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The Influence of Climate on the Demography of Woodland Caribou

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EXECUTIVE SUMMARY

Understanding how species respond to climate variability has become fundamentally important to wildlife conservation and management in light of global climate change. Variation in climate can impact a species' distribution and demography by influencing resource availability and energy expenditure and by altering interactions within and among trophic levels. Because species differ in their life history traits and adaptive potential, responses to climate effects are likely to be species-specific and may further vary depending on the ecological context.

In this report, we evaluate how annual variation in climate affects the demography of woodland caribou (*Rangifer tarandus caribou*) with a particular focus on the boreal and central mountain ecotypes. Across much of their distribution, populations of woodland caribou have been declining due to increasing predation, which ultimately is linked to altered predator-prey dynamics stemming from human-mediated landscape alteration and climate change. Because of this predation-driven mechanism, hypothesized impacts of climate change have primarily focused on its role in the expansion of other ungulate species into caribou range and the subsequent increase in predators that incidentally prey on caribou. Climate change, however, may potentially impact caribou populations in other ways. Specific to predation, increasing freeze-thaw events in winter may enhance predator movements on snow, leading to increased caribou-predator encounters. Climate variability may also directly affect caribou reproduction and survival through metabolic mechanisms (e.g. forage availability, energy expenditure).

We evaluated climate effects on the demography of 21 caribou populations, each monitored for various intervals between 1994 and 2015. We specifically assessed how annual changes in seasonal minimum and maximum temperatures, seasonal precipitation, the frequency of freeze-thaw events and metrics of plant phenology impacted adult female survival and calf-to-adult female ratios, two demographics rates with high influence on caribou population dynamics. We used a mixed-effects modelling approach to evaluate five temporally-driven hypotheses, each relating season-specific climate effects to the two demographic rates.

Calf-to-adult female ratios and adult female survival were both impacted by climate variability although each rate was affected by different climate variables occurring within different seasons. Calf-to-adult female ratios were negatively affected by increasing mean temperatures across the majority of seasonal analyses with effects particularly strong in the winter before birth. During this time period, an increase in the mean minimum temperature from -20 °C to -15 °C resulted in a predicted decrease in calf-to-adult female ratios from 0.135 to 0.098 (a 38% decline). Calf-to-adult female ratios also responded positively to increasing snowfall in the year before birth. Adult female survival was more impacted by climate effects during the preceding spring and autumn, suggesting that climate impacts on this demographic rate are lagged. In both seasons, adult female survival responded to metrics of plant phenology, which collectively indexed forage quality and availability. These results suggested that a female's balance of body reserves from the preceding year influences annual survival and that this balance is dictated by resource accumulation in the previous autumn and spring. Comparing the two demographic rates, climate-mediated effects on calf-to-adult female ratios and adult female survival appeared to have similar impacts on caribou population dynamics.

In general, climate models had low explanatory power for both demographic rates, suggesting that other factors (e.g. landscape disturbance) have a higher influence on caribou population dynamics.

Future work will evaluate the potential influence of other climatic variables (e.g. length of snow cover, average daily snow depth), varying the temporal scales of analysis, and assessing for potential interactions between climate variability and landscape disturbance.

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INTRODUCTION

Climate exerts direct and indirect effects on a species' population dynamics (Sæther 1997; Sillett *et al.* 2000; Coulson *et al.* 2001; Post & Forchhammer 2002) and is a key determinant of a species' distribution (Guisan & Thuiller 2005). Direct climate effects include those related to temperature and precipitation, which dictate seasonal and annual resource availability and energy expenditure, thereby impacting survival and reproductive rates (Loison & Langvatn 1998; Coulson *et al.* 2001; Giroux *et al.* 2014). Climate can also impact a species' demography by altering interactions within and among trophic levels (e.g., Huggard 1993; Montgomery *et al.* 2013; Shepard & Lambertucci 2013). Despite the variable nature of climate effects, species are expected to be adapted to the normal climatic variation of local environments. Current and predicted rates of global climate change, however, will likely challenge the adaptive potential of many species (Hoffmann & Sgrò 2011; Vázquez *et al.* 2017) and, consequently, an increased emphasis has been placed on understanding how species respond to varying climatic conditions (Visser 2008).

Among vertebrates, climate effects on ungulate population dynamics have been relatively well-studied, particularly in temperate climates. Studies have primarily focused on how climate impacts juvenile recruitment and adult female survival as these demographic rates have the highest influence on ungulate demography (Gaillard *et al.* 2000; DeCesare *et al.* 2012a). Juvenile recruitment represents a combination of rates – pregnancy, fetal survival to parturition and juvenile survival – and each rate can be influenced by climate effects. For example, climate can influence late summer and early fall range conditions, which can impact pregnancy rates and over-winter fetal survival (Adams & Dale 1998; Cook *et al.* 2004; Parker *et al.* 2009). Climate during the winter and early spring can impact fetal survival by affecting maternal energy expenditures and consequently allocation of resources to the fetus (Barboza & Parker 2008). Conditions during these seasons can also affect juvenile survival as smaller offspring may have lower survival probabilities (Gaillard *et al.* 1997, 2013; Carstensen *et al.* 2009). Juvenile survival is further influenced by summer / fall range conditions and winter severity as these time periods influence the accumulation and depletion of body reserves critical to over-winter survival (Parker *et al.* 2009; Hurley *et al.* 2017). Adult female survival over winter is also affected by similar mechanisms (Parker *et al.* 2009) and for both rates, severe winters likely expose adults and juveniles to increased predation risk (Huggard 1993; Mech *et al.* 2001; Montgomery *et al.* 2013). The above examples illustrate relatively direct climate relationships, but both juvenile recruitment and adult female survival can be influenced by lagged climate effects as well; for instance, severe winters may limit pregnancy rates and influence juvenile recruitment in the following year (Larter & Nagy 2001).

While it is well-established that climatic variation impacts ungulate demography, there is still considerable uncertainty as to the exact nature of many climate-demography relationships (Tyler 2010). For example, Hegel *et al*. (2010) found that variability in juvenile recruitment in northern mountain caribou was best explained by winter climate whereas Chen *et al.* (2014) reported that recruitment variability in barren-ground caribou was best explained by summer range conditions. Responses to specific climate effects may also be variable. Huggard (1993) and Hebblewhite (2005) reported that increasing snow depth interacted with predation to lower survival in elk (*Cervus elaphus*) yet Larter *et al.* (2017) found snow depth had no effect of juvenile recruitment in the boreal ecotype of woodland caribou. Joly *et al.* (2011) found that climatic conditions indexed by the Pacific Decadal Oscillation had contrasting effects on the growth rates of two caribou herds in Alaska. Similarly, Tyler *et al.* (2008) and

Hansen *et al.* (2011) reported contrasting effects of warmer winters on growth rates of spatially separated populations of Svalbard reindeer (*Rangifer tarandus platyrhynchus*). Collectively, these examples suggest that although general trends may be apparent, ungulate responses to changing climatic conditions will likely be context- and species-specific.

In this report, we evaluate the potential influence of climate effects on the demography of woodland caribou. Populations of woodland caribou have been declining throughout most of their distribution due to increasing predation facilitated by human-mediated landscape alteration and climate change (Sorensen *et al.* 2008; Latham *et al.* 2011; Apps *et al.* 2013; Masood *et al.* 2017). Increasing predation from climate change has been predominantly linked to the expansion of other ungulate species (e.g. white-tailed deer [*Odocoileus virginianus*]) into caribou range, which increases the abundance of predators that incidentally prey on caribou (Latham *et al.* 2011; Dawe *et al.* 2014). Climatic conditions, however, may affect woodland caribou populations via some of the more direct mechanisms described above. Such effects have been demonstrated for woodland caribou populations in northeastern British Columbia where adult female survival and juvenile recruitment were both comparatively low in 2014 following a protracted winter with heavy snow accumulation extending through the end of April 2013 (Culling & Culling 2013, 2014). In this example, lowered adult survival was attributed to increases in both condition-related deaths (e.g. starvation) and predation.

We assessed climate effects on the population dynamics of woodland caribou by evaluating five temporally-driven hypotheses (Table 1). These hypotheses link both direct and indirect indicators of climate effects to rates of adult female survival and juvenile recruitment. Direct indicators included measures of seasonal temperatures and precipitation. Indirect indicators included seasonal metrics of plant phenology that indexed forage quality and quantity. We further considered the number of freeze-thaw (or icing) events occurring within a winter. Such events can negatively impact caribou populations by limiting forage availability, which can lower survival and recruitment rates via body condition-related mechanisms potentially interacting with predation, or by enhancing predator movement on snow (Murray & Boutin 1991) leading to an increase in caribou-predator encounters.

Table 1: Five temporally-driven hypotheses for explaining climate effects on demographic rates of woodland caribou. Effects are described as phenoclimatic because they include typical climate indicators (i.e. temperature and precipitation) and indirect indicators reflected by changes in plant phenology. The monitoring year is measured from April 1 – March 31 for British Columbia and Northwest Territory herds and from May 1 – April 30 for Alberta herds.

Hypothesis	References
1. Phenoclimatic effects during the late summer and autumn before the monitoring year affects juvenile recruitment and adult female survival. *Mechanisms:* – Forage availability can affect pregnancy rates. – Forage availability affects body reserves for winter, influencing over-winter survival and energy allocation for reproduction.	Cook *et al.* 2004; Parker *et al.* 2009
2. Phenoclimatic effects during the winter before the monitoring year affects juvenile recruitment and adult female survival. *Mechanisms:* – Winter severity affects resource availability and energy expenditure, impacting over-winter survival and energy allocation for reproduction.	Coulson *et al.* 2001; Parker *et al.* 2009; Hegel *et al.* 2010; Hansen *et al.* 2011
3. Phenoclimatic effects during calving (spring) affects juvenile recruitment and adult female survival. *Mechanisms:* – Affects female's ability to replenish body reserves and meet lactation demands; therefore, also affects body fat accumulation of calf. – "Slow green-up" hypothesis posits that slow development of plant phenology in spring has a positive effect on ungulate population dynamics because it increases the temporal availability of peak forage quality.	Parker *et al.* 2009; Christianson *et al.* 2013
4. Phenoclimatic effects during the late summer and autumn of the monitoring year affects juvenile recruitment and adult female survival. *Mechanisms:* – Similar to Hypothesis 1. Affects resource accumulation and energy allocation of female and calf, which influences over-winter survival of both.	Parker *et al.* 2009; Chen *et al.* 2014; Hurley *et al.* 2017
5. Phenoclimatic effects during the winter of the monitoring year affects juvenile recruitment and adult female survival. *Mechanisms:* – Similar to Hypothesis 2. Winter severity affects resource depletion and energy expenditure of female and calf, influencing over-winter survival of both.	Tyler 1986; Coulson *et al.* 2001; Parker *et al.* 2009; Hansen *et al.* 2011; Hurley *et al.* 2017

METHODS

Caribou Demographic Data

We used demographic data from 21 herds (or populations) of woodland caribou (Fig. 1), each monitored for various periods from 1994 – 2015. Eighteen herds were from the boreal ecotype (Designatable Unit 6) and three herds (A La Peche, Redrock-Prairie Creek, and Narraway) were from the central mountain ecotype (Designatable Unit 8; COSEWIC 2011). Of the boreal herds, ten were situated in Alberta (Bischto, Caribou Mountains, East Side Athabasca River, Little Smoky, Nipisi, Red Earth, Richardson, Slave Lake, West Side Athabasca River, and Yates), four were in British Columbia (Calendar, Maxhamish, Snake-Sahtaneh, and West Side Fort Nelson) and two were in the Northwest Territories (Decho and Hay River Lowlands). Two boreal herds were transboundary: the Chinchaga herd, which spanned the Alberta-British Columbia border, and the Cold Lake herd, which spanned the Alberta-Saskatchewan border. Note that West Side Fort Nelson in British Columbia is an amalgamation of the Prophet and Parker ranges and an area of core caribou use north of Fort Nelson. This amalgamation was necessary because of small sample sizes of radio-collared caribou, the small spatial extents of these areas, and their close proximity to each other, which suggests that they should share similar climatic conditions.

Data delineating herd boundaries (or ranges) were provided by provincial governments (Fig. 1). In general, these boundaries were similar to those described by Environment Canada (Environment Canada 2012, 2014) except for the above mentioned West Side Fort Nelson area, which amalgamates two ranges (Prophet and Parker) and a currently unrecognized area of caribou use (the Fort Nelson core; Culling & Culling 2013). For transboundary herds (e.g. Chinchaga and Cold Lake), we used polygons spanning both provinces.

We assessed caribou response to varying climatic conditions using two demographic rates: calf-adult female (CAF) ratios, which index juvenile recruitment (DeCesare *et al.* 2012a), and adult female survival (AFS). These herd-specific demographic data were provided by provincial governments. Data estimating CAF ratios (Fig. 2) were collected during aerial surveys conducted in March. These surveys recorded the total number of calves and adult females observed. Because our focus was not on population growth *per se*, CAF ratios were not adjusted to reflect the number of female calves to the total number of females across all age classes (DeCesare *et al.* 2012a). For AFS (Fig. 3), monitoring data from radio-collared females in each herd were used to derive Kaplan-Meier estimates of annual survival rates. The monitoring interval for estimating survival differed slightly among jurisdictions, with Alberta using a monitoring year of May 1 – April 30 while BC and the NWT used April 1 – March 31. For trans-boundary herds where both boundary provinces were monitoring demographic rates independently (i.e., Chinchaga herd, AB and BC), we combined data for CAF ratios (i.e. summed the total number of calves observed across jurisdictions and summed the total number of adult females observed across jurisdictions) and derived combined estimates of AFS using means weighted by sample sizes from each province and year. Across herds, CAF and AFS were generally uncorrelated (Spearman's correlation coefficient [r] = -0.01) and AFS was more highly correlated (r = 0.92) with a population's growth rate than CAF (r = 0.38; Fig. 4).

The total number of monitoring years differed among herds and by demographic rate. In general, CAF ratios were monitored for a longer period (277 herd-years) than AFS (268 herd-years). As a result, the mean per-herd number of years monitored was higher for CAF ratios ($\bar{x}$ = 13.2; range: 4 – 22) than for AFS ($\bar{x}$ = 12.8; range: 3 – 22). Jurisdiction also influenced monitoring timespans with all BC herds having four years of CAF ratios and three years of AFS data while all Alberta and NWT herds had at least eight years of both demographic rates.

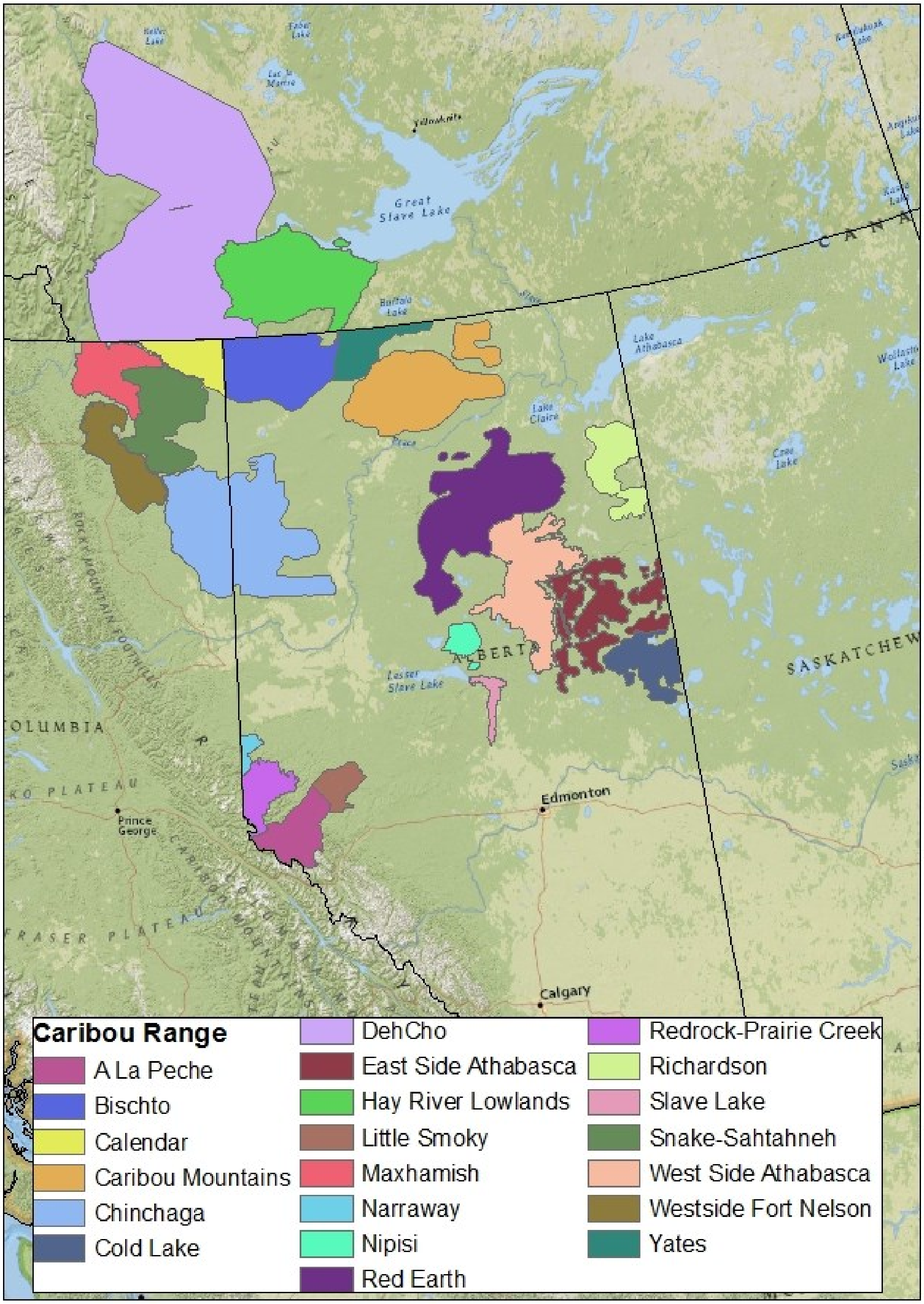

Figure 1: Range delineations of 21 populations of woodland caribou. Calf-adult female ratios and adult female survival were monitored annually for various periods within each range between 1994 and 2015. Note that the Cold Lake range extends into Saskatchewan and this portion of the range is not shown. Also the Westside Fort Nelson area in British Columbia is an amalgamation of the Prophet and Parker ranges and an area used by caribou north of Fort Nelson.

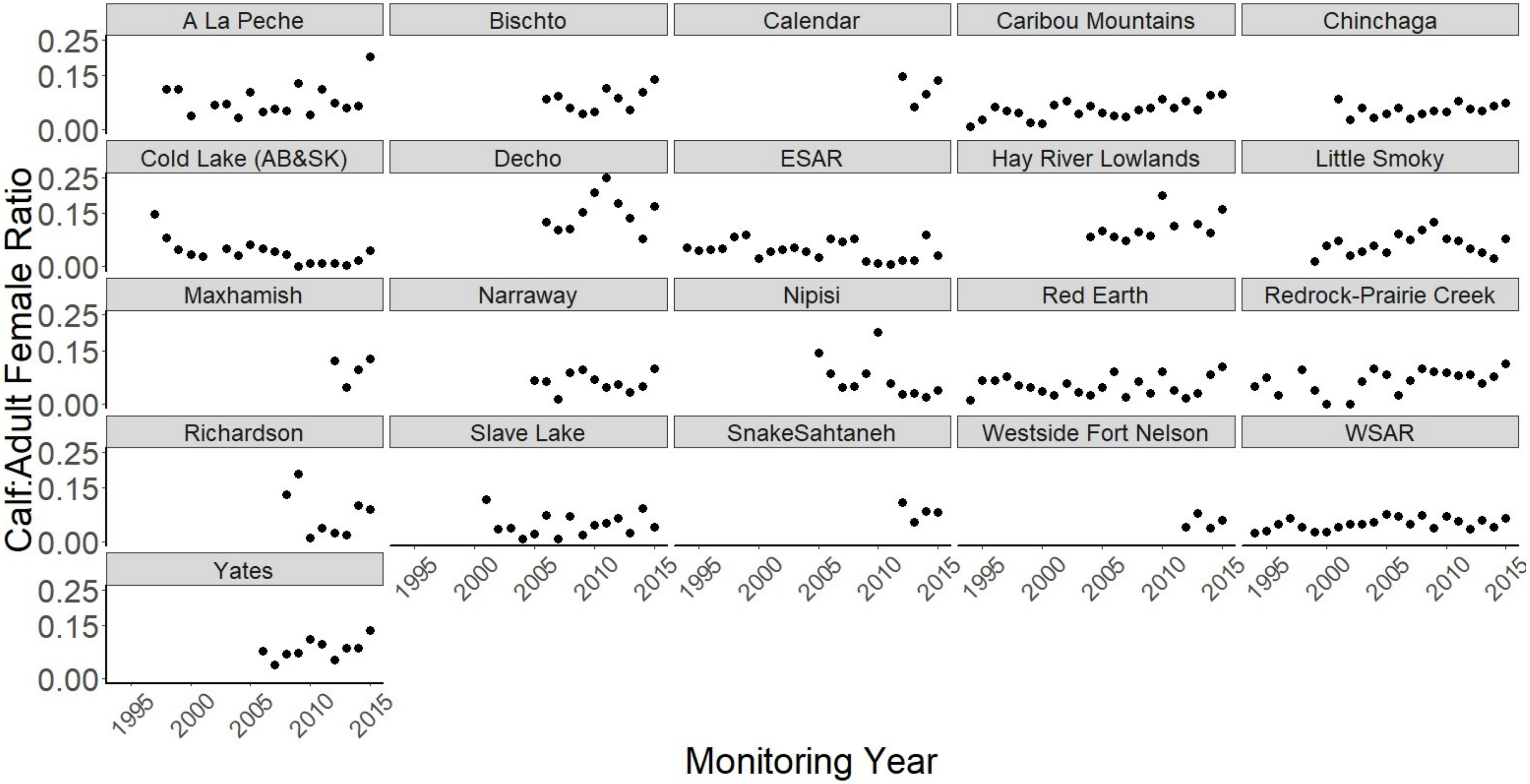

Figure 2: Annual calf-to-adult female ratios estimated for 21 herds of woodland caribou monitored for various intervals from 1995 – 2015. Data used to estimate ratios were collected during aerial surveys conducted during March when calves are ~ 9 -10 months old. [ESAR = East Side Athabasca River; WSAR = West Side Athabasca River].

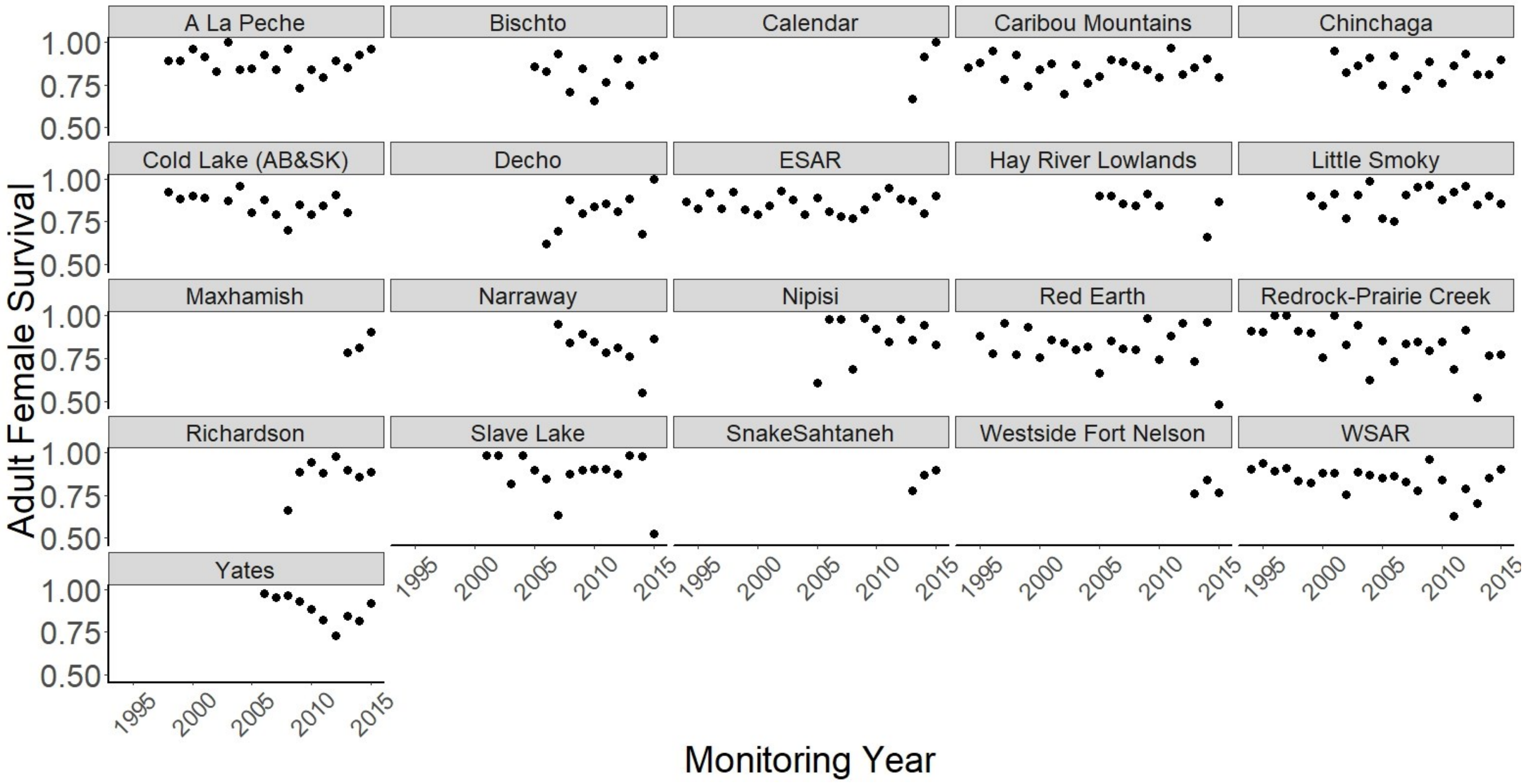

Figure 3: Annual estimates of adult female survival estimated for 21 herds of woodland caribou monitored for various intervals from 1995 – 2015. Estimates were derived using data from radio-collared females in each herd. [ESAR = East Side Athabasca River; WSAR = West Side Athabasca River].

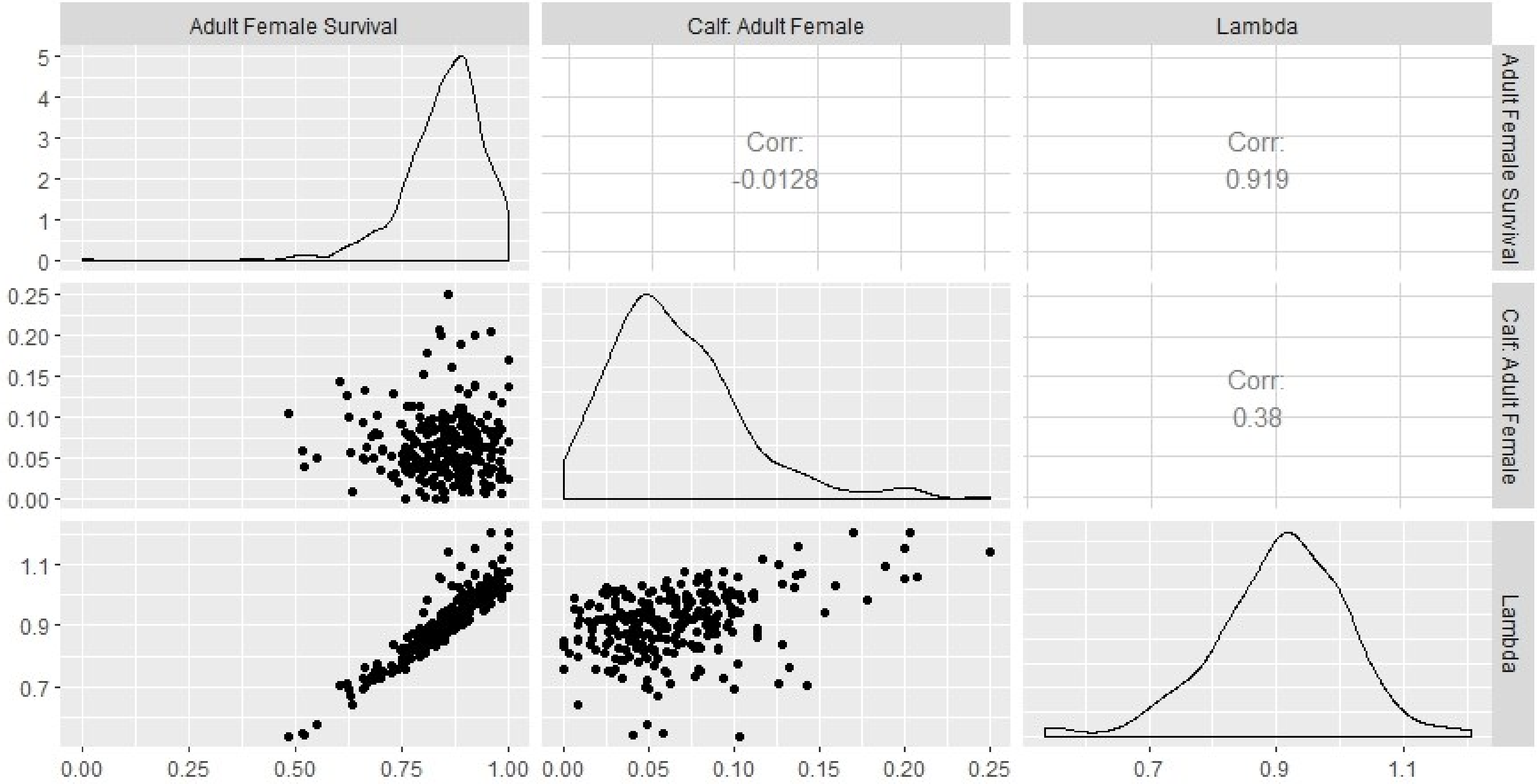

Figure 4: Relationships among adult female survival, calf: adult female ratios and population growth rate (lambda) for 21 herds of woodland caribou. “Corr” indicates the strength of the correlation (measured by Spearman’s correlation coefficient) between the column and row variables.

Climate Data

To model potential variation in climate, we used a suite of explanatory variables, including seasonal minimum and maximum temperatures, seasonal accumulations of snowfall or rainfall, the number of freeze-thaw events in a given winter and metrics derived from normalized difference vegetation index (NDVI) data representing temporal changes in forage quality and availability (Table 2). Because our *a priori* hypotheses considered effects prior to a given demographic year, we considered lag effects up to one year prior for all explanatory variables.

We modelled seasonal metrics of temperature and precipitation using ClimateNA data (https://sites.ualberta.ca/~ahamann/data/climatena.html). These data, which span 1961 – 2015, estimate minimum and maximum temperatures and accumulated precipitation at a resolution of 1-km. We calculated mean temperature and precipitation values across four seasons: winter (December [previous year] – February), spring (March – May), summer (June – August) and autumn (September – November). We calculated the mean minimum temperature for winter and the mean maximum temperature for the other seasons. For precipitation, we estimated the mean rainfall across all seasons and the mean snowfall for autumn, winter and spring. We also estimated the total annual snowfall within a given year.

To model the number of freeze-thaw events in a given winter, we used data from the Freeze/Thaw Earth System Data Record (http://freezethaw.ntsg.umt.edu/). These data measure the number of thaw events (units = weeks/year) during a winter (November – April), excluding "transition" events (i.e., fall freeze-up and spring thaw periods), and only in areas with snow cover. Thaw events are determined by classifying temporal changes in the time-series of microwave brightness temperature observations remotely collected by global satellites. These freeze-thaw data span 1979-2015 and have a 25-km resolution.

We used NDVI data to model temporal changes in plant phenology. NDVI is calculated from spectral reflectance measurements from the red (or visible) and near-infrared regions with higher values indicating greater vegetation density and greenness. Increasingly, NDVI has been used to model forage productivity and availability for ungulates (e.g., Pettorelli *et al.* 2007; DeCesare *et al.* 2012b; Bastille-Rousseau *et al.* 2016; Hurley *et al.* 2017). NDVI data are available from a number of sources but no one source covered the entire monitoring period of the caribou demographic data (1994 – 2015). For 2000-2015, we used NDVI data from MODIS (https://lpdaac.usgs.gov/dataset_discovery/modis/modis_products_table/mod13q1). These data are derived from 16-day composite imagery and have a 250-m spatial resolution. For pre-2000, we used NDVI data derived from Advanced Very High Resolution Radiometer (AVHRR) imagery available from Ecocast (https://ecocast.arc.nasa.gov/data/pub/gimms/3g.v0/). These data are produced bi-monthly and have a spatial resolution of 8-km. Although the resolutions of the two data sets differ substantially, this difference is likely not problematic because we calculated mean NDVI values over a large spatial extent (i.e., a herd's range) and comparisons of AVHRR and MODIS metrics of NDVI have found high levels of agreement (Eidenshink 2006). Because NDVI is most appropriate for modelling ungulate forage dynamics in open areas, we clipped NDVI layers to include only non-forested areas.

We developed five metrics describing changing plant phenology using the NDVI data. The first was the integrated NDVI (iNDVI), which is the sum of NDVI values in a given area within a specific time frame (Pettorelli *et al.* 2005; Christianson *et al.* 2013). We calculated iNDVI values in spring during an interval when green-up is expected to occur in the boreal forest (9 May to 9 June) and in autumn when plant senescence is expected (30 September – 30 October) . Compared to other years in a given area, higher iNDVI values indicate earlier green-up in spring and later plant senescence in autumn. The second and third metrics were the annual maximum NDVI value and the timing (or date) of the annual NDVI maximum. The former metric provides an index of annual vegetation productivity while the latter provides the timing of maximum forage availability (Pettorelli *et al.* 2005). The final two metrics represented rates of spring green-up and autumn senescence. To index the overall rate of spring green-up, we used linear regression to estimate the rate of NDVI change between 9 May and the date of the maximum NDVI value, regressing NDVI against Julian day (Pettorelli *et al.* 2005). Within this same time frame, we also estimated the maximum rate of spring green-up, defined as the maximum difference between any two 16-day (or bimonthly) NDVI intervals (Pettorelli *et al.* 2005; Bastille-Rousseau *et al.* 2016). We repeated this same process to estimate the overall rate of autumn senescence and the maximum rate of senescence.

Table 2: Explanatory variables used to model phenoclimatic effects on demographic rates of woodland caribou.

Phenoclimatic Effect	Variable	References
Weather	mean spring maximum temperature	Stenseth *et al.* 2002; Wittmer *et al.* 2007; Tyler 2010
	mean summer maximum temperature	
	mean autumn maximum temperature	
	mean winter minimum temperature	
	mean spring snowfall accumulation	
	mean autumn snowfall accumulation	
	mean winter snowfall accumulation	
	mean total snowfall accumulation for the year	
	mean spring rainfall	
	mean autumn rainfall	
	mean winter rainfall	
Freeze-thaw Events	cumulative count during periods with snow cover (units = weeks / year)	Tyler 2010; Hansen *et al.* 2011
NDVI	Integrate NDVI – The sum of NDVI values from May 9 to June 9. High values suggest early spring while low values indicate late spring. Repeated for fall (September 30 to October 31)	Pettorelli *et al.* 2005, 2007; Christianson *et al.* 2013; Bastille-Rousseau *et al.* 2016; Hurley *et al.* 2017
	Maximum annual NDVI value	
	Date of maximum NDVI value	
	Rate of spring green-up – Estimated slope of NDVI increase from May 9 to date of maximum NDVI value	
	Maximum rate of spring green-up – The maximum difference between consecutive 16-day averages occurring between May 9 and the date of the maximum NDVI value	
	Rate of autumn senescence – Estimated slope of NDVI decrease from the date of maximum NDVI value to October 31	
	Maximum rate of autumn senescence – The maximum absolute difference between consecutive 16-day averages occurring between the date of the maximum NDVI value and October 31	

Data Analysis

We evaluated climate effects on caribou demographic rates using generalized linear mixed-effects models (GLMMs), which account for the hierarchical structure of the data (i.e. repeated annual measures of demography and climate variables for each herd; Zuur *et al.* 2009). Following Hegel *et al.* (2010), we specified year and herd as crossed random grouping factors (i.e., random intercepts) for all models to capture baseline differences among herds and years. We also created a "trend" variable to account for possible long-term trends in both demographic rates and thus potentially increase discrimination of true climate effects. To maintain herd as the primary sampling unit and generate appropriate standard errors (Schielzeth & Forstmeier 2009), we specified all climate and trend variables as random slopes within GLMMs, thereby generating herd-specific coefficients. These models took the form

$$\text{CAF ratio or AFS} = \beta_0 + \beta_1 x_{1ijk} + \beta_2 x_{2ijk} + \beta_3 Trend_{ijk} + \gamma_{0j} + \gamma_{0k} + \gamma_{nij} x_{nij}$$

(Gillies *et al.* 2006)

where β_0 is the fixed-effect intercept, β_n is the fixed-effect – or population mean – coefficient for covariate x_n, γ_{0j} is the random intercept for herd *j*, γ_{0k} is the random intercept for year *k*, and γ_{nij} is the random slope (or coefficient) of covariate x_n for herd *j*. Given this formulation, we restricted the number of explanatory variables within a model to a maximum of three because of the small number of herds ($n = 21$). To adequately assess all potential climate effects within each *a priori* hypothesis, we ran multiple models, one assessing weather variables (temperature and precipitation), one evaluating freeze-thaw events, and one assessing NDVI metrics (Table 2). Prior to model fitting, we assessed for correlations among explanatory variables using Pearson's correlation coefficient (*r*). For highly correlated variables ($r \geq |0.60|$), we retained the variable with the highest correlation to the two response variables. We further assessed for multicollinearity using variance inflation factors (VIFs), retaining all variables with VIFs < 2 (Graham 2003). All explanatory variables were centered to improve model convergence and facilitate the comparison of effect sizes.

For response variables, modelled distributions depended on the demographic rate. Because rates of AFS were recorded as proportions (i.e. between 0 and 1), we first subtracted a small constant (0.0005) from each survival estimate then applied a logit transformation, which allowed modelling with a Gaussian distribution. In all survival models, we specified the maximum number of radio-collared females in a given year (e.g. 1 April – 31 March) as a sample weight. CAF ratios were considered binomial count data and thus models used a binomial distribution and the number of adult females observed was specified as a sample weight.

For this report, we evaluate effect sizes within each individual model and provide two R^2 statistics to assess model fit: the marginal $R^2_{\text{GLMM}(m)}$, which is the explained variation of the fixed effects, and the conditional $R^2_{\text{GLMM}(c)}$, which is the explained variation provided by both the fixed and random effects (Johnson 2014). We do not specifically discriminate among hypotheses using information-theoretic approaches (Burnham & Anderson 2002) because comparing non-nested mixed-effects models can be problematic due to the co-dependence between the fixed and random effect structures (i.e., selection of the random effect structure affects selection of the fixed effects; Zuur *et al.* 2009; Lewis *et al.* 2011; Smith 2015).

All analyses were performed in R, version 3.3.2 (R Core Team 2016), using the packages 'lme4' (Bates et al. 2015) to estimate GLMMs, and 'piecewiseSEM' to estimate R^2 for mixed-effects models (Lefcheck 2015).

RESULTS

Climate Effects on Calf-Adult Female Ratios

Model outputs across the five hypotheses suggested that CAF ratios were positively influenced by colder climate effects (Table 3). In the autumn, winter and spring before parturition and in the autumn and winter after parturition, CAF ratios were negatively correlated with mean temperatures with the largest effect occurring in the winter before parturition (Fig. 2). CAF ratios also generally increased with increasing snowfall in the winter before birth. During this same time period, an increasing frequency of freeze-thaw events negatively affected CAF ratios though the effect size was relatively small ($\beta = -0.079$, SE = 0.041). Indices of forage productivity, as indexed by NDVI, appeared to have little effect on CAF ratios except for a negative correlation with the maximum annual NDVI value. This relationship may further reflect that CAF ratios seem to be higher in colder years if lower maximum NDVI values are associated with shorter growing seasons and lower summer temperatures. Among models, the fixed – or population-level – effects of the model describing temperature and snowfall effects in the winter before parturition had the highest explanatory power although the explained variation was generally low ($R^2_M = 0.030$).

Table 3: Parameter estimates (β) and standard errors (SE) for weather and NDVI variables used in linear mixed-effects models representing five hypotheses for explaining climate effects on calf-adult female ratios of woodland caribou. Model fit is represented by the marginal R^2 (R^2_M; variance explained by the fixed effects) and conditional R^2 (R^2_C; variance explained by the fixed and random factors). All variables were specified as random slopes with caribou herd as a random intercept; thus, standard errors reflect herd as the sampling unit. Climate variables in bold indicate $p \leq 0.10$.

Hypothesis	Model	Variable	β	SE	*p*	R^2_M	R^2_C
H1	Autumn Weather Before Birth	**Mean maximum temperature**	**-0.207**	**0.109**	**0.059**	0.015	0.205
		Snowfall	0.071	0.108	0.510		
		Trend	-0.125	0.196	0.521		
	Autumn NDVI Before Birth	**Maximum annual NDVI value**	**-0.287**	**0.084**	**0.001**	0.027	0.140
		Integrated NDVI index	0.094	0.066	0.156		
		Trend	-0.443	0.159	0.005		
H2	Winter Weather Before Birth	**Mean minimum temperature**	**-0.364**	**0.101**	**< 0.001**	0.030	0.128
		Total snowfall for year	**0.275**	**0.118**	**0.020**		
		Trend *	-0.008	0.116	0.948		
	Winter Freeze-Thaw Before Birth	**Number of freeze-thaw weeks**	**-0.079**	**0.041**	**0.052**	0.013	0.152
		Trend	-0.371	0.208	0.074		
H3	Spring Weather Before Birth	**Mean maximum temperature**	**-0.199**	**0.066**	**0.003**	0.016	0.201
		Snowfall	-0.017	0.133	0.897		
		Trend	-0.303	0.212	0.153		
	Spring NDVI During Calving	Integrated NDVI index	0.04	0.098	0.682	0.008	0.182
		Green-up rate	0.047	0.056	0.397		
		Trend	-0.297	0.231	0.199		
H4	Autumn Weather Year of Birth	**Mean maximum temperature**	**-0.168**	**0.08**	**0.035**	0.011	0.159
		Snowfall	0.069	0.131	0.599		
		Trend	-0.104	0.186	0.574		

(cont'd)

Hypothesis	Model	Variable	β	SE	*p*	R^2_M	R^2_C
	Autumn NDVI Year of Birth	Maximum NDVI value	0.096	0.154	0.533	0.004	0.191
		Integrated NDVI value	-0.147	0.098	0.133		
		Trend	-0.004	0.220	0.985		
H5	Winter Weather Year of Birth	**Mean minimum temperature**	**-0.17**	**0.105**	**0.104**	0.008	0.177
		Total annual snowfall	0.149	0.162	0.360		
		Trend	-0.131	0.190	0.490		
	Winter Freeze-Thaw Year of Birth	Number of freeze-thaw weeks	0.011	0.049	0.826	0.010	0.167
		Trend	-0.348	0.221	0.115		

* Model would not converge with trend as a random coefficient; therefore, trend was specified as a fixed effect only.

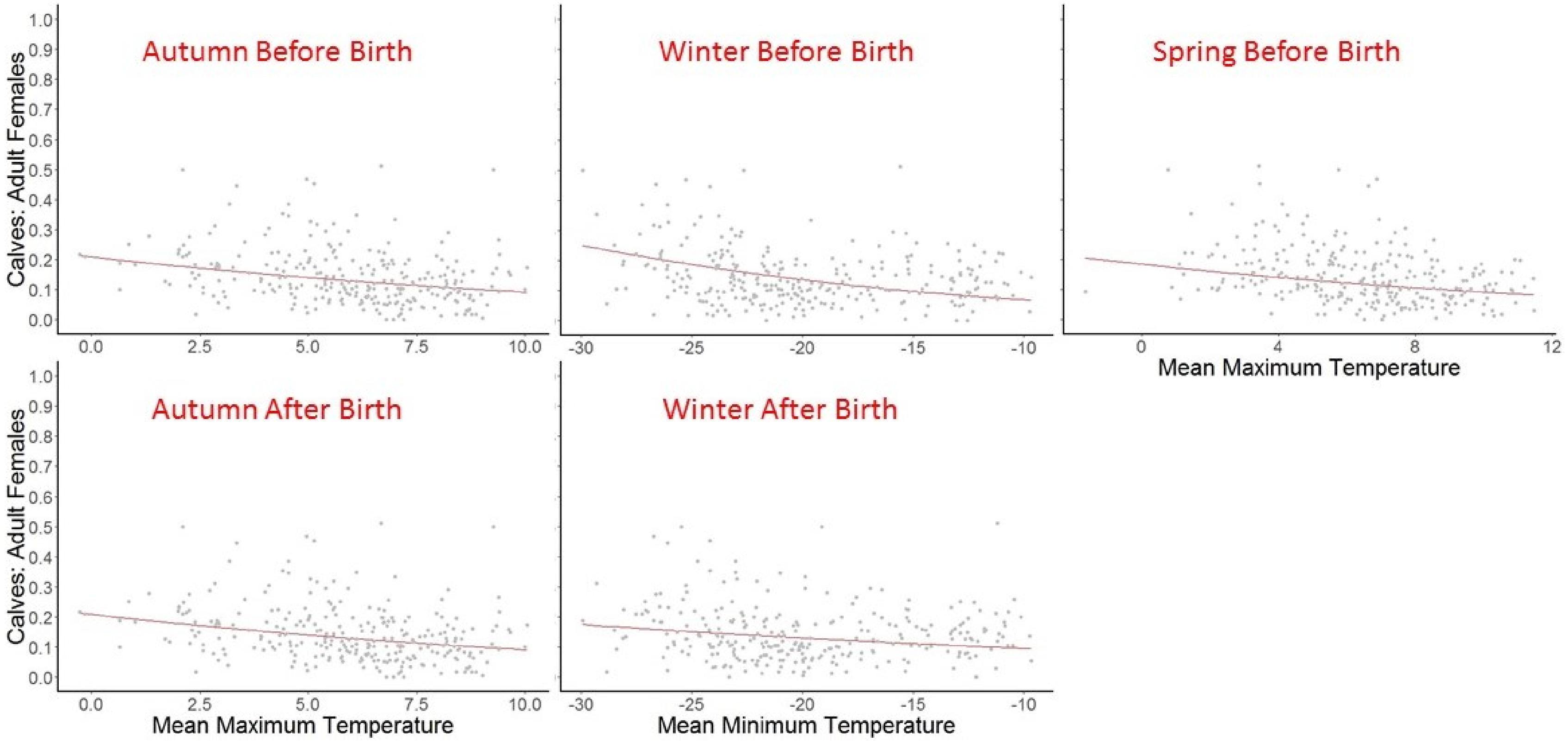

Figure 5: The predicted effects of seasonal mean maximum (spring and autumn) or minimum (winter) temperatures on the ratio of calves to adult females across 21 populations of woodland caribou, each monitored for various periods from 1994 – 2015. Calf-adult female ratios were recorded during March when calves are ~ 10 months old.

Climate Effects on Adult Female Survival

Adult female survival seemed to be more influenced by climate effects during the autumn and spring compared to the winter (Table 4). The strongest effects occurred in the autumn prior to the monitoring year as AFS was positively correlated with the mean maximum temperature and the date of the maximum annual NDVI value with the latter appearing to have a slightly greater effect (Fig. 3). These relationships may suggest that AFS is affected by late summer and early autumn growing conditions. Rainfall in the autumn after parturition also had a positive effect on AFS. During spring, AFS was positively correlated with increasing snowfall accumulation and had a weak negative correlation with iNDVI (Fig. 4). Collectively, these two relationships suggest that AFS is generally higher during late versus early springs. Across models, the fixed effects of the model representing NDVI indices in the autumn before parturition had the highest explanatory power though the percent variation explained was small ($R^2_M = 0.004$) and overall, climate models explained less variation in AFS than CAF ratios.

Table 4: Parameter estimates (β) and standard errors (SE) for weather and NDVI variables used in linear mixed-effects models representing five hypotheses for explaining climate effects on adult female survival of woodland caribou. Model fit is represented by the marginal R^2 (R^2_M; variance explained by the fixed effects) and conditional R^2 (R^2_C; variance explained by the fixed and random factors). All variables were specified as random slopes with caribou herd as a random intercept; thus, standard errors reflect herd as the sampling unit. Climate variables in bold indicate $p < 0.10$

Hypothesis	Model	Variable	β	SE	*p*	R^2_M	R^2_C
H1	Autumn Weather Prior to MY †	**Mean maximum temperature**	**0.172**	**0.091**	**0.073**	0.003	0.020
		Snowfall	0.209	0.2	0.383		
		Trend	-0.322	0.156	0.057		
	Autumn NDVI Prior to MY	**Date of maximum annual NDVI value**	**0.243**	**0.078**	**0.006**	0.004	0.011
		Integrated NDVI index	-0.112	0.115	0.345		
		Trend *	-0.24	0.112	0.033		
H2	Winter Weather Prior to MY	Mean minimum temperature	0.06	0.087	0.496	0.001	0.005
		Snowfall	0.075	0.079	0.349		
		Trend	-0.308	0.153	0.071		
	Winter Freeze-Thaw Prior to MY	Number of freeze-thaw weeks	0.002	0.07	0.98	0.001	0.004
		Trend	-0.291	0.139	0.045		
H3	Spring Weather Prior to MY	Mean maximum temperature	-0.027	0.08	0.739	0.001	0.005
		Snowfall	**0.141**	**0.068**	**0.046**		
		Trend	-0.296	0.147	0.056		
	Spring NDVI During Calving of MY	**Integrated NDVI index**	**-0.124**	**0.074**	**0.096**	0.001	0.007
		Maximum green-up rate	-0.048	0.092	0.612		
		Trend	-0.297	0.166	0.113		
H4	Autumn Weather of MY	Mean maximum temperature	0.032	0.084	0.722	0.001	0.006
		Rainfall	**0.128**	**0.067**	**0.073**		
		Trend	-0.293	0.174	0.175		

(cont'd)

Hypothesis	Model	Variable	β	SE	*p*	R^2_M	R^2_C
	Autumn NDVI of MY	Maximum NDVI value	-0.002	0.117	0.99	0.001	0.006
		Maximum senescence rate	0.004	0.08	0.96		
		Trend	-0.222	0.118	0.062		
H5	Winter Weather of MY	Mean minimum temperature	0.075	0.087	0.394	0.001	0.005
		Total annual snowfall	0.079	0.08	0.326		
		Trend	-0.298	0.148	0.065		
	Winter Freeze-Thaw of MY	Number of freeze-thaw weeks	-0.052	0.07	0.464	0.001	0.005
		Trend	-0.3	0.138	0.04		

[†] MY= monitoring year

* Model would not converge with trend as a random coefficient; therefore, trend was specified as a fixed effect only.

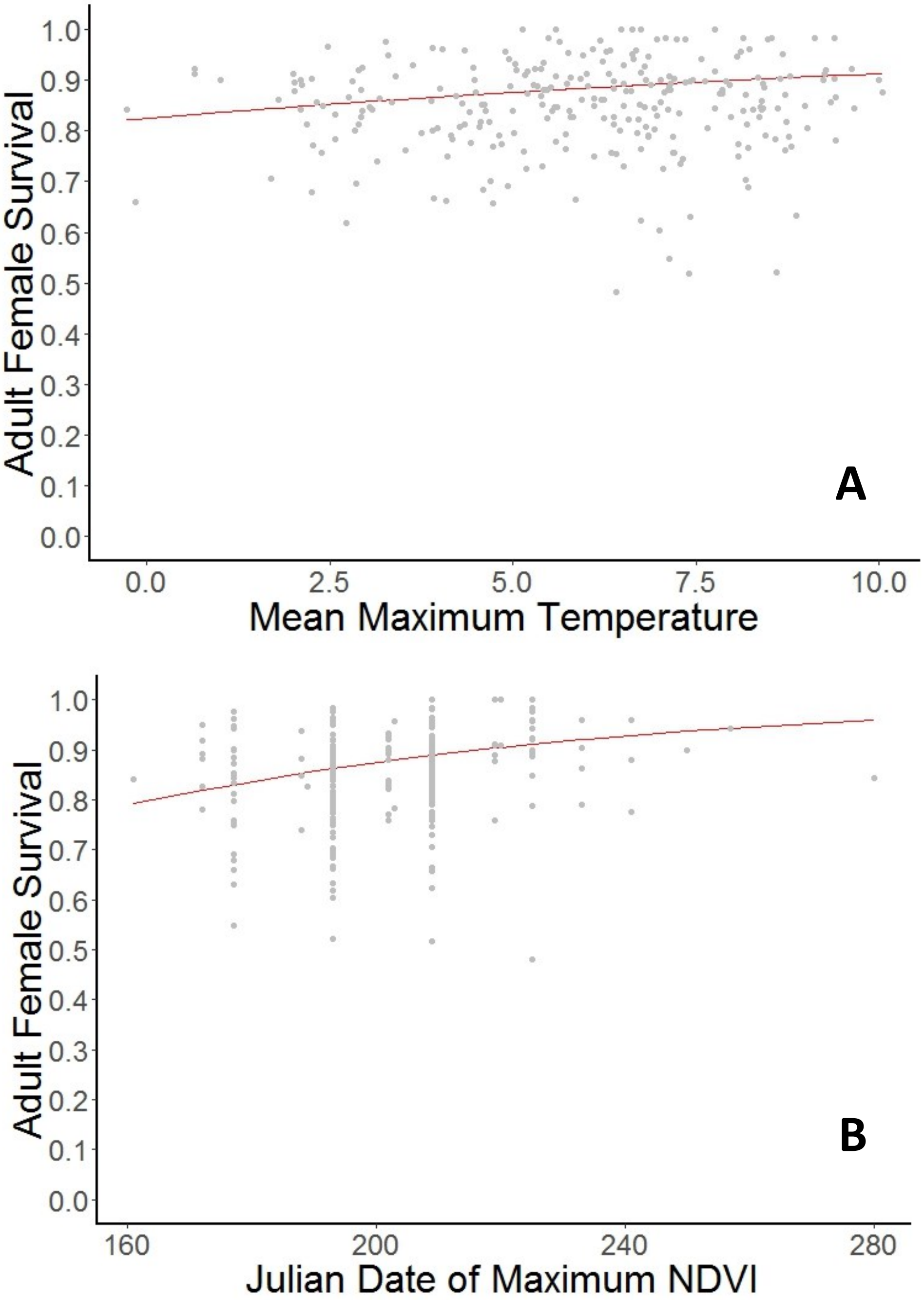

Figure 6: Predicted effects of the mean maximum temperature (A) and the date of the maximum annual NDVI value (B) in the previous autumn on adult female survival of woodland caribou during the following year (April 1 – March 30).

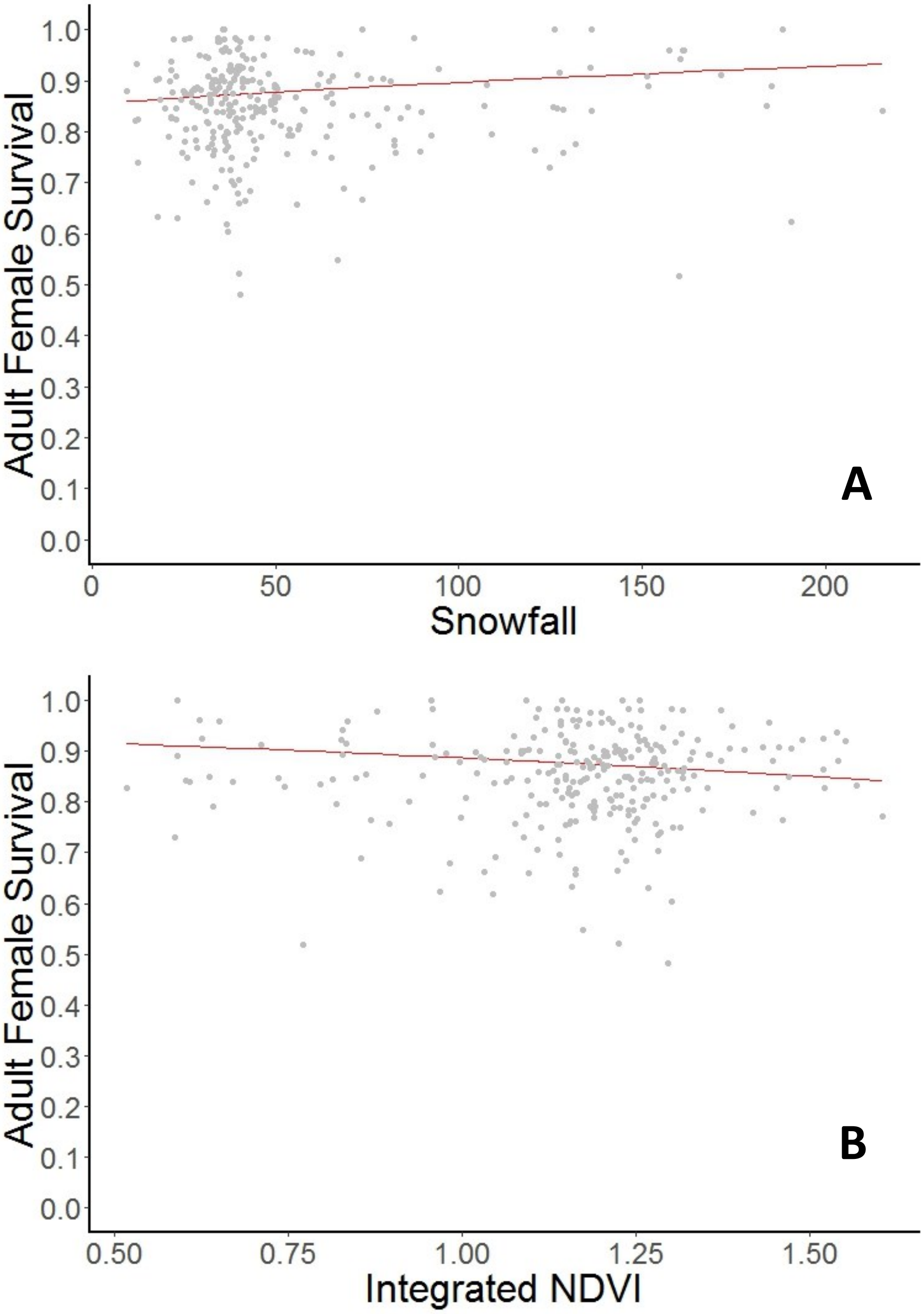

Figure 7: Predicted effects of snowfall accumulation (A) and the integrated NDVI value (B) in the spring on adult female survival of woodland caribou during the following year (April 1 – March 30).

DISCUSSION

Ungulate population dynamics are expected to be impacted by annual variation in climate because such variability influences forage quality and availability, affects energy expenditure, and exerts direct and indirect effects on predation (Sæther 1997; Stenseth *et al.* 2002; Montgomery *et al.* 2013). This expectation held true for woodland caribou as we documented demographic responses to annual variation in seasonal temperatures, seasonal precipitation and plant phenology. Between the two rates assessed, CAF ratios were most sensitive to climate effects, which is perhaps unsurprising given that juvenile survival and fecundity have high temporal variability and are the first demographic rates affected when resources become limited (Eberhardt 1977; Gaillard *et al.* 2000).

Across the majority of seasonal analyses, CAF ratios were negatively affected by increasing mean temperatures with this effect being particularly strong in the winter before parturition. During this same time period, CAF ratios also had a positive correlation with snowfall. Together, these results suggest that CAF ratios respond positively to increasing winter severity, a finding that contradicts previous work in the Yukon reporting increased CAF ratios in northern mountain caribou following less severe winters (Hegel *et al.* 2010). These contrasting results may be due to differences in the range of climatic conditions measured and the range of conditions that might be considered optimal for caribou. In our study, most of the populations evaluated are situated near the southern edge of caribou distribution; consequently, these populations likely experience warmer winters, which are associated with increased disease and parasite prevalence in caribou, potentially leading to lowered reproductive performance (Schwantje *et al.* 2014).

The effect size of temperature on CAF ratios was relatively large (although explained variation was low – see below). If mean minimum temperatures in winter lowered from -20°C to -25°C, CAF ratios increased from 0.135 to 0.183 (35% increase). While climate change is not amenable to local management actions, these effect sizes are notable when considered against other management actions aimed at increasing CAF ratios. In the Little Smoky range, the CAF ratio increased from 0.115 to 0.186 (62% increase), on average, following six years of wolf control (Hervieux *et al.* 2014). In the Yukon, CAF ratios increased two-fold in the Aishihik caribou herd following five years of wolf reduction (Hayes *et al.* 2003). In other instances, however, wolf control had limited or no effects on CAF ratios (Valkenburg *et al.* 2004; Boertje *et al.* 2017). Our results here suggest that relatively strong climate effects could confound interpretation of predator control effects, particularly if control herds are not concurrently monitored (e.g. Valkenburg *et al.* 2004). The inclusion of control herds, however, does not necessarily overcome this potential confound as spatial variation in climate effects and caribou responses may impact treatment-control comparisons (e.g., Coulson *et al.* 2001; Joly *et al.* 2011).

Adult female survival was more affected by spring and autumn conditions than winter. These effects were more pronounced prior to the monitoring year, suggesting that climate effects on AFS are lagged. In the preceding autumn, AFS was positively correlated to increasing temperature and the date of the maximum NDVI value, perhaps indicating that longer growing seasons extending into warm autumns allow for increased accumulation of body reserves critical to meeting survival and reproductive demands over winter (Parker *et al.* 2009). In spring, the negative association with iNDVI and positive association with increased snowfall is consistent with the "slow green-up" hypothesis (Christianson *et al.* 2013), which states that slow development of plant phenology in spring increases the temporal availability of peak forage quality, potentially allowing females to more efficiently replenish body reserves depleted during winter (Cebrian *et al.* 2008). Collectively, these results suggest that AFS is strongly influenced by a female's balance of body reserves from the preceding year and that this balance is dictated by resource accumulation in the previous autumn and spring. Because AFS has high influence on caribou population dynamics (DeCesare *et al.* 2012a), relatively small changes in autumn and spring conditions can have significant impacts on population growth rates. For example, if the peak of the growing season extends 15 days beyond its mean value (~ 20 July), AFS is predicted to increase from 88% to 90%. Given a CAF ratio of 25%, which is near values associated with population stability (Bergerud 1996), this 2% increase in AFS will result in populations going from decline ($\lambda = 0.99$) to growth ($\lambda = 1.02$).

Determining whether climate has a greater impact on caribou population dynamics via its effects on AFS versus CAF ratios is not straightforward based on our results because each demographic rate was generally affected by different climate variables occurring in different seasons. One comparison, however, that might yield insights into these relationships is assessing the differential impact of increasing snowfall as this variable positively affected both demographic rates, albeit in different seasons. For CAF ratios, increasing snowfall by one standard deviation (~ 88 cm) during the year before parturition equated to an increase in the population growth rate from 0.929 to 0.944 (0.015 difference), holding mean minimum winter temperature constant and assuming 87% AFS (increasing AFS to 90% yielded a difference of 0.016). For AFS, increasing snowfall by one standard deviation (~ 36 cm) in the spring prior to the monitoring year equated to an increase in the population growth rate from 0.989 to 1.005 (0.016 difference), holding mean spring maximum temperature constant and assuming a CAF ratio of 25% (increasing the CAF ratio to 30% also yielded a difference of 0.16). These results suggest that climate-mediated effects on CAF ratios and AFS have similar impacts on caribou population dynamics, a finding consistent with DeCesare *et al.'s* (2012a) work showing that, in general, explained variation in population growth rates is similar between CAF ratios (43.3%) and AFS (54.0%).

Overall, colder temperatures and increasing snowfall appeared to have a positive effect on caribou population dynamics. While this relationship may make intuitive sense for a species that is generally cold-adapted, it is counter to observed trends of climate in the study area and population trajectories of caribou. Over the course of the monitoring period (1994-2015), snowfall has been slightly increasing and mean minimum winter temperatures slightly decreasing in most caribou ranges (Appendix 1). Yet, despite these apparently positive climate conditions, most caribou populations have been declining over the same monitoring period (Hervieux *et al.* 2013; see also the negative coefficients for 'trend' variables in all climate models in Tables 3-4). This contradiction, combined with the relatively low explanatory power of our climate models, suggests that other factors have a higher influence than climate on current trends in caribou populations. The most cited factor is the degree of anthropogenic disturbance within caribou range (Wittmer *et al.* 2007; Environment Canada 2008; Sorensen *et al.* 2008; Apps *et al.* 2013). Indeed, in the federal review of critical habitat for boreal caribou, the proportion of the range disturbed by industrial activities explained 49% of the variation in CAF ratios across 24 caribou populations (Environment Canada 2008). This effect is an order of magnitude larger than the percent variation explained the climate models presented here. A similar analysis by Wittmer *et al*. (2007) found range disturbance to have much higher influence on AFS than fluctuating snow depths. We did not include effects of range disturbance in our models because most caribou ranges only have periodic snapshots of range disturbance (i.e., a 2012 calculation for boreal caribou ranges in Alberta; Alberta Biodiversity Monitoring Institute data) rather than annual measurements. Nevertheless, future analyses should seek to assess the simultaneous effects of climate, range disturbance and their interaction on caribou population dynamics. This latter assessment – the climate-disturbance interaction – is particularly relevant if climate works synergistically with disturbance to facilitate the expansion of other ungulate species (e.g. white-tailed deer) into caribou range, a dynamic that would likely result in increasing predation of caribou (Latham *et al.* 2011; Dawe *et al.* 2014; Fisher *et al.* 2017).

Limitations

We evaluated climate effects on caribou demography at a relatively coarse scale. This scale was dictated by demographic metrics recorded annually at the population-level and the measurement interval of some of the climate variables (e.g. mean temperatures and snow accumulation were available over 3-month intervals). While this scale of analysis is appropriate for evaluating for general trends, it may obscure fine-scale changes in climate that have high influence on demographic rates. For example, a high number of caribou mortalities occurred in northeast British Columbia during the spring of 2013 (Culling & Culling 2014). These mortalities were attributed to a moderately severe winter followed by a heavy snow event occurring during the last week of April. Because climate effects were averaged over longer periods (e.g. 3 months), such events can be obscured. Averaging over large spatial scales can have similar effects to averaging over long time scales. We tracked mean snow accumulation across caribou ranges, which may obscure fine-scale variation in snow depths that can highly influence population dynamics via predation (Brennan *et al.* 2013).

The temporal scale of analysis also impacts inferences on potential responses to long-term, systemic changes in climate. We assessed demographic responses to annual changes in various climate variables and such year-to-year responses may not correlate with how caribou might respond to longer-term climate trends. Moreover, climate effects on ungulate populations may occur at longer-time lags than the one-year lag assessed here (e.g. up to seven years; Mech *et al*. 1987).

We further caution that our analyses focused on linear relationships between climate effects and caribou demography. Clearly, one of our key findings – that CAF ratios increase with increasing snowfall and deceasing minimum winter temperatures – cannot be linear indefinitely; at some point, increasing snowfall and decreasing temperatures will negatively impact reproduction and juvenile survival. Such climate thresholds are to be expected given that a species' distribution is often dictated by a climate envelope (Pearson & Dawson 2003) and these thresholds may not be static, often interacting with density-dependent factors (Tyler *et al.* 2008).

Future Directions

We assessed annual variation of climate on caribou demography using four main climate effects: temperature, accumulated precipitation, freeze-thaw events, and NDVI. Moving forward, additional climate variables will be investigated, including the annual length of snow cover and daily snow depth, which can influence forage availability, energy expenditure, and predation. Such variables may have a better explanatory power on caribou demographic rates than those analysed here. We will also investigate alternate data sources for existing climate variables to try and generate variables that temporally match biologically relevant periods for caribou (e.g. calving in May to mid-June). To overcome the limited number of variables that can be evaluated in a given model, future modelling will investigate principal component analysis, which can capture important aspects of multiple variables into one metric. This approach may also be useful for quantifying high-dimensional data sources such as NDVI (e.g., Hurley *et al.* 2017).

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APPENDIX 1

Snow and Temperature Trends within Caribou Ranges

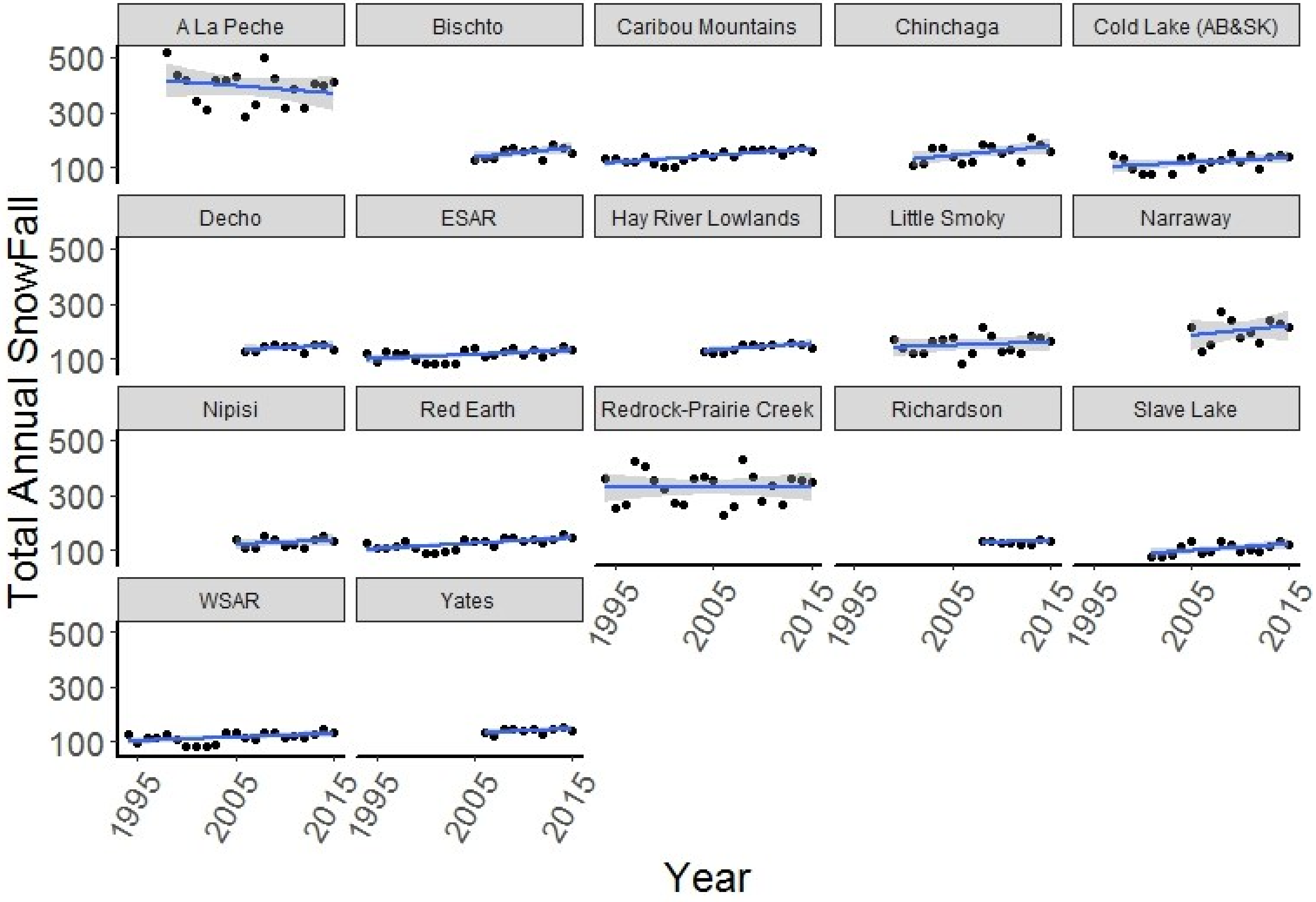

Figure A1: Total annual snowfall (cm) within 17 ranges of woodland caribou, each monitored for various intervals between 1994 and 2015. British Columbia ranges (*n* = 4) have been excluded due to their short monitoring interval (3 years).

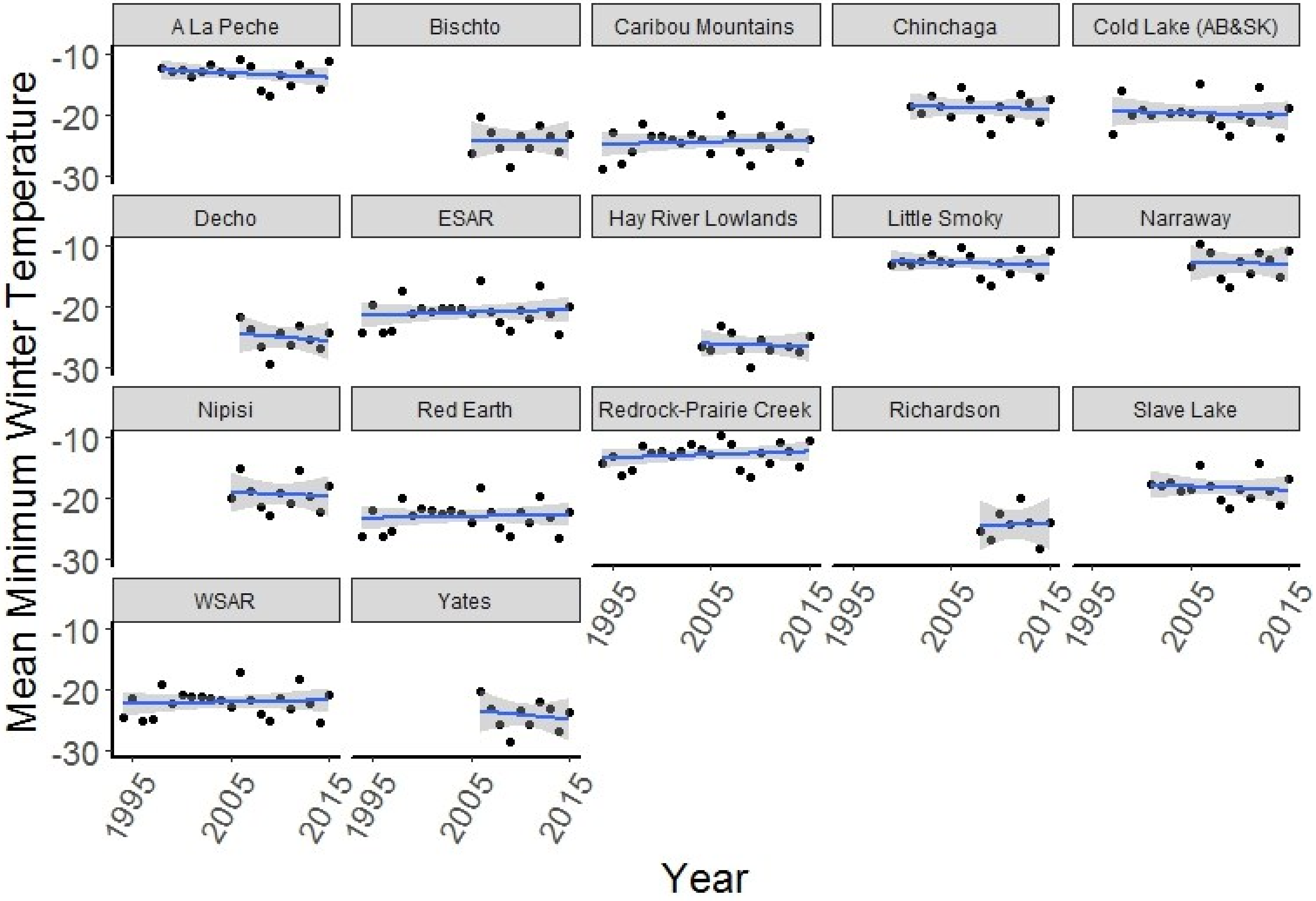

Figure A2: Mean minimum winter temperatures (°C) within 17 ranges of woodland caribou, each monitored for various intervals between 1994 and 2015. British Columbia ranges (*n* = 4) have been excluded due to their short monitoring interval (3 years).