



Weather conditions and variation in timing of spring and fall migrations of migratory caribou

MAEL LE CORRE,* CHRISTIAN DUSSAULT, AND STEEVE D. CÔTÉ

Caribou Ungava, Département de Biologie and Centre d'Études Nordiques, Université Laval, 1045, av. de la Médecine, Québec, Québec G1V 0A6, Canada (MLC, CD, SDC)

Direction de la faune terrestre et de l'avifaune, Ministère des Forêts, de la Faune et des Parcs du Québec, 880, chemin Sainte-Foy, Québec, Québec G1S 4X4, Canada (CD)

* Correspondent: mael.le-corre.1@ulaval.ca

Species that make long-distance migrations face changes in the phenology of natural processes linked to global climate changes. Mismatch between the onset of resources and arrival on breeding grounds or changes in the conditions faced during migration such as early snowmelt in northern environments could have severe impacts on migrant populations. We investigated the impact of local weather and broad-scale climate and of the availability of forage resources on timing of spring and fall migrations of migratory caribou (*Rangifer tarandus*) from the Rivière-George and Rivière-aux-Feuilles herds in northern Québec and Labrador, Canada. We tested the effect of local weather using data provided by the Canadian Regional Climate Model, a large-scale climate index, snow and ice cover, and the Normalized Difference Vegetation Index on departure and arrival dates of 377 spring migrations and 499 fall migrations of female caribou. Since 2000, except for the spring arrival, migrations tended to occur earlier. Spring arrival was delayed when caribou encountered mild temperatures and abundant precipitation during migration, as early snowmelt may increase cost of movements. At greater population sizes, caribou seemed to limit the time spent on summer range by arriving later and departing earlier, possibly to limit competition for summer forage. During fall, caribou adjusted their migration to conditions *en route* because they arrived earlier if November was snowy and mild, possibly to limit the costs of moving through deep snow. Like numerous migrant species, most caribou herds are declining, and it is crucial to assess which environmental factors affect migrant populations. Our study contributes to the understanding of the impact of local weather conditions and climate change on migratory land mammals.

Key words: climate change, fall migration, long-distance migration, *Rangifer tarandus*, spring migration, timing

Migration is a key habitat selection strategy allowing species to follow broad-scale changes in resource availability and abundance (van der Graaf et al. 2006) and reduce the risk of predation (McKinnon et al. 2010). Migration is expected to improve survival rate of adults and reproductive success (Rasmussen et al. 2007). Migrant species, however, face threats related to human development and climate change (Bolger et al. 2008; Robinson et al. 2009), and several migrant populations are currently decreasing (Bolger et al. 2008; Both et al. 2010). Climate change likely is responsible for some observed declines (Robinson et al. 2009), particularly in northern environments where changes appear to be more drastic (Graversen et al. 2008), notably by modifying phenology of several natural processes (Parmesan and Yohe 2003).

Migrations to breeding areas often coincide with peaks in resource emergence or productivity (Møller et al. 2008). This synchronicity is essential to provide females with sufficient energy to rear offspring (Jonzén et al. 2007; Post and Forchhammer 2008). Observed changes in resource phenology with a progressive advancement of the onset of resource availability (Parmesan and Yohe 2003) could lead to a mismatch between time of arrival on breeding areas and peak in resource productivity. Such a mismatch has been reported for numerous migratory species of birds (Møller et al. 2008), terrestrial mammals (Post and Forchhammer 2008), and marine mammals (Anderson et al. 2013). This asynchrony may translate into lower reproductive success for females, with ultimately negative consequences for population dynamics (Møller et al. 2008;

Post and Forchhammer 2008). Individuals mostly rely on photoperiod (Bauer et al. 2011) or circannual cycles (Helm et al. 2013) to time their migrations. However, fine-tuning can be achieved through environmental cues (Visser et al. 2010) such as local weather (Gordo et al. 2005) or resource availability, notably when these resources are used to build energy reserves needed for migration (Gordo et al. 2005).

Factors that may influence the timing of migration in northern regions include onset and duration of the growing season (Post and Forchhammer 2008). Species could benefit by arriving earlier on summer ranges in response to earlier onset of vegetation growth (Jonzén et al. 2007). A longer period during which suitable conditions prevail on summer ranges could delay the date of departure toward wintering ranges (Jenni and Kéry 2003). Conditions encountered during migration also could influence arrival on seasonal ranges. Animals may use environmental cues during migration to adjust their pace (Tøttrup et al. 2008) or arrival dates, or they may follow the emergence of resources along the migration route (van der Graaf et al. 2006). On the other hand, adverse weather conditions can increase cost of movements and slow down migration (Gordo 2007; Robinson et al. 2009). For terrestrial mammals, early snowmelt or abundant fresh, powdery snow may increase costs of locomotion because energy expenditures increase with sinking depth (Fancy and White 1987). Changes in the phenology of ice formation and thawing also could alter migration, because individuals must wait for suitable ice conditions to cross large water bodies and limit risk of drowning (Poole et al. 2010).

Migratory caribou (*Rangifer tarandus*) are long-distance migrant ungulates widespread in northern environments. They undertake migrations from boreal forests in spring to reach calving grounds located in tundra where they spend summer (Taillon et al. 2012). A mismatch has been observed between the arrival date on calving grounds and the onset of vegetation growth in 1 herd (Post and Forchhammer 2008), but other components of caribou migration, such as timing of fall migration, also could be affected by climate change. In the context of a global decline in *Rangifer* populations (Vors and Boyce 2009) and pan-arctic global changes, it is crucial to assess how climate variables affect timing of migrations in caribou.

Using a long-term database, we investigated effects of snow and ice cover, temperature, precipitation, broad-scale climatic variations, and resource abundance on departure and arrival dates of spring and fall migrations of migratory caribou from the Rivière-George (RGH) and Rivière-aux-Feuilles (RFH) herds in northern Québec and Labrador, Canada. We also considered population size because it can affect the timing of migration (Hinkes et al. 2005). We hypothesized that adverse snow conditions would impede migration and that caribou would adjust their departure dates to migrate under favorable conditions according to local and broad-scale environmental cues. During mild winters, we expected caribou to depart earlier in anticipation of an early spring but also expected that conditions promoting an early snowmelt during spring migration would delay arrival on calving grounds. We also expected arrival on calving grounds to be delayed during years when snow was abundant on the calving grounds. In fall, we expected departure date

would be delayed as long as forage resources were available on the summer range. Similar to spring migrations, we expected arrival on winter grounds to be delayed as snow precipitation along caribou migratory routes increased.

MATERIALS AND METHODS

Study area and caribou herds.—The RGH and RFH range about 1,000,000 km² in northern Québec and Labrador (Fig. 1). Although wintering areas of the 2 herds may overlap in some years, their calving grounds are usually located > 800 km apart (approximately 57°N–65°W for RGH; 58°N–73°W for RFH). Females usually leave their winter range in April and arrive on calving grounds in late May after a migration of several hundreds of kilometers (RGH: $\bar{X}$ = 350 km, SD = 161; RFH: $\bar{X}$ = 615 km, SD = 248). They migrate back to their wintering areas between October and December.

Tracking data.—We used the locations of 120 females for RGH and 116 females for RFH equipped with ARGOS satellite-tracking collars (Telonics, ARGOS platform, Mesa, Arizona) between January 2000 and December 2011 (females/year RGH: $\bar{X}$ = 23, SD = 8; RFH: $\bar{X}$ = 27, SD = 15). We captured most females using a net-gun fired from a helicopter (Bookhout 1996) on wintering areas in February or March. We considered individuals to be independent because capture sites within a given year were spread over several thousands of km². We monitored females on average 2.1 years (SD = 0.1), but some individuals were followed for up to 8 years. We usually collected locations every 5 days (85.4% of the database), but frequency ranged from 1 location every day (0.2%) to 1 location every 7 days (0.7%). We filtered the data using an algorithm similar to that of Austin et al. (2003) to eliminate aberrant locations leading to movements greater than 50 km/day (Boulet et al. 2007). Capture, handling, and monitoring of caribou complied with the guidelines of the American Society of Mammalogists (Sikes et al. 2011) and the Canadian Council on Animal Care, and all procedures were approved by the University of Laval Animal Care Committee and by the Ministère des Forêts, de la Faune et des Parcs du Québec (MFFP) Animal Care Committee.

Demographic data.—Since the 1950s, RGH and RFH have varied widely in population size. RGH numbers increased from at least 60,000 individuals in the 1950s (Rasiulis 2015) to 823,000 (90% CI = 104,000) individuals in 1993, and then decreased to 385,000 (90% CI = 108,000) caribou in 2001 (Couturier et al. 2004), 27,600 (90% CI = 2,760) caribou in 2012 (V. Brodeur, MFFP, Chibougamau, Québec, pers. comm.), and 14,200 (90% CI = 710) caribou in 2014 (V. Brodeur, MFFP, Chibougamau, Québec, pers. comm.). RFH was identified in 1975 when its size was estimated at 56,000 individuals (Le Hénaff 1976). The herd reached approximately 628,000 caribou in 2001 (Couturier et al. 2004) and declined to 430,000 (90% CI = 98,900) individuals in 2011 (V. Brodeur, MFFP, Chibougamau, Québec, pers. comm.). We computed annual population sizes by fitting a polynomial regression spline to these estimates with the “loess” function in R software (R Core Team 2015).

Climate data.—To describe local weather, we used data from the Canadian Regional Climate Model (CRCM, v4.3) produced

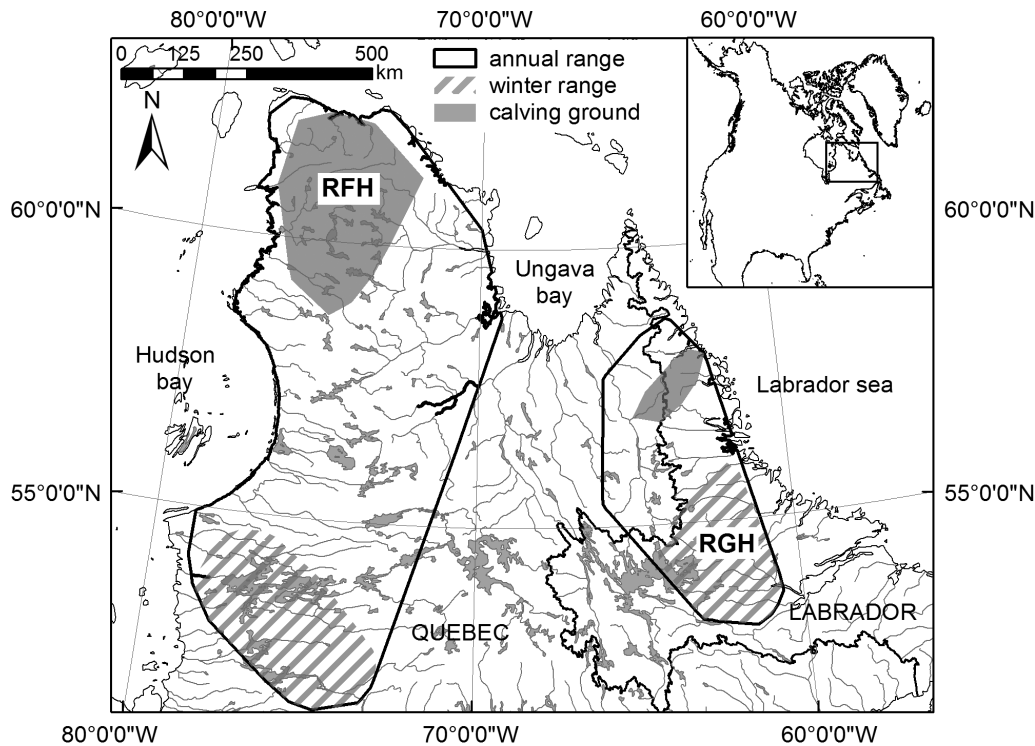


Fig. 1.—Annual ranges, winter ranges (striped areas) and calving grounds (shaded areas) of the Rivière-George (RGH) and Rivière-aux-Feuilles (RFH) migratory caribou (*Rangifer tarandus*) herds, located in northern Québec and Labrador. We delineated ranges using 100% minimum convex polygons based on ARGOS locations collected on 54 females for RGH and 60 females for RFH in 2010.

by the Ouranos Consortium (Music and Caya 2007; de Elía and Côté 2010). The domain of the CRCM simulation is centered over the province of Québec (111 × 87 grid cells of 45 × 45 km). The CRCM simulation is driven by a time series of atmospheric variables produced by the global atmospheric reanalyses ERA-Interim that give a numerical description of climate since 1979 (Dee et al. 2011). Details about the CRCM simulation are provided by de Elía and Côté (2010). We used the CRCM to obtain temperature, precipitation, snow water equivalent, and snow depth data. We used monthly averages of the mean daily temperature (°C), daily precipitation (mm/day), and snow water equivalent (mm). We did not use snow depth because it was highly correlated ($r = 0.99$) with snow water equivalent. We associated monthly weather data with each caribou location using the corresponding grid cell of the CRCM. As caribou commonly used different cells during a given month, we computed average monthly values of weather variables by taking all locations occurring during a given month and calculating the mean value of weather variables associated with these locations. We computed mean winter values of weather variables using the same method from January to March.

For broad-scale climate, we used the North Atlantic Oscillation index (NAO). NAO integrates precipitation and temperature data, and it is based on the difference in atmospheric pressure between subpolar and subtropical regions of the North Atlantic (Hurrell 1995). We used monthly and winter NAO values. In northern Québec, winter NAO is negatively correlated with snowfall and winter temperature (Couturier et al. 2009); however, these relationships are weaker for the other seasons (Coulbaly 2006). To interpret the effect of NAO

on departure or arrival dates when it was significant, we related weather variables with monthly NAO values using weather data from 4 weather stations of Environment Canada (Kuujuaq: 58°06'N–68°25'W, data spanning from 1947 to 2005; Schefferville: 54°48'N–66°49'W, 1949–1993; La Grande: 53°38'N–77°42'W, 1976–2005; Goose Bay: 53°19'N–60°25'W, 1942–2011; climat.meteo.gc.ca). We fitted linear mixed models using the “lme4” package (Bates et al. 2014) in R software with monthly NAO as the response variable, monthly average temperature, total rainfall, and total snowfall as explanatory variables, and weather station as a random factor.

Snow and ice cover.—We assessed snow and ice cover at each caribou location using snow cover data from MODIS satellite images (Hall et al. 2006). The MODIS/Terra Snow cover images represent the maximum snow cover extent over an 8-day period. At each location, we estimated snow cover (snow pixels/land pixels) and ice cover (ice pixels/water pixels) within a 10-km radius circle centered on the location. Pixels with a cloud value were excluded from the snow and ice cover calculations. We set the radius of the circle at 10 km, which was the mean daily distance travelled by females when excluding the winter break ($\bar{X} = 10.2$ km/day, $SD = 7.7$, $n = 236$ —Le Corre et al. 2014). We considered snow and ice cover values as missing values when clouds covered more than 50% of the 10-km buffer area. We computed mean monthly values of snow and ice cover as described in the “Climate data” section.

Plant productivity.—We used the Normalized Difference Vegetation Index (NDVI) as an index of plant productivity. NDVI has been used to describe plant productivity and phenology in arctic habitats (Myneni et al. 1997) and to assess their

effects on life-history traits in ungulates (Couturier et al. 2009). We used NDVI data from the Advanced Very High Resolution Radiometer (AVHRR) satellite images processed by the Canada Centre for Remote Sensing (Latifovic et al. 2005). AVHRR images are 10-day image composites at a resolution of 1 km. At each location, we calculated the mean NDVI value within the same 10-km buffer areas used to estimate snow and ice cover. We excluded pixels corresponding to water and pixels with a thick cloud shadow according to the quality mask layer of the AVHRR images. We considered NDVI value as missing when clouds represented more than 50% of the buffer area. We computed mean monthly NDVI values as described in the “Climate data” section.

Departure and arrival dates.—Movement rates differ when caribou are migrating and when they are residing on seasonal ranges (Le Corre et al. 2014). We assessed departure and arrival dates of migrations by looking at abrupt changes in caribou movement patterns over the year. We characterized movements of caribou using the First-Passage Time analysis (FPT—Fauchald and Tveraa 2003), which summarizes the velocity and tortuosity of movement along a path. FPT corresponds to the time needed by an individual to cross a circle of given radius centered on each location of an animal path. Fast, long-distance movements result in low FPT values, whereas pauses in annual movements result in high FPT values (Le Corre et al. 2014). Based on the work of Le Corre et al. (2014) on the same database, we used a circle of 25 km radius to compute FPT (see Supplementary Data SD1 for details). We then applied a segmentation process (Lavielle 2005) on FPT profiles to detect departures and arrivals of migrations. This method allows detection of changes in a signal by locating breakpoints along the signal (see Supplementary Data SD1 for details). We segmented FPT profiles into low and high FPT value segments, discriminating between fast, directional movements such as migration and slow, tortuous movements expected on seasonal ranges. Hereafter, we use “breaks” to designate pauses in annual movement, i.e., periods of the year during which individuals slow their displacements and are associated with high FPT values. For each female, the departure date corresponded to the breakpoint, along its FPT profile, marking the end of the winter break. Arrival date was the breakpoint marking the beginning of the calving break (see Le Corre et al. [2014] for details). Among 377 spring migrations made by 178 females, we identified 372 departure and 354 arrival dates. In fall, we distinguished 2 types of movement: pre-migration, from departure of the summer range until the rutting period, and fall migration, corresponding to the long-distance movement, following the rutting period, toward the winter range. We only considered the 2nd movement during fall in the analyses. A break in October preceded the fall migration in 47% of paths. We used the breakpoint marking the end of this break as the departure date. When this break was missing, we completed the analysis by computing the Net-Squared Displacements (NSD—Bunnfeld et al. 2011), i.e., the squared distance between fall locations and a reference location, here the 1st location of the winter break. We used the location for which the NSD started to decrease steadily as departure date because migration movement was associated with a strong decrease in NSD. Arriving on winter

range, individuals slowed down, leading to a sudden increase in FPT. We used this breakpoint as arrival date. Among 499 fall migrations made by 230 females, we identified 464 departure dates and 471 arrival dates. Finally, we calculated migration distance in spring and fall using the Euclidean distance between departure and arrival locations of the migrations.

For each migration phase, we tested the effect of climate variables measured during the month for which most departures or arrivals occurred and during the preceding month. For spring departure, we tested the effect of conditions in April (65.6% of departures) and during winter. For fall departure, we tested effects of conditions in October (78.0% of departures) and September. For arrival dates, we used June (64.7% of arrivals) and May in spring, and December (55.0% of arrivals) and November in fall. We grouped explanatory variables into 5 categories (Table 1): snow and ice (ice cover, snow cover, snow water equivalent), local weather (precipitation, temperature), broad-scale climate (NAO), vegetation (NDVI), and herd characteristics (herd identity, population size, migration distance). Vegetation was always included in models as an interaction with population size. We did not use snow and ice cover to model spring departure dates because cover values were 100% from January to April. We used the vegetation category only in June, September, and October. We tested for multicollinearity among all explanatory variables for each migration phase with the variance inflation factor (VIF—Zuur et al. 2010). We discarded snow water equivalent in October for fall departure ($VIF > 5$). Snow water equivalent in April for spring departure also had $VIF > 5$, but it was essentially correlated with snow water equivalent in winter ($r = 0.83$). We kept both variables but never used them in the same models.

Statistical analyses.—We fitted linear mixed models for spring departure, spring arrival, fall departure, and fall arrival to detect temporal trends in timing of migrations from 2000 to 2011. We included female identity as a random factor and year as the explanatory variable. We transformed spring departure dates (x^2) to meet assumptions of normality of the residuals and homogeneity of variance.

We used linear mixed models to assess effects of local weather and broad-scale climate variables on spring and fall departure and arrival dates with female identity as a random factor. We built biologically meaningful candidate models composed of various combinations of the categories of variables defined above to test hypotheses (see Supplementary Data SD2 for the complete list of models). We ranked all models, including a null model with no explanatory variable, using AICc (Akaike’s information criterion) weights. We considered models with $\Delta AICc \leq 2$ as equivalent and calculated parameter estimates and 95% CI using model averaging (Burnham and Anderson 2002). We provide parameter estimates with SE and 95% CI.

RESULTS

Spring departure.—Caribou started spring migration increasingly earlier and advanced their departure by approximately 14 days during the study period (year: $\beta = -304.1$, $SE = 45.87$, 95% CI = $[-394.0; -214.2]$; Fig. 2a). According to the most parsimonious models for spring departure date (Table 2), caribou

Table 1.—Variables used to investigate changes in phenology of spring and fall migrations of the Rivière-aux-Feuilles and Rivière-George (RGH) migratory caribou (*Rangifer tarandus*) herds in Québec and Labrador, Canada, 2000–2011. We indicate, for each variable, the time period over which we averaged the data. NAO: North Atlantic Oscillation index; NDVI: Normalized Difference Vegetation Index; swe: snow water equivalent; sc: snow cover; ic: ice cover; st: temperature; pcpr: precipitation; herd_ID: RGH used as the reference category; pop_size: estimated population size ($\times 10^3$); dist_mig: distance of migration.

Migration phase	Period over which data were averaged	Variable categories				
		Snow and ice	Local weather	Broad-scale climate	Vegetation	Herd characteristics
Spring departure	Winter (January–March)	Swe	St + pcpr	NAO		herd_ID + pop_size + dist_mig
	April	(swe) ^a	St + pcpr	NAO		
Spring arrival	May	sc + ic + swe	St + pcpr	NAO		herd_ID + pop_size + dist_mig
	June	sc + ic + swe	St + pcpr	NAO	NDVI	
Fall departure	September	sc + ic + swe	st + pcpr	NAO	NDVI	herd_ID + pop_size + dist_mig
	October	sc + ic + (swe) ^a	st + pcpr	NAO	NDVI	
Fall arrival	November	sc + ic + swe	st + pcpr	NAO		herd_ID + pop_size + dist_mig
	December	sc + ic + swe	st + pcpr	NAO		

^aBrackets indicate variables with a variance inflation factor > 5.

from RFH started migration on average 7.4 days ($SE = 2.98$) sooner than caribou from RGH (Table 3a). Spring departure occurred earlier at smaller population sizes, and an increase of 100,000 individuals delayed departure by 3.5 days ($SE = 0.78$). Caribou also departed earlier in years with mild winter temperatures (Table 3a), with migration starting 1.9 days earlier for each increase of 1° ($SE = 0.3$; Fig. 3a). Departure was delayed in years with abundant precipitation in April. Finally, longer migration led to earlier departure, with caribou advancing their migration by 1.8 days ($SE = 0.45$) for an increase of 100 km of migration distance. We did not detect changes in spring migration distance over the study period (linear mixed model with distance of migration as dependent variable, year as factor, and female identity as a random factor; $\beta = 8.0$, $SE = 4.30$, 95% $CI = [-0.4; 16.4]$). Other parameter estimates did not differ from 0 (Table 3a).

Spring arrival.—We found no trend in arrival date of spring migration over the study period (year: $\beta = -0.2$, $SE = 0.21$, 95% $CI = [-0.6; 0.2]$; Fig. 2b). Few variables included in the best models for the spring arrival date (Table 2) had a significant influence on arrival date (Table 3b). Herd (RFH or RGH) did not influence arrival date, but longer migration led to late arrivals (Table 3b); an increase of 100 km of migration distance delayed arrival by 2.8 days ($SE = 0.40$). At small population sizes (e.g., 200,000 individuals in Fig. 4a), arrival dates were positively related with NDVI in June, whereas at greater population sizes, arrivals were late even for low NDVI values (e.g., 500,000 individuals in Fig. 4a). Arrival date was delayed in years when caribou faced abundant precipitation and warm temperatures during migration (Fig. 3b), with an increase of 1° in daily temperature in May delaying arrival by 1.6 days ($SE = 0.59$) and an increase of 1 mm in daily precipitation in May by 3.3 days ($SE = 0.91$). Finally, we observed a positive relationship between NAO in May and arrival date. NAO in May was negatively related to temperature (temperature: $\beta = -0.04$, $SE = 0.02$, 95% $CI = [-0.1; -0.003]$) but not with precipitation (rainfall: $\beta = -0.002$, $SE = 0.002$, 95% $CI = [-0.002; 0.007]$; snowfall: $\beta = -0.0003$, $SE = 0.004$, 95% $CI = [-0.007; 0.007]$).

Fall departure.—Departure at fall occurred progressively earlier, shifting by 6.2 days ($SE = 1.61$) during the study period (year: $\beta = -0.6$, $SE = 0.15$, 95% $CI = [-0.9; -0.3]$; Fig. 2c).

According to the most parsimonious model for fall departure date (Table 2), departure occurred earlier as distance of migration increased (Table 4a); a 100 km increase in migration distance advanced departure by 1.8 days ($SE = 0.30$). Fall migration distance increased during the study period (linear mixed model with distance of migration as dependent variable, year as factor, and female identity as a random factor; $\beta = 7.2$, $SE = 3.30$, 95% $CI = [0.7; 13.6]$). Departure date was delayed in years when snow water equivalent was high in September and when there was little precipitation in October (Fig. 3c), with a decrease of 1 mm in mean daily precipitation delaying departure by 3.3 days ($SE = 0.82$). Departure date occurred earlier as NDVI values in October increased; however, this relationship tended to disappear as population size increased (Fig. 4b).

Fall arrival.—Caribou advanced arrival on winter range by 5.6 days ($SE = 1.91$) during the study period (year: $\beta = -0.5$, $SE = 0.17$, 95% $CI = [-0.9; -0.2]$; Fig. 2d). According to the most parsimonious models (Table 2), caribou from RFH arrived on their winter range 6.9 days ($SE = 2.51$) earlier than caribou from RGH. Arrival date was positively related to population size; increasing population size by 100,000 individuals delayed arrival by 2.0 days ($SE = 0.64$), and increasing migration distance by 100 km delayed arrival by 2.4 days ($SE = 0.38$). Caribou terminated fall migration sooner in years when snow water equivalent was high and temperature was mild in November (Fig. 3d) because an increase of 10 mm of snow water equivalent in November advanced arrival by 1.4 days ($SE = 0.50$) and an increase of 1° in November temperature advanced arrival by 1.1 days ($SE = 0.30$). Caribou also arrived earlier when precipitation was abundant on the winter range in December because they arrived 2.8 days ($SE = 1.05$) earlier for each increase of 1 mm in daily precipitation. Finally, fall arrival dates were negatively related with NAO in November and positively related with NAO in December. In November, NAO was negatively related with temperature ($\beta = -0.1$, $SE = 0.03$, 95% $CI = [-0.2; -0.09]$) and snow precipitation ($\beta = -0.006$, $SE = 0.003$, 95% $CI = [-0.01; -0.001]$) but not with rainfall ($\beta = -0.01$, $SE = 0.006$, 95% $CI = [-0.001; 0.02]$). In December, NAO was negatively related with temperature ($\beta = -0.2$, $SE = 0.02$, 95% $CI = [-0.2; -0.1]$) but not with precipitation

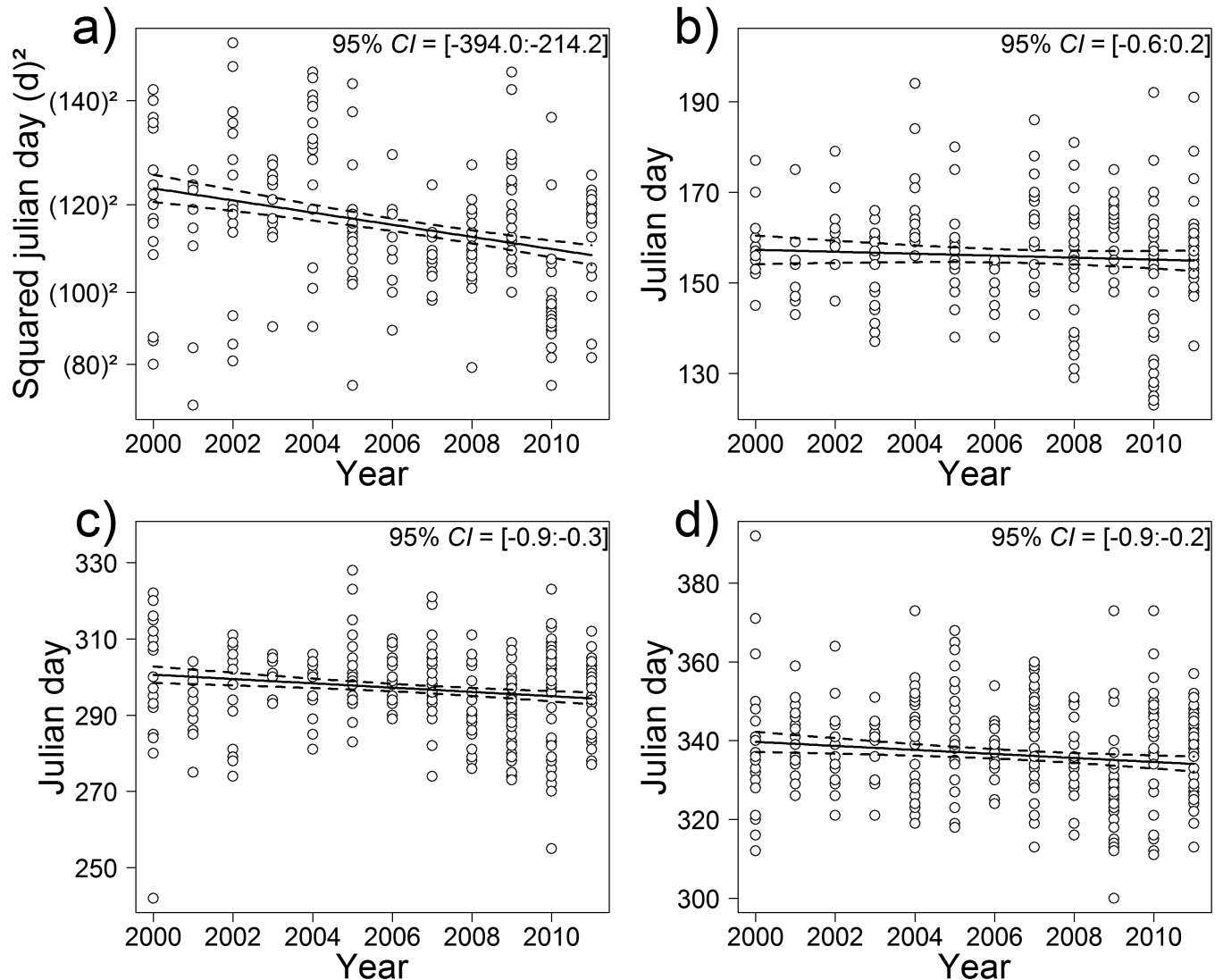


Fig. 2.—Changes in migration phenology of migratory caribou (*Rangifer tarandus*) from northern Québec and Labrador between 2000 and 2011 with fitted trends and 95% CI (dashed lines). a) Spring migration departure (dates in squared Julian days); b) spring migration arrival; c) fall migration departure; d) fall migration arrival.

Table 2.—Most parsimonious mixed-effects models explaining variation in the phenology of spring and fall migrations of the Rivière-aux-Feuilles and Rivière-George (RGH) migratory caribou (*Rangifer tarandus*) herds in Québec and Labrador, Canada, 2000–2011, for each migration phase, with their AICc (Akaike's information criterion) weight (ω_i). Models that received equivalent support from the data ($\Delta\text{AIC} < 2$) are presented. NAO: North Atlantic Oscillation index; NDVI: Normalized Difference Vegetation Index; swe: snow water equivalent; sc: snow cover; ic: ice cover; st: temperature; pc: precipitation; herd_ID: RGH used as the reference category; pop_size: estimated population size ($\times 10^3$); dist_mig: distance of migration; sept: September; oct: October; nov: November; dec: December.

Migration phase	Most parsimonious models	ω_i
Spring departure	swe_apr + st_winter + pc_winter + st_apr + pc_apr + herd_ID + pop_size + dist_mig	0.60
	swe_winter + st_winter + pc_winter + st_apr + pc_apr + herd_ID + pop_size + dist_mig	0.25
Spring arrival	swe_may + sc_may + ic_may + swe_june + sc_june + ic_june + NAO_may + NAO_june + NDVI_june * pop_size + herd_ID + dist_mig	0.71
	swe_may + sc_may + ic_may + swe_june + sc_june + ic_june + st_may + pc_may + st_june + pc_june + NDVI_june * pop_size + herd_ID + dist_mig	0.26
Fall departure	swe_sept + sc_sept + ic_sept + sc_oct + ic_oct + st_sept + pc_sept + st_oct + pc_oct + NDVI_sept * pop_size + NDVI_oct * pop_size + herd_ID + dist_mig	0.99
Fall arrival	swe_nov + sc_nov + ic_nov + swe_dec + sc_dec + ic_dec + st_nov + pc_nov + st_dec + pc_dec + herd_ID + pop_size + dist_mig	0.60
	swe_nov + sc_nov + ic_nov + swe_dec + sc_dec + ic_dec + NAO_dec + herd_ID + pop_size + dist_mig	0.40

Table 3.—Parameter estimates from the best mixed-effects models (female identity as a random factor) explaining variation in a) departure date and b) arrival date of the spring migration of caribou (*Rangifer tarandus*) in Québec and Labrador, Canada, 2000–2011. Parameters were calculated by model averaging. Variables for which 95% *CI* exclude 0 are considered statistically significant and are indicated in bold. NAO: North Atlantic Oscillation index; NDVI: Normalized Difference Vegetation Index; RGH: Rivière-George; swe: snow water equivalent; sc: snow cover; ic: ice cover; st: temperature; pc: precipitation; herd_ID: RGH used as the reference category; pop_size: estimated population size ($\times 10^3$); dist_mig: distance of migration; wint: winter; apr: April.

Variable category	a) Spring migration departure					b) Spring migration arrival				
	Variable	Estimate	SE	95% CI		Variable	Estimate	SE	95% CI	
Snow and ice	swe_wint	0.01	0.02	−0.03	0.05	swe_may	0.01	0.02	−0.03	0.05
	swe_apr	0.03	0.02	−0.01	0.07	sc_may	0.70	7.31	−13.63	15.02
Local weather	st_wint	−1.88	0.28	−2.43	−1.32	ic_may	−3.33	8.58	−20.14	13.48
	pcp_wint	−1.41	2.43	−6.16	3.35	swe_june	0.04	0.02	−0.003	0.08
	st_apr	0.65	0.37	−0.07	1.38	sc_june	4.12	4.02	−3.77	12.01
	pcp_apr	3.70	0.97	1.80	5.61	ic_june	1.08	2.27	−3.37	5.53
						st_may	1.60	0.59	0.44	2.77
Broad-scale climate						pcp_may	3.26	0.91	1.48	5.04
						st_june	0.21	0.59	−0.94	1.36
Vegetation						pcp_june	−0.46	0.98	−2.39	1.46
						NAO_may	4.97	1.14	2.75	7.20
Herd characteristics	pop_size	0.03	0.01	0.02	0.05	NAO_june	−0.32	1.36	−2.99	2.35
	herd_ID	−7.44	2.98	−13.28	−1.60	NDVI_june * pop_size	−0.10	0.05	−0.19	−0.01
	dist_mig	−0.02	0.005	−0.03	−0.01	herd_ID	−4.71	3.65	−11.87	2.45
						dist_mig	0.03	0.00	0.02	0.04

(rainfall: $\beta = -0.002$, $SE = 0.02$, 95% $CI = [-0.03; 0.03]$; snow-fall: $\beta = -0.004$, $SE = 0.003$, 95% $CI = [-0.002; -0.01]$).

DISCUSSION

We assessed effects of weather and broad-scale climate variables and vegetation productivity on the timing of migrations in 2 large migratory caribou herds in northern Québec and Labrador. Contrary to our predictions, snow and ice cover did not influence timing of migrations. Resource availability, possibly through intraspecific competition, affected timing of migration, but changes in departure and arrival dates mostly were related to local weather variables that affected snow quality, that likely also affected the costs of locomotion for migratory caribou.

Except for spring arrival date, migrations occurred earlier throughout the 12-year study period. This trend is consistent with most observations of other long-distance migrants, e.g., earlier departures in spring have been reported for bird species (Tøttrup et al. 2006). In contrast to short-distance migrants that stay longer on summer ranges and gradually move toward their winter ranges, long-distance migrants usually depart early in fall in anticipation of the environmental conditions that they will encounter during migration (Jenni and Kéry 2003; Gordo 2007). Schaefer and Mahoney (2013) studied long-term changes in the timing of migration of a woodland caribou population in Newfoundland, but caribou from their study corresponded more to a short-distance migrant species, with migration < 100 km. Changes in the timing of spring and fall migrations in their study were more related to changes in herd population size, with individuals limiting time spent on the summer range at greater population size.

We reported earlier departures and later arrivals for long migrations in spring and fall. Differences in timing of migrations have been reported between long- and short-distance

migrants, the former leaving sooner and arriving later on breeding sites (Tøttrup et al. 2006). Accordingly, difference in spring departure dates between the 2 herds likely was related to differences in the length of migrations. Caribou from the RFH started their spring migration earlier than caribou from RGH. The main winter range of the RFH is located much farther away from its calving ground than the winter range used by RGH. Caribou from the RFH migrated over a distance almost twice as long as those of the RGH (615 versus 350 km, on average). The shift in fall departure date during the study period could be explained partly by the increase in fall migration distance. However, fall migration only increased by 79 km, and the change observed for departure date was greater than expected if caribou only responded to migration distance. Moreover, migration distance can be affected by changes in population size, with caribou wintering farther from their calving ground at greater population size to limit competition (Schaefer et al. 2000; Schmelzer and Otto 2003). However, during the study period, despite both herds declining, we did not detect changes in migration distance in spring and we observed longer migrations in fall, suggesting that changes in departure and arrival dates were mostly related to changes in conditions encountered during migration.

Timing of spring migration was linked to weather conditions encountered by caribou during migration. Departure dates in spring occurred earlier in mild winters and were delayed when precipitation was abundant in April. On the other hand, arrival dates of the spring migration were delayed in years of mild temperatures and abundant precipitation during migration. Taillon (2013) found the opposite effect of the May temperature for RFH. Here, we used estimated conditions encountered at each caribou location. In contrast, temperatures used by Taillon (2013) were collected from a weather station located about 300 km east of the calving ground and provided general weather conditions on the calving ground.

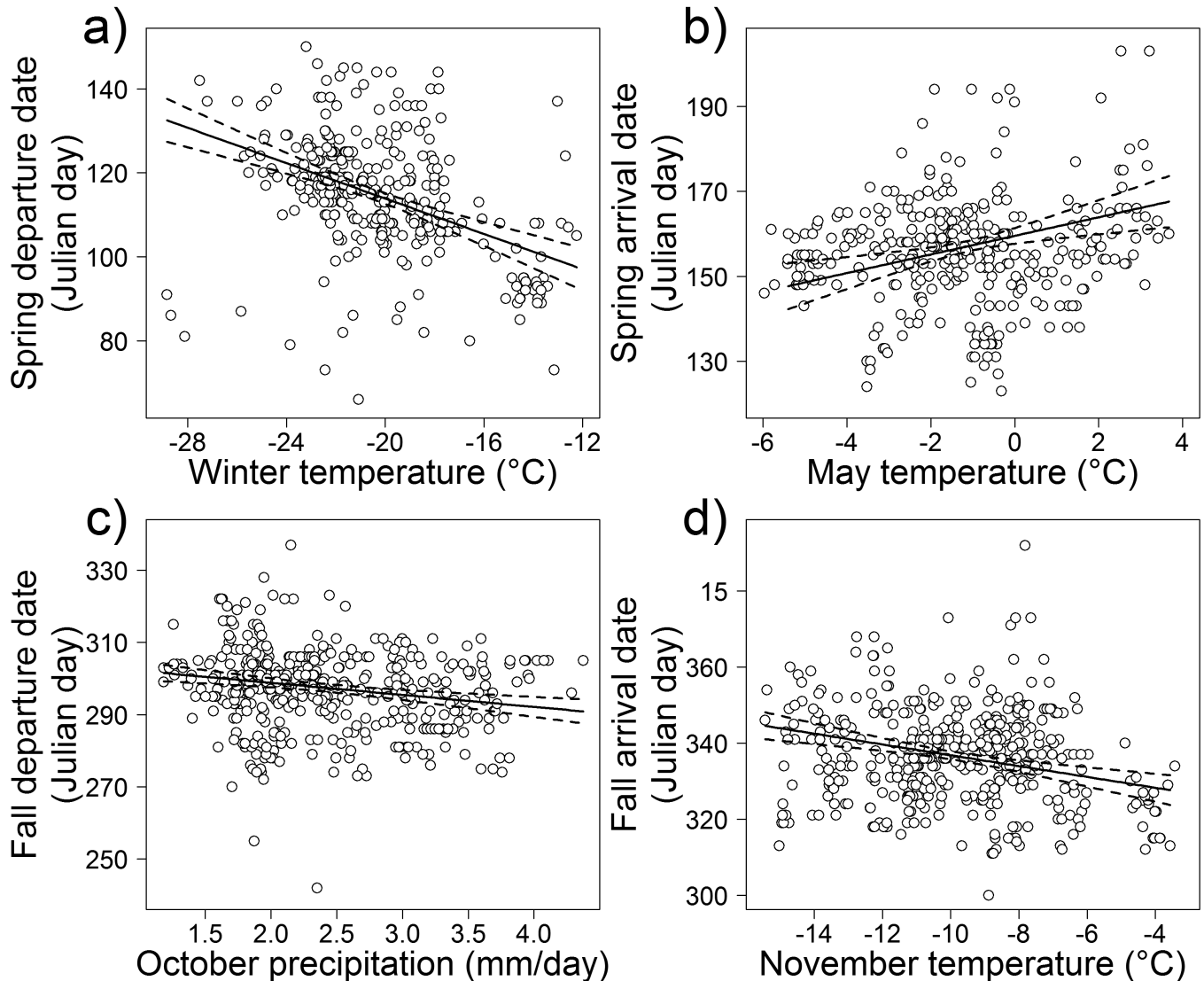


Fig. 3.—Significant relationships with fitted trends and 95% CI (dashed lines) between a) spring migration departure date and mean daily temperature for winter (January to March), b) spring migration arrival date and mean daily temperature in May, c) fall migration departure date and daily October precipitation, and d) fall migration arrival date and mean daily temperature in November for migratory caribou (*Rangifer tarandus*) from Northern Québec and Labrador, 2000–2011.

Migrants that minimize costs of movements during migration should have increased fitness; birds may use favorable winds (Alerstam 2011), and caribou may travel on frozen lakes and rivers (Fancy and White 1987; Leblond et al. 2016) or use trails of packed snow. Deep, soft snow increases energetic costs of movements for ungulates (Fancy and White 1987; Hénault-Richard et al. 2014). Duquette (1988) reported that caribou avoided moving in soft snow and delayed migration in such conditions as we observed in years with abundant snow on the ground and heavy snowfall in April. Furthermore, migrating through melting snow could increase energy expenditures (Fancy and White 1987) and possibly slow migration. One effect of climate change in northern environments is the earlier onset of snowmelt caused by rising spring temperatures (Derksen and Brown 2012). Caribou could use winter temperature as a cue for upcoming spring weather conditions. Early departure dates during mild winters could limit the impact of poor snow conditions during migration.

In fall, contrary to our predictions, we observed an early arrival when caribou encountered abundant snow and mild temperatures during migration and abundant precipitation at the arrival site, 2 variables that are expected to increase in fall with climate change (IPCC 2014). In birds, long-distance migrants depart earlier when individuals are expected to encounter harsh conditions during migration (Jenni and Kéry 2003; Gordo 2007). Therefore, timing of the fall migration seemed to depend more on conditions *en route* than for spring migration (Gordo 2007). Thus, caribou could use the amount of precipitation in October as a cue to predict snow abundance during migration and adjust migration to limit costs of moving through deep snow. The effect of temperature on the timing of fall migration was more variable, possibly because temperatures were relatively cold throughout the fall migration, with low perceived effects on snow quality. Mild temperatures in fall, however, could delay ice formation (Magnuson et al.

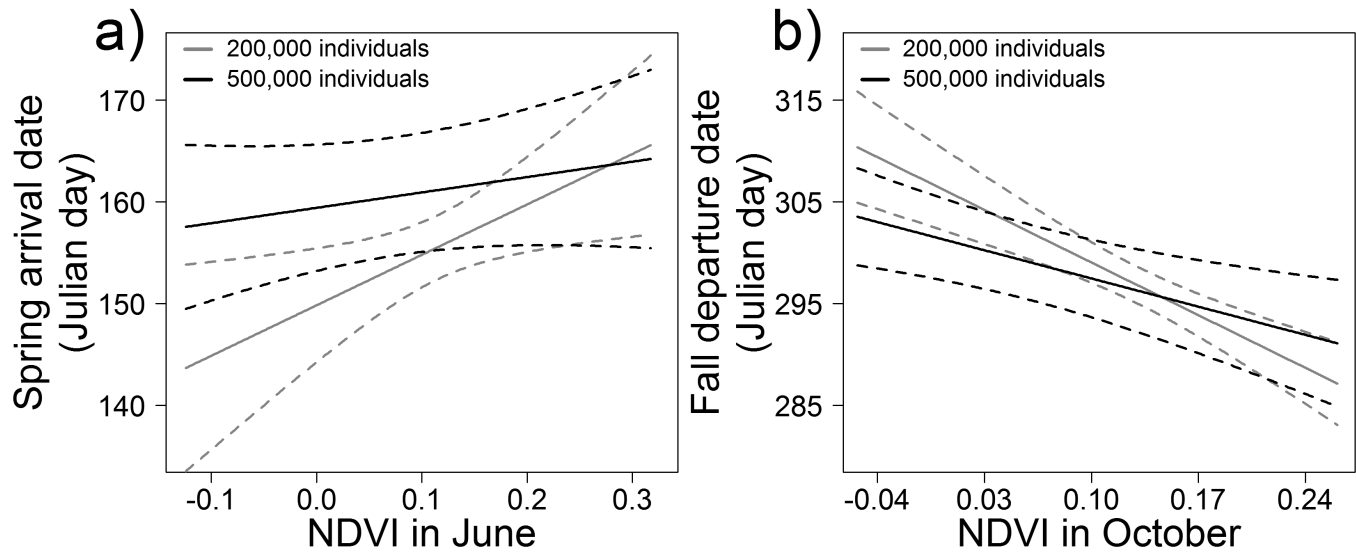


Fig. 4.—Effect of a) NDVI in June on spring migration arrival date, and b) NDVI in October on fall migration departure date for migratory caribou (*Rangifer tarandus*) from northern Québec and Labrador between 2000 and 2011, according to population size (gray: 200,000 individuals; black: 500,000 individuals). Fitted trends are presented with 95% CI (dashed lines). NDVI: Normalized Difference Vegetation Index.

Table 4.—Parameter estimates from the best mixed-effects models (female identity as a random factor) explaining variation in a) departure date and b) arrival date of the fall migration of caribou (*Rangifer tarandus*) in Québec and Labrador, Canada, 2000–2011. Parameters were calculated by model averaging. Variables for which 95% CI exclude 0 are considered statistically significant and are indicated in bold. NAO: North Atlantic Oscillation index; NDVI: Normalized Difference Vegetation Index; RGH: Rivière-George; swe: snow water equivalent; sc: snow cover; ic: ice cover; st: temperature; pcpr: precipitation; herd_ID: RGH used as the reference category; pop_size: estimated population size ($\times 10^3$); dits_mig: distance of migration; sept: September; oct: October; nov: November; dec: December.

Variable category	a) Fall migration departure					b) Fall migration arrival				
	Variable	Estimate	SE	95% CI		Variable	Estimate	SE	95% CI	
Snow and ice	swe_sept	2.50	0.52	1.48	3.52	swe_nov	-0.14	0.05	-0.24	-0.05
	sc_sept	3.80	7.88	-11.64	19.24	sc_nov	-5.24	10.20	-25.23	14.75
	ic_sept	6.28	7.14	-7.72	20.28	ic_nov	0.12	3.59	-6.91	7.15
	sc_oct	-2.48	3.41	-9.16	4.20	swe_dec	0.04	0.03	-0.03	0.10
	ic_oct	-2.02	2.43	-6.79	2.74	sc_dec	29.90	41.22	-50.90	110.70
Local weather						ic_dec	-6.00	8.38	-22.42	10.42
	st_sept	1.07	0.55	-0.004	2.15	st_nov	-1.10	0.30	-1.69	-0.50
	pcp_sept	-0.19	0.52	-1.20	0.83	pcp_nov	0.39	1.13	-1.82	2.60
	st_oct	0.39	0.41	-0.41	1.20	st_dec	0.22	0.19	-0.16	0.60
Broad-scale climate	pcp_oct	-3.33	0.82	-4.95	-1.72	pcp_dec	-2.79	1.05	-4.84	-0.74
						NAO_nov	-2.78	0.78	-4.31	-1.26
						NAO_dec	1.46	0.35	0.78	2.14
Vegetation	NDVI_sept * pop_size	0.001	0.04	-0.08	0.09					
	NDVI_oct * pop_size	0.11	0.05	0.02	0.21					
Herd characteristics						pop_size	0.02	0.01	0.01	0.03
	herd_ID	1.90	2.42	-2.84	6.65	herd_ID	-6.88	2.51	-11.80	-1.96
	dist_mig	-0.02	0.003	-0.02	-0.01	dist_mig	0.02	0.004	0.02	0.03

2000), and past observations have shown that crossing partially frozen lakes could increase the risk of injuries and drowning for caribou (Miller and Gunn 1986). Caribou could attempt to migrate before freeze-up, but the index of ice cover we used was too coarse to reliably test this idea.

Population size and resource availability on seasonal ranges influenced departure and arrival dates of caribou in spring and fall. We observed a delay in spring departure dates at greater population sizes and in fall departure dates when snow water equivalent was high and NDVI was low during the pre-migration movement. Various responses to resource abundance and

availability on departure range can be observed among migrant species (Gordo et al. 2005; Tøttrup et al. 2008). Individuals may stay on seasonal ranges as long as conditions remain favorable, delaying departure when resources are abundant (Tøttrup et al. 2008). Conversely, when individuals need to build energetic reserves before starting migration, a decrease in food availability, such as in fall, can slow down the build-up of reserves and delay departure (Gordo et al. 2005). At greater population sizes, competition for food could increase, leading to a decrease in food availability at the individual level (Bonenfant et al. 2009), which could explain, at least partly, the

delay we observed in departure dates in spring. Greater population size also appeared to delay arrival on calving grounds when NDVI in June was low, as also observed by [Schaefer and Mahoney \(2013\)](#). Summer food has been suggested as a key regulating factor of caribou populations ([Crête and Huot 1993](#); [Mahoney and Schaefer 2002](#)). Caribou can limit the impact of competition for summer forage by limiting time spent on the summer range ([Schaefer and Mahoney 2013](#)). Because arrival was late for high NDVI in June even at small population sizes, NDVI might not indicate an effect of resources on arrival date. Individuals arrived on calving grounds before the onset of vegetation growth ([Bergerud et al. 2008](#)), which is linked to snowmelt ([Høye et al. 2007](#)). Thus, high NDVI in June may have reflected earlier spring conditions, with high temperature and an early snowmelt ([Taillon 2013](#)) impeding migratory movements. In fall, the interaction between NDVI and population size seemed to indicate that competition also may delay the build-up of reserves necessary to migrate, but if resources are too scarce, condition could deteriorate faster and individuals could be forced to migrate prematurely to escape competition ([Nelson 1995](#); [Schaefer and Mahoney 2013](#)). Finally, arrival was delayed at greater population sizes, possibly because of increased competition for resources on the winter range. Caribou from RFH and RGH showed variability in use of winter ranges ([Schaefer et al. 2000](#)), and in a context of low resource availability, they may pursue migration until they reach a suitable winter range. We interpret our results assuming that high population size and low resource availability led to increased competition; however, to test this hypothesis, we would need additional information on caribou density and resource abundance, notably in fall and winter when caribou essentially rely on lichens ([Bergerud et al. 2008](#)), as NDVI mostly reflects vascular plant productivity ([Myneni et al. 1997](#)).

Global climate indices such as NAO are known to affect long-distance migrant species ([Vähätalo et al. 2004](#)). We detected an effect on the arrival date of the NAO of May in spring, which was negatively related to temperature, and of the NAO of November in fall, which was negatively related to temperature and precipitation. Thus, effects of NAO appeared to contradict effects of local weather variables encountered by caribou during spring and fall migrations. NAO, however, provides composite information about climate conditions prevailing in the entire range of caribou; early arrival in spring thus could be a response to broad-scale early spring conditions, and late arrival in fall could be a response to broad-scale delay in the onset of winter. However, at a finer scale, individuals seemed to adjust their migration according to local conditions encountered during the migration ([Gordo 2007](#); [Tøttrup et al. 2008](#)).

We provide new insights on the influence of local weather on timing of the spring caribou migration. Our study is also the first to highlight effects of weather on the fall migration of caribou. According to actual observations of climate and climate projections, temperature and precipitation are expected to increase in spring and fall in forthcoming decades ([IPCC 2014](#)). Interpreting our findings in this context of climate change, we expect a more limited impact of climate change during fall than

spring because of variation in the use of winter ranges by caribou ([Schaefer et al. 2000](#); [Couturier et al. 2009](#)). Moreover, in contrast to spring migration that just precedes calving, a critical biological period for female caribou, fall migration does not impose such a strong constraint. However, individuals remain exposed to different weather events that may delay freeze-up and then increase the risk of injuries and drowning when crossing lakes on a thin ice layer ([Miller and Gunn 1986](#)). Early spring conditions appeared to slow migration. Despite a clear trend for individuals to leave winter ranges earlier, migration distance and arrival date on calving grounds did not change. In Greenland, females calved gradually earlier in response to earlier onset of vegetation, but change in the timing of calving occurred at a slower pace than change in the onset of vegetation growth ([Post and Forchhammer 2008](#)). Thus, the capacity of caribou to maintain synchrony with the onset of vegetation growth could be limited by weather conditions encountered during migration. This synchrony is crucial for survival of newborn calves ([Post and Forchhammer 2008](#)), which is a critical component of the population dynamics of ungulates ([Gaillard et al. 2000](#)). A mismatch between the date of arrival on calving grounds and vegetation green-up could be the most proximate negative impact of climate change for migratory caribou. Further investigations are now required to assess how changes in timing of spring and fall migrations affect the fitness of migratory caribou.

ACKNOWLEDGEMENTS

We thank the Ministère des Forêts, de la Faune et des Parcs du Québec and Caribou Ungava for providing the Argos database. We thank M. Leblond as well as 2 anonymous reviewers for constructive comments on earlier versions of the manuscript. Caribou Ungava is funded by ArcticNet, Natural Sciences and Engineering Research Council of Canada, Hydro-Québec, GlenCore-Mine Raglan, Fédération des Pourvoiries du Québec, CircumArctic Rangifer Monitoring and Assessment Network, International Polar Year, Ministère des Forêts, de la Faune et des Parcs du Québec, Labrador and Newfoundland Wildlife Division, First Air, Fédération québécoise des chasseurs et pêcheurs, Fondation de la Faune du Québec, Institute for Environmental Monitoring and Research, Canadian Wildlife Federation, and Canada Foundation for Innovation. MLC was supported by Ouranos through the Fonds Vert Québec and Caribou Ungava. We thank M. Bélanger, T. Chubbs, S. Couturier, J.-D. Daoust, P. Duncan, D. Elliott, P. Jefford, C. Jutras, J.-Y. Lacasse, L. Lambert, P. May, Y. Michaud, M. Pachkowski, Y. Pépin, R. Perron, A. Thiffault, and A.-A. Tremblay for their help with data collection. We especially thank V. Brodeur and S. Rivard for providing help with caribou monitoring, and C. Hins for logistical support and advice.

SUPPLEMENTARY DATA

Supplementary Data SD1.—Detailed process to assess spring and fall migration movements, as well as timing, from changes

in the structure of caribou displacements using First-Passage time and Net-Squared Displacement analyses.

Supplementary Data SD2.—Summary of the selection procedure for linear mixed models examining departure and arrival dates for spring migration and departure and arrival dates for fall migration of female migratory caribou from northern Québec and Labrador.

LITERATURE CITED

- ALERSTAM, T. 2011. Optimal bird migration revisited. *Journal of Ornithology* 152:5–23.
- ANDERSON, J. J., E. GURARIE, C. BRACIS, B. J. BURKE, AND K. L. LAIDRE. 2013. Modeling climate change impacts on phenology and population dynamics of migratory marine species. *Ecological Modelling* 264:83–97.
- AUSTIN, D., J. I. McMILLAN, AND W. D. BOWEN. 2003. A three-stage algorithm for filtering erroneous Argos satellite locations. *Marine Mammal Science* 19:371–383.
- BATES, D., M. MAECHLER, B. M. BOLKER, AND S. WALKER. 2014. lme4: linear mixed-effects models using Eigen and S4. R package version 1.1-12. <https://cran.r-project.org/web/packages/lme4/index.html>. Accessed 20 April 2016.
- BAUER, S., ET AL. 2011. Cues and decision rules in animal migration. Pp. 68–87 in *Animal migration: a synthesis* (E. J. Milner-Gulland, J. M. Fryxell, and A. R. E. Sinclair, eds.). Oxford University Press, New York.
- BERGERUD, A. T., S. N. LUTTICH, AND L. CAMPS. 2008. The return of caribou to Ungava. McGill-Queen's University Press, Montréal, Quebec, Canada.
- BOLGER, D. T., W. D. NEWMARK, T. A. MORRISON, AND D. F. DOAK. 2008. The need for integrative approaches to understand and conserve migratory ungulates. *Ecology Letters* 11:63–77.
- BONENFANT, C., ET AL. 2009. Empirical evidence of density-dependence in populations of large herbivores. Pp. 313–357 in *Advances in ecological research*, Vol. 41 (H. Caswell, ed.). Elsevier Academic Press Inc., San Diego, California.
- BOOKHOUT, T. A. 1996. Research and management techniques for wildlife and habitats. The Wildlife Society, Bethesda, Maryland.
- BOTH, C., C. A. M. VAN TURNHOUT, R. G. BULSMA, H. SIEPEL, A. J. VAN STRIEN, AND R. P. B. FOPPEN. 2010. Avian population consequences of climate change are most severe for long-distance migrants in seasonal habitats. *Proceedings of the Royal Society of London, B. Biological Sciences* 277:1259–1266.
- BOULET, M., S. COUTURIER, S. D. CÔTÉ, R. D. OTTO, AND L. BERNATCHEZ. 2007. Integrative use of spatial, genetic, and demographic analyses for investigating genetic connectivity between migratory, montane, and sedentary caribou herds. *Molecular Ecology* 16:4223–4240.
- BUNNEFELD, N., ET AL. 2011. A model-driven approach to quantify migration patterns: individual, regional and yearly differences. *Journal of Animal Ecology* 80:466–476.
- BURNHAM, K. P., AND D. R. ANDERSON. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York.
- COULIBALY, P. 2006. Spatial and temporal variability of Canadian seasonal precipitation (1900–2000). *Advances in Water Resources* 29:1846–1865.
- COUTURIER, S., S. D. CÔTÉ, R. D. OTTO, R. B. WELADJI, AND J. HUOT. 2009. Variation in calf body mass in migratory caribou: the role of habitat, climate, and movements. *Journal of Mammalogy* 90:442–452.
- COUTURIER, S., D. JEAN, R. D. OTTO, AND S. RIVARD. 2004. Demography of the migratory tundra caribou (*Rangifer tarandus*) of the Nord-du-Québec region and Labrador. Ministère des Ressources naturelles, de la Faune et des Parcs, Québec, Canada.
- CRÊTE, M., AND J. HUOT. 1993. Regulation of large herd of migratory caribou: summer nutrition affects calf growth and body reserves of dams. *Canadian Journal of Zoology* 71:2291–2296.
- DE ELÍA, R., AND H. CÔTÉ. 2010. Climate and climate change sensitivity to model configuration in the Canadian RCM over North America. *Meteorologische Zeitschrift* 19:325–339.
- DEE, D. P., ET AL. 2011. The ERA-Interim reanalysis: configuration and performance of the data assimilation system. *Quarterly Journal of the Royal Meteorological Society* 137:553–597.
- DERKSEN, C., AND R. BROWN. 2012. Spring snow cover extent reductions in the 2008–2012 period exceeding climate model projections. *Geophysical Research Letters* 39:L19504.
- DUQUETTE, L. S. 1988. Snow characteristics along caribou trails and within feeding areas during spring migration. *Arctic* 41:143–144.
- FANCY, S. G., AND R. G. WHITE. 1987. Energy expenditures for locomotion by barren-ground caribou. *Canadian Journal of Zoology* 65:122–128.
- FAUCHALD, P., AND T. TVERAA. 2003. Using first-passage time in the analysis of area-restricted search and habitat selection. *Ecology* 84:282–288.
- GAILLARD, J. M., M. FESTA-BIANCHET, N. G. YOCOZ, A. LOISON, AND C. TOÏGO. 2000. Temporal variation in fitness components and population dynamics of large herbivores. *Annual Review of Ecology and Systematics* 31:367–393.
- GORDO, O. 2007. Why are bird migration dates shifting? A review of weather and climate effects on avian migratory phenology. *Climate Research* 35:37–58.
- GORDO, O., L. BROTONS, X. FERRER, AND P. COMAS. 2005. Do changes in climate patterns in wintering areas affect the timing of the spring arrival of trans-Saharan migrant birds? *Global Change Biology* 11:12–21.
- GRAVERSEN, R. G., T. MAURITSEN, M. TIERNSTRÖM, E. KÄLLEN, AND G. SVENSSON. 2008. Vertical structure of recent Arctic warming. *Nature* 451:53–U54.
- HALL, D., G. RIGGS, AND V. SALOMONSON. 2006. MODIS/Terra Snow Cover 8-day L3 Global 500m Grid V005, February 2000 to December 2011. NASA National Snow and Ice Data Center Distributed Active Archive Center, Boulder, Colorado. <https://nsidc.org/data/MOD10A2/versions/5>. Accessed 20 April 2016.
- HELM, B., ET AL. 2013. Annual rhythms that underlie phenology: biological time-keeping meets environmental change. *Proceedings of the Royal Society of London, B. Biological Sciences* 280:20130016.
- HÉNAULT-RICHARD, J., J. WILMSHURST, AND S. D. CÔTÉ. 2014. The effect of snow on space use of an alpine ungulate: recently fallen snow tells more than cumulative snow depth. *Canadian Journal of Zoology* 92:1067–1074.
- HINKES, M. T., ET AL. 2005. Influence of population growth on caribou herd identity, calving ground fidelity, and behavior. *Journal of Wildlife Management* 69:1147–1162.
- HØYE, T. T., E. POST, H. MELTOFTE, N. M. SCHMIDT, AND M. C. FORCHHAMMER. 2007. Rapid advancement of spring in the High Arctic. *Current Biology* 17:R449–R451.
- HURRELL, J. W. 1995. Decadal trends in the North Atlantic Oscillation: regional temperatures and precipitation. *Science* 269:676–679.

- IPCC. 2014. Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, New York.
- JENNI, L., AND M. KÉRY. 2003. Timing of autumn bird migration under climate change: advances in long-distance migrants, delays in short-distance migrants. *Proceedings of the Royal Society of London, B. Biological Sciences* 270:1467–1471.
- JONZÉN, N., A. HEDENSTRÖM, AND P. LUNDBERG. 2007. Climate change and the optimal arrival of migratory birds. *Proceedings of the Royal Society of London, B. Biological Sciences* 274:269–274.
- LATIFOVIC, R., ET AL. 2005. Generating historical AVHRR 1 km baseline satellite data records over Canada suitable for climate change studies. *Canadian Journal of Remote Sensing* 31:324–346.
- LAVIELLE, M. 2005. Using penalized contrasts for the change-point problem. *Signal Processing* 85:1501–1510.
- LEBLOND, M., M. H. ST-LAURENT, AND S. D. CÔTÉ. 2016. Caribou, water, and ice – fine-scale movements of a migratory arctic ungulate in the context of climate change. *Movement Ecology* 4:14.
- LE CORRE, M., C. DUSSAULT, AND S. D. CÔTÉ. 2014. Detecting changes in the annual movements of terrestrial migratory species: using the first-passage time to document the spring migration of caribou. *Movement Ecology* 2:19.
- LE HÉNAFF, D. 1976. Inventaire aérien des terrains de vêlage du caribou dans la région nord et au nord du territoire de la municipalité de la Baie James (mai–juin 1975). Service de la recherche biologique, Ministère du Tourisme, de la Chasse et de la Pêche, Québec, Canada (in French).
- MAGNUSON, J. J., ET AL. 2000. Historical trends in lake and river ice cover in the Northern Hemisphere. *Science* 289:1743–1746.
- MAHONEY, S. P., AND J. A. SCHAEFER. 2002. Long-term changes in demography and migration of Newfoundland caribou. *Journal of Mammalogy* 83:957–963.
- MCKINNON, L., ET AL. 2010. Lower Predation Risk for Migratory Birds at High Latitudes. *Science* 327:326–327.
- MILLER, F. L., AND A. GUNN. 1986. Observations of Barren-Ground Caribou traveling on thin ice during autumn migration. *Arctic* 39:85–88.
- MØLLER, A. P., D. RUBOLINI, AND E. LEHIKONEN. 2008. Populations of migratory bird species that did not show a phenological response to climate change are declining. *Proceedings of the National Academy of Sciences* 105:16195–16200.
- MUSIC, B., AND D. CAYA. 2007. Evaluation of the hydrological cycle over the Mississippi river basin as simulated by the Canadian Regional Climate Model (CRCM). *Journal of Hydrometeorology* 8:969–988.
- MYNENI, R. B., C. D. KEELING, C. J. TUCKER, G. ASRAR, AND R. R. NEMANI. 1997. Increased plant growth in the northern high latitudes from 1981 to 1991. *Nature* 386:698–702.
- NELSON, M. E. 1995. Winter range arrival and departure of white-tailed deer in northeastern Minnesota. *Canadian Journal of Zoology* 73:1069–1076.
- PARMESAN, C., AND G. YOHE. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421:37–42.
- POOLE, K. G., A. GUNN, B. R. PATTERSON, AND M. DUMOND. 2010. Sea ice and migration of the Dolphin and Union caribou herd in the Canadian Arctic: an uncertain future. *Arctic* 63:414–428.
- POST, E., AND M. C. FORCHHAMMER. 2008. Climate change reduces reproductive success of an Arctic herbivore through trophic mismatch. *Philosophical Transactions of the Royal Society of London, B. Biological Sciences* 363:2369–2375.
- R CORE TEAM. 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://cran.r-project.org/>. Accessed 20 April 2016.
- RASIULIS, A. 2015. Survie et dynamique de population des caribous migrants du Québec-Labrador. M.S. thesis, Laval University, Québec, Canada.
- RASMUSSEN, K., ET AL. 2007. Southern Hemisphere humpback whales wintering off Central America: insights from water temperature into the longest mammalian migration. *Biology Letters* 3:302–305.
- ROBINSON, R. A., ET AL. 2009. Travelling through a warming world: climate change and migratory species. *Endangered Species Research* 7:87–99.
- SCHAEFER, J. A., C. M. BERGMAN, AND S. N. LUTTICH. 2000. Site fidelity of female caribou at multiple spatial scales. *Landscape Ecology* 15:731–739.
- SCHAEFER, J. A., AND S. P. MAHONEY. 2013. Spatial dynamics of the rise and fall of caribou (*Rangifer tarandus*) in Newfoundland. *Canadian Journal of Zoology* 91:767–774.
- SCHMELZER, I., AND R. OTTO. 2003. Winter range drift in the George River Caribou Herd: a response to summer forage limitation? *Rangifer* 14:113–122.
- SIKES, R. S., W. L. GANNON, AND THE ANIMAL CARE AND USE COMMITTEE OF THE AMERICAN SOCIETY OF MAMMALOGISTS. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy* 92:235–253.
- TAILLON, J. 2013. Condition physique, allocation maternelle et utilisation spatio-temporelle des aires de mise bas du caribou migrant, *Rangifer tarandus*. Ph.D. dissertation, Laval University, Québec, Canada.
- TAILLON, J., M. FESTA-BIANCHET, AND S. D. CÔTÉ. 2012. Shifting targets in the tundra: protection of migratory caribou calving grounds must account for spatial changes over time. *Biological Conservation* 147:163–173.
- TØTTRUP, A. P., K. THORUP, AND C. RAHBK. 2006. Patterns of change in timing of spring migration in North European songbird populations. *Journal of Avian Biology* 37:84–92.
- TØTTRUP, A. P., K. THORUP, K. RAINIO, R. YOSEF, E. LEHIKONEN, AND C. RAHBK. 2008. Avian migrants adjust migration in response to environmental conditions en route. *Biology Letters* 4:685–688.
- VÄHÄTALO, A. V., K. RAINIO, A. LEHIKONEN, AND E. LEHIKONEN. 2004. Spring arrival of birds depends on the North Atlantic Oscillation. *Journal of Avian Biology* 35:210–216.
- VAN DER GRAAF, S. A. J., J. STAHL, A. KLIMKOWSKA, J. P. BAKKER, AND R. H. DRENT. 2006. Surfing on a green wave - how plant growth drives spring migration in the Barnacle Goose *Branta leucopsis*. *Ardea* 94:567–577.
- VISSER, M. E., S. P. CARO, K. VAN OERS, S. V. SCHAPER, AND B. HELM. 2010. Phenology, seasonal timing and circannual rhythms: towards a unified framework. *Philosophical Transactions of the Royal Society of London, B. Biological Sciences* 365:3113–3127.
- VORS, L. S., AND M. S. BOYCE. 2009. Global declines of caribou and reindeer. *Global Change Biology* 15:2626–2633.
- ZUUR, A. F., E. N. IENO, AND C. S. ELPHICK. 2010. A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution* 1:3–14.

Submitted 20 April 2016. Accepted 14 October 2016.

Associate Editor was Christine Maher.