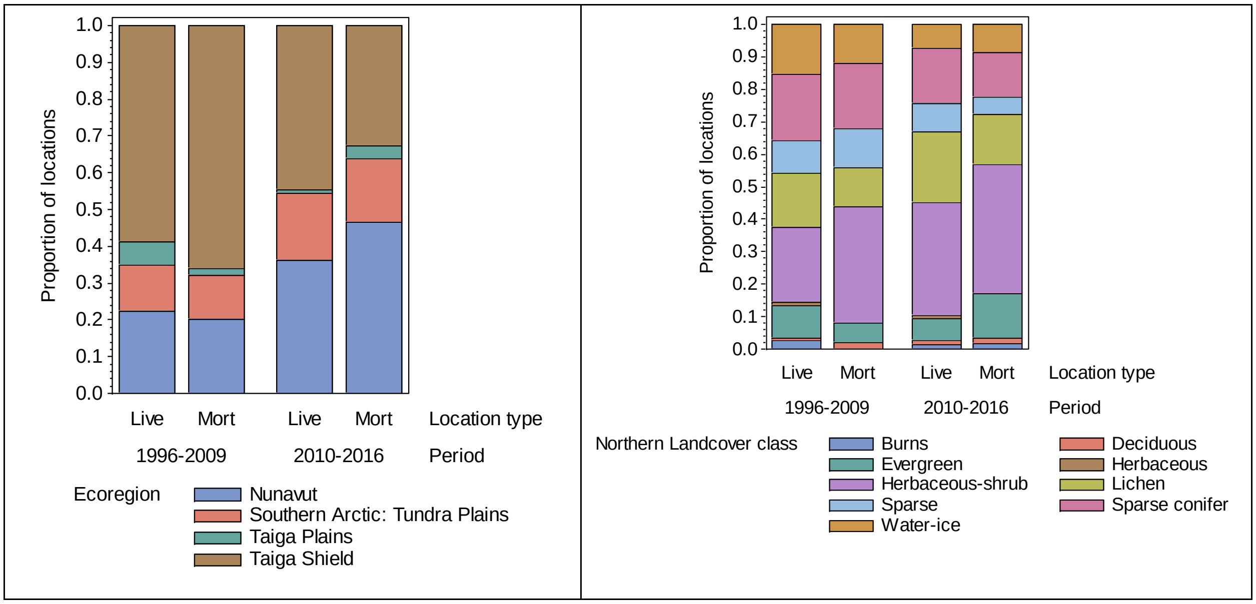

Figure 14. Proportions of live and mortality collared cow locations in each habitat type as a function of period and eco-region or land-cover class.

Comparison of proportions of collared cow mortalities by seasons reveals an increase in the proportion of mortalities in the summer and slight decrease of proportion of mortalities in the winter in 2010-2016 compared to 1996-2009 (Figure 15).

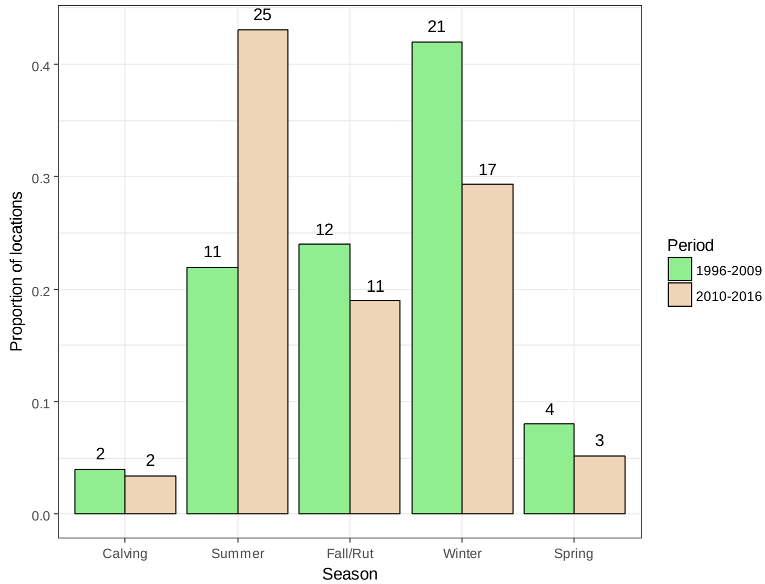

Figure 15. Proportions of Bathurst collared cow mortalities by season. The number of mortalities is given with each bar. The total numbers of mortalities for 1996-2009 and 2010-2016 were 45 and 62 respectively.

Summary Using Plots of Location and Heat Maps

A plot of the live and mortality locations with hotspots denoted for 1996-2009 and 2010-2016 reveals that caribou were much more aggregated in 2010-2016, especially on the winter range. From this it can be seen that in 1996-2009 mortality was primarily centered in a U-shape around Wekweètì, which was similar to the pattern of use. In 2010-2016 use and mortality hotspots occurred around Contwoyto Lake (Lupin Mine area) and just south of Wekweètì (Figure 16).

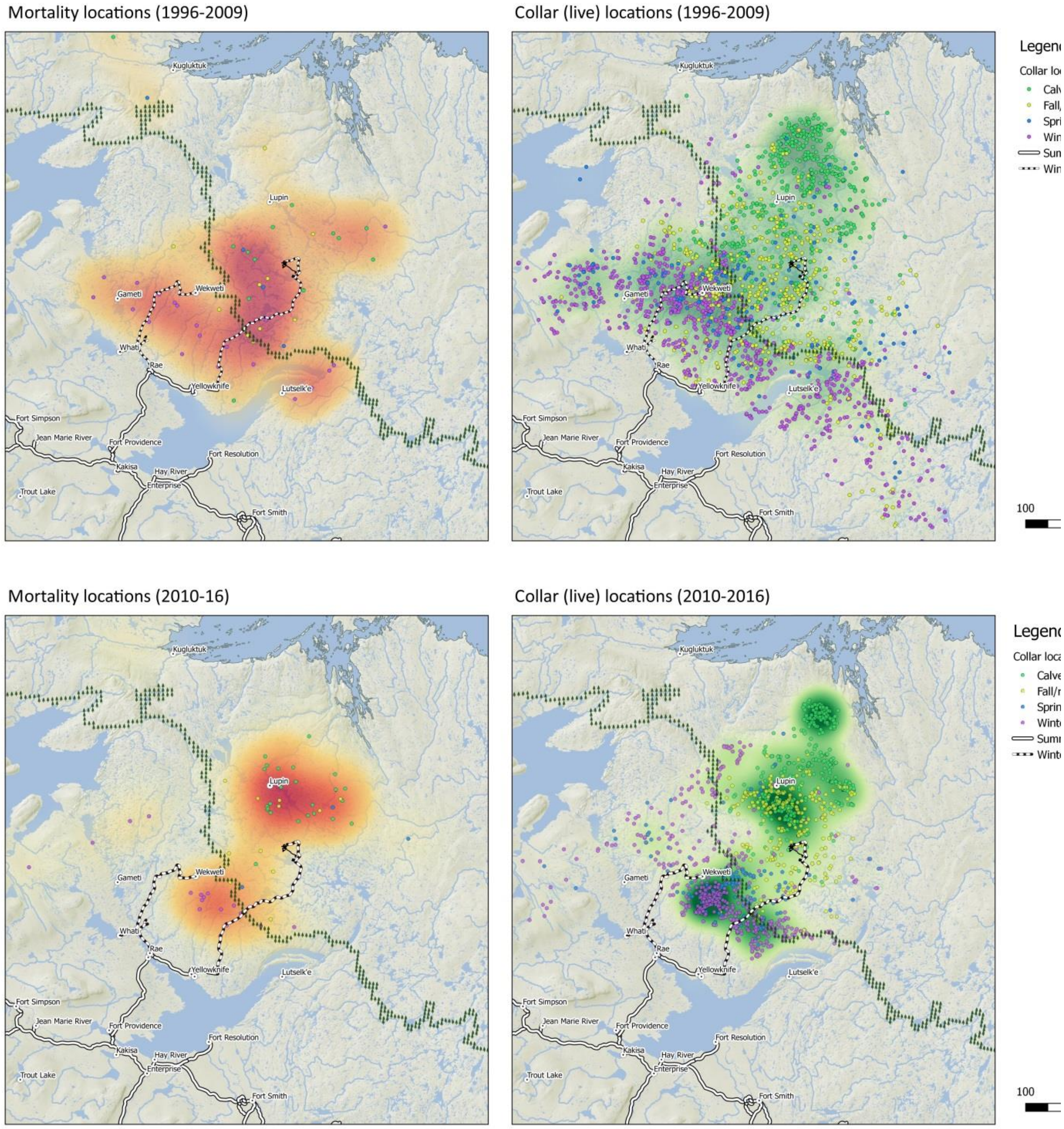

Figure 16. Comparison of mortality locations (left maps) and use locations (right maps) for 1996-2009 (upper maps) and 2010-2016 (lower maps). A heat map smoothing method in QGIS (QGIS Foundation 2020) was used to define areas of higher mortality and use. This approach used a moving window with a 100 km and 60 km search radius for mortality and live locations.

The clustering of locations especially on the winter range in 2010-2016 may have been partially due to recent fire activity during the 2010-2016 period (Figure 17) as well as reduced herd size and associated range contractions. Of collar locations, 0.76% (n=27 of 3531) occurred in areas that were recently burned (within five years of the date of the location) with the majority (22) occurring in the winter season. Caribou locations occurred within 10 km of recent fires in 179 (5%) of locations. We speculate that recent fires reduced travel to areas utilized in 1996-2009. Restricted movement and reduced numbers of caribou partially created the aggregated distribution on the winter range.

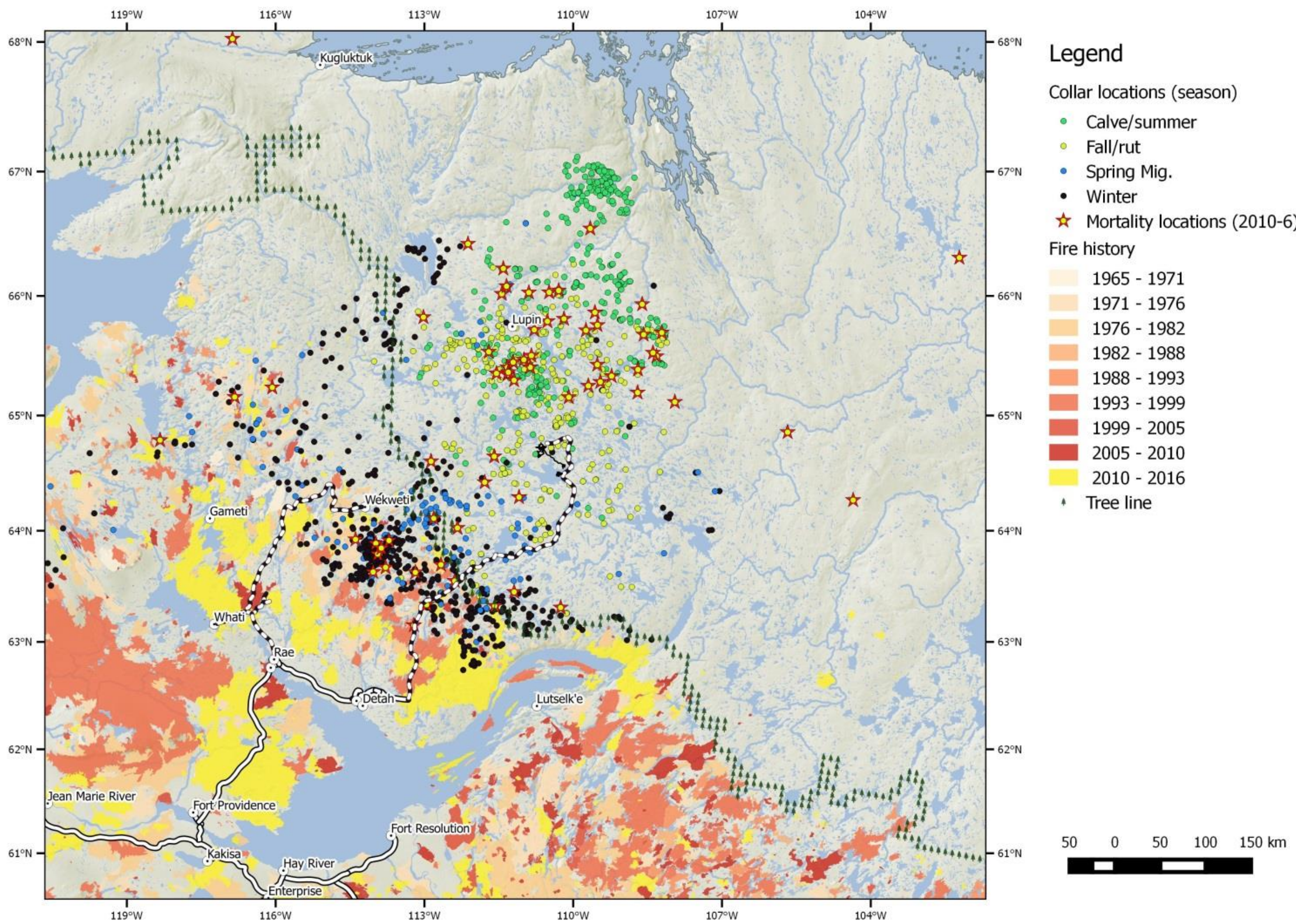

Figure 17. Live and mortality locations with fire history indicated. The 2010-2016 fire areas are indicated by yellow.

Survival Analyses

Model selection initially considered the effects of season, land-cover class, and ecoregions on spatial and temporal mortality risk of collared caribou. Of ecoregions, only NU, which would be primarily tundra plains, was a significant predictor when interacted with season. Of northern land-cover types, the evergreen cover class was a significant predictor when interacted with season or period. Season and the interaction of season and period was also a significant predictor. The log of distance from roads was significant but distance from communities was not significant. Underlying directional temporal trends in survival were modelled using polynomial year terms with a quadratic model being significant (Table 6). This model was much more supported than a base model that varied survival by year

(ΔAIC_c=44.5) as was used for the OLS model analysis. The ROC score, which indicates relative fit of the model to the data, was 0.68 which indicates marginal fit. Ideally the ROC score of the model should be 0.7 or higher. Therefore, the results and predictions of the model should be interpreted cautiously. In the discussion, strategies to improve model fit are discussed.

Table 6. Slope parameters (β) for Bathurst mortality risk model and associated significance tests. Wald chi-square tests and p-values (P(χ2)) are given for each parameter.

Variable	Category	Period	β	SE(β)	X^2	$P(X^2)$
Intercept			2.27	0.75	9.12	0.003
Year			-0.14	0.08	3.29	0.070
$Year^2$			0.01	0.00	3.73	0.053
Evergreen*period	1996-2009		1.16	0.38	9.29	0.002
Evergreen*summer			-2.12	0.97	4.74	0.029
Season	Calving		-1.07	0.63	2.88	0.090
	Fall/rut		0.12	0.29	0.16	0.689
	Spring Migration		1.02	0.46	4.93	0.026
	Summer		-0.75	0.32	5.58	0.018
Season*period	Calving	1996-2009	-0.14	0.46	0.09	0.766
	Fall/rut	1996-2009	0.13	0.24	0.32	0.570
	Spring Migration	1996-2009	-0.47	0.37	1.65	0.200
	Summer	1996-2009	0.53	0.20	6.82	0.009
NU*season	Calving		2.42	0.87	7.80	0.005
	Fall/rut		-0.49	0.48	1.02	0.312
	Spring Migration		-2.22	0.73	9.35	0.002
	Summer		-0.03	0.37	0.01	0.925
Log (distance from road)			0.33	0.12	7.82	0.005

A model with March 31 snow depth replacing the polynomial year terms was marginally supported (ΔAIC_c=0.55) with estimated survival rates increasing slightly with higher snowfall levels as suggested by the OLS model. Annual survival in this case was estimated by monthly survival raised to the 12^{th} power. This approach is not as appropriate as methods that multiply successive months of the year together to estimate yearly survival, however, it still provides a general estimate of trends in survival rates (Figure 18).

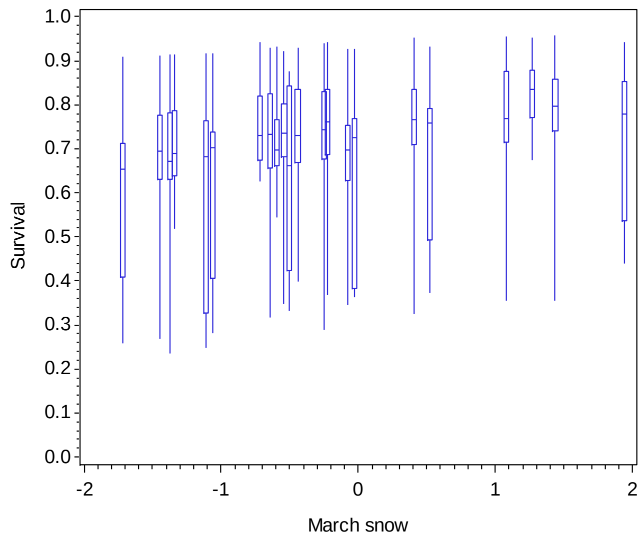

Figure 18. Predicted Bathurst cow survival as a function of March snow depth for Model 1 (Table 20) with March snow depth replacing the polynomial trend terms (Year and $Year^2$).

The predicted effects of season and period on survival rates can be illustrated by the distribution of monthly survival estimates by month and period. Monthly survival rates in this case will be affected by season, proximity of caribou to roads, and habitat (i.e., evergreen cover and ecoregion) as well as period. Monthly survival rates will be higher than yearly survival rates. For example, a monthly survival rate of 0.97 would equal a yearly survival rate of 0.69 (0.97^{12}). The actual yearly survival rate will therefore be the product of the series of monthly survival rates (Figure 19). Regardless, the analysis shows that monthly survival rates were relatively similar for the two periods, with the exception of the summer months where survival was reduced in the 2010-2016 period. Cow survival rates were highest during calving, during both periods.

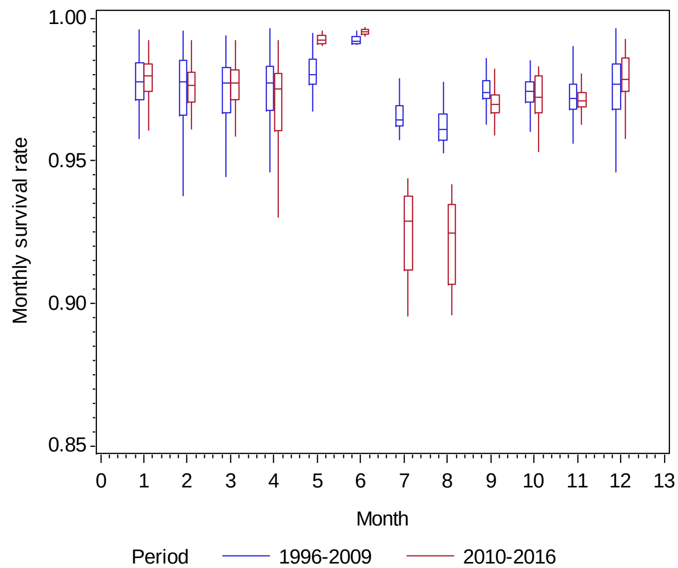

Figure 19. Predicted distributions of monthly survival rates as a function of month and period from Model 1 (Table 20).

The effect of distance from road on mortality risk is illustrated by a plot of predictions as a function of distance from road with season delineated. The main effect of roads occurs in the winter season (in purple) when caribou are near the roads and in the immediate proximity of the roads (<25 km) (Figure 20).

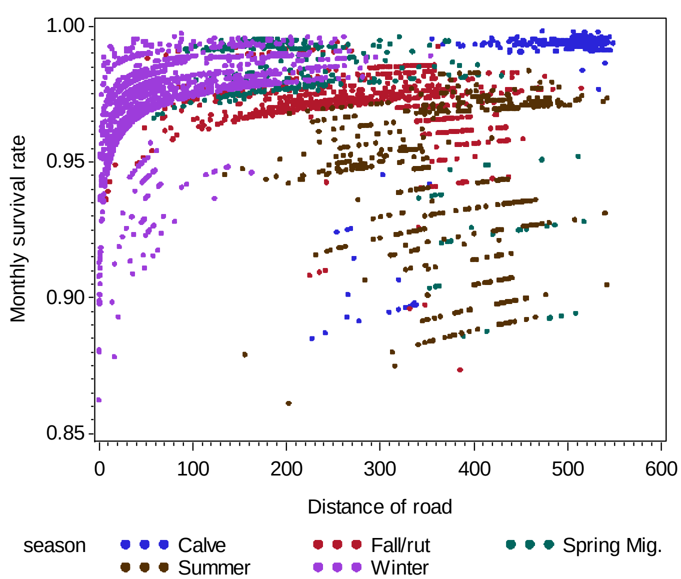

Figure 20. Predicted monthly survival rates as function of distance from roads and season for Model 1 (Table 20).

The predictions from the mortality risk model were plotted for the 1996-2009 (Figure 21) and 2010-2016 period (Figure 22). Prediction from the model were roughly similar to the heatmaps (Figure 16) with diffuse mortality risk in 1996-2009 compared to the 2010-2016 time period.

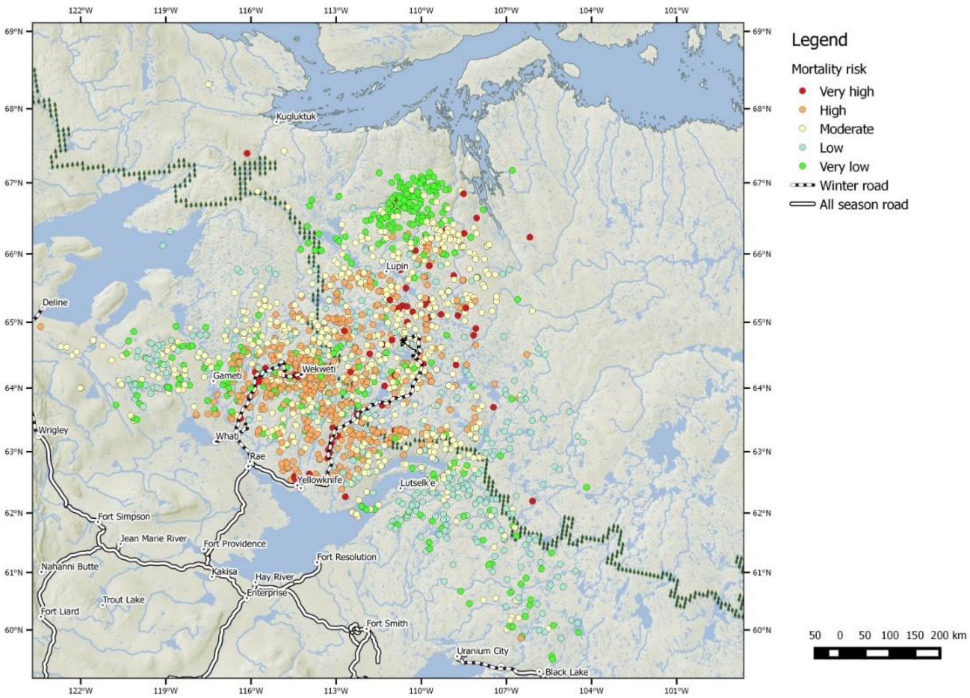

Figure 21. Predictions of the Bathurst collared caribou mortality risk model for the 1996-2009 period (Table 6).

As with the heat map for 2010-2016 (Figure 16) an area of higher mortality risk is indicated around the Contwoyto Lake area for the 2010-2016 period (Figure 22). Intermittent areas of higher mortality risk occur in the winter range areas which are likely due to land cover (evergreen northern land cover class) or distance from road.

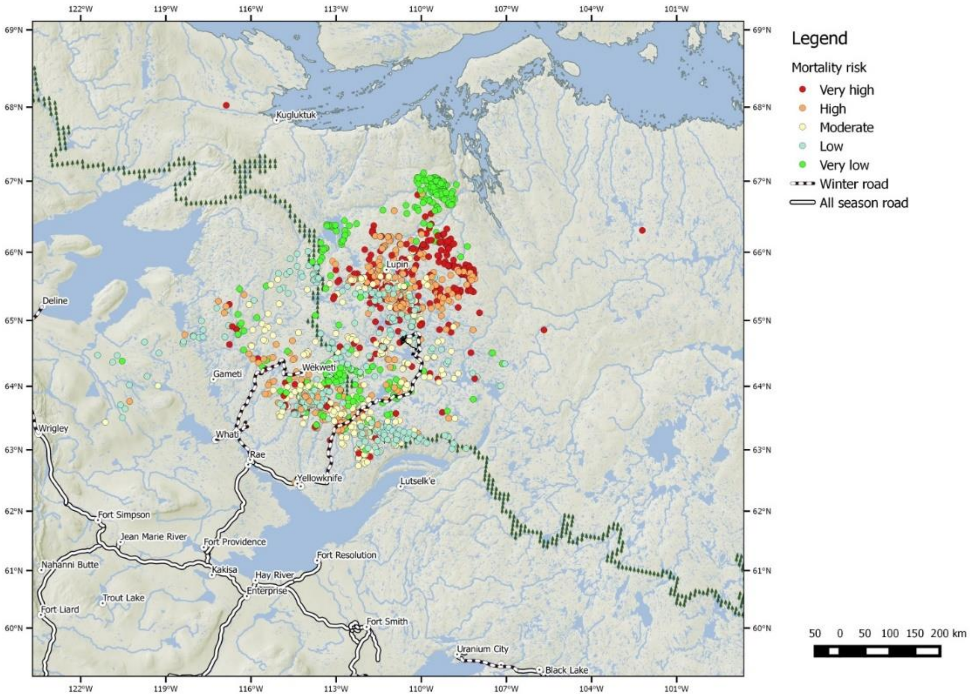

Figure 22. Predictions of the Bathurst collared caribou mortality risk model for the 2010-2016 period (Table 6).

Bluenose-East Herd

Summary of Data

Overall, 54 mortalities of cows were documented for the Bluenose-East herd from 2010-2016 (Table 7). As with the Bathurst herd, collar locations for caribou were summarized by month fate (alive or dead) for each collared caribou. The mean number of collars monitored per month varied from 15.1 in 2011 to 29 per month in 2015 (Table 7). The number of yearly cow mortalities varied partially as a function of how many collars were monitored in a given year. The annual Kaplan Meir survival rate estimate (used in the integrated population model analysis) is given for reference with survival rates varying from 0.53 in 2012 to 0.93 in 2015. An annual survival rate estimate is not possible for the 2016 caribou year given that it extends from June 2016 to May 2017 and the data for the year was still being collected. We note that often collar survival rates are lower than the most likely demographic survival rates as shown in the previous demographic analysis of Bluenose-East data (Figure 12).

Table 7. Summary of sample sizes for Bluenose-East collared cow survival analysis. Collar months are the cumulative number of months that collared caribou were monitored, summed over all caribou. The annual Kaplan-Meir (KM) survival rate estimate used in the OLS analysis (Figure 9) is given for reference.

Caribou year	Collared cow mortalities	Months monitored	Mean # collars	Std. dev	Min	Max	Collar months	KM survival	SE(S)
2010	10	12	22.8	5.1	17	30	274	0.64	0.09
2011	2	12	15.1	13.5	5	42	181	0.95	0.03
2012	20	12	38.4	5.5	30	50	461	0.53	0.08
2013	7	12	18.2	3.1	14	23	218	0.68	0.10
2014	8	12	25.1	5.9	19	35	301	0.71	0.09
2015	2	12	29.0	5.4	23	36	348	0.93	0.05
2016	5	8	28.3	8.9	8	36	226		

Mortality frequencies were also summarized by season which suggests roughly even frequencies for all seasons except calving where frequencies are low (Figure 23). This contrasts with the Bathurst herd for the 2010-2016 interval which had higher frequencies for the summer season. We note that the comparison of frequencies will not indicate seasonal survival rate given that the length of seasons in time is different. However, it still provides a general comparison of mortality risk between herds. A more formal survival analysis could be used to estimate seasonal survival rates for the Bluenose-East herd.

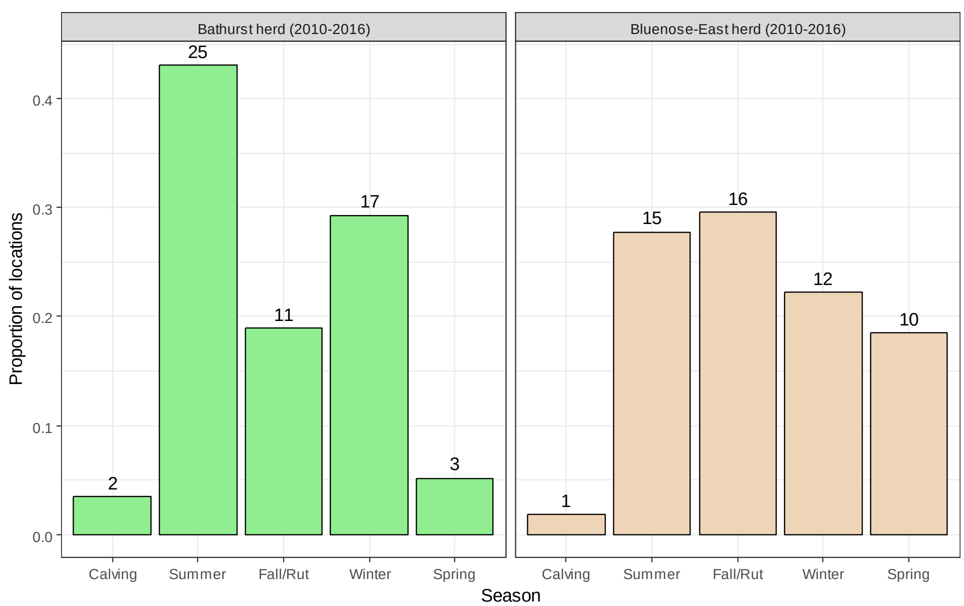

Figure 23. Mortality frequencies from 2010-2016 for Bathurst and Bluenose-East herds.

Heatmaps were generated for the 2010-2016 cow data set (Figure 24) which suggests that highest areas of mortality occur to the east of Great Bear Lake with less mortality to the south and north. The winter, fall, and summer ranges for the Bluenose-East overlap in many years therefore making it more difficult to ascribe mortality risk to a particular season.

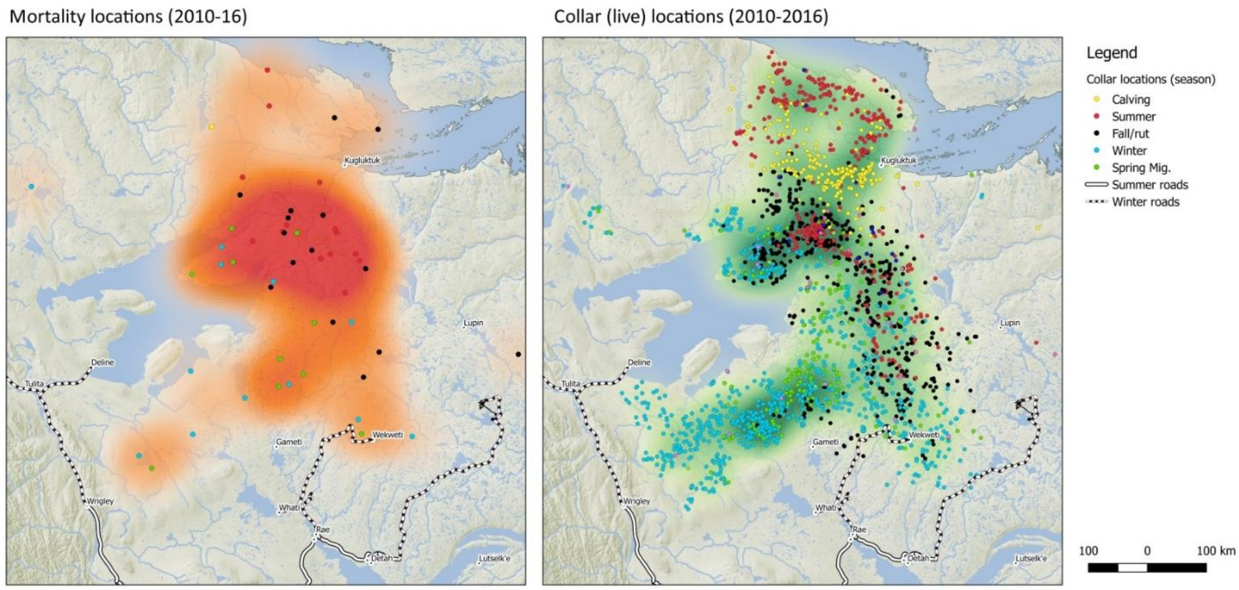

Figure 24. Heatmaps of mortality and live collar locations for collared cows in the Bluenose-East herd from 2010-2016. A heat map smoothing method in QGIS (QGIS Foundation 2020) was used to define areas of higher mortality and use. This approach used a moving window with a 100 km and 60 km search radius for mortality and live locations. Areas of darker red and green indicate interpolated areas of higher mortality or use.

DISCUSSION

The analyses in this report suggest potential associations of caribou demography with environmental variables as well as spatial and temporal variation in survival rate within the range of the Bathurst herd. Each component analysis is discussed separately.

Integrated Population Model

The integrated population model analysis suggested associations between all three of the main demographic parameters and environmental covariates (Table 7). Of particular interest was the potential influence of environmental variation on adult survival and the proportion of females breeding, which could help explain recent variation in calf-cow ratios for the Bathurst herd (Figure 6). This result further demonstrates the covariance between parameters and field measurements as well as the likelihood that multiple environmental factors are influencing all parameters to a certain degree. One other significant finding was that different environmental factors influenced the proportion of females breeding and calf survival, further demonstrating the utility of a demographic model to explore variation in productivity compared to using calf-cow ratios, which may be affected by cow survival, calf survival and pregnancy rate.

There were strong associations detected by the analysis for adult female survival. March 31 snow depth was positively associated with adult female survival for both the Bathurst and Bluenose-East herds. March 31 snow depth has displayed periodic cycles (Figure 2) with recent high points in 2012 and 2015 and recent lows in 2010 and 2013. Trends in the Bathurst and Bluenose-East herds have been quite similar, which makes sense given that the winter ranges of these two herds overlap. Potential placement of caribou relative to wolves and other predators as well as harvesters may influence survival in higher snow depth years. June growing degree days were also positively related to cow survival. Cow survival is high during the calving season; the potential effect in this case could indicate early snow-melt and green-up, which may mean good range condition during early lactation, when cows have their highest nutrient needs (Russell and White 2000). High early calf survival in Porcupine caribou was associated with early green-up (Griffith et al. 2002) The effect of freezing rain on cow survival was marginal and may have been influenced by an outlier data point, however, the relationship was still apparent if this data point was set to a mean value. The negative effects of ice layers in snow cover on caribou have been well known for some time, particularly for high-arctic Peary caribou (Miller and Barry 2009).

The proportion of females breeding was influenced by insect harassment prior to the fall rut for the Bathurst herd as well as by the PDO. One explanation for the linkage of insect harassment is that it likely will reduce cow condition in the breeding season (Bergerud et al. 2008), thereby reducing pregnancy rate. The probability of pregnancy is strongly linked to cow condition in the breeding season (Gerhart et al. 1997, Russell et al. 1998). Insect activity on the Bathurst summer range was strongly linked to environmental variables, and behavioural responses of caribou were particularly pronounced in the presence of oestrid flies (Witter et al. 2011). Other studies have linked trend in the PDO to productivity (Joly et al. 2011) as further demonstrated in this analysis. However, Joly et al. (2011) found a different relationship of the PDO to herd trend in the Western Arctic and Teshekpuk herds, and no relation to herd trend in the Porcupine and Central Arctic herds, underscoring the complexity of environmental influences on caribou. June growing degree days may reflect a more pronounced growing season and favourable summer foraging conditions (Chen et al. 2014) which might positively influence pregnancy rates.

The relationship between calf survival and environmental factors was less clear. For both herds directional trends in calf survival were apparent (as indicated by directional linear or polynomial terms) suggesting that other factors beyond the environment, such as predation, likely influenced calf survival. Positive associations of calf survival with the mushroom index were suggested for the Bathurst herd. Mushrooms are a preferred food, high in mineral nutrients, for reindeer in the fall (Staaland et al. 1990) and may also be consumed in early winter (Inga 2007). A high mushroom index may also be indicative of more generally good late summer/early fall foraging conditions; this period is important for caribou to regain condition after the insect season (Russell and McNeil 2005). Negative associations with insect harassment and rain on snow days were suggested for calf survival in the Bluenose-East herd. These associations are biologically plausible in driving shorter term variation in calf survival rates; calves may enter winter in poor condition after a severe insect season and the negative effects of ice layers in snow cover are widely recognized for caribou and reindeer (Collins and Glenn 1991).

Univariate tests (Figures 5 and 10) suggested that many environmental covariates had some degree of linkage with demographic parameters as suggested by increased support over base models. However, the univariate tests were simplistic in that they assumed that the only covariate creating yearly variation (beyond the base model parameters) was the covariate being tested. Often the strength of association (as reflected by its odds ratio) was reduced once other covariates were added to the model. Therefore, the univariate results should be interpreted cautiously. Basically, these tests were the first step to identifying potential covariates for the next step of the analysis where more complex models were built. Multiple environmental variables affect caribou every year.

The most supported models for both the Bathurst and Bluenose-East contained six environmental covariates which further suggest the complex nature of the relationship between environmental covariates and caribou demography (Table 8). As demonstrated in Figure 3 many of the environmental variables are correlated and it is likely that they are linked across seasonal and yearly time scales. A single indicator, such as March 31 snow depth, will relate to other factors such as range condition the next summer (due to increased moisture), however, this will depend on temperature indices in the preceding spring and summer. May snow depth will be related to growing degree days and May temperature which would affect the rate of snow melt. Therefore, the actual "true model" would most likely contain even more covariates and therefore the main assumption of the model in this analysis is that the covariates that are included are indicators of larger scale environmental variation within any given year of the analysis. As an example, a high oestrid index in July may well coincide with a high drought index, as warm dry weather may readily contribute to both, and both are likely to affect caribou negatively.

Table 8. Summary of results of the integrated population model and environmental covariate analysis. The herd (Bathurst=BA, Bluenose-East = BNE) and direction of association is given for each association. The main correlated covariates from Figure 3 are given also.

Description	Cow survival (S_f)	Proportion females breeding (F_a)	Calf survival (S_c)	Correlated with
March 31 snow depth (m)	BA &BNE (+)			Rain on snow Freeze rain
Freeze rain	BA(-)		BA(+)	Rain on snow March 31 snow
Mushroom index			BA(+)	
Oesterid index		BA(-)	BNE(-)	Most temperature covariates
Pacific Decadal Oscillation		BA(-)		
May 15 snow	BNE(+)			May temperature GDD covariates SRCI
June 10 GDD	BNE(+)			
ROS days			BNE(-)	Freeze rain days
June Temperature		BNE(+)		Most temperature covariates
Arctic Oscillation		BNE(-)		

The results of this demographic model analysis will assist in partially determining factors influencing recent demographic trends. For example, adult female survival has been lower in past years than required for population recovery. The results of this analysis suggest that adult female survival is positively linked with March 31 snow depth. Further year by year comparison of caribou distribution and mortality locations may help further determine actual mechanisms that are creating this trend. Pregnancy rates (as indicated by proportions of females breeding) are related to oesterid indices during the year prior to calving. Input of these covariates into the OLS model may sharpen predictions of herd trend and help identify conditions favouring potential recovery.

Spatial and Temporal Analysis Collared Caribou Mortalities

The spatial and temporal analysis illustrated that there is considerable information available from the location patterns of mortalities that is not utilized in traditional aspatial survival analyses. For example, analyses suggest association between distance from roads, ecoregion, and northern landcover classes and mortality risk. This information, as well as temporal (seasonal and environmental) trends results in a more refined model of survival compared to a simple KM analysis. Analysis predictions can be used to further understand factors influencing mortality as well as provide spatial predictions of mortality risk that can be compared to observed locations and heat-maps.

Bathurst Herd

The results for the earlier period (1996-2009) demonstrate a fairly diffuse pattern of cow mortality, with some concentration of mortalities on the winter range near Wekweètì and Gamètì and the winter roads to these communities (Figure 18), and a reduced survival probability in winter within 25 km of roads (Figure 20). These patterns may be in part indicative of the harvest levels from this herd over this period; in the 1990s harvest was estimated at about 15,000 caribou/year, and in 2006-2009 at a still substantial 6,000/year (Figure 4), and the largest part of this harvest was from winter roads to Wekweètì and Gamètì (Adamczewski et al. 2009). A portion of the winter mortalities 1996-2009 is also likely associated with wolf predation.

The concentration of collared cow mortalities on the summer range in the more recent period (2010-2016) appears to be the main season of cow mortality, and it is most likely associated with predation by bears and wolves. Hunter harvest has been highly limited and focused on bulls (up to 70 bulls/year taken by sports hunters in NU associated with the small community of Bathurst Inlet). Winter mortalities have decreased proportionately in the herd in the more recent period, which may in part reflect severe harvest restriction for this herd 2010-2014 (a limit of 300 Bathurst caribou/year) and harvest closure in the Northwest Territories (NWT) in 2015-2016. Although wolves associated with the Bathurst herd have likely declined substantially with the herd at much lower numbers (Klaczek et al. 2016) the remaining wolves may still have a limiting effect on the herd. The high mortality risk on the summer range 2010-2016 (Figure 19) may be an indicator of the recent significance of predation on the herd during this season, however, lack of direct estimates of predation numbers precludes testing for the effect of predation as part of the demographic model analysis.

The low mortality risk for collared cows during calving (Figures 16, 19) is quite striking and was consistent through the earlier period 1996-2009 and the more recent period 2010-2016. These results may provide confirmation of the longstanding theory that cows calve in remote northern locations in June to distance themselves from most of their predators (Heard et al. 1996). The Bathurst calving grounds 1996-2016 are well north of the main concentration of denning wolves (see Klaczek et al. 2016). Early calf survival in calving Porcupine caribou was highest when they calved on their preferred North Slope calving grounds, where abundance of their main predators was reduced from areas further south (Griffith et al. 2002, Russell and McNeil 2005).

The main current limiting factor for this analysis is updated landcover/habitat data and more detailed information on anthropogenic influences as discussed in the future research section. As a result, the fit of the Bathurst model is marginal as indicated by ROC scores. It is suggested that the current iteration of this analysis be used as a means to identify more exact habitat and spatial covariates especially for some range areas where higher mortality levels are occurring.

One interesting peripheral finding of this analysis was the contracted range of the Bathurst herd in the more recent period (2010-2016), with wintering Bathurst caribou near treeline or on the tundra. This may in part reflect potential influence of recent fires on caribou movements. Namely, the core winter range of the Bathurst herd 2010-2016 is removed from areas that were recently burned (Figure 17) which might partially explain the more clustered distribution of caribou compared to the 1996-2009 time period. It is also possible that the contracted range in large part reflects the herd's much lower numbers over this time period; Bergerud et al. (2008) demonstrated the much-expanded range of the George River herd at high numbers in the 1980s than at low numbers in the 1950s. The use of more peripheral winter range areas by caribou at high numbers only has long been recognized by Indigenous elders (Beaulieu 2010).

Bluenose-East Herd

A preliminary analysis of the Bluenose-East collar data was conducted to assess dominant temporal and spatial survival rate patterns. A more in-depth approach as was done for the Bathurst herd is discussed further in the future research section. The summary analysis revealed a more diffuse pattern of mortalities by season as well as across the landscape. Mortalities were more spread out by season when compared with the Bathurst herd (Figure 23) which may have been due to the relatively large difference in size of the two herds. More generally, the larger size of the Bluenose-East herd resulted in less aggregation so that the spatial patterning of mortalities (Figure 24) more resembles the Bathurst herd from 1996-2009 (Figure 16).

Future Research

Integrated Population Model.

The following aspects of the integrated population model could be developed or explored further:

- The present analysis is mainly deterministic and therefore the actual effects of sampling and model-based variation has not been quantified beyond the use of the AIC_c model selection method. Bootstrapping method to estimate standard errors and confidence limits as was done in previous analyses (Boulanger et al. 2016, Boulanger et al. 2017) on parameters should be run once models have been reviewed and finalized. Monte Carlo simulation methods could also be used to further explore the effect of stochasticity on model predictions. An eventual goal is to use a Bayesian Markov Chain Monte Carlo methodology which will allow more direct estimation of confidence intervals as well as more direct modelling of the different data types used in the analysis (Kery and Schaub 2012).
- Harvest levels were assumed for the analysis to allow inference on true rather that observed survival (which contains hunting mortality). These levels were conservative and could have been higher; harvest was not well documented in all years. A sensitivity analysis of assumed harvest levels to model findings and estimates could be conducted to further assess the effect of harvest level on model outcomes.
- The time step for the OLS model is the caribou year and it is likely that some environmental covariates apply to certain seasons. The OLS model of adult female survival or calf survival could be further generalized into a summer and winter survival model which would allow more exact matching of covariates with the seasons of interest.
- It is possible that there are time-lags in the effects of some of the covariates on demography as well as interactions between covariates. In addition, non-linear trend could be possible for some covariates. For this analysis only additive main effects were considered, however, future analyses could assess more complex relationships. A workshop format to discuss more complex biologically based models would aid in development of these models.
- The estimation of male survival rate and incorporation into the OLS model would be useful. Males have been collared in the Bluenose-East herd and more recently collared for the Bathurst herd (starting in 2015) and therefore it should be possible to estimate survival for males as an added field parameter for the OLS model. This could potentially help with bull-cow ratio estimation; however, it is likely that estimates will still be imprecise therefore not affecting model estimates substantially.
- One question of management interest is what annual survival rate estimates will result from the demographic model and if survival is increasing in 2016 compared to previous years. Estimates could be derived for the environmental covariate and non-covariate models. In this case bootstrap or simulation methods could also be used to test if these estimates are different than those derived from previous analyses.
- The effect of predation was mainly modelled under the assumption that it would create a directional trend (as indicated by linear or polynomial terms) that was additive with

environmental variation. More elaborate methods to model predation could be employed especially if indices of predator abundance are available.

- The summer range cumulative indicator (Chen et al. 2014) provides a direct remote sensing measure of range condition. It was only available up to 2011 for the current analysis which precluded its use in the full analysis. If updated, it could be included in future model runs.

Spatial and Temporal Mortality Analysis

The Bathurst collared caribou mortality risk model provides a first cut at this type of analysis and demonstrated some interesting trends and changes over time. The following aspects of the spatial survival analysis could be developed further as listed below. It could be applied to the Bluenose-East herd, although the shorter period of collar information would limit the analysis temporally.

- **The use of updated habitat layers:** The present northern land-cover database used most likely does not reflect current range condition beyond broad scale habitat. Ecoregions are only classified for NWT, however, it is likely that some of the NWT ecoregions could be extended into NU. Further refinement of these layers may help better indicate areas of habitat-based mortality risk
- **The use of a shorter time step than once a month locations:** A monthly time step was used for the analysis to make the results most comparable to other collar-based survival estimates. In addition, from a survival estimation context, it is simplest if a similar time step is used for all the caribou in the analysis and using a month time step accounts for differences in collar reporting rates and helps ensure independence of locations. However, reducing the time step to weekly might provide more resolution on habitat use especially during migration or other times in which the caribou are moving.
- **More information on areas of higher hunting pressure:** Information about trails used by hunters on skidoos as well as more precise schedules of winter ice road operation would help define harvest pressure risk more precisely.
- **Inclusion of male collar mortality data:** The present Bathurst analysis only considers female collar data given that males have only recently been collared. Inclusion of males would confound comparison of past collar data (all females) with the current data set. However, it would be possible to further consider male collar data as separate stratum in the analysis.
- **Further analysis of March snow depth as an influence on caribou demography:** The association of March 31 snow depth with cow survival was suggested in both the demographic and spatial survival analyses. Further investigation of this factor on a year-by-year basis to assess differences in mortality locations, herd distribution, and other factors on high and low snow depth years may provide more inference on potential mechanisms behind this association.

ACKNOWLEDGEMENTS

Don Russell (Yukon College, Whitehorse, YT) provided CARMA climate covariates and discussion on their interpretation. Judy Williams and Bonnie Fournier (Environment and Natural Resources, Yellowknife, NWT) provided collar fate data and assistance in error-checking the collar data analysis used for survival. Jason Shaw (Caslys Consulting, Saanich, BC) extracted northern landcover covariates for the collar locations. Wenjen Chen provided the summer range condition index. Ashley McLaren (Environment and Natural Resources, Fort Smith, NWT) provided a useful review of an earlier version of this report. This study was funded by Environment and Natural Resources, Government of the Northwest Territories, Yellowknife, NWT.

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APPENDIX 1. CORRPLOT WITH CORRELATIONS COEFFICIENTS

	YEAR	SRCI	Drought_June	Tmp_June	Jun_10_gdd	June20_gdd	July20_gdd	Drought_July	aug5_oesterid	Temp_July	Temp_May	Rain_on_snow	FreezeRain	March31_snow	Mushroom_index	PDO	Rain_on_snow_days	Freeze_Rain_days	AO	FreezeThaw	May_15_snow	June_10_snow
YEAR	1	0.2	0.29	0.24	0.22	0.19	0.29	0.2	0.33	0.21	0.2	0.22	0.21	-0.18	-0.26	-0.26	-0.31	-0.31	-0.11	-0.12	-0.18	-0.28
SRCI	0.2	1	0.42	0.2	0.43	0.55	0.43	0.05	0.19	0.22	0.64	0.19	-0.22	-0.01	-0.04	0.01	-0.16	-0.13	-0.22	-0.27	-0.61	-0.19
Drought_June	0.29	0.42	1	0.68	0.59	0.72	0.72	0.64	0.66	0.34	0.46	0.2	0.11	-0.07	-0.14	-0.22	-0.2	-0.14	0.11	-0.34	-0.41	-0.18
Tmp_June	0.24	0.2	0.68	1	0.74	0.8	0.8	0.46	0.64	0.21	0.33	0.08	0.12	-0.15	-0.04	-0.1	-0.01	-0.1	-0.1	-0.09	-0.15	-0.27
Jun_10_gdd	0.22	0.43	0.59	0.74	1	0.91	0.85	0.49	0.57	0.34	0.61	0.1	0.08	0	0.11	0.17	-0.05	-0.18	-0.22	-0.19	-0.36	-0.37
June20_gdd	0.19	0.55	0.72	0.8	0.91	1	0.89	0.53	0.67	0.38	0.71	0.19	0.08	0.07	0.05	0.05	-0.02	-0.12	-0.19	-0.26	-0.54	-0.31
July20_gdd	0.29	0.43	0.72	0.8	0.85	0.89	1	0.63	0.86	0.63	0.65	0.16	0.1	-0.06	0.1	0.04	-0.01	-0.1	-0.13	-0.13	-0.37	-0.29
Drought_July	0.2	0.05	0.64	0.46	0.49	0.53	0.63	1	0.64	0.57	0.3	0.17	-0.04	-0.05	-0.09	0.01	0.07	-0.04	0.05	-0.07	-0.21	-0.15
aug5_oesterid	0.33	0.19	0.66	0.64	0.57	0.67	0.86	0.64	1	0.8	0.47	0.21	0.2	-0.13	0.12	-0.11	-0.01	-0.08	-0.05	-0.01	-0.21	-0.17
Temp_July	0.21	0.22	0.34	0.21	0.34	0.38	0.63	0.57	0.8	1	0.33	0.12	0.01	-0.12	0.17	-0.06	-0.04	-0.04	0.03	0.03	-0.16	-0.19
Temp_May	0.2	0.64	0.46	0.33	0.61	0.71	0.65	0.3	0.47	0.33	1	0.22	0.11	0.24	0	0.08	0.05	-0.01	-0.16	-0.17	-0.79	-0.15
Rain_on_snow	0.22	0.19	0.2	0.08	0.1	0.19	0.16	0.17	0.21	0.12	0.22	1	0.63	0.66	0.03	0.04	0.39	-0.01	0.27	0.09	-0.24	-0.22
FreezeRain	0.21	-0.22	0.11	0.12	0.08	0.08	0.1	-0.04	0.2	0.01	0.11	0.63	1	0.31	0.13	0.16	0.3	0.18	0.09	0.21	-0.18	-0.07
March31_snow	-0.18	-0.01	-0.07	-0.15	0	0.07	-0.06	-0.05	-0.13	-0.12	0.24	0.66	0.31	1	0.09	0.17	0.29	0.07	0.32	-0.04	-0.23	-0.09
Mushroom_index	-0.26	-0.04	-0.14	-0.04	0.11	0.05	0.1	-0.09	0.12	0.17	0	0.03	0.13	0.09	1	0.25	0.15	0.18	0.1	0.16	0.2	-0.21
PDO	-0.26	0.01	-0.22	-0.1	0.17	0.05	0.04	0.01	-0.11	-0.06	0.08	0.04	0.16	0.17	0.25	1	0.27	0.03	-0.29	0.05	-0.01	-0.16
Rain_on_snow_days	-0.31	-0.16	-0.2	-0.01	-0.05	-0.02	-0.01	0.07	-0.01	-0.04	0.05	0.39	0.3	0.29	0.15	0.27	1	0.59	0.15	0.76	-0.05	0.04
Freeze_Rain_days	-0.31	-0.13	-0.14	-0.1	-0.18	-0.12	-0.1	-0.04	-0.08	-0.04	-0.01	-0.01	0.18	0.07	0.18	0.03	0.59	1	0.16	0.59	-0.14	-0.03
AO	-0.11	-0.22	0.11	-0.1	-0.22	-0.19	-0.13	0.05	-0.05	0.03	-0.16	0.27	0.09	0.32	0.1	-0.29	0.15	0.16	1	0.01	0.05	-0.09
FreezeThaw	-0.12	-0.27	-0.34	-0.09	-0.19	-0.26	-0.13	-0.07	-0.01	0.03	-0.17	0.09	0.21	-0.04	0.16	0.05	0.76	0.59	0.01	1	0.19	0.08
May_15_snow	-0.18	-0.61	-0.41	-0.15	-0.36	-0.54	-0.37	-0.21	-0.21	-0.16	-0.79	-0.24	-0.18	-0.23	0.2	-0.01	-0.05	-0.14	0.05	0.19	1	0.16
June_10_snow	-0.28	-0.19	-0.18	-0.27	-0.37	-0.31	-0.29	-0.15	-0.17	-0.19	-0.15	-0.22	-0.07	-0.09	-0.21	-0.16	0.04	-0.03	-0.09	0.08	0.16	1

APPENDIX 2. DETAILS ON NORTHERN LANDCOVER CLASSIFICATION POOLING.

Table 9 provides details on northern landcover used in the spatial mortality analysis and number of caribou locations for each class.

Table 9. Northern landcover classes used in the spatial mortality analysis, pooled classes, and number of live locations for each class. Pooling was roughly based on previous RSF analyses (Boulanger et al. 2012).

Northern Landcover class	Pooled NLC class	Locations
Deciduous forest (>75% cover)	Deciduous	5
Deciduous shrubland (>75% cover)	Deciduous	55
Evergreen forest (>75% cover) - old	Evergreen	78
Evergreen open canopy (25-40% cover) - shrub-moss understory	Evergreen	287
Evergreen open canopy (40-60% cover) - lichen-shrub understory	Evergreen	85
Evergreen open canopy (40-60% cover) - moss-shrub understory	Evergreen	178
Herb-shrub-bare cover, mostly after perturbations	Herbaceous	75
Herb-shrub	Herbaceous-shrub	1683
Lichen barren	Lichen	717
Lichen-shrub-herb-bare	Lichen	574
Lichen-shrubs-herb, bare soil or rock outcrop	Lichen	162
Low regenerating to young mixed cover	Sparse	155
Low vegetation cover (bare soil, rock outcrop)	Sparse	148
Low vegetation cover	Sparse	572
Mixed coniferous (50-75% coniferous) - old	Evergreen	1
Mixed deciduous (25-50% coniferous trees; 25-60% cover)	Evergreen	11
Mixed evergreen-deciduous open canopy (25-60% cover)	Evergreen	4
Recent burns	Burns	137
Rock outcrop, low vegetation cover	Sparse	36
Shrub-herb-lichen-bare	Herbaceous-shrub	60
Shrub-herb-lichen-water bodies	Herbaceous-shrub	452
Shrubs-herb-lichen-bare	Herbaceous-shrub	92
Sparse coniferous (density 10-25%), herb-shrub cover	Sparse conifer	857
Sparse coniferous (density 10-25%), lichens-shrub-herb cover	Sparse conifer	174
Sparse coniferous (density 10-25%), shrub-herb-lichens cover	Sparse conifer	399
Water bodies	Water-ice	703
Wetlands	Water-ice	28