Impacts of climate change on the seasonal distribution of migratory caribou

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Abstract

Arctic ecosystems are especially vulnerable to global climate change as temperature and precipitation regimes are altered. An ecologically and socially highly important northern terrestrial species that may be impacted by climate change is the caribou, *Rangifer tarandus*. We predicted the current and potential future occurrence of two migratory herds of caribou [Rivière George herd (RG) and Rivière-aux-Feuilles (RAF) herd] under a Canadian General Circulation Model climate change scenario, across all seasons in the Québec–Labrador peninsula, using climatic and habitat predictor variables. Argos satellite-tracking collars have been deployed on 213 caribou between 1988 and 2003 with locations recorded every 4–5 days. In addition, we assembled a database of climate (temperature, precipitation, snowfall, timing and length of growing season) and habitat data obtained from the SPOT VEGETATION satellite sensor. Logistic regression models indicated that both climatic and physical habitat variables were significant predictors of current migratory caribou occurrence. Migratory caribou appeared to prefer regions with higher snowfall and lichen availability in the fall and winter. In the summer, caribou preferred cooler areas likely corresponding to a lower prevalence of insects, and they avoided disturbed and recently burnt areas. Climate change projections using climate data predicted an increased range for the RAF herd and decreased range for the RG herd during 2040–2069, limiting the herds to northeastern regions of the Québec–Labrador peninsula. Direct and indirect consequences of climate change on these migratory caribou herds possibly include alteration in habitat use, migration patterns, foraging behaviour, and demography, in addition to social and economic stress to arctic and subarctic native human populations.

Keywords: caribou (*Rangifer tarandus*), climate change, occurrence models, seasonal habitat selection

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Introduction

Global climatic change is predicted to impact a myriad of ecosystems, for example by altering species distributions, community composition, and ecosystem structure (Walther *et al.*, 2002; Parmesan & Yohe, 2003). Global mean air temperatures are predicted to increase between 1.4 and 5.8 °C by the year 2100, with variability among estimates due to different expectations about economic development and assumptions in the General Circulation Models used to forecast temperatures (IPCC, 2001). Arctic ecosystems are especially vulnerable to

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global warming as polar regions are expected to exhibit the greatest degree of change (ACIA, 2004; Graverson *et al.*, 2008). In regions closer to the north and south poles, temperatures are predicted to increase at a faster rate estimated between 4 and 7 °C by 2100 (ACIA, 2004). As temperature regulates many processes across numerous taxa, increases in air temperature will impact many species, including the abundance of polar bears (*Ursus maritimus*, Stirling & Parkinson, 2006) and the distribution of freshwater fishes, such as smallmouth bass (*Micropterus dolomieu*, Sharma *et al.*, 2007). Climate change has also been associated with phenology, the seasonal timing of plant and animal activities. For example, increases in spring air temperature have been associated with earlier onsets of bird singing and

breeding, amphibian choruses and spawning, and plant shooting and flowering (see Walther *et al.*, 2002; Parmesan & Yohe, 2003 for a review).

A key species in Arctic ecosystems is the caribou (*Rangifer tarandus*). Alterations to the distribution of caribou attributed to global climatic change could have biological, social, and economical implications. Caribou is a species with one of the highest biomass of terrestrial vertebrates in northeastern Canada and thus plays a central role in the ecology of predators and the structure of Arctic plant communities (Crête, 1999; Bergerud *et al.*, 2008). The traditional lifestyle of arctic and subarctic native communities still exhibits a strong cultural and economic reliance on caribou for food (Miller, 2003). For example, an analysis of 24 rural communities in the interior of Alaska revealed that caribou harvest can be as high as $22 \, kg \, person^{-1} \, yr^{-1}$ (median harvest of $3.5 \, kg \, person^{-1} \, yr^{-1}$) (*sensu* Nelson *et al.*, 2008). The distribution of caribou may be altered in response to climate change, potentially away from northern villages and thus increasing the difficulty of hunting.

Migratory caribou population dynamics are influenced by a suite of variables including climate, habitat, predation, and anthropogenic activities (Messier *et al.*, 1988; Post & Forchhammer, 2002; Bergerud *et al.*, 2008). Migratory caribou demonstrate spatial and temporal variation in habitat use, corresponding to different life-history strategies in an effort to maximize opportunities for access to abundant and high-quality forage and minimize interactions with predators and insects. In particular, high-quality habitat is a strong indicator of caribou distribution (O'Brien *et al.*, 2006).

Seasonally, wintering grounds for migratory caribou are typically at the southern extent of their range. Winter habitat selection tends to be characterized by regions with increased lichen coverage, the staple food for caribou in the winter (Théau & Duguay, 2004; Théau *et al.*, 2005; O'Brien *et al.*, 2006). During winter, migratory caribou partially overlap with sedentary caribou that live solitary or in much smaller groups and use the same areas year round (Boulet *et al.*, 2007). In sedentary caribou, regions with decreased snow depth are also selected to ease mobility and provide access to forage (Johnson *et al.*, 2001). Quality and abundance of winter forage are crucial as low birth mass of calves and low parturition rates may be a consequence of insufficient winter forage quality (Couturier *et al.*, 1990). In the spring, migratory caribou aggregate into larger groups and begin moving northwards to calving grounds as snow depth decreases and day length increases (Miller, 2003). In early summer, caribou reach calving grounds located on the tundra away from the tree-line and on higher elevations with sparsely vegetated lands, likely to minimize encounters with predators Bergerud *et al.*,

2008). Postcalving, migratory caribou expand their distribution in tundra seeking habitats with high-quality forage to increase growth and survival of their fawns (Miller, 2003; Couturier, 2007), in addition to areas with reduced densities of insects (Morschel & Klein, 1997). Inadequate high-quality forage in the summer may result in lower pregnancy rates (Rettie & Messier, 1998), in deterioration of the body condition of adult females (Couturier *et al.*, 1990) and smaller fawn body mass at birth and in late October (Couturier *et al.*, 2009). In the fall, caribou migrate southward from tundra habitats to taiga, and normally breed before reaching wintering grounds (Miller, 2003).

Two migratory caribou populations occur in eastern North America: the Rivière-George (RG) herd and the Rivière-aux-Feuilles (RAF) herd (Boulet *et al.*, 2007). These migratory caribou herds travel up to $6000 \, km \, yr^{-1}$ searching for forage or to avoid predators and insects (Bergerud *et al.*, 2008). Although not genetically different (Boulet *et al.*, 2007), these two herds showed some differences in body size and condition, in movement rates and in demography (Couturier, 2007). Both herds have exhibited dramatic population fluctuations over recent decades. In the 1950s, there were only about 5000 individuals in the RG herd (Banfield & Tener, 1958). By 1993, the population had increased to >775 000 individuals (Couturier *et al.*, 1996). In the subsequent decade and by 2001, the population size had decreased to about 385 000 individuals (Couturier *et al.*, 2004), while the RAF herd increased from 56 000 individuals estimated during its first census in 1975 to at least 628 000 individuals in 2001 (Couturier *et al.*, 2004).

The objectives of this study were two-fold. First, we predicted the current winter, spring, summer, and fall occurrence of the RG and RAF migratory caribou herds in the Québec–Labrador peninsula using climatic and habitat predictor variables. Second, using projections from a Canadian General Circulation Model climate change scenario for 2040–2069, we predicted future winter, spring, summer, and fall occurrence for migratory caribou in the Québec–Labrador peninsula.

Materials and methods

Data acquisition

Caribou were captured using darts or nets fired from a helicopter. ARGOS satellite-tracking collars (Service ARGOS Inc., Largo, Maryland, USA) were used to track adult (≥ 1.5 years old) caribou from the RG and RAF herds. Efforts were made to recapture radio-collared individuals and to replace radio-collars before the end of the batteries. The average duration of individual

Table 1 Number of marked individuals monitored by year for Rivière-George (RG) and Rivière-aux-Feuilles (RAF) migratory caribou (*Rangifer tarandus*) herds in the Québec–Labrador peninsula

Year	No. of marked RG caribou	No. of marked RAF caribou
1988	9	–
1989	7	–
1990	19	–
1991	20	–
1992	19	–
1993	21	–
1994	27	3
1995	26	3
1996	30	4
1997	26	7
1998	27	7
1999	21	9
2000	26	11
2001	20	11
2002	21	9
2003	23	6

monitoring was 2.5 years but some animals were followed for up to 10 years. Twenty-four males and 147 females were tracked from the RG herd between 1988 and 2003 (Table 1; Fig. 1). Eight males and 34 females from the RAF herd were tracked between 1994 and 2003 (Table 1; Fig. 2). Locations were obtained every 4 or 5 days and were generally accurate within 1 km. Satellite telemetry positions were checked for error according to a custom filtering tool and erroneous locations were discarded (Couturier, 2007).

Air temperature data were compiled for each month over the Québec–Labrador peninsula. Climate data were obtained from IPCC Data Distribution Centre as 1961–1990 averages. The data were interpolated from meteorological stations using thin-plate splines and summarized on a $0.5°$ latitude $× 0.5°$ longitude grid (IPCC Data Distribution Centre). Total rainfall (mm), total snowfall (cm), timing of the start and end of the growing season, and effective growing degree days data were obtained from the National Land and Water Information Service (http://sis.agr.gc.ca/cansis/nsdb/ecostrat/district/climate.html) as monthly means
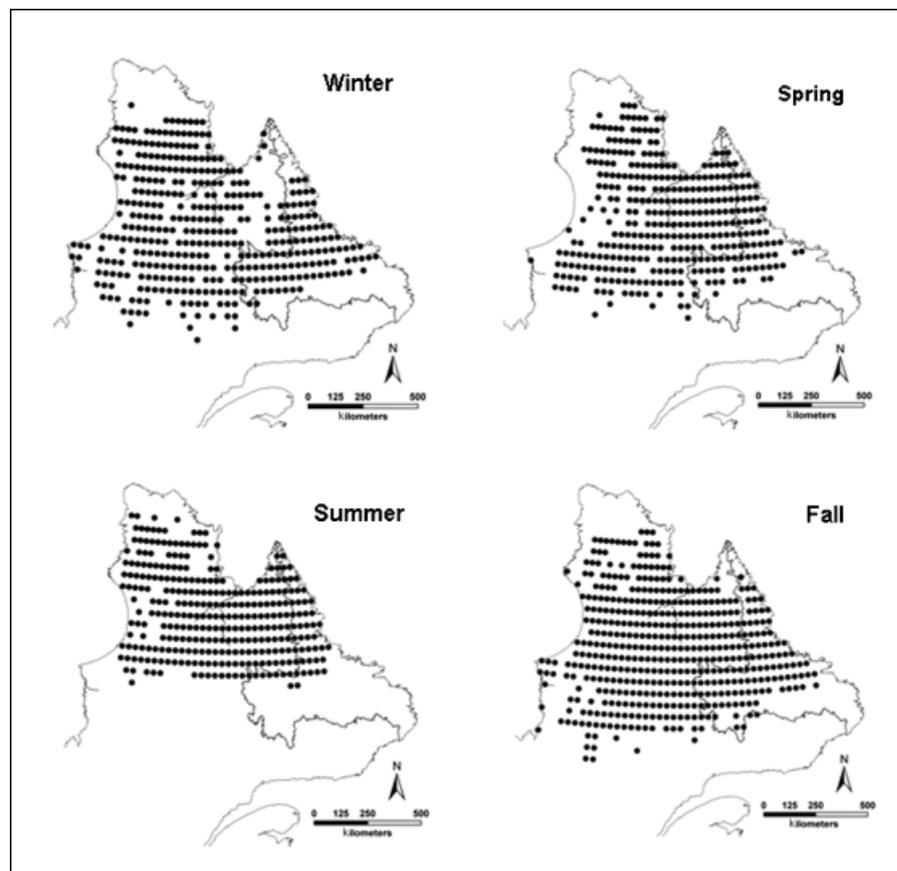

Fig. 1 Rivière-George migratory caribou occurrence for 1988–2003, Québec–Labrador peninsula. Points represent at least one occurrence of satellite-tagged caribou between 1988 and 2003.
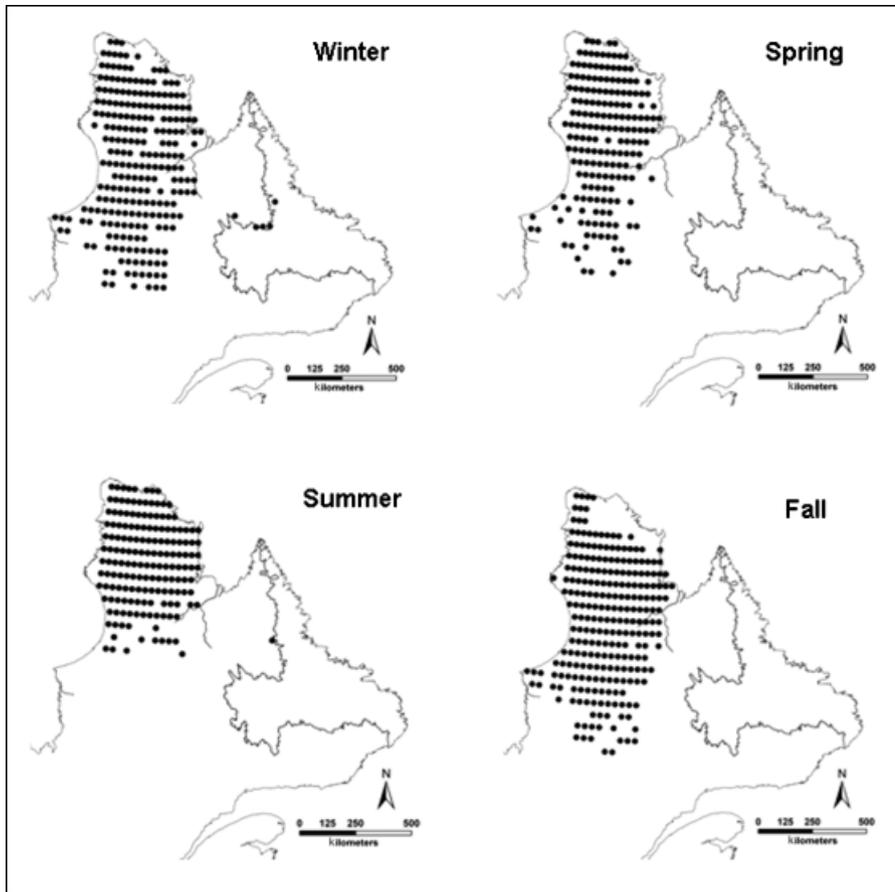
Fig. 2 Rivière-aux-Feuilles migratory caribou occurrence for 1994–2003, Québec–Labrador peninsula. Points represent at least one occurrence of satellite-tagged caribou between 1994 and 2003.

summarized for 1961–1990. The first and last day of the year when mean daily air temperature surpassed 5 °C dictated the start and end of the growing season. Effective growing degree days were defined as growing degree days exceeding 5 °C, using an algorithm that accounted for season and day length (http://sis.agr. gc.ca/cansis/nsdb/ecostrat/district/climate.html).

We obtained North America Land Cover data for 2000 (http://landcover.usgs.gov/landcoverdata.php). Land cover data were summarized at a spatial resolution of 1 km and compiled using the SPOT VEGETATION sensor between April and October 2000. We used the terminology of the Land Cover data for habitat description. The visualization of habitat can be accessed at: http://www.ccrs.nrcan.gc.ca/optic/coarse/images/nalandcover.jpg.

Future projections of climate (Canadian General Circulation Model Version 1 including greenhouse gas and aerosol emissions) were acquired from Canadian Climate Impact and Scenarios (http://www.cics.uvic.ca) for eastern Canada between 2040 and 2069. Monthly mean air temperatures, precipitation, timing of the start and end of growing season, and effective growing

degree days were summarized on a $0.5° \times 0.5°$ latitude and longitude grid. For the time period between 1961–1990 and 2040–2069, mean temperatures and precipitation are predicted to increase by approximately 3.3 °C and 3.85 mm, respectively, for northeastern Canada. Additionally, the growing season is predicted to increase by 12 days over the same time period (Table 2).

Data analyses

Using the RG and RAF caribou distribution data for 1988–2003 and 1994–2003 respectively, we summarized the information of migratory caribou occurrence (categorized as either present or absent for each herd) on a $0.5° \times 0.5°$ latitude and longitude grid for each season in the Québec–Labrador peninsula to correspond to climate normal data. The use of presence–absence data by site reduces the possibility of introducing sampling error and bias in the analyses. Because the estimates of population size include large errors, typically 30–50% of the estimates (Couturier *et al.*, 2009), it was not possible to consider density in the analyses as it would have introduced large amounts of uncertainty. The

Table 2 Mean deviation of climate normals between 1961–1990 and 2040–2069 in the Québec–Labrador peninsula

Variables	Mean deviation
Start date of growing season (days)	−10.14
End date of growing season (days)	2.13
Effective growing degree days	185.62
Winter temperature (°C)	4.71
Spring temperature (°C)	3.27
Summer temperature (°C)	2.35
Fall temperature (°C)	2.81
Winter precipitation (mm)	2.85
Spring precipitation (mm)	4.37
Summer precipitation (mm)	5.11
Fall precipitation (mm)	3.07

Data source: Canadian Institute for Climate Studies.

Table 3 Proportion of each habitat type used in the analyses of caribou occurrence in the Québec–Labrador peninsula

Habitat type	Proportion
Needleleaved evergreen forest – closed canopy	0.14
Needleleaved evergreen forest – open canopy	0.09
Needleleaved evergreen shrubland – open canopy	0.04
Grassland with a sparse tree layer	0.1
Grassland with a sparse shrub layer	0.002
Polar grassland with a sparse shrub layer	0.07
Polar grassland with a dwarf-sparse shrub layer	0.16
Needleleaved evergreen forest open canopy – lichen understory	0.18
Unconsolidated material sparse vegetation (old burnt or other disturbance)	0.02
Water bodies	0.1
Recently burnt area	0.02

Habitat type descriptions were obtained from North American Land cover 2000.

spatial extent of the study was determined by the limit of all RG and RAF caribou locations between 1988 and 2003. Based on this grid, the RG caribou dataset consisted of 12 865 sites by year for each season. The RAF caribou dataset was composed of 8067 sites by year for each season. All datasets were randomly divided into independent training and validation datasets, with the same large-scale geographic coverage in both datasets, based on a 70 : 30 ratio.

For all analyses, seasons were designated based on migratory caribou biology. Winter months for caribou occurrence and climate data were classified as January to April, a period where snow is ecologically significant (Bergman *et al.*, 2000; Couturier, 2007). Spring months were categorized as May and June corresponding to the spring migration and calving. July and August were classified as summer months corresponding to the postcalving season. Finally, the fall months were September to December and correspond to the breeding season and autumn migration.

Land cover habitat classes were also summarized on a 0.5° × 0.5° grid to correspond to caribou occurrence and climate normal data. Habitat data were summarized as a proportion of each habitat type in each 0.5° × 0.5° grid square. Only habitat types that were found through the majority of the study area were included in the analyses (Table 3).

Multicollinearity between variables was evaluated using bivariate plots and correlational analyses before regression analyses in order to determine which variables should be retained. Normality of variables was assessed to determine if transformation of variables was required. Variables included in the models were: winter, spring, summer, and fall temperature and precipitation; winter, fall and total snowfall, total rainfall, timing of the start and end of growing season, effective growing degree days, and habitat type.

Stepwise multiple logistic regression models were constructed for both RG and RAF herds for each season in SAS using the training datasets to evaluate the relationships between caribou occurrence and climate and physical habitat. As sampling year was a significant predictor variable, the logistic regression models were constrained by year to account for the interannual variability (represented by β-coefficients) in caribou occurrence. Significance values were set at 0.01 for predictor variables to enter and remain in the models. Subsequently, logistic regression models were tested on the independent validation datasets for each season and herd.

Instead of designating caribou presence by the traditional decision threshold of 0.50, we constructed Receiver Operating Curves (ROC) to identify the threshold that would maximize species sensitivity and specificity (Fielding & Bell, 1997; Olden & Jackson, 2002). ROCs are particularly useful with datasets that have unequal species presence and absence as logistic regression tends to produce scores that are biased towards the more prevalent group (Fielding & Bell, 1997). ROC analyses were used to identify thresholds that would predict sensitivity (correctly predicting species presence) and specificity (correctly predicting species absence) equally well. Based on the ROC analyses and the optimal decision threshold, we constructed 'confusion matrices' using the independent, validation datasets (Fielding & Bell, 1997). The confusion matrix summarizes true absence, true presence, false absence, and false presence, which can then be used to calculate overall classification rate, sensitivity and specificity (Fielding & Bell, 1997; Olden & Jackson, 2002).

We incorporated projected mean temperatures, precipitation, timing of growing season, and effective growing degree days for the years between 2040 and 2069 from the Canadian General Circulation Model climate change scenario to derive our predictions for migratory caribou occurrence across seasons. We set the interannual coefficient (β) to zero to apply the model in the years 2040 and 2069 because the average β was close to 0 among all years, seasons, and herds, suggesting that $\beta = 0$ would be indicative of a typical year. Owing to the limitations in the climate change projections available for the region, we only assumed changes in climate and not in habitat to predict future caribou occurrences.

To assess the spatial distribution of the RG and RAF herds, we calculated the spatial overlap, range expansion, range contraction, and overall change in range under climate change for each season. In addition, we calculated the spatial overlap between the two migratory caribou herds in each season under present and climate change conditions.

Results

RG herd

The distribution of the RG herd among all seasons was significantly predicted by climatic and habitat variables (Table 4). For all seasons, year was a significant factor indicating strong temporal variation in caribou occurrence (Table 4). Evaluation of the stepwise logistic regression models on the independent validation datasets for the RG caribou population across seasons resulted in overall classification success between 65% and 80%, with at least 70% of species presence being correctly predicted for all seasons (Table 5).

In the winter, caribou occurrence was predicted to occur in regions with a later start of the growing season and increased amounts of total snowfall. Furthermore, migratory caribou tended to avoid regions with evergreen forests, polar grasslands with a dwarf-sparse shrub layer, and water bodies.

In the spring, caribou tended to occur in regions with an earlier commencement of the growing season and fewer effective growing degree days (Table 4). Caribou avoided closed evergreen forests, old burnt or disturbed forests, and grasslands with a sparse tree layer. Conversely, in the spring, caribou tended to be found in open evergreen shrublands, and polar grasslands with a sparse shrub layer.

The summer distribution of the RG caribou herd was related to regions with cooler and wetter summers, earlier start dates of the growing season, and fewer effective growing degree days. In the summer, caribou

tended to prefer regions with open evergreen shrublands, and polar grasslands with a sparse shrub layer. Conversely, caribou avoided old burnt and disturbed habitats, closed evergreen forests, and open evergreen forests with a lichen understory.

In the fall, caribou from the RG herd were found in cooler habitats with increased levels of total snowfall, and decreased levels of total rain. Fall caribou occurrence was also related to earlier start and later end dates of the growing season. Furthermore, caribou were found in open evergreen shrublands, and open evergreen forests with a lichen understory. Conversely, caribou tended to be absent near water bodies, polar grasslands with a dwarf-sparse shrub layer, and evergreen forests.

Based on future climate projections by 2040–2069, winter, spring, and summer RG caribou occurrences will tend to be restricted to the northeastern portion of our study area (Northern Québec and Labrador). In the fall, however, climatic conditions are likely to be suitable for caribou from the RG herd throughout most of its range (Fig. 3). Under a climate change scenario, the RG migratory caribou herd is predicted to undergo significant range contractions for each season, with the exception of fall (Table 6).

RAF herd

The occurrence of the RAF migratory caribou was influenced by both climate and habitat. For all seasons, year was a significant factor indicating strong temporal variation in caribou occurrence (Table 7). Evaluation of the stepwise logistic regression models on the independent validation datasets for the RAF caribou population across seasons resulted in overall classification success between 36% and 76%. High sensitivity success was achieved for the fall and winter, while high specificity success was attained for winter, spring, and summer seasons. Sensitivity was low for spring and summer due to chance and the inability of the models to predict species presence on these independent datasets (Table 8).

In the winter, RAF caribou preferred areas with warmer and drier climate, and later end dates of the growing season (Table 7). Additionally in the winter, RAF caribou were found in regions with a high abundance of lakes, grasslands with a sparse shrub layer, and open evergreen forests with a lichen understory.

In the spring, caribou from the RAF herd were found in areas with cooler and drier climate, and later end dates of the growing season. They were also found in regions with more water bodies and open evergreen forests with a lichen understory.

Table 4 Coefficients for stepwise multiple logistic regression models ($P < 0.01$) predicting the occurrence of the Rivière-George migratory caribou (*Rangifer tarandus*) during winter, spring, summer and fall seasons between 1988 and 2003 in the Québec–Labrador peninsula ($n = 9005$ occurrences)

Variables	Winter	Spring	Summer	Fall
Intercept	−10.6	81.0	94.3	14.4
Winter temperature	ns	–	–	–
Spring temperature	–	ns	–	–
Summer temperature	–	–	−0.2	–
Fall temperature	–	–	–	−0.4
Winter precipitation	ns	–	–	–
Spring precipitation	–	ns	–	–
Summer precipitation	–	–	0.06	–
Fall precipitation	–	–	–	ns
Total snowfall	0.01	–	–	0.01
Winter snowfall	ns	–	–	–
Fall snowfall	–	–	–	ns
Total rain	–	ns	ns	−0.01
Start of growing season	0.05	−0.4	−0.5	−0.1
End of growing season	ns	ns	ns	0.03
Effective growing degree days	ns	−0.03	−0.04	−0.01
Needleleaved evergreen forest – closed canopy	−4.9	−9.2	−7.9	−2.9
Needleleaved evergreen forest – open canopy	−3.2	ns	ns	−2.95
Needleleaved evergreen shrubland – open canopy	ns	8.8	16.9	6.9
Grassland with a sparse tree layer	ns	−2.4	ns	ns
Grassland with a sparse shrub layer	ns	ns	ns	ns
Polar grassland with a sparse shrub layer	ns	2.1	3.3	ns
Polar grassland with a dwarf-sparse shrub layer	−2.8	ns	ns	−4.4
Subpolar needleleaved evergreen forest open canopy – lichen understory	ns	ns	−1.4	1.3
Unconsolidated material Sparse vegetation (old burnt or other disturbance)	ns	−6.4	−29.7	ns
Water bodies	−1.8	ns	ns	−2.9
Recently burnt area	ns	ns	ns	ns
Year 1988	−0.7	−0.4	−1.0	−1.1
Year 1989	−0.4	−1.0	−1.0	−0.6
Year 1990	−0.5	−1.2	−1.1	−0.2
Year 1991	0.3	0.6	0.7	0.5
Year 1992	1.0	0.5	0.5	0.7
Year 1993	0.4	1.1	0.7	0.5
Year 1994	0.1	0.4	0.5	0.02
Year 1995	−0.5	0.3	0.03	−0.3
Year 1996	−0.1	−0.4	0.4	0.02
Year 1997	0.4	−0.2	0.02	−0.3
Year 1998	0.2	0.2	0.5	0.003
Year 1999	0.3	−0.1	−0.3	−0.1
Year 2000	0.2	−0.3	−0.4	−0.1
Year 2001	0.1	0.1	−0.1	0.2
Year 2002	−0.5	0.3	0.3	0.02
Year 2003	0	0	0	0

ns, nonsignificant.

–, the variable was not tested in the model.

Summer caribou occurrence was related to regions with cooler temperature, lower amounts of total rainfall, and later end dates of the growing season. Caribou preferred grasslands with a sparse tree layer and strongly avoided open evergreen forests and recently burnt areas.

In the fall, the RAF caribou were found in regions with greater amounts of fall snowfall, but decreased levels of fall rain. Furthermore, caribou distribution was related to regions with earlier start and later end dates of the growing season. With respect to habitat, RAF caribou preferred open evergreen forests with a lichen

understory and polar grasslands with a sparse shrub layer, but avoided areas with open evergreen forests and no lichen understory.

Based on future climate projections, spring and summer RAF caribou occurrences should tend to occur in northern Québec–Labrador by 2040–2069 (Fig. 4). In the winter and fall, however, climatic conditions should be suitable for caribou from the RAF herd throughout most of the study region (Fig. 4). The

RAF migratory caribou herd is predicted to expand its range across all seasons, by as much as 47.4% in the winter (Table 6). Furthermore, the spatial overlap between the two migratory caribou herds under present and climate change conditions is predicted to increase in the spring and fall, and decrease in the winter and summer (Table 9).

Discussion

Climate and physical habitat were important predictors of the occurrence of migratory caribou in the Québec–Labrador peninsula across all seasons. In addition, we found strong temporal variation in caribou occurrence across seasons. Significant temporal variation in caribou occurrence suggests that caribou are using different habitats based on climatic and habitat conditions available each year. The two migratory herds exhibit similarities but also differences in habitat use. The similarities in habitat use can be attributed to migratory caribou preferences of habitat and climatic conditions corresponding to similar life-history strategies in different seasons. The differences in habitat use may be a
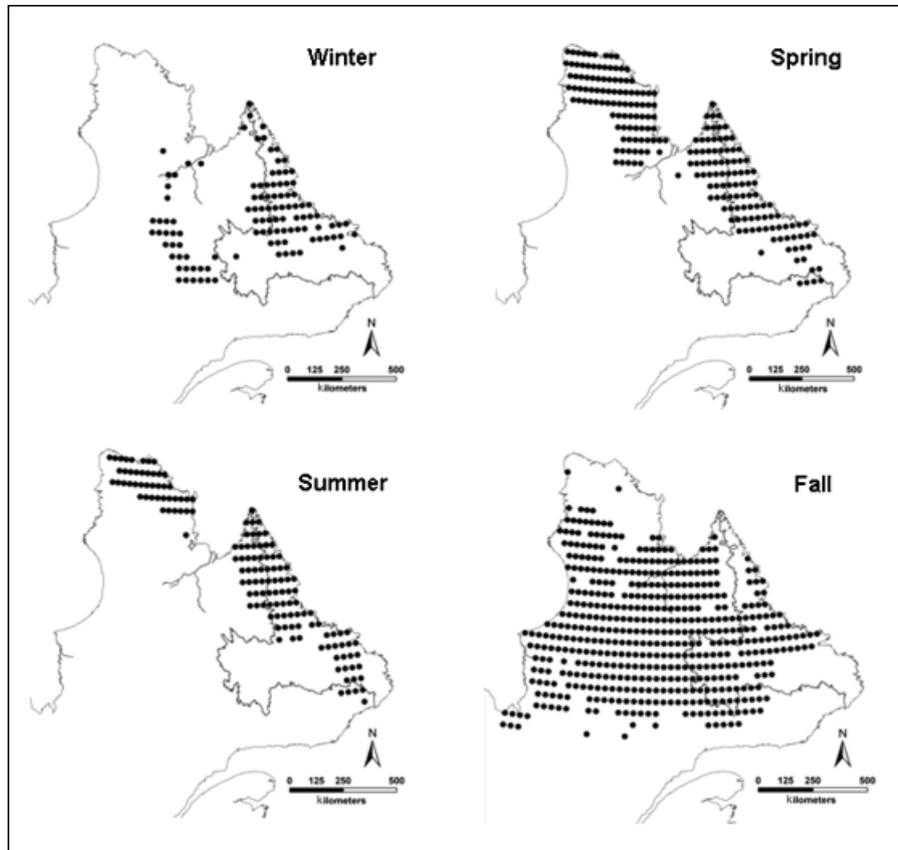
Table 5 Overall classification rate, model sensitivity, and model specificity of the performance of the stepwise multiple logistic regression models on the RG caribou occurrence validation datasets for winter, spring, summer, and fall ($n = 3859$ occurrences)

Season	Overall classification rate (%)	Sensitivity (%)	Specificity (%)
Winter	65.4	70.9	65.0
Spring	77.9	78.5	77.9
Summer	79.8	77.6	80.1
Fall	76.8	76.8	76.8

Fig. 3 Predicted caribou distribution for 2040–2069 under a climate-change scenario (CGCM2) for the Rivière-George caribou, Québec–Labrador peninsula.

Table 6 Spatial overlap (%), range expansion (%), range contraction (%), and overall change in range (%) under a climate-change scenario (CGCM2) for each season in the Rivière-George (RG) and Rivière-aux-Feuilles (RAF) caribou herds

Caribou herd	Season	Spatial overlap	Range expansion	Range contraction	Overall change
RG	Winter	59	2.1	38.2	−36.1
RG	Spring	58.8	12.4	28.8	−16.4
RG	Summer	60.7	9.8	29.5	−19.7
RG	Fall	76.1	14.2	9.7	4.5
RAF	Winter	52.6	47.4	0	47.4
RAF	Spring	82.8	10.2	7	3.2
RAF	Summer	81.4	12.5	6.1	6.4
RAF	Fall	61.1	38.5	0.4	38.1

Table 7 Coefficients for stepwise multiple logistic regression models ($P < 0.01$) predicting the occurrence of the Rivière-aux-Feuilles migratory caribou (*Rangifer tarandus*) during winter, spring, summer and fall seasons between 1994 and 2003 in Québec and Labrador ($n = 5636$ occurrences)

Variables	Winter	Spring	Summer	Fall
Intercept	−36.6	−25.9	−103.7	−11.6
Winter temperature	−0.6	–	–	–
Spring temperature	–	−0.7	–	–
Summer temperature	–	–	−0.8	–
Fall temperature	–	–	–	ns
Winter precipitation	−0.1	–	–	–
Spring precipitation	–	−0.1	–	–
Summer precipitation	–	–	ns	–
Fall precipitation	–	–	–	−0.1
Total snowfall	ns	–	–	−0.03
Winter snowfall	ns	–	–	–
Fall snowfall	–	–	–	0.3
Total rain	–	ns	−0.1	ns
Start of growing season	ns	ns	ns	−0.04
End of growing season	0.1	0.1	0.5	0.1
Effective growing degree days	ns	ns	ns	ns
Needleleaved evergreen forest – closed canopy	ns	ns	ns	ns
Needleleaved evergreen forest – open canopy	ns	ns	−73.4	−14.5
Needleleaved evergreen shrubland – open canopy	ns	ns	ns	ns
Grassland with a sparse tree layer	ns	ns	3.1	ns
Grassland with a sparse shrub layer	22.3	ns	ns	ns
Polar grassland with a sparse shrub layer	ns	ns	ns	1.9
Polar grassland with a dwarf-sparse shrub layer	ns	ns	ns	ns
Subpolar needleleaved evergreen forest open canopy – lichen understory	2.8	3.9	ns	2.5
Unconsolidated material sparse vegetation (old burnt or other disturbance)	ns	ns	ns	ns
Water bodies	5.0	4.9	ns	ns
Recently burnt area	ns	ns	−12.5	ns
Year 1994	−0.6	−0.2	0.2	0.3
Year 1995	0.1	−0.4	−0.2	0.1
Year 1996	0.1	0.04	0.2	−0.02
Year 1997	0.4	−0.04	0.4	−0.03
Year 1998	0.3	−0.05	−0.3	−0.1
Year 1999	−0.2	0.1	0.3	0.5
Year 2000	0.1	0.6	0.2	0.1
Year 2001	0.2	0.1	0.03	0.3
Year 2002	0.4	−0.1	−0.4	−0.3
Year 2003	0	0	0	0

ns, nonsignificant.
–, the variable was not tested in the model.

function of the different geographic locations in which these two herds of migratory caribou reside during part of the year as the summer landscape of the RG herd is mainly composed of higher elevation alpine tundra plateaus, while the RAF herd occurs in summer in a less productive habitat characterized by many lakes and rocks. We have summarized the influences of abiotic and biotic conditions on migratory caribou distribution and demography (Table 10).

Table 8 Overall classification rate, model sensitivity, and model specificity of the performance of the stepwise multiple logistic regression models on the Rivière-aux-Feuilles caribou occurrence validation datasets for winter, spring, summer, and fall ($n = 2430$)

Season	Overall classification rate (%)	Sensitivity (%)	Specificity (%)
Winter	76.4	69.1	77.0
Spring	72.4	20.3	76.7
Summer	69.0	0	75.9
Fall	36.2	100	29.1

Projections using the Canadian General Circulation Model suggest that by the 2050s, as temperature and precipitation increase in the Québec–Labrador peninsula, the occurrence of the migratory RG and RAF caribou herds will shift. The RG herd should be restricted to the northeastern sections of the Québec–Labrador peninsula in the winter, spring, and summer. However, in the fall, RG caribou occurrence is predicted to be distributed throughout northern Québec and Labrador. Under climate change projections, the RAF herd is expected to expand its distribution relative to its current range. Furthermore, the spatial overlap between the two migratory caribou herds under present and climate change conditions is expected to increase in the spring and fall, and decrease in the winter and summer. It should be noted, however, that these projections are based on current climate and habitat use. In addition, they are based on a period when both herds were abundant. If migratory caribou population numbers decrease in the future, there may be range constrictions independent of climate change (Messier *et al.*, 1988; Bergerud *et al.*, 2008), underlining the
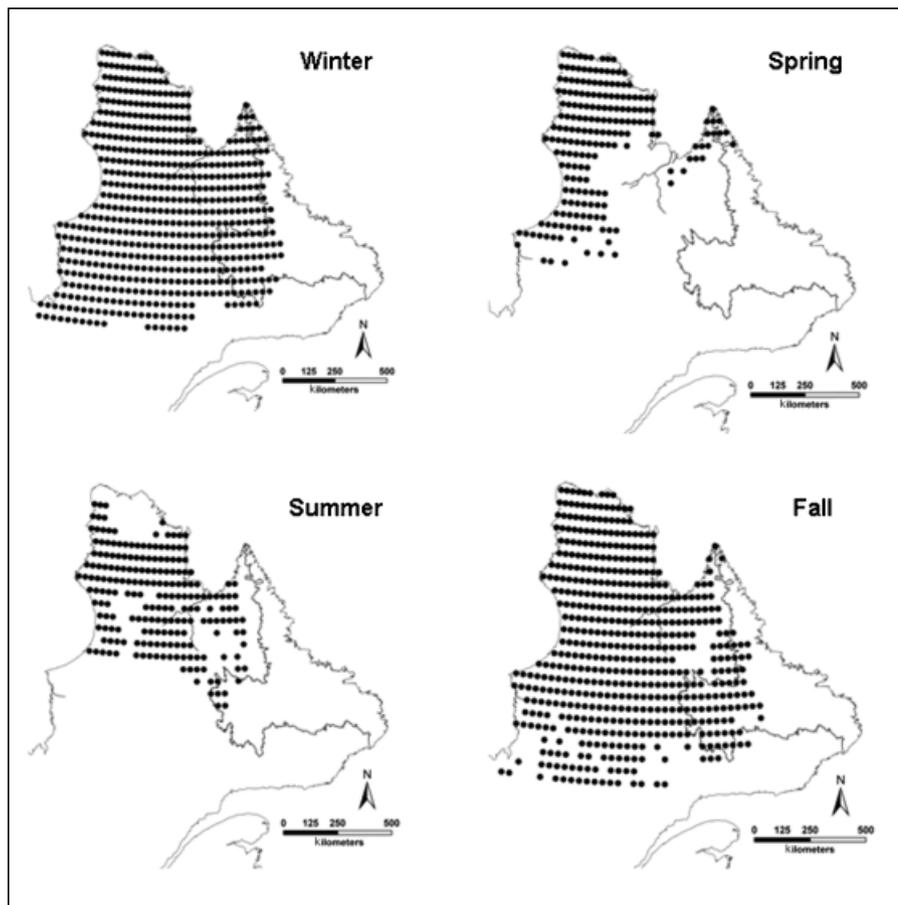

Fig. 4 Predicted caribou distribution for 2040–2069 under a climate-change scenario (CGCM2) for the Rivière-aux-Feuilles caribou, Québec–Labrador peninsula.

Table 9 Spatial overlap (%) between the two migratory caribou herds (Rivière-George (RG) and Rivière-aux-Feuilles (RAF)) of the Québec–Labrador peninsula in each season under present and climate change conditions

Season	Spatial overlap (1986–2003)	Spatial overlap (2040–2069)	Overall change
Winter	61.8	24.3	37.5
Spring	56.2	69.6	−13.4
Summer	66.8	60.7	6.1
Fall	58.7	69.5	−10.8

Table 10 Summary of the influences of abiotic and biotic conditions on migratory caribou distribution and demography

Environmental condition	References
Snow depth	For example, Pruitt (1959), Fancy & White (1985), Johnson et al. (2000), Johnson et al. (2001), Couturier et al. (2009)
Increased lichen coverage	For example, Brown & Theberge (1990), Mosnier et al. (2003), Théau & Duguay (2004), Théau et al. (2005), O'Brien et al. (2006)
Avoidance of water bodies	For example, Ferguson & Elkie (2005)
Avoidance of disturbed forests	For example, Moser et al. (1979), Rettie & Messier (1998), Mosnier et al. (2003), Joly et al. (2003), Vistnes & Nellemann (2008)
Avoidance of insects	For example, Toupin et al. (1996), Morschel & Klein (1997), Morschel (1999), Weladji et al. (2003), Couturier et al. (2009)
Avoidance of predators	For example, Bergerud (1988, 1996)

difficulty of modelling range use and population dynamics of large migratory herds.

Migratory caribou traverse frozen water bodies when migrating to ease migration. The absence or incomplete formation of ice can result in delays in the caribou migration and possibly the drowning of some animals. In the past, difficult water conditions (flow, waves, etc.) in the Québec–Labrador peninsula have resulted in the drowning of up to 10 000 caribou on thin ice in the fall or during summer in large rivers (Nault & et LeHénaff, 1988), in lakes or even in salt waters during bay crossing (S. Couturier, unpublished data). In our study area, precipitation is expected to increase in all seasons (Table 2) which may increase the flow regime of large rivers increasing the risk of drowning for migratory caribou.

Under climate change regimes as temperatures warm, the ice-free period is predicted to lengthen coincident with earlier ice break-up dates (Anderson et al., 1996; Magnuson et al., 2000). As a consequence of earlier ice break-up dates and snow melt, migratory caribou will have to start the spring migration earlier to ensure safe passage over large water bodies (e.g. Brotton & Wall, 1997) or will have to shift their distribution further north. Spring migration may also be affected under climate change scenarios as plant phenology occurs earlier resulting in a mismatch for reproducing caribou between the timing of increased resource demands and resource availability (Post & Forchhammer, 2008). The mismatch in the availability of resources has resulted in an increase in offspring mortality and a decrease in offspring production in response to a $4\,°C$ temperature rise for a migratory caribou herd in West Greenland (Post & Forchhammer, 2008).

In addition, the overlap between the RG and RAF herds in the spring should increase according to climate change scenarios. This may increase competition on the calving grounds but may also change their distribution. In the last 2–3 decades, the calving grounds of the RG and RAF herds have been separated by about 800 km and the vast majority of females have been philopatric to very specific calving grounds (Boulet et al., 2007).

Under climate change scenarios, winter precipitation and extreme events are expected to increase in central and northern Québec (Bourque & Simonet, 2008). In years with extreme winter weather conditions such as increased snowfall and icing events, Peary caribou populations in the Canadian High Arctic have crashed (Tews et al., 2007) as animals experienced poorer body condition (Brotton & Wall, 1997). The population dynamics and growth rate of Svalbard reindeer are limited by winter climatic conditions, particularly in years with increased snow levels, potentially due to decreased forage availability and reduced mobility, thereby increasing starvation and death of unhealthy individuals (Aanes et al., 2000; Solberg et al., 2001). More adverse snow and ice conditions are expected under climate change scenarios and predicted to negatively impact caribou body condition (Couturier et al., 2009) and demography (Miller & Gunn, 2003).

Primary productivity is also predicted to increase in Québec and Labrador as climate warms (Bourque & Simonet, 2008). A longer growing season and increased primary production could increase the amount of plant biomass and thus, available forage for caribou (Tews et al., 2007). An increase in forage production would likely decreases calf abortion, improve the birth mass of calves (Couturier et al., 2009), and increase parturition rates (Tews et al., 2007), thereby increasing the survival and fecundity of migratory caribou. Increased plant

productivity may also reduce the dependency of caribou on lichens.

Increases in air temperatures and declines in surface moisture since the 1950s have resulted in an increase in the frequency and size of forest fires, which is projected to continue in the future under climate change scenarios (Joly et al., 2003; Flannigan et al., 2005; Nelson et al., 2008). This will result in increased abundance of early successional forest and reduced the abundance of mature forests (Flannigan et al., 2005; Nelson et al., 2008). Specifically, the immediate consequences of wildland fire include loss of habitat and forage, such as lichens (Joly et al., 2003; Rupp et al., 2006). The alteration in fire regime may result in a change in distribution of migratory caribou populations further north in their range above the tree-line.

Summer air temperatures and wind speed are important predictors of insect distribution (Morschel, 1999; Weladji et al., 2003). As summer temperatures increase, the intensity and duration of caribou harassment by insects such as oestrid flies could increase (Brotton & Wall, 1997), as insect distribution increase to the north (Weladji et al., 2003). Morschel & Klein (1997) reported increased rates of activity change of caribou and movements to snow ridges with low-quality forage in the presence of insects. Reindeer in Norway exhibited lower carcass weight, decreased summer growth rate, and reduced levels of lactation in the presence of insect harassment, likely due to increased energy expenditure and reduced grazing time in an effort to escape (Weladji et al., 2003).

Caribou population and movement dynamics are also influenced by predator distribution. In order to reduce predation risk and increase predator detectability, caribou migrate to calving grounds in the north to avoid predators, such as wolves (Canis lupus; Bergerud, 1988, 1996). As older forests are replaced with younger ones and habitat productivity increases in the north, increased abundances of moose (Alces alces) and wolves are expected, possibly negatively impacting caribou populations. Under climate change regimes, wolves may further increase in abundance. In response to the northerly distribution of predator populations, caribou are concomitantly expected to increase their distribution to the north. However, under climate change scenarios, there may not be enough space available for migratory caribou to avoid predators if predators move to the north.

Our climate change analyses revealed a significant decrease in the occurrence of the RG migratory caribou herd, and an increase in the occurrence of the RAF migratory caribou herd based on current environmental preferences, such as habitat and climatic conditions. In addition to the direct effects of climate on caribou occurrence modelled in this study, it is expected that the migratory caribou herds will experience a further northerly shift in distribution due to several factors including longer ice-free periods, increases in snowfall and extreme weather events, alterations in the fire regime, and changes in the distribution of insects and predators. The predicted poleward shifts for caribou mirror the patterns documented for many other species (Parmesan & Yohe, 2003). Reductions in the predicted distributions of these two migratory caribou herds could result in changes in population sizes, and conversely changes in population demography could also affect caribou distribution (Couturier, 2007; Bergerud et al., 2008).

Currently, the RG and RAF migratory caribou herds are two of the largest migratory caribou populations in the world, and declines in their numbers could have negative social and economical implications, particularly for northern arctic and subarctic native cultures that rely on caribou for subsistence (Miller, 2003). Management efforts focusing on mitigating greenhouse gases to reduce the potential effects of climate change, preserving high-quality habitat, and limiting anthropogenic landscape disturbances (Schaefer, 2003), could alleviate stressors on migratory caribou populations in North America.

Acknowledgements

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