esa

ECOSPHERE

Tactical departures and strategic arrivals: Divergent effects of climate and weather on caribou spring migrations

Eliezer Gurarie,[1,2,]† Mark Hebblewhite,[2] Kyle Joly,[3] Allicia P. Kelly,[4] Jan Adamczewski,[5] Sarah C. Davidson,[6,7] Tracy Davison,[8] Anne Gunn,[9] Michael J. Suitor,[10] William F. Fagan,[1] and Natalie Boelman[11]

[1]*Department of Biology, University of Maryland, College Park, Maryland 20742 USA*
[2]*Wildlife Biology Program, Department of Ecosystem and Conservation Sciences, W.A. Franke College of Forestry and Conservation, University of Montana, Missoula, Montana 59812 USA*
[3]*National Park Service, Gates of the Arctic National Park and Preserve, Arctic Inventory and Monitoring Network, Fairbanks, Alaska 99709 USA*
[4]*Department of Environment and Natural Resources, Government of the Northwest Territories, Fort Smith, Northwest Territories, Canada*
[5]*Department of Environment and Natural Resources, Government of the Northwest Territories, Yellowknife, Northwest Territories, Canada*
[6]*Max Planck Institute of Animal Behavior, Am Obstberg 1, Radolfzell 78315 Germany*
[7]*Department of Civil, Environmental and Geodetic Engineering, The Ohio State University, Columbus, Ohio 43210 USA*
[8]*Department of Environment and Natural Resources, Government of the Northwest Territories, Inuvik, Northwest Territories, Canada*
[9]*Circumarctic Rangifer Monitoring and Assessment Network (CARMA), Salt Spring Island, British Columbia V8K 1V1 Canada*
[10]*Fish and Wildlife Branch, Environment Yukon, Yukon Government, Dawson City, Yukon, Canada*
[11]*Lamont-Doherty Earth Observatory, Columbia University, Palisades, New York 10964 USA*

Citation: Gurarie, E., M. Hebblewhite, K. Joly, A. P. Kelly, J. Adamczewski, S. C. Davidson, T. Davison, A. Gunn, M. J. Suitor, W. F. Fagan, and N. Boelman. 2019. Tactical departures and strategic arrivals: Divergent effects of climate and weather on caribou spring migrations. Ecosphere 10(12):e02971. 10.1002/ecs2.2971

Abstract. The Arctic has been warming rapidly, affecting ecological processes across the region. Caribou and reindeer (*Rangifer tarandus*) is a keystone Arctic species undergoing declines in many parts of its range, but definitive links between climate and populations remain elusive. The conspicuous and dramatic mass migration of many caribou populations, during which nearly all pregnant females move from wintering ranges to calving grounds shortly before giving birth, may be an important link between climate and caribou populations. The drivers of migration, however, are similarly mysterious. It is unknown, for example, whether caribou respond to immediate phenological cues, anticipate conditions on calving grounds, or are driven by lagged effects related to physical condition. To investigate the drivers of migration, we analyzed movement data from over 1000 individual caribou from seven major herds, spanning 3000 km across Alaska, Yukon, Northwest Territories (NWT), and Nunavut in Canada, from 1995 to 2017. We developed a hierarchical model to estimate migration departure and arrival times, and analyzed these variables against global climate indices and local weather conditions, exploring immediate and lagged effects, as well as snowmelt timing and vegetation indices. We discovered a continent-wide synchrony in spring migration departure times, driven mainly by large-scale, ocean-driven climate indices (Pacific Decadal Oscillation, Arctic Oscillation, and North Atlantic Oscillation). However, we also found that the speed of migration was highly plastic with later migration departure times followed by shorter migration durations. This plasticity made arrival timing independent of departure timing and its respective drivers. Rather, arrival timing depended strongly on weather conditions from the previous summer: cooler and windier summers generally led to earlier arrival at calving grounds the following year. We suggest that maternal body condition, mainly influenced by conditions that limit insect harassment, is a major factor for earlier spring migration arrival timing, and therefore earlier calving and higher survival rates. We place these results in the context of mechanistic links between climate and caribou population dynamics. Long-term and large-scale observations of migratory animals can provide insights into the mechanisms by which long-distance, collective migrants may adapt to dynamic and unpredictable environments.

Key words: Arctic; climate; herbivore; lagged effects; phenology; Rangifer; weather.

Received 20 September 2019; accepted 7 October 2019. Corresponding Editor: Debra P. C. Peters.

† **E-mail:** egurarie@umd.edu

Introduction

Understanding how climate change affects species demography, behavior, life history, and community interactions is a pressing applied ecology issue (Parmesan 2006, Post et al. 2009). This is particularly true in Arctic and northern temperate regions, where rapid changes in temperature, precipitation, snow dynamics, sea ice, fire regimes, permafrost thaw, and vegetative growth have been well-documented (Walther et al. 2002, Post et al. 2009, 2013, Pearson et al. 2013, Descamps et al. 2017). Increases in temperature and precipitation are most marked in winter and spring (Moritz et al. 2002, Boisvert and Stroeve 2015), leading to a higher frequency of rain-on-snow or related icing events (Rennert et al. 2009) and significantly earlier snowmelt and growth phenology throughout the Arctic (Høye et al. 2007, Park et al. 2016).

A central challenge in arctic ecology is understanding the potential effects of a changing climate on caribou and reindeer (*Rangifer tarandus*), the most widespread terrestrial herbivore in the Arctic (Hummel and Ray 2008). The centrality of caribou to high latitude ecosystems is reflected in their high circumpolar abundance, their strong impacts on tundra vegetation (Väisänen et al. 2014, Rickbeil et al. 2015, Bichet et al. 2016, Bråthen et al. 2017, Schmitz et al. 2018), their importance as prey species for predators and scavengers (Reynolds et al. 1987, Bergerud 1996, Young and McCabe 1997, Legagneux et al. 2014), and their importance to the subsistence and culture of human groups throughout the Arctic (Burch 1972, Wolfe and Walker 1987, Hummel and Ray 2008). In North America, the most numerically abundant ecotype of caribou are the migratory barren-ground caribou, which undertake long-distance movements of several hundred kilometers between wintering, calving, and post-calving summer ranges (Fig. 1). These migrations, and the collective behavior of the caribou, are an outstanding and conspicuous ecological phenomenon comparable in scale to the migrations of African blue wildebeest *Connochaetes taurinus* or the saiga antelope *Saiga tatarica* in Asia (Joly et al. 2019). Like other long-distance terrestrial migrations, they also require unhindered passage through extensive landscapes (Berger 2004, Joly et al. 2019). Throughout the Arctic, barren-ground caribou herd ranges overlap with areas with existing or earmarked industrial development, in particular mineral and oil and gas exploitation (Klein 2000, Johnson et al. 2005, Boulanger et al. 2012). Between the globally declining populations, the ever-increasing rate of anthropogenic activity throughout the Arctic, and the central role of caribou and reindeer to Arctic human-natural systems, there is a high level of conservation concern throughout their range.

Sub-populations of migratory barren-ground caribou, commonly referred to as *herds*, are identified by site fidelity to particular calving grounds where they aggregate in early summer (Lent 1968, Skoog 1968). A single herd's population can attain several hundred thousand individuals, but undergo large fluctuations on a multi-decadal scale (Klein 1991*b*, Gunn 2003, Vors and Boyce 2009, Joly et al. 2011, COSEWIC 2016). In recent years, many herds globally have been in decline, including several precipitous declines. For example, since the 1990s, the Bathurst Caribou herd in north-central Canada has fallen from over 400,000 animals to under 10,000 (COSEWIC 2016, Adamczewski et al. 2019) and the George River herd in northern Québec and Labrador has fallen from 800,000 animals to under 10,000 (Boulanger et al. 2011, COSEWIC 2016). Other major herds, such as the Porcupine Caribou herd that straddles northeastern Alaska and Yukon, appear to be stable or increasing (COSEWIC 2016, Caikoski 2018).

While the mechanisms of caribou population dynamics are not well-understood, and likely locally idiosyncratic (Klein 1991*a*, Gunn 2003, Tyler 2010, Mallory and Boyce 2017), the role of abiotic climate forcing has long been a major focus of research efforts. Studies on the effects of

Fig. 1. Caribou (*Rangifer tarandus*) from the Porcupine herd on their spring migration crossing the Porcupine River in Yukon, Canada (photo: Karsten Heuer).

temperatures, snow conditions, vegetation quality, and phenology and insect harassment on caribou have, however, revealed complex and occasionally contradictory relationships (Tyler 2010, Albon et al. 2017). Female body condition, which is critical to fecundity rates and calf survival (Crête and Huot 1993, Cameron and Ver Hoef 1994, Gerhart et al. 1997*b*, Veiberg et al. 2017), depends on forage availability during the summer and winter months preceding parturition. Thus, research has mainly focused on direct and indirect effects of climate on forage availability. For example, caribou winter forage comprises primarily slow-growing terrestrial lichens (Joly et al. 2007, 2010) which are negatively impacted by the warming-induced increases in drought, wildfire regimes, and tree pathogens occurring throughout boreal regions (Joly et al. 2009, de Groot et al. 2013, Flannigan et al. 2013, Whitman et al. 2017). Furthermore, warmer winters may lead to more frequent thaw-freeze or rain-on-snow icing events which can make vegetation under the snow inaccessible (Gunn 2003, Albon et al. 2017), causing mass mortalities in exceptional cases (Miller and Barry 2009, Forbes et al. 2016). However, differences among caribou ranges (e.g., coastal plains versus forest versus mountainous, colder versus warmer, more vs. less precipitation) and the complexity of the snow and icing process make the directionality of warming effects vary across ranges. In some populations, warmer winters have been reported to enhance animal abundance (Tyler 2010). Similarly, summer conditions can strongly influence demography in the following year, but the direction of the effect is debated. Warmer, longer summers generally increase vegetative growth in tundra, thereby increasing the quantity of summer forage available to caribou (Albon et al. 2017, Zamin et al. 2017, Mallory et al. 2018). However, in places summer warming can increase the relative abundance of shrubs with anti-browsing chemical defenses (Bryant et al. 2014, Zamin et al. 2017) or can lead to increased insect harassment (Walsh et al. 1992), which has significant impacts on caribou physical condition (Helle and Tarvainen 1984, Helle and Kojola 1994, Walsh et al. 1992, Weladji et al. 2003, Witter et al. 2012*a*,*b*). Further, the advance of spring environmental conditions may lead to temporal mismatches between vegetation phenology and the reproductive timing of Arctic caribou, which

may be partially responsible for population declines in some populations (Post and Forchhammer 2008, Post 2013). These mismatches and demographic outcomes are similar to those observed across a variety of ecosystems (Both et al. 2009, Anderson et al. 2013) and for several ungulates (Pettorelli et al. 2007, Plard et al. 2014, Doiron et al. 2015), though its role for caribou populations has been questioned (Veiberg et al. 2017).

The complexity of the links between abiotic drivers and caribou population dynamics is, in part, a consequence of their high level of mobility, which makes them dependent at various life stages on different ecosystems (Klein 1991*a*). The annual spring migration links the winter ranges, which are often in the boreal taiga, to the calving and summer calf-rearing seasons in the Arctic tundra. The timing and duration of spring migrations may also be related to the physical condition of females, which depends on a year's worth of integrated environmental conditions: in the summering period, during the fall migration, and in their wintering ranges. Female physical condition can, in turn, play an important role for parturition and calf survival (Albon et al. 2017, Veiberg et al. 2017).

Understanding how variability in environmental conditions throughout the caribou annual lifecycle affects the timing of spring migration is the central goal of this study. These relationships may also provide insights into the demographic mechanisms affecting recent, ongoing, and expected shifts in caribou demography. To date, the triggers of caribou migration are poorly known, aside from a widely held assumption that day length is a fundamental cue to initiate migration (Miller 2003). While day length remains stable across years, migration timing varies significantly across individuals, populations, and years. For example, in a large-scale (~350 collared females over 12 yr) study of barren-ground caribou migrations in the George River and Leaf River herds in northern Québec and Labrador (NQL), Le Corre et al. (2017) showed a ~60-d variation in the timing of departure from wintering ranges and in the timing of arrival times at calving grounds. The authors attributed this variation, in part, to late winter weather conditions that affect locomotion costs: heavier, deeper, and later spring snow tended to delay migrations.

Climate trends lead to phenological shifts which can lead to a shift in parturition dates, and, consequently, migration dates in other cervids. Parturition dates of a non-migratory insular red deer (*Cervus elaphus*) population have advanced about 12 d over 28 yr, matching a concurrent advance in local vegetation phenology (Moyes et al. 2011). Other migratory cervids follow shifting peaks of high-quality forage in the spring, surfing a "green wave" of vegetation productivity, before reaching areas conducive to successful calving and calf-rearing (Merkle et al. 2016, Aikens et al. 2017). Because this strategy is essentially "tactical," responding to immediately available information, it presumably allows the population to adapt to changes in timing of immediate green-up or resource availability by adjusting the migration timing (Anderson et al. 2013). In contrast, many long-distance migrants cannot rely on local information and must anticipate disparate, often unpredictable changes in the seasonality of abiotic conditions and vegetation phenology from great distances to encounter favorable conditions and exploit maximum resources. This is particularly true for birds (Both et al. 2009, Møller et al. 2010), many of which are shifting the timing of their arrival to breeding grounds to match changes in local climate and phenology (Cotton 2003, Marra et al. 2005, Rubolini et al. 2007, Barrett 2011, Ward et al. 2016), though this trend has also been observed for terrestrial herbivores (Bastille-Rousseau et al. 2019). Analogous long-range strategies have been observed for migratory red deer that "jump the green wave" to maximize resources at the end of their migration (Bischof et al. 2012), and for zebras (*Equus burchelli*), that show evidence of memory-based forecasting of water resources (Bracis and Mueller 2017).

It is unclear whether caribou are more similar to green wave surfers or green wave jumpers, that is, whether they are responding to immediate conditions or are driven by longer-term goals. While caribou migrations coincide, roughly, with that of many temperate ungulates, beginning in April, and calving in late May or early June (Couturier et al. 2009, Parker et al. 2009, Albon et al. 2017, Cameron et al. 2018), there is typically very little spring vegetation growth on the northern taiga or tundra during the migration period, and Arctic barren-ground migrations can

take place over largely snow-covered landscapes (Boelman et al. 2019). While there is consequently no green wave to surf, caribou may lead or pursue the front of melting snow in a "surfing the snow edge" Arctic analogue. In the case of barren-ground caribou, however, previous studies have shown weak relationships between spring migration timing and snowmelt timing at the respective calving and wintering grounds (Le Corre et al. 2017, Boelman et al. 2019). Rather than respond to immediate conditions, caribou may be anticipating resources at calving sites in a manner similar to long-distant migrant birds.

Though migration is central to caribou population ecology, there are large gaps in understanding the interaction between migration timing, climate and spring phenology. To help fill these gaps, we adopted a synthetic approach to explore the migratory behavioral response of caribou to changing environmental conditions. We set out to test two broad hypotheses: a *spring weather-driven* hypothesis and a *parturition and body condition* hypothesis. The first hypothesis, which we refer to as the "tactical" hypothesis, proposes that the timing of spring migration is driven by immediate weather conditions in late winter and early spring in overwintering grounds. Under this hypothesis, we would expect that earlier spring onset in the Arctic would lead to earlier spring migration dates. Similarly, we would expect migration to be closely linked to snowmelt phenology, that is, "surfing the snow edge," and that later migration start times would lead to later arrival times at the calving grounds. Finally, we might expect large-scale correlation and synchronization of migration timing, since weather conditions are often determined on a continental scale by large-scale climate forcing (Koenig 2002). We would expect this synchronization effect to decline in strength with distance between herds, analogous to the Moran effect that synchronizes population dynamics according to the spatial correlation of environmental covariates (Moran 1953, Koenig 2002), a mechanism that has been proposed to explain synchrony in some Arctic herbivores (Post and Forchhammer 2002).

In contrast, the "strategic" hypothesis suggests that the timing of spring migration is mainly driven by the need to give birth, that is, it is driven by the need to arrive at the calving grounds at a particular time, possibly in synchrony with other cows (Rutberg 1987, Adams and Dale 1998), with relatively less dependence on immediate environmental conditions. A central component of this hypothesis is the centrality of maternal body condition, which is associated with earlier parturition timing (Adams and Dale 1998), which in turn can be related to higher calf survival and recruitment (Flydal and Reimers 2002, Veiberg et al. 2017). Maternal body condition itself is affected by growing conditions and weather in the previous summer, in particular as it relates to insect harassment (Weladji et al. 2003, Witter et al. 2012*a*), and by winter conditions, primarily via snow and ice conditions influencing access to food (Vors and Boyce 2009, Albon et al. 2017). Thus, we predicted that caribou would migrate earlier when and where environmental conditions of the preceding summer and winter seasons were favorable to female body condition, reflecting the strength of energetic stores typical of a capital breeder (Veiberg et al. 2017). Environmental conditions that lead to better condition include: cooler and windier summers which mitigate insect harassment, leading to more time allocated to foraging and better body condition (Witter et al. 2012*a*), or, in contrast, warmer and longer summers which can lead to higher forage productivity (Mallory et al. 2018). Because the drivers of migration under this hypothesis are longer-scaled than in the "tactical" hypothesis, we characterize this hypothesis as a "strategic" mechanism, without, however, making any explicit claims about caribou cognition.

While these hypotheses are not mutually exclusive, they do lead to different sets of specific predictions that can be tested directly by regressing migration parameters against environmental predictors. Under the tactical hypothesis, we predicted that: (1) Spring covariates are more significant predictors of migration timing than winter or previous summer covariates; (2) earlier snowmelt would lead to earlier migrations; (3) departure times would determine arrival times; (4) there would be a large-scale cross-correlation in migration timing that would be attenuated by distance between herds. Under the strategic hypothesis, we predicted that: (1) Environmental covariates from the previous summer or winter would be more significant in predicting migration timing than spring conditions; (2) migration timing would not depend strongly on snow phenology; (3) migration patterns across the range

would not be highly synchronized. Responses to climate change can be reflected under either hypothesis, but under the tactical hypothesis we predicted that they vary in tandem with interannual variation, whereas under the strategic hypothesis, we expected a longer-scaled response that integrates the interaction of the caribou to the environment over multiple seasons or even years.

Methods

Overview

We analyzed migration timing from the compiled dataset of over 1000 individual caribou from seven major barren-ground caribou herds across western North America against an array of immediate and lagged environmental covariates. The first step was to develop a robust, hierarchical tool to estimate population-level spring migration parameters, including timing of departure from wintering ranges, timing of arrival to calving ranges, and the spatial coordinates and areas of the respective ranges. Existing approaches to estimate migration timing have been developed with application to individuals in mind (Börger and Fryxell 2012, Le Corre et al. 2014, Cagnacci et al. 2016, Gurarie et al. 2017, Spitz et al. 2017), but few robust approaches have been developed for estimating migration timing and seasonal ranges at a population level (though see Calabrese et al. 2018). We obtained these estimates against a set of large-scale climate drivers, such as the Pacific Decadal Oscillation (PDO), Arctic Oscillation (AO), and North Atlantic Oscillations (NAO), which have been shown to be related to demographic rates of high latitude ungulates (Forchhammer et al. 2002, Hegel et al. 2010, Joly et al. 2011), and against a set of local weather conditions, including temperature, wind speeds, precipitation, and snow water equivalent. Importantly, we collected those covariates across seasons: previous summer, winter, early spring, and migration periods. We additionally compared migration timing against spring snowmelt, and to summer productivity as indexed by the normalized difference vegetation index (NDVI; Pettorelli 2013).

Study area and caribou movement data

We analyzed data from 1048 adult female caribou from seven major herds (from west to east: Western Arctic, Porcupine, Cape Bathurst, Bluenose West, Bluenose East, Bathurst, and Beverly herds, Fig. 2, Table 1) in Northern Alaska and Canada. Caribou were collared with GPS and ARGOS collars from 1995 to 2017 by state, federal, territorial, and First Nation government agencies as part of ongoing monitoring efforts (Table 1). The data span a geographic range over 3000 km from the Bering Sea (Western Arctic, median longitude ~160° W) to the Canadian Shield lowlands west of Hudson Bay (Beverly herd, median longitude ~103° W). The collared animals represent herds that, in total, account for roughly 90% of all the coastal barren-ground caribou within this range.

While all seven populations are migratory and have calving grounds on the tundra near the continent's northern coast, there are several notable geographical differences. For example, the Western Arctic and Porcupine ranges (orange colors in Fig. 2) are roughly bisected by the Brooks Range mountains. Rather than follow a direct path, the Porcupine herd typically migrates around the eastern edge of the mountains during spring migration. Unique among the seven herds, the Western Arctic herd does not typically overwinter in taiga woodlands, but is generally found in tundra year-round. In contrast, the five populations east of the Mackenzie River (pink and purplish colors, henceforth referred to as Northwest Territories (NWT) herds because their wintering ranges are found mainly within the NWT, though several herds calve in Nunavut), have no major topographical features to navigate. There is a clear gradient in distance between wintering grounds and calving ranges between the western-most (Cape Bathurst) and the eastern-most (Beverly) of the five NWT herds, reflecting the increased distance of the boreal forest tree line from the coast. The two western-most herds have traditionally been considered to be distinct subspecies (*R.t. granti*) from the NWT herds (*R.t. groenlandicus*), though genetic differentiation is limited (Weckworth et al. 2012).

Wildlife management bodies and government agencies across North America have been monitoring these populations for several decades. In that period, technology has varied from early adoption of very-high-frequency radiocollars, to ARGOS satellite tags with occasionally large spatial errors on the order of tens of kilometers, to

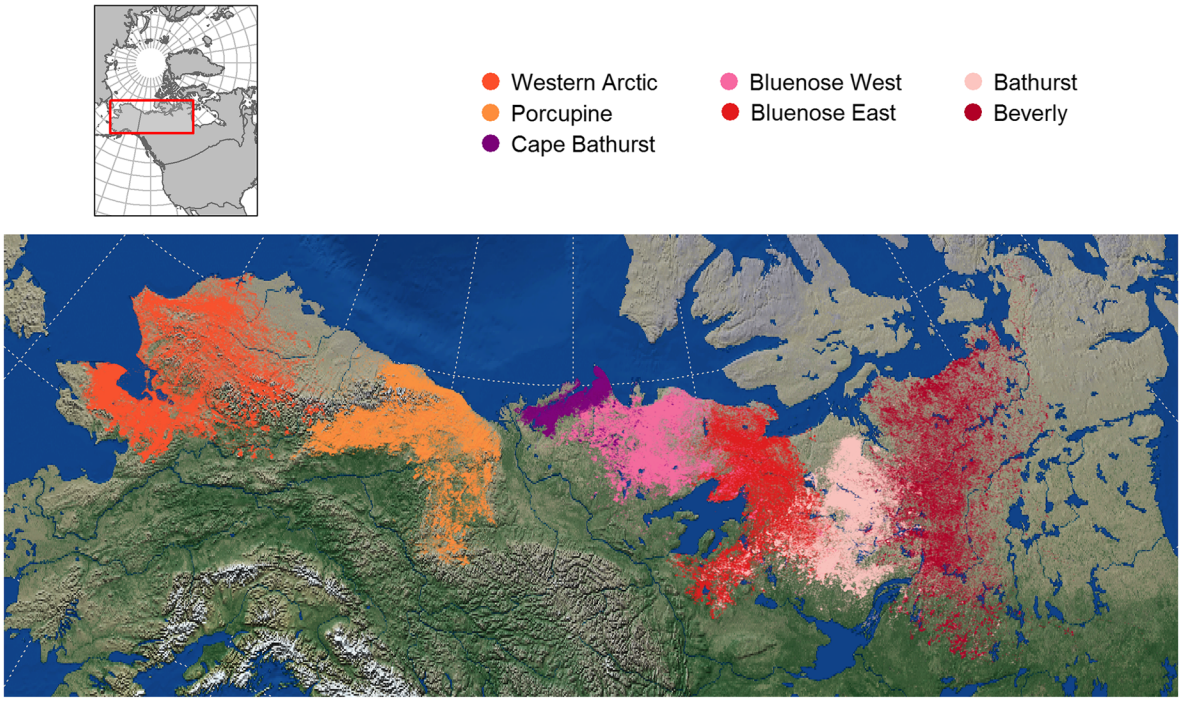

Fig. 2. Movement data were analyzed in this study from seven barren-ground caribou (*Rangifer tarandus* sspp.) populations across Alaska and Northwest Canada from 1995 to 2017.

more recent, highly accurate global positioning system (GPS) technology. Because of the wide variety of devices used across two decades and across multiple studies, the technology and duty cycle of the transmitters varied considerably. In earlier years, particularly before 2000, most collars were ARGOS collars with median intervals between transmissions typically up to 8 d, whereas in later years all collars were GPS collars and duty cycle intervals as low as 2 h. This variability was partly dealt with by filtering out low-quality ARGOS locations and using daily average positions for all subsequent analysis, a choice justified by the multi-week scale of migration (Gurarie et al. 2017). Additional irregularities in the data, such as multi-day intervals between location fixes and missing data, were dealt with by designing the migration analysis to account for irregular sampling (see *Estimating migration timing*).

Note, the Beverly herd refers to animals that calve near Queen Maud Gulf and are termed Beverly by the Government of Nunavut and Nagy et al. (2011), though they are sometimes

Table 1. Summary of female barren-ground caribou (*Rangifer tarandus*) satellite telemetry data across Alaska and northwest Canada, 1995–2017.

Herd	Agency	N_{ind}	Years	N_{years}	N_{ind}/y: mean (SD)
Western Arctic	NPS	128	2009–2018	10	37.12 (5.4)
Porcupine	PCMB	175	1998–2018	21	24.3 (17.2)
Cape Bathurst	NT-ENR	83	1996–2017	22	14.1 (5.2)
Bluenose West	NT-ENR	159	1996–2017	22	19.3 (13.5)
Bluenose East	NT-ENR	219	2005–2017	14	27.5 (12.8)
Bathurst	NT-ENR	179	1996–2017	23	15.6 (7.5)
Beverly	NT-ENR	105	1995–2017	17	18.5 (8.4)

Note: SD, standard deviation.

referred to as "Beverly and Ahiak" or "Beverly/Ahiak" due to a hypothesized merging of a depleted Beverly herd and a more eastern Ahiak herd (Adamczewski et al. 2015). For those animals where herd assignments were ambiguous due to overlapping wintering ranges, we assigned herd status based on methods outlined in Nagy et al. (2011).

Estimating migration timing

Statistical tools for identifying migrations and range shifts are almost entirely based on analysis of individual trajectories (Börger and Fryxell 2012, Cagnacci et al. 2016, Gurarie et al. 2017, Spitz et al. 2017; though see Dalziel et al. 2016, Calabrese et al. 2018). While effective, these tools require some individual supervision, a prohibitive task when a single movement dataset contains hundreds of individuals with diverse sampling regimes across multiple decades. Furthermore, caribou are social animals: Despite variability in their wintering and post-calving summering areas, they exhibit largely collective migrations to their calving grounds (Skoog 1968, Dalziel et al. 2016).

To address these issues, we developed a robust, population-level statistical method, the hierarchical range-shift analysis (HRSA) to quantitatively characterize caribou spring migrations. We designed the model to provide population-level inference with minimal supervision to estimate the timing of spring migration and the locations of wintering and calving grounds. Additionally, we designed the model to be robust to varying sampling regimes (frequency of observations varied from one location every eight days to multiple observations per day) and to observation error (especially in those years where data were collected with ARGOS satellites; Gurarie et al. 2017). The framework is directly applicable to any dataset where multiple individuals undergo collective range shifts.

The model assumes that an individual moves according to a modified version of the migratory white noise (MWN process) as described by Gurarie et al. (2017). Each individual i's movement $\mathbf{Z}_i(t)$ is modeled as an individual ranging process ($\mathbf{r}_i(t)$) around a mean process ($\mathbf{m}_i(t)$):

$$\mathbf{Z}_i(t) = \mathbf{r}_i(t) + \mathbf{m}_i(t)$$

The mean process shifts linearly between the first range ($\mathbf{m}_1 = (\mu_{x,1,i}, \mu_{y,1,i})$) and a second range ($\mathbf{m}_2 = (\mu_{x,2,i}, \mu_{y,2,i})$) at some unknown time t_i^*. The transition lasts for a migration duration Δt, such that:

$$\mathbf{m}(t) = \begin{cases} \mathbf{m}_1 & \text{where } t \le t^* \\ \mathbf{m}_1 + (\mathbf{m}_2 - \mathbf{m}_1)\frac{(t-t^*)}{\Delta t} & \text{where } t^* \le t < t^* + \Delta t \\ \mathbf{m}_2 & \text{where } t > t^* + \Delta \end{cases}$$

The ranging component, which corresponds to the spatial displacements around the mean process, is modeled as "white noise," that is, random locations in x and y dimensions with mean 0 and a standard deviation $\sigma(t)$ which itself steps from a seasonal ranging standard deviation (σ_r) to a migratory standard deviation (σ_m) once migration begins ($t = t^*$), and back down to σ_r when the migration is complete ($t = t^* + \Delta t$). This shift between the magnitudes of the ranging standard deviation account for individual caribou to be constrained to a relatively small range in winter and during calving, while deviating far from the straight-line path that connects the two ranges during migration.

The migratory process describes an individual caribou. We place this individual model into a population-level hierarchy by specifying two population-level ranges for winter and calving. Thus, the end-point centroids of the individual caribou ranges ($\mu_{1,i}$ and $\mu_{2,i}$) are modeled as bivariate normal distributions in x and y with a non-zero covariance, such that the vector of centroids $\mathbf{M}$:

$$\mathbf{M}_1 \sim \text{BivarNormal}(\mu_1, \Sigma_1)$$

$$\mathbf{M}_2 \sim \text{BivarNormal}(\mu_2, \Sigma_2)$$

where (for range 1) $\mu_1 = (\mu_{x,1}, \mu_{y,1})$ and Σ_1 is a 2×2 matrix:

$$\Sigma_1 = \begin{bmatrix} \sigma_{x,1}^2 & \rho_1 \sigma_{x,1} \sigma_{y,1} \\ \rho_1 \sigma_{x,1} \sigma_{y,1} & \sigma_{y,1}^2 \end{bmatrix}$$

The parameters $\sigma_{1,x}$ and $\sigma_{1,y}$ describe the spatial extent of the population-level range, while ρ describes the shape and orientation of the modeled elliptical range (Fig. 3): $\rho = 0$ is a horizontal or vertically aligned range, values between 0 and 1 indicate a range with a northeast to southwest

orientation, and values between −1 and 0 indicate a northwest to southeast orientation. An exactly analogous set of parameters is estimated for the calving range.

Finally, the migration timing parameters t^* and Δt are modeled at the population level as:

$$t^* \sim \mathcal{N}(\mu_t, \sigma_t)$$
$$\Delta t^* \sim \mathcal{N}(\mu_{\Delta t}, \sigma_\Delta).$$

In total, 16 parameters are needed to specify the hierarchical spring migration model: five range location and shape parameters for each

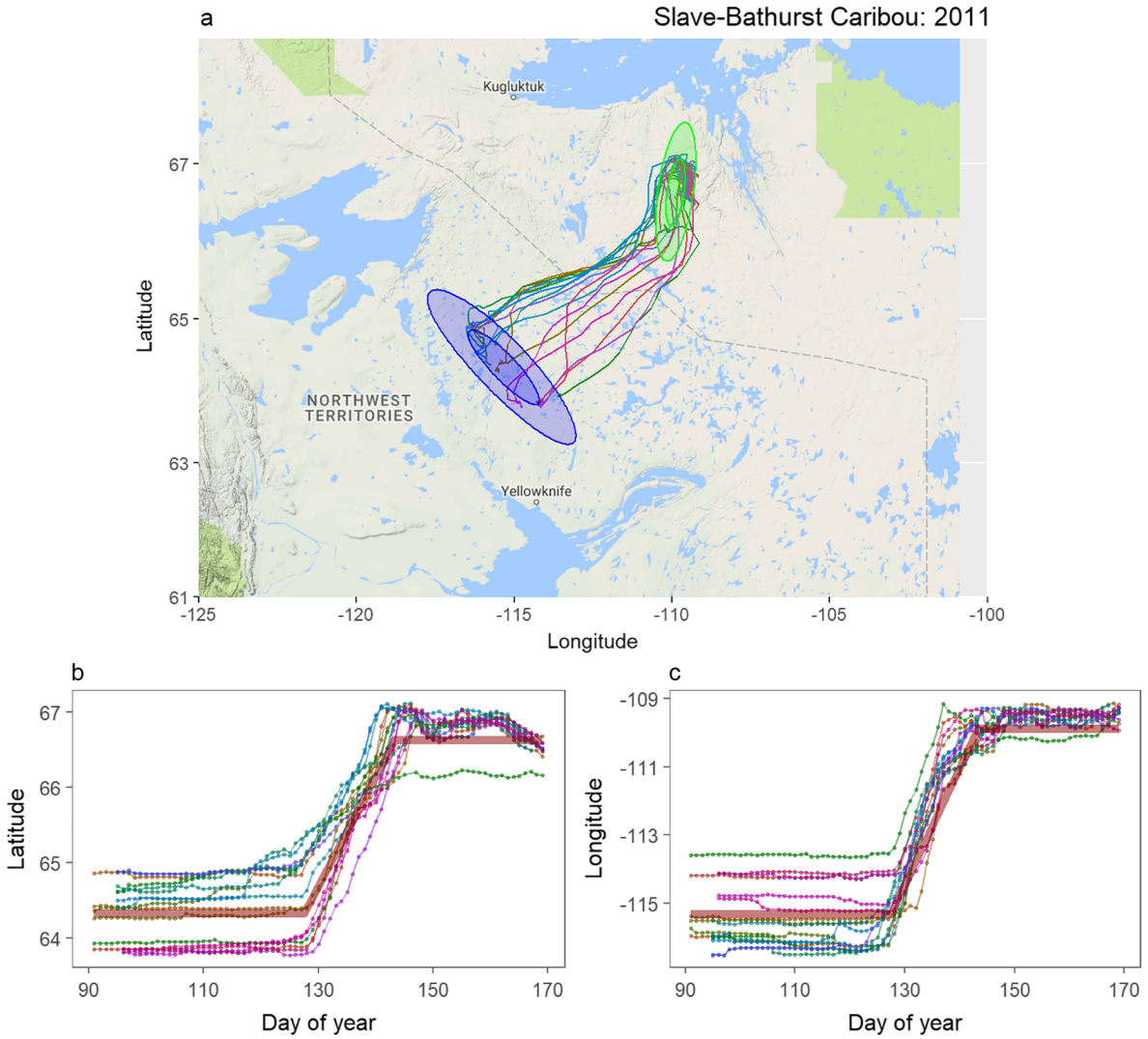

Fig. 3. Spring migration estimation illustrated for the Bathurst Herd in the Northwest Territories, Canada, 2011. In all panels, the different colored tracks represent unique individuals. (a) The movement data analyzed between 1 April (day of year 90) and 20 June (day 170). The ellipses illustrate the posterior fit of the population-wide wintering range (blue ellipses) and calving range (green ellipses); darker and lighter ellipses indicate the 50% and 95% percentile estimate, respectively. (b, c) The movement of the caribou in terms of (b) latitude and (c) longitude, and the thicker red shaded line indicates the fitted estimate of the mean spring migration departure, duration, and arrival dates.

season, four for the migration timing, and two for the variance of the MWN process while ranging and during migration. Because of the hierarchical nature of the model and the considerable amount of prior information on range locations and migration timings, we fitted the model using Bayesian Markov chain Monte Carlo (MCMC), using a Hamiltonian No-U Turn Sampler (NUTS) as implemented in the STAN programming language (Carpenter et al. 2017) via the R package rstan (Stan Development Team 2018) (complete STAN code and implementation in R are provided in Appendix S1). Prior distributions for the parameters were either drawn from straightforward summary statistics of the data or were uninformative. For each year of data, we ran four chains of length 800 with a burn-in period of 600 and assessed convergence visually. We report medians of the posterior distributions as point estimates and 95% quantile ranges as credible intervals.

The fitted models provided herd-year specific estimates of the timing and duration of migration along with population-level variability estimates. The model also estimated the centroid location, overall area, ellipticity, and orientation of the seasonal (winter and calving) ranges of each herd-year, as well as migration timing and ranging location estimates for each individual caribou. The model was designed to be robust against irregular or sparse sampling, and against location error typical of ARGOS data (Douglas et al. 2012, Rozylowicz et al. 2019). To illustrate the robustness of the method, we took a sample dataset and (1) randomly retained 33% of the locations and re-estimated the parameters, and (2) added a spatial error with a standard error of 10 km, re-estimated the parameters, and compared the results to estimates obtained from the complete and unaltered data (Appendix S1).

Migration timing and duration

Having obtained estimates of date of departure from the wintering range, date of arrival at calving grounds, and the duration of migration across the seven herds and the available years, we fully characterized and analyzed these variables to assess trends, variability across herds and years, and autocorrelation and cross-correlations for departure, arrival and duration. We further tested the relationship between these migration measures. We refer to this set of covariates variables (the measures themselves, year, and herd) as "intrinsic variables." The relative contribution of trend, autocorrelation, inter-annual variation, and variation across herds in predicting departure and arrival time was assessed by sequentially including the set of explanatory covariates as additive linear effects and computed the resulting r^2 of each fitted linear model. Note, autocorrelation here refers not to the autocorrelation in the movement process itself, but in potential lagged effects of migration timing, for example, if later and earlier migrations tend to be followed by later and earlier migrations in the following year. For most other analyses (e.g., duration against departure time, departure or arrival against year to assess trends, etc.), we fitted linear mixed-effects models weighted by the posterior estimate of the standard deviation of the respective variables with herd as a random effect.

Synchrony in migration timing was estimated as a joint cross-correlation across all the time series. To do this, we developed an estimator that combines pairwise Pearson correlation coefficients with a weighting based on sample sizes and bias correction (details in Appendix S2). We obtained a *P*-value on the hypothesis test that the cross-correlation is zero by randomizing the data and recalculating the cross-correlation, thereby generating a null distribution against which to compare the observed estimate. Where synchrony was significant, we assessed whether those cross-correlations depended on great-circle distance between respective herd wintering ranges by regressing the cross-correlation against pairwise distance between herds, allowing us to estimate a characteristic spatial range of synchrony.

Climate, weather, snowmelt, and vegetation covariates

We extracted several types of covariates by intersecting the environmental data with the movement data as potential predictors of the migration variables: climate, weather, snowmelt timing, and vegetation (Table 2). Climate and weather covariates were summarized for a subset of seasons (winter, early spring, pre-migration, migration, calving, summer) using cutoffs determined, in part, by migration timing estimates.

Table 2. Summary of estimated migration response variables and climate, weather, and phenology explanatory covariates broken down into seasons.

Variables	Season	Definition	No. variables
Predictors			
Climate: PDO, NAO, AO†	Previous summer	July, August	3
	Winter	January, February	3
	Spring	April	3
Weather: temp., precip., swe, wind‡	Previous summer	15 July to 31 August	4
	Winter	1 January to 28 February	4
	Spring	15 March to (T_{start} − 14 d)	4
	Pre-migration	(T_{start} − 14 d) to T_{start}	4
	Migration	T_{start} to T_{end}	4
Phenology: SDD§	Winter range	75% MCP 14 d pre-migration	1
	Calving range	75% MCP 14 d post-migration	1
Vegetation: max-NDVI¶	Summer range	75% MCP previous 1 July to 31 August	1
Response			
Migration: T_{start}; dT; T_{end}			3

Notes: The dates separating "spring" and "pre-migration" are determined by the herd-year specific estimate of migration departure timing. MCP, minimum convex polygon.

† Pacific Decadal Oscillation; North Atlantic Oscillations; Arctic Oscillation, global monthly.

‡ Temperature, precipitation, snow-water equivalent, wind, averaged daily per herd-year.

§ Snow disappearance day, averaged across seasonal ranges.

¶ Maximum normalized difference vegetation index, averaged across ranges.

Start date; duration and end date of migration, estimated via hierarchical migration model.

Climatic variables included PDO (Mochizuki et al. 2010, data source: research.jisao.washington.edu/pdo/), AO (Ambaum et al. 2001, data source: cpc.ncep.noaa.gov/products/precip/CWlink/daily_ao_index/ao.shtml), and NAO (Ambaum et al. 2001, data source: https://www.cpc.ncep.noaa.gov/products/precip/CWlink/pna/nao.shtml). All three are large-scaled ocean-driven climate indicators with direct impacts on seasonal temperatures and precipitation across the Arctic-boreal regions of northern North America. We defined "previous summer" as July and August, "winter" as January and February, and "spring" as March and April and took the respective means of all three indices for each of the three seasons.

We obtained daily temperatures, precipitation, and snow water equivalent (SWE) at 1000 m resolution from the Daymet NASA gridded estimate of weather parameters (Thornton et al. 2017), and obtained modeled daily average wind speed at 0.25 arc-second resolution from the Global Land Data Assimilation System 2.0 (GLDAS Rodell et al. 2004). We then associated each caribou mean daily location at each day of the temperature, precipitation, wind speed, and SWE data to reflect conditions that the caribou actually experienced. We then summarized these variables over five nominal seasons: previous summer (15 July–31 August), corresponding to a period that is typically entirely post-calving and preceding fall migration, winter (1 January–28 February), early spring (15 March–two weeks prior to migration date), pre-migration (the two-week period prior to migration), and migration (the period of migration; Table 2). Within each of these seasons, we took the means of all the variables directly experienced by each caribou.

To understand the relationship between weather covariates experienced by caribou and large-scale climate drivers, we regressed all of the season-specific variables against the climate variables for each herd in each of three seasons (summer, winter, and spring). We similarly assessed the nature of the trends in the weather covariates by regressing against year for each herd and season to see whether the caribou were experiencing generally warmer, rainier, snowier and windier summers, springs, and winters.

Perhaps, the most important driver of spring phenology in the Arctic is snowmelt patterns (Buus-Hinkler et al. 2006, Tamstorf et al. 2007, Macander et al. 2015, Boelman et al. 2019). To quantify snow phenology, we used images from

NASA's satellite mounted Moderate Resolution Imaging Spectroradiometer (MODIS), obtaining normalized snow difference index at 500-m resolution. From these images, we computed a snow disappearance day (SDD), defined as the end of the last consecutive stretch of 3 d with any snow in a given spring season, averaging neighbors in space and time to fill gaps. To quantify the imminent snowmelt in given range, we defined the "winter range" as the 75% minimum convex polygon (MCP) of locations in the two-week interval preceding the estimated start date of migration, and the "calving range" as the 75% MCP of the locations spanning the two-week interval after the end date of migration using the adehabitat R package (Calenge 2006). Similarly, for vegetation, we summarized available NDVI values with the domain of the caribou to a maximum annual NDVI across the spatial extent, and obtained averages of maximum NDVI within a 75% MCP of all caribou locations in summer, defined as 15 June–31 August. This quantity roughly indexed the productivity of the preceding summer range, which we hypothesize may be linked to physical condition of the caribou.

We also obtained a surface of maximum annual NDVI from MODIS imagery (Huete et al. 2002) at a 250-m resolution. In open tundra environments, NDVI indices are correlated with growing season forage quality for large herbivores (Ellebjerg et al. 2008, Johnson et al. 2018). We therefore interpreted NDVI as a coarse, indirect index of the previous summer foraging conditions. Because NDVI has been shown to be a poor predictor of forage quality for caribou in the early growing season (Johnson et al. 2018), we used only maximum NDVI, averaged over the summer range (July and August) of the caribou from the previous year. We obtained and combined all spatial data into uniform 1-km rasters, and performed all geospatial calculations (e.g., to obtain the SDD and maximum NDVI) using Google Earth Engine (Gorelick et al. 2017).

Identifying drivers of migration

In total, we regressed the three main migration response variables (departure date, arrival date, and duration) against 35 potential predictors (Table 2). We used linear mixed-effects models, exploring relevant covariates using Akaike's information criterion, corrected for sample sizes (AIC_c) as a criterion (Burnham and Anderson 2004), herd as a random effect, and weighted by the standard deviation estimates from the HRSA. Because of the large number of potential covariates, we selected a model iteratively in two steps. First, we compared models with only main effects, selecting the best covariates to keep from the set of models with $\Delta AIC_c < 2$. Next, we compared models using those best covariates to fit a complete set of two-way interactions before settling on a final second-order model. While we report coefficient values from a single "best" model, we also discuss and report the prevalence of certain covariates across several of the best models, that is, those that account for over 90% of the cumulative model weights. For more detailed explorations, we performed herd-specific regressions of migration timing parameters against covariates.

We performed all analyses using R version 3.4.3 (R Core Team 2017). To test relationships between migration response variables and potential covariates, we used randomization ANOVA, which is robust to unbalanced designs, and then determined the impact of outlying points on small sample sizes, fitted with the lmPerm package (Wheeler and Torchiano 2016). We fitted mixed-effects models with the nlme package (Pinheiro et al. 2017) and guided multi-model selection using MuMIn (Barton 2018).

Results

The hierarchical range-shift analysis (HRSA) converged for every herd-year combination that had at least five individuals collared during the period of migration (see example in Fig. 3 and https://terpconnect.umd.edu/~egurarie/research/ABoVE/springmigration/AllFits for remaining fits, including MCMC chain convergence). In total, we obtained 101 sets of migration parameter estimates across the seven herds, ranging from a maximum of 21 yr for the Bathurst herd (1996–2017) to a minimum of 8 yr for the Western Arctic herd (2010–2017). All results are tabulated in Appendix S4.

Differences among herds

On average, across herd-year combinations, the mean departure date from wintering ranges

was 26 April (standard deviation [SD] = 8.1 d), migrations lasted 33 d (SD = 7.8), and the mean arrival date on calving grounds was 29 May (SD = 6.9). The earliest herds to start migration were Cape Bathurst and Beverly (mean departure date: 19 April), significantly earlier than Bathurst, Bluenose East, and Bluenose West; otherwise, there were no significant differences (Wilcoxon ranked sum test $P > 0.25$ for all other pairs). Interestingly, Cape Bathurst and Beverly herds, the two earliest to migrate, represented the two extremes of the shortest and longest migration distances, respectively.

The duration of migration varied significantly across studies, with Beverly taking on average 42.6 d (SD 4.0) compared to 30–35 d for the other herds. This variation is largely explained by the longer migration distance: The estimated linear distance between the centroids of the Beverly wintering range and calving range was 483 km, compared to 360–380 km for Western Arctic, Bathurst, and Bluenose. Note that while the Porcupine calving and wintering grounds are geographically relatively close (mean 245 km, SD 85), the migrations themselves are considerably longer due to a route that typically skirts the Brooks Range by heading northeast into the Yukon's North Slope before heading west into Alaska. Overall, durations were related to distance, increasing by ~2 d for every additional 100 km (randomization linear model $P = 0.04$), but with a significant main effect of herd (permutation ANOVA $P < 2 \times 10^{-16}$).

Most strikingly, migration duration was very strongly, linearly and negatively dependent on departure timing (Fig. 4b): Later migrations were on average 0.6 d (standard error [SE] 0.10) faster for every day of departure delay ($P < 1 \times 10^{6}$). This dependence was consistent across herds (departure × herd interaction $P = 0.22$). Arrival dates at spring calving grounds, in contrast, varied very little across the herds: Average mean arrival dates ranged between 25 May (Cape Bathurst) and 1 June (Bluenose West and Beverly), with no significant differences among the herds (all Wilcoxon rank-sum test $P > 0.3$).

Trends, autocorrelation, and synchrony

Overall trends in spring migration parameters were very weak for departure date ($\beta = -0.17$ d/yr; $P = 0.65$) and migration duration ($\beta = -1.2$ d/yr; $P = 0.21$). Broken down by individual herds, only Bluenose West caribou tended to migrate significantly earlier over time ($\beta = -0.61$ d/yr, $P = 0.02$, $n = 20$) with correspondingly significantly longer migration durations ($\beta = 0.5$ d/yr; $P = 0.04$). The Porcupine was the only herd that trended toward later departure dates ($\beta = 1.89$, $P = 0.022$, $n = 15$) and Bathurst was the only herd that showed a trend toward shorter migration duration over time ($\beta = -1.23$, $P < 1 \times 10^{-3}$, $n = 21$).

We observed a remarkably high level of synchrony across the seven herds in departure timing (Fig. 4a, see also animation in https://terpconnect.umd.edu/~egurarie/research/ABoVE/springmigration/migrationanimation6.mp4). The estimated cross-correlation coefficient across the time series was 0.46 (randomization $P < 0.001$). Several pairwise correlations were notably high: Bluenose West and Bathurst departure timing had a correlation of 0.84, and the correlations between these two and Bluenose East were 0.79 and 0.63, respectively. We also found a few surprisingly long-distance correlations. Stark differences can be observed among some particularly early and late years. For example, the correlation in departure dates between the Western Arctic and Beverly herds, located over 2500 km from each other, was 0.71. In 2010, the overall mean start date of migration was 17 April, and the *latest* migration departure was 24 April (Western Arctic), whereas in 2013 the mean date of departure was 5 May and the *earliest* mean departure was 3 May (Bluenose East), such that there was no overlap in mean migration departure timing in these two years.

Regressing cross-correlation coefficients against distance revealed some dependence (Fig. 5). A simple exponential regression of pairwise correlation against pairwise distances was not significant ($P = 0.374$, $n = 21$), an exponential fit that fixed the intercept at zero distance equal to 1 yielded a significant regression coefficient of -0.0014 ($P < 0.001$), corresponding to a characteristic spatial correlation distance of 712 km (95% confidence interval [CI] 457–1610; Fig. 5). This characteristic distance provides a rough estimate of the distance at which spatial correlations are significant. If Western Arctic (the westernmost herd showing surprisingly high correlation with the eastern-most Beverly and other NWT

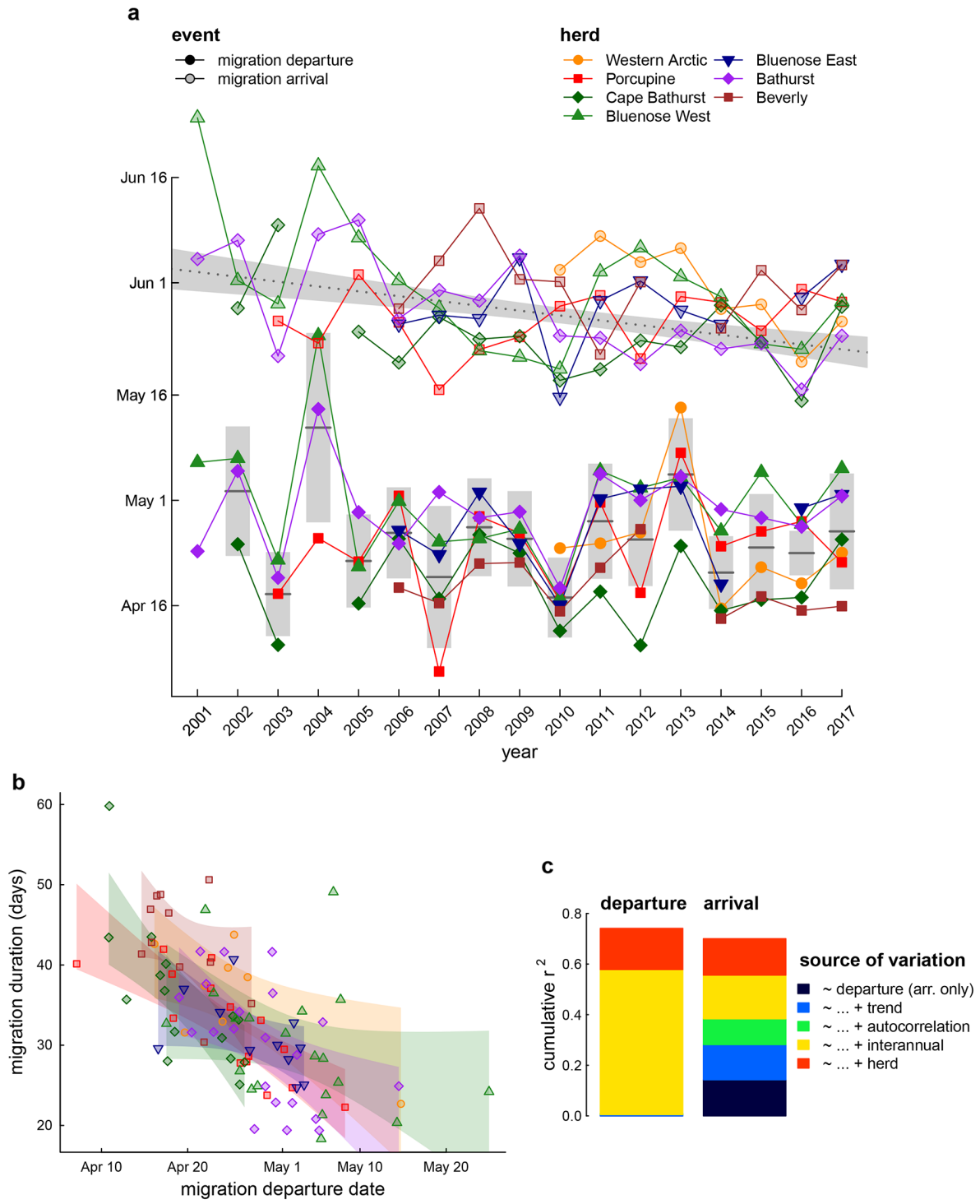

Fig. 4. Summaries and analysis of estimated barren-ground caribou migration timing in northern North America, focusing on intrinsic variables. (a) Spring migration departure from wintering ranges (lower lines, solid symbols) and arrival dates at calving grounds (upper lines, shaded symbols) across years for all herds (color-symbol combinations). The boxes behind the departure dates indicate means and standard deviation, which showed the

greatest variation among years, with no significant trends. The shaded area behind the arrival dates indicates the overall trend (excluding 2001, with only two data points and a potential outlier in Bluenose West). (b) Duration of migration (y-axis) against departure date (x-axis) for seven caribou herds, color coded as in (a); shaded areas indicate herd-specific linear regression prediction intervals. (c) Cumulative R^2 plot contrasting the role of intrinsic explanatory variables for spring migration departure and arrival dates. The areas of rectangles indicate the approximate amount of variation explained by including each of the following variables sequentially to additive linear models: *departure* (for arrival date only), *trend* (year as a continuous covariate), *autocorrelation* (using previous year's date as covariate), *interannual variation* (year as discrete factor), *herd* (as discrete factor).

herds) is conservatively removed from the analysis an exponential fit with a free intercept indicates a significant negative relationship between the two ($\beta = -0.003$, $P = 0.0348$, $n = 16$), corresponding to a characteristic spatial correlation distance of 337 km (95% CI 266–458).

Even though arrival date is simply the sum of departure date and duration, both of which exhibited weak or no trends, arrival dates did significantly trend earlier at −0.713 d/yr (SE 0.15, $P < 1 \times 10^{-3}$). Individually, arrival date trended significantly earlier for four herds: Western Arctic ($\beta = -2.89$ d/yr, $P = 0.003$), Cape Bathurst ($\beta = -0.57$, $P = 0.02$), Bluenose West ($\beta = -0.61$, $P = 0.02$), and Bathurst ($\beta = -0.80$, $P < 1 \times 10^{-3}$). Serial autocorrelation was significant for arrival dates, with an estimated coefficient $\phi = 0.225$ (likelihood ratio test comparing mixed-effects model with and without autocorrelation: $P = 0.03$), whereas departure dates

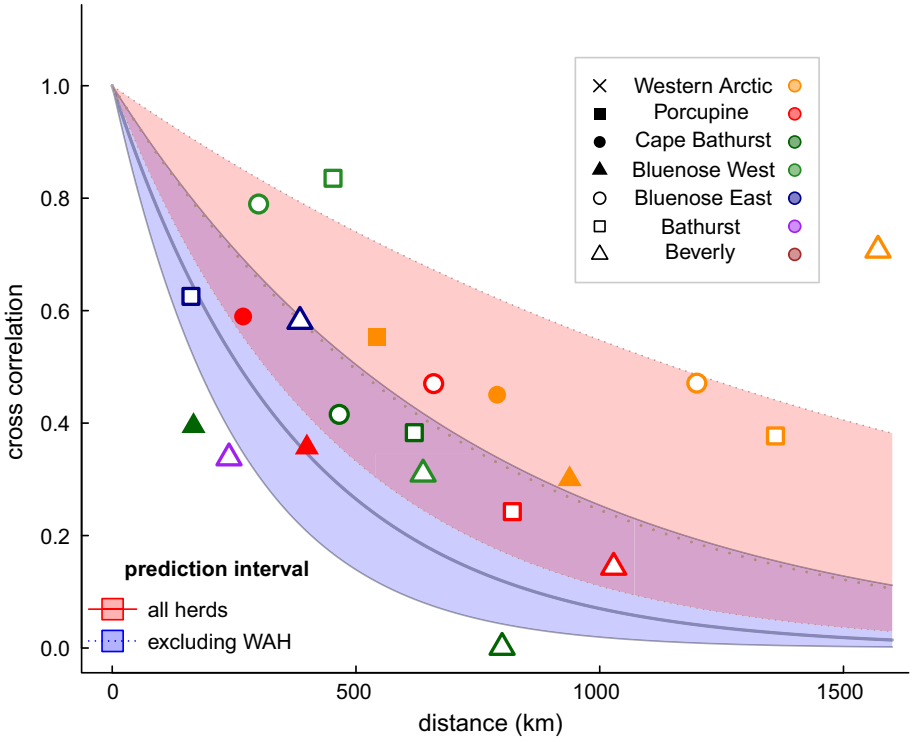

Fig. 5. Pairwise correlations (ρ) in spring migration departure timing against distance between wintering grounds for seven caribou herds in northern North America. Symbols and colors indicate the specific herds in each pair, as summarized in the key (upper right). The curves indicate two exponential fits, red indicating all of the herds, blue indicating a fit that excludes the Western Arctic herd (orange dots). The, respectively, colored shaded area are the corresponding 95% prediction intervals.

showed none ($P = 0.67$). Autocorrelation was taken into account when regressing arrival dates against year using generalized least squares, which controls for spuriously small or large P-values in dependent time series. Arrival dates were also completely unsynchronized across the herds (cross-correlation coefficient: 0.06, $P = 0.20$), and duration was only weakly cross-correlated (0.29, $P = 0.02$).

The contrast between the intrinsic statistical properties of spring departure and arrival dates is illustrated in the cumulative variance explained analysis in Fig. 4c. For departures, autocorrelation and trend explained <1% of the variation, whereas interannual differences (related closely to synchrony) explained 57.3% of the variation in start timing, far more than differences among herds (16.3%). For arrival timing, even after accounting for departure date as an initial covariate, trend, autocorrelation, interannual variation, and differences among herds all contributed between 10% and 17% to the total variance explained.

Snow phenology and vegetation

For all herds, in both wintering and calving grounds, SDD trended earlier over the time frame of the study, with overall regression coefficients −1.18 d/yr in wintering ranges (SE 0.23, $P < 1 \times 10^{-10}$) and −1.5 d/yr in calving ranges (SE 0.15, $P < 1 \times 10^{-10}$), with significant differences across herds. Notably, Porcupine ranges were the only ones to experience a slightly later (but non-significant) snowmelt trend over time. The difference in SDD between the more southern wintering ranges and the more northern calving ranges overall was 19.9 d (SD = 15), with wide variation among herds (Fig. 6). The smallest difference was for the Porcupine, which at just 6.1 d (SD = 6.7) contrasted strongly with the 37.7 d (SD = 18) average difference between the two SDDs for the Bluenose East.

On average, spring migration began 14.5 d (SD 15.9 d) before snowmelt in the calving ground (Fig. 6, filled circles) and ended very close to snowmelt on calving grounds: The difference between the two was just 0.87 d (SD 9.2). However, there were significant differences among the herds. Notably, the Beverly herd began migration, on average, 31.1 d (SD 13.4) before snowmelt, significantly earlier than three of the other NWT herds. The Bluenose East was the only herd where departure date occurred after snowmelt on average (−1.68 d), but with a very large standard deviation (20.3). For arrival dates, the Western Arctic arrived consistently 2 weeks *after* snowmelt (−13.8 d, SD 3.15 d), and the Porcupine similarly arrived, on average, 5.8 d after snowmelt (SD 6.70), while the other herds arrived between 0 and 7.2 d before snowmelt.

Departure dates were weakly related to snowmelt phenology. A model selection comparing models with all combinations of main and interactions effects between herd, year trend, and winter range SDD for departure date did not retain SDD in the final model. In contrast, arrival date was positively related to calving range SDD while controlling for trends and inter-herd variability, with an overall SDD coefficient of 0.31 arrival days/snowmelt days (SE 0.07, $P < 0.01$). In a herd-specific comparison, Western Arctic, Bluenose West, Bathurst, and Beverly herds all showed a significant relationship between arrival and calving SDD (coefficients between 0.56 and 0.916, $P < 0.017$).

Climate and weather drivers of migration

We present model weights of the top ten spring departure models against large-scale climate variables in Table 3. All but one of these models included all summer and spring PDO, NAO, and AO, while fewer included those variables in winter. Positive NAO values in spring and in the previous summer were associated with later migrations, while positive PDO and AO values in spring and previous summer were associated with earlier migrations. The conditional R^2—a measure of variance explained for mixed-effects models (Nakagawa and Schielzeth 2013)—was 0.54 for the main-effects model with summer and spring PDO, AO, and NAO.

In stark contrast to the departures, arrival dates revealed no significant effects of any large-scale climate variables. The top selected model was the intercept only model and the following nine models were all single main-effect models from each of the oscillation—season combinations, with winter variables appearing in the lower ranked models (Table 4).

To test the effect of the weather conditions that the animals experience on the ground during

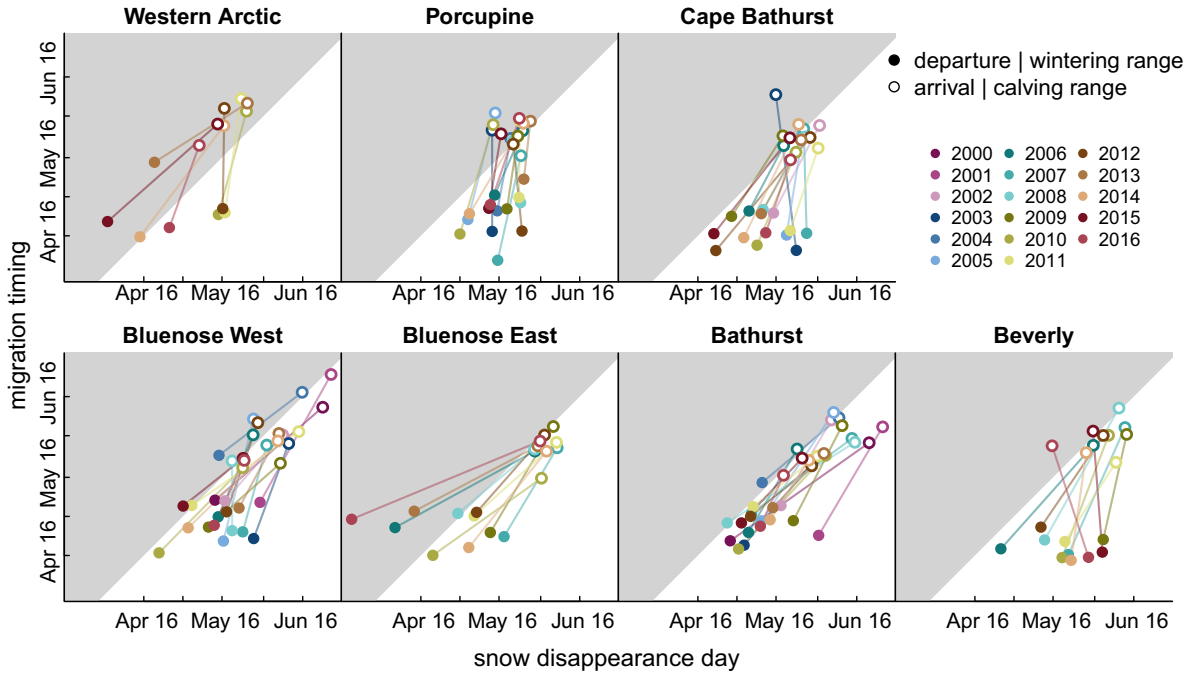

Fig. 6. Estimated spring migration timing (*y*-axis) plotted against snow disappearance day (SDD, *x*-axis) for seven caribou herds, northern North America, 2000–2016. Filled in circles represent the start of migration against the winter range SDD, open circles represent the end of migration against calving range SDD. Each set of connected points represents one year of estimates. Points in the lower right of each panel (shaded white) represent events that occurred while there was still snow on the ground while points in the gray area (upper left) represent events that occurred once the snow had melted. Nearly all departures occurred while snow was on the ground. In Alaskan calving grounds (Western Arctic and Porcupine herds, upper left panels), most arrivals occurred after the snow had melted on the calving grounds, largely because the SDD was not significantly later on the calving grounds. In contrast, in NWT herds (remaining panels), arrival generally occurred while the ground was still largely snow covered.

Table 3. Model selection table for spring migration departure date against climate indices computed during the preceding summer ("sum": July–August), winter ("win": January–February), and spring ("spr": March and April).

	PDO			AO			NAO						
Rank	sum	win	spr	sum	win	spr	sum	win	spr	df	AIC_c	ΔAIC_c	Weight
1	−1.24		−2.03	−7.55		−4.17	3.08		5.25	9	676.4	0.00	0.272
2	−1.39		−2.24	−9.06		−3.83	3.23	1.10	4.72	10	677.4	0.93	0.171
3	−1.50		−1.99	−8.71	0.68	−4.09	3.31		4.87	10	678.2	1.78	0.112
4			−3.01	−6.77	−3.42	−3.14	2.18	4.31	4.86	10	678.4	2.02	0.099
5	−1.24	0.41	−2.40	−7.15		−4.27	2.91		5.34	10	678.8	2.35	0.084
6			−2.02	−5.46		−3.99	2.31		4.69	8	679.1	2.69	0.071
7	−0.99		−2.61	−8.50	−1.59	−3.52	2.90	2.67	4.85	11	679.3	2.85	0.065
8	−1.38	0.42	−2.61	−8.66		−3.93	3.06	1.10	4.80	11	679.7	3.33	0.052
9	−1.26	−1.69		−9.30		−3.61	3.71		4.69	9	680.2	3.82	0.040
10	−1.50	0.39	−2.35	−8.33	0.68	−4.19	3.15		4.95	11	680.6	4.20	0.033

Notes: The top ten models according to Akaike's information criterion, corrected for sample sizes (AIC_c) are presented, with the numbers indicating the value of the respective coefficients: positive (or negative) values indicate later (or earlier) departure dates for higher values of the respective index. PDO, Pacific Decadal Oscillation; AO, Arctic Oscillation, NAO, North Atlantic Oscillations.

Table 4. Model selection table for spring migration arrival date.

	PDO			AO			NAO						
Rank	sum	win	spr	sum	win	spr	sum	win	spr	df	AIC_c	ΔAIC_c	Weight
1										3	707.03	0.00	0.21
2							1.01			4	707.98	0.95	0.13
3				1.66						4	708.48	1.44	0.10
4			−0.49							4	708.63	1.60	0.09
5						−0.57				4	708.67	1.64	0.09
6									−0.48	4	708.95	1.92	0.08
7		−0.19								4	709.11	2.08	0.07
8								0.21		4	709.15	2.12	0.07
9					−0.13					4	709.17	2.14	0.07
10	−0.11									4	709.17	2.14	0.07

Note: Details as in Table 3. AIC_c, Akaike's information criterion, corrected for sample sizes; sum, summer; win, winter; spr, Spring; PDO, Pacific Decadal Oscillation; AO, Arctic Oscillation, NAO, North Atlantic Oscillations.

migration times, we used a similar procedure as for the large-scale climate variables, fitting models using the complete set of weather predictors (temperature, precipitation, snowwater equivalent, and wind magnitude) in the previous summer, winter, early spring, and the two-week period preceding migration. We also included previous summer's maximum NDVI in this analysis as the best available proxy for vegetation productivity.

For the start of spring migration, the final selected model included spring temperatures, pre-migration snow water equivalent, and winter snow water equivalent, as well as a winter snow and spring temperature interaction, all with significant effects (Fig. 7b). More snow and warmer temperatures immediately preceding migration were associated with later migrations, with the combination of the two interacting positively, that is, pushing migration even later. However, more winter snow was associated with earlier migrations. This relatively simple model, with three main effects and one interaction, explained 46% of the variation in start of spring migration according to conditional R^2.

For migration duration, we only explored the weather variables that were associated with the two-week pre-migration and migration periods. Of these, temperature during migration and wind pre-migration were the only variables

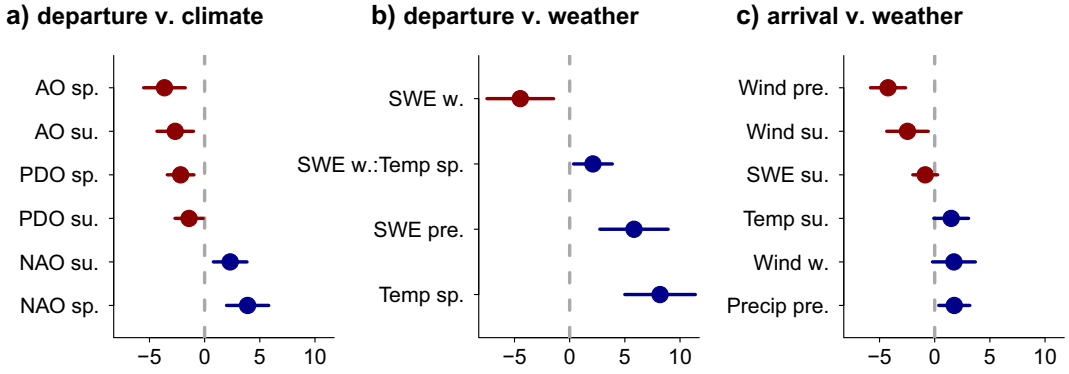

Fig. 7. Effects plot for models of (a) migration start timing against climate predictors, (b) migration start timing against weather predictors, and (c) arrival at calving grounds against weather predictors. Positive (blue) and negative (red) colors correspond to later and earlier migration timing, respectively, at higher values of the coefficient. All weather covariates were scaled. The dotted line indicate variables that were retained in the final model but were not significantly non-zero at the $\alpha = 0.05$ level.

retained in the final model, both with negative coefficients. Warmer temperatures predicted faster migrations by 0.72 d/°C (SE 0.30, $P = 0.02$), and higher average winds predicted faster migrations by −3.5 d per m/s wind speed (SE 1.54, $P = 0.019$). The start date of migration is by far the most significant single factor predicting durations: Later migrations are faster by about 0.72 d per day delay in migration start (SE 0.11, $P < 0.001$). When controlling for the start date, the temperature covariate ceased to be significant while wind became more significant.

Arrival dates analyzed against all weather covariates revealed a very different set of predictors (Fig. 7), including several weather variables from the previous summer and from the pre-migration period, but none from early spring. The previous summer variables include snow water equivalent (negative effect), temperature (positive), and wind speed (negative); the pre-migration variables also include snow water equivalent (positive) and wind (negative). The conditional r^2 value for the weather arrival model was 0.48. In no models was NDVI during the previous summer selected as a significant predictor for departure or arrival dates in the following spring.

Seasonal weather trends and relationship to climate

Many of the weather covariates showed significant trends over the period of our analysis, but these trends were variable across herds and seasons (Fig. 8; Appendix S3). Winter temperatures, for example, generally trended positive over the study, but these trends were only significant for two herds (Porcupine and Cape Bathurst). In summer and spring, there were no significant trends except for the Western Arctic, which experienced generally cooler summers over its study period (slope −0.28°C/yr, $P = 0.014$). Curiously, winds showed the most consistent trends across seasons and herds, with five of the seven herds experiencing significantly stronger average winds over the study period, and only the Porcupine showing a strong negative trend in average wind magnitude in winter (slope $-0.085\ \mathrm{m{\cdot}s^{-1}{\cdot}yr^{-1}}$, $P < 10^{-4}$). Spring weather showed the starkest geographic variability, with the Alaskan herds (Western Arctic and Porcupine) experiencing generally less snow and precipitation over time, whereas the NWT herds experienced conditions that have become significantly windier and snowier over this period (Fig. 8c).

Relationships between the weather covariates and large-scale oscillations revealed complex patterns, but relatively few significant relationships (Appendix S3). The PDO and NAO were most strongly related to weather variables across seasons, but of 80 possible regressions across all weather covariate and season combinations, only 11 PDO and 10 NAO relationships were significant. The AO, in contrast, was significant in only one relationship (higher winter AO was related to significantly less snow for Western Arctic). Generally, high winter PDO was linked to warmer temperatures, while high summer PDO was associated with cooler temperatures across the range, though both tendencies displayed a gradient from stronger effects in Alaska to weaker effects eastward. For example, for the easternmost herd (Beverly), PDO was associated with *cooler* winters and somewhat *warmer* summers, though neither relationship was significant (Appendix S3: Fig. S3). Positive PDO was generally related to more precipitation, more snow and windier conditions across seasons. Positive winter NAO was associated with windier and slightly cooler conditions in most places, while positive summer NAO was almost universally less windy, cooler, and with less precipitation (Appendix S3: Fig. S5). Arctic Oscillation results were generally not significant, but echoed the patterns of NAO, with which it was particularly strongly correlated in winter and spring ($r = 0.82$ and 0.72, respectively; Appendix S3: Figs. S1 and S2).

Discussion

By aggregating an unprecedentedly large dataset of caribou locations, developing a robust hierarchical modeling framework to distill the behaviors to the relevant ecological unit of herd-year, and analyzing the results against various environmental covariates, we made several novel and unexpected discoveries. We found that variation in the onset of spring migration was, indeed, primarily driven by immediate weather conditions, consistent with the tactical migration hypothesis. Consequently, the onset of spring

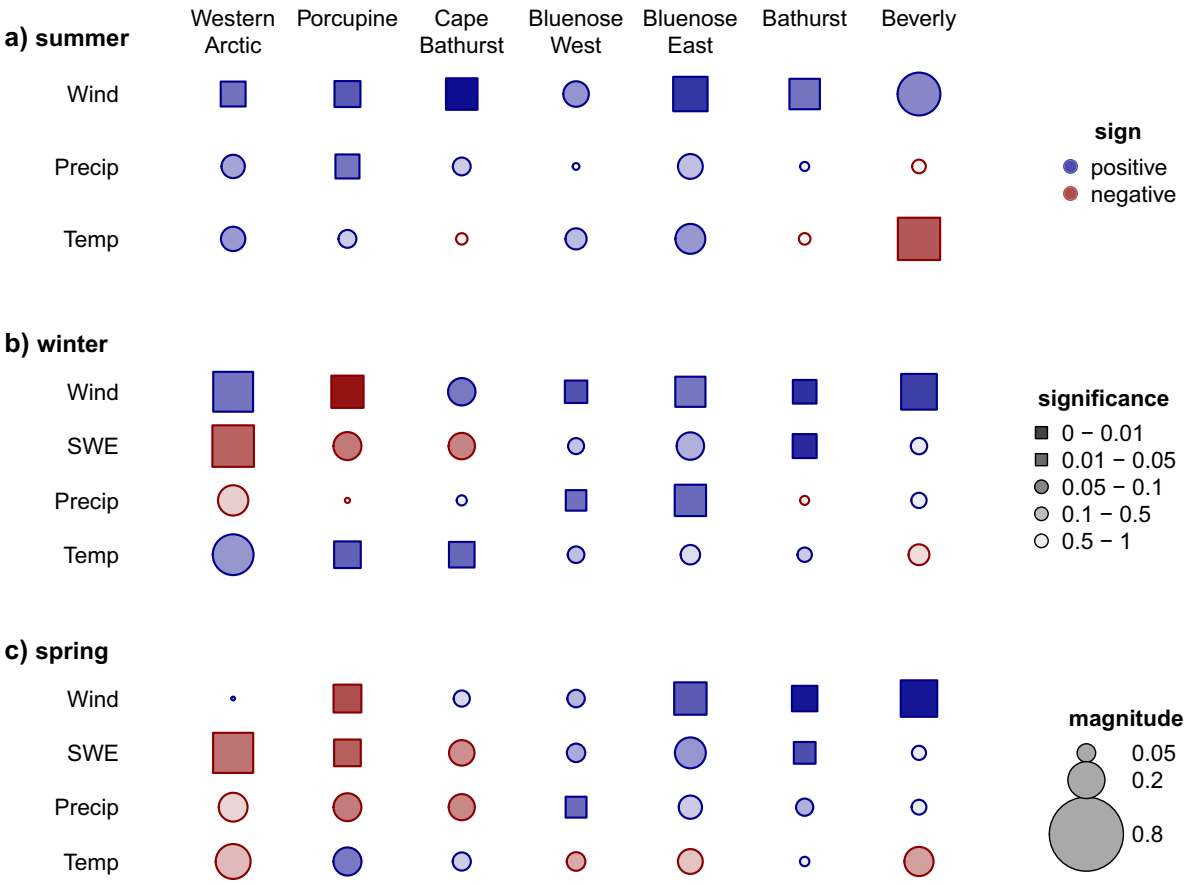

Fig. 8. Magnitude and significance of trends in the weather covariates (temperature, precipitation, snow water equivalent, and wind) experienced by seven caribou herds in northern North America in three seasons. Red and blue colors indicate negative and positive trends, respectively. Squares represent trends that were significant at the $\alpha = 0.05$ level, circles represent non-significant trends with shading reflecting the *P*-value. The sizes of the symbols represent the magnitude of the regression slopes for the respective covariates, all of which were first scaled to facilitate comparisons. Snow water equivalent (SWE) was negligible in most places in summer and is therefore omitted in the top panel. All trends are illustrated in Appendix S3: Figs. S1 and S2.

migrations exhibited an astonishing level of synchrony across herds and over a spatial scale on the order of many hundreds of kilometers. However, caribou also showed remarkable plasticity in the duration of their migrations, significantly speeding up migrations that started later in the season. This plasticity essentially decoupled departure timing from arrival timing at the calving grounds, such that arrival timing depended on a completely different set of environmental variables, notably influenced by weather conditions from the previous summer. This result indirectly suggests that maternal body condition was the ultimate driver of arrival timing to calving grounds, consistent with the strategic migration hypothesis. We discuss these main findings in more detail and place them in a larger ecological context of caribou population dynamics.

Migration phenology and climate

We observed considerable variability in spring departure timing across herds and, despite major differences in the habitats, migration distances, and geography of different herds, no herds began their migrations consistently earlier or later than others. However, the timing of the start

of migration was largely synchronized across western North America. For example, and without exception, every herd began their migration earlier in 2010 than either 2009 or 2011, later in 2013 than either 2012 or 2014, and earlier in 2014 than in 2015 (Fig. 4a). Further, we found that herds began migrating later when conditions were snowier and warmer in the period immediately preceding migration (Fig. 7b). These findings echo those reported for the George River and Leaf River herds in NQL, on the eastern edge of the North American continent (Le Corre et al. 2017). As in our study, Le Corre et al. (2017) report that 2003 and 2010 were earlier migration years relative to years immediately before and after, when spring snowfall was heavier. Thus, we conclude that the triggers of migration onset are continental in scale, consistent with the typically large scales of spatial correlation in temperature and precipitation in North America. Koenig (2002) reported spatial correlations in precipitation and temperature across continents on the order of 500–650 km, comparable to the distance scale of correlation in onset of migration timing. Our results therefore provide empirical evidence for a behavioral synchronization analogous to the Moran effect that synchronizes population dynamics. It is an open question to what extent this continental-scaled synchrony extends across other terrestrial migratory species, including birds, in the Arctic and boreal regions.

The reasons caribou may have delayed their migrations remain mysterious. There was little evidence that start of migration was influenced by the timing of snowmelt; in fact, the majority of migrations occurred while the ground was largely snow covered (Fig. 6). However, there are limitations to using simple satellite-derived snow presence metrics (Mahoney et al. 2018, Boelman et al. 2019). The snow disappearance day that we used to capture snowmelt timing on a large scale is a fairly coarse measure derived from MODIS imagery, which is notoriously prone to missing pixels due to cloud cover. Furthermore, the 500-m resolution masks a great deal of fine structure in the process and distribution of snowmelt, particularly where terrain is complex. The *presence* of snow is of less importance than understanding the *properties* of the snow, such as depth, surface hardness, and density, which are fundamental to an animal's ability to move and access food or shelter (Boelman et al. 2019). These properties are, to date, difficult to infer from remotely sensed observations or to acquire via alternative approaches (Boelman et al. 2019).

Our analyses do, however, provide some indirect indication that snow properties may be important determinants of the speed and duration of migration via the influence of wind on snowpack conditions along migratory routes. After controlling for migration start time, we found that higher wind speeds were associated with shorter migration durations. During winter and spring months, wind over snow leads to the hard-packed snow known locally as *upsik* (Pruitt 2005). Landscapes covered by hard snowpacks are measurably more difficult for caribou to forage in than those with soft snow (Collins and Smith 1991), but easier to move on than deep, wet snow (Henshaw 1968), both of which contribute to faster migrations. Given our overarching conclusion that caribou mainly set the pace of migration to arrive at a particular time, the presence of hard-packed snow may make attaining that goal mechanically easier, even if it restricts access to food along the way. Another indirect indication that snow properties might be important was the curious result of the weather model for departure times (Fig. 7b). Our analysis suggested that snowier conditions immediately preceding migration delayed migrations, consistent with Le Corre et al. (2017). However, more *winter* snow was linked to earlier migrations, and there was a significant positive interaction between spring temperatures and winter snow, meaning that warm temperatures after a snowy winter delayed migrations. One possible explanation is that a hardened winter snowpack (i.e., cold spring following winter snow) is suitable for migration, whereas warmer, slushier snow makes movement more difficult, leading caribou to wait for better conditions. Warmer temperatures and increased winds may also accelerate onset of snow disappearance as wind affects the rate of snow sublimation, leading to easier foraging or new foraging access on late winter ranges, thereby delaying migrations and further decoupling migration from snow phenology. A better understanding of the factors that influence snow quality with respect to caribou mobility would be gained via improved snow property

observations of improved modeling of snow quality from remote sensing (Pan et al. 2018, Boelman et al. 2019).

Once migration began, caribou displayed remarkable plasticity in the duration of their migrations. A given herd's migration was as likely to last fewer than 25 d as over 40 d (22% probability of either). Caribou compensated for later departure dates with more rapid rates of migration, and took much more time to migrate if the departure was earlier. We were surprised to find that <14% of the variability in arrival times was explained by departure timing. This compensatory behavior suggests that arrival at calving grounds is driven by the physiological prerogative to give birth, and that the caribou's mobility gives it the ability to largely compensate for the constraints imposed by the proximal triggers for initiating migration.

As a consequence of this decoupling of arrival and departure times, we found little overlap in the environmental variables predicting these times. No large-scale climate indices influenced arrival timing, which resulted in an effective desynchronization of arrival timing across the range. In contrast, a prominent role was played by specific local weather conditions experienced by the caribou in the previous year's summer. In particular, cooler, windier, and even rare summers with snowfall were generally followed by earlier arrival time at calving grounds. One possible explanation for this unexpected result is related to insect harassment and physical condition. It is well-established that harassment by blood-sucking and parasitic insects, including mosquitoes (*Culicidae*), black flies (*Simuliidae*), and botflies (*Oestridae*), significantly influences caribou behavior and habitat selection. Indeed, Russell et al. (1993) point to insect harassment as the principle driver of caribou movements in the summer months. Specifically, when harassment levels are high, caribou tend to aggregate spatially (Russell et al. 1993), move to less productive habitats (Walsh et al. 1992, Skarin et al. 2008), and spend less time feeding (Russell et al. 1993, Witter et al. 2012*b*), all leading to worse physical condition of the females. Cooler, windier conditions all lead to lower insect densities (Walsh et al. 1992, Russell et al. 1993, Weladji et al. 2003, Witter et al. 2012*a*), and, consequently, to better physical condition of females, and as our analysis has shown, to earlier migration arrival times and, consequently, to earlier calving times. The link between female condition and earlier parturition was demonstrated experimentally in captive caribou from the George River herd in Québec and Labrador, whose calving dates advanced by two weeks over two years of ad libitum feeding and corresponding increase in female body mass (Crête et al. 1993). Thus, our analysis—while limited to movement and large-scale climate weather data—provides strong indirect evidence that better physical condition leads to earlier spring migration arrival times and likely earlier calving. Note that the physical condition hypothesis may also explain our otherwise mysterious finding of significant serial autocorrelation in arrival timing (but not departure timing), which might reflect a carry-over effect of body condition across years.

Other studies on temperate ungulate dynamics similarly point to the importance of summer and early fall conditions (Cook et al. 2004, Monteith et al. 2013, Hurley et al. 2017, Hebblewhite et al. 2018). For example, overwinter survival and reproduction of mule deer (*Odoicoleus hemionus*) and elk (*Cervus elaphus*) were most strongly explained by late summer and autumn growing conditions across the western United States. However, in caribou the fundamental mechanism appears to be insect harassment rather than vegetation. In fact, the vegetation index we used to assess summer productivity (annual maximum NDVI) had no predictive power in any of our models for any of the migration variables. While it is tempting to conclude that the effects of insect harassment, which most directly lowers the amount of time caribou can spend foraging, outweigh the benefits of greater forage quantity which might be associated with warmer conditions, this assertion requires more focused study based on direct observations, since NDVI is a relatively poor measure of variation in the abundance of caribou specific forage (Bryant et al. 2014, Johnson et al. 2018), especially since caribou are generally selective foragers (Denryter et al. 2017).

Our results also show that unlike departure timing from wintering grounds, arrival timing at calving ranges trended somewhat earlier over a 16-yr study period (Fig. 4). This trend was driven primarily by the trio of NWT herds—Cape

Bathurst, Bluenose West, and Bathurst—which have been tracked for the longest period and have undergone the steepest population declines over the time period of the study (COSEWIC 2016, Adamczewski et al. 2019). For the Bluenose West and Bathurst herds, the trend toward earlier arrival has also corresponded with a decline in migration distance as the annual range of each of these herds has contracted and shifted. Thus, population decline rather than phenology matching is the most parsimonious explanation for the general trend of earlier arrival at calving ranges. Another possibility is that given the highly social nature of both spring migration and calving, large drops in population size may themselves influence the timing and within-herd synchrony of migration phenology.

It bears reiterating that in contrast to temperate ungulate populations, for which migrations are driven by surfing (Merkle et al. 2016, Aikens et al. 2017) or jumping (Bischof et al. 2012) green waves of maturing forage, vegetation and green-up timing likely play a minimal role in driving caribou migration. Many of our herd-year populations began and ended their migration before any meaningful green-up has begun, based on remotely sensed observations. More reliable field-based observations of several of the herds in our study have indicated that the quality and quantity of food on calving grounds during the calving period, in fact, inferior to food available for non-reproductive animals that typically delay migration (Heard et al. 1996), providing further evidence that proximal food quality and vegetation are not important drivers of migration.

In summary, barren-ground caribou appear to be ultimately driven by an intrinsic "strategic" drive to give birth, but their migrations triggered by "tactical" decisions that balance energetic reserves and forage availability in the wintering range against their ability to attain calving grounds in time given immediate environmental constraints. This combination of tactical and strategic behaviors, in conjunction with the impressive plasticity in migration speeds related to the array of physiological adaptations that allow caribou to move in snow-covered environments (e.g., via extremely high foot-loading index; Telfer and Kelsall 1984), provides caribou with a strong ability to hedge against long-term trends and variability in spring conditions.

These observations raise further questions regarding the adaptive mechanisms and evolutionary-scale benefits of the collective migration behavior. In particular, collective memory and access to non-local information, both of which may help caribou hedge against environmental variability and unpredictable dynamics, may be key adaptations for explaining the success of migratory caribou and to anticipate population-level responses to ongoing rapid climate change. In this context, it will be important to continue to monitor the migrations of the caribou to see if the early evidence of trends toward earlier arrivals in some herds extends across other populations and continues apace with the general warming trends of the Arctic. In parallel, it will be important to monitor the extent to which the caribou may be shifting the locations — and therefore the habitat features — of their calving grounds. Both of these are potential adaptive mechanisms, and both can be studied using the analytical framework developed here.

Climate, migration, and population dynamics

The ability of animals to track the environmental changes due to a changing climate is a central problem in ecology, and one that is particularly relevant for caribou (Vors and Boyce 2009). It is also one that ultimately requires linking animal movement to population dynamics (Morales et al. 2010). Our study was focused on linking climate variables to mass movements, but the main interest of these movements—generally, the main motivation in collaring the animals originally—is to understand their population dynamics. We therefore conclude by placing our results into a mechanistic framework that might guide future investigations exploring climate and population links.

A schematic of the complex links between climate, migration, and population processes is presented in Fig. 9, emphasizing the mediating role played by adult female body condition (Albon et al. 2017). Our results highlight the links between spring climate and spring migration departure timing, the surprisingly weak link between departure and arrival timing, and a strongly inferred link between summer climate and arrival timing via mechanistic pathways related to insect harassment, vegetation, body condition, rut timing, and gestation periods.

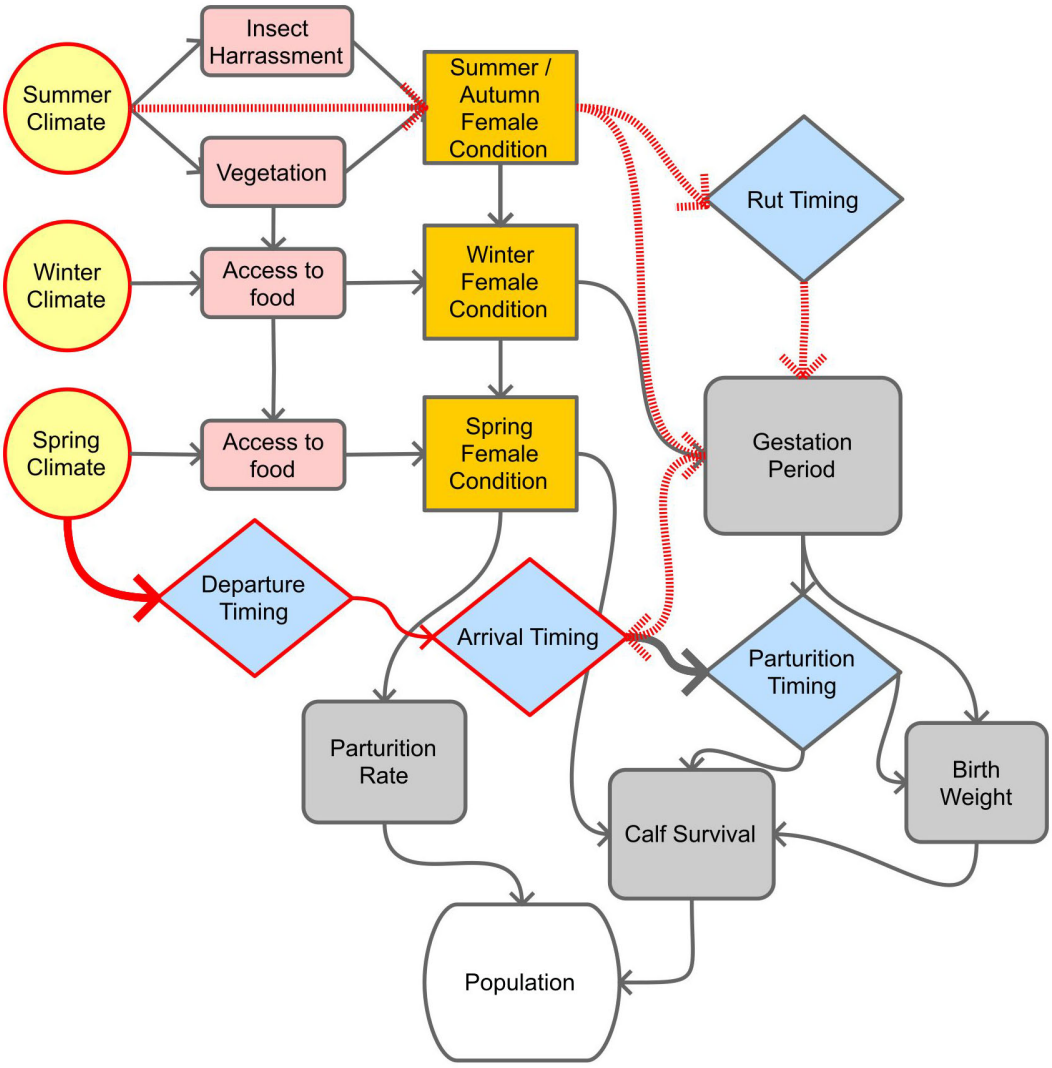

Fig. 9. Conceptual model of hypothesized relationships linking seasonal climate (circles on left) to body condition (rectangles) to phenological events (diamonds), to reproductive processes (rounded rectangles), and ultimately to populations. Red outlines indicate those variables which we have studied or estimated in this study. Thicker arrows indicate stronger relationships (e.g., between spring climate and departure time), thinner arrows indicate week relationships (e.g., between departure and arrival times), and solid red arrows indicate links that we obtained in this study. The thick dotted red lines indicate a proposed mechanistic pathway that explains earlier arrival timing following favorable summers. Many of the other pathways in the schematic have been explored in other studies (see *Discussion* text).

Many of the other links in Fig. 9 have been studied and quantified over many decades of studies on the reproductive ecology, behavior, and physiology of caribou and reindeer, while others can be considered knowledge gaps.

For example, the effect of climate and weather on body condition is especially well-studied in the summer through the effects of insect harassment which also has a direct effect on growth and weight of calves (Helle and Tarvainen 1984, Helle and Kojola 1994). In winter, perhaps the most direct impact of climate on body condition comes from rain on snow events, which can catastrophically cut off access to food (Vors and

Boyce 2009, Albon et al. 2017). Climate also influences parturition timing, which has been linked with autumn (rather than winter or spring) physical condition in caribou in central Alaska (Adams and Dale 1998) and reindeer in Norway (Flydal and Reimers 2002) with larger females in fall generally giving birth earlier. The effect of body condition on reproduction is also fairly well-known. Poorer female body condition leads to lower parturition rates (Gerhart et al. 1997*a*, *b*), lower calf birth weights (Skogland 1986), and lower summer calf survival (Cameron et al. 1993). Similarly, poor maternal body condition has been shown to lead to longer gestation periods in caribou and reindeer (Cameron et al. 1993, Adams and Dale 1998, Rowell and Shipka 2009), with several studies pointing out explicitly a correlation with autumn (rather than winter or spring) condition (Adams and Dale 1998, Flydal and Reimers 2002).

Probably, the greatest gap in our understanding of caribou reproductive behavior is the timing of the rut, which, unlike migrations and parturitions, is very difficult to infer from existing satellite movement data. Examinations of harvested animals from the Qaminirjuaq herd, immediately to the east of our study, indicated that breeding was highly synchronous and uncorrelated with female body condition within a year (Dauphiné and McClure 1974), but the design of the study did not allow for a comparison across higher and lower-productivity years. If gestation periods are relatively inflexible, earlier arrival and parturition times would suggest that animals in better physical condition breed earlier in the season, and earlier parturition times may increase calf survival due to the additional time available to gain body condition and size during the important summer and autumn foraging periods. In other ungulates, however, gestation timing has been shown to depend on mother's condition and diet (Cook et al. 2004). Thus, even if rut timing is fairly stable across years, the effect of body condition on gestation time may be an important mechanistic driver of migration arrival times, and subsequent parturition timing.

Preliminary analysis of our movement data supports the well-documented relationship between arrival timing and parturition timing. We compared arrival times estimated in this study with independently estimated and validated parturition dates for the Western Arctic herd caribou (Cameron et al. 2018, M. Cameron, E. Gurarie, K. Joly, *unpublished data*), and found that parturition occurred on average 4.0 d (SD 3.4, $n = 100$) after the individual mean posterior arrival date. Similarly, Gunn and Poole (2009) identified peak calving times roughly within a week of our estimated arrival times for the Bathurst herd, with 2005 identified as the latest peak calving period (14–20 June), corresponding to the latest estimated mean arrival time in our analysis (10 June). A large-scale and detailed analysis comparing individual migration timing with individual parturition timing, and herd-level parturition rates will provide additional insights to the links between climate and population processes. In particular, there are anecdotal cases of calving occurring before caribou arrive at the calving grounds (M. Cameron, E. Gurarie, K. Joly, *unpublished data*). These events may reflect a situation in which a greatly delayed onset of migration cannot be adequately compensated for by faster movements because of poor conditions for migration, leading to much lower calf survival. Understanding the combination of conditions which lead to too-early calving, and the potential for an increased frequency of such events with climate change, could be an important additional piece of the caribou population puzzle.

Hierarchical movement modeling

Our results were made possible by developing a robust hierarchical modeling framework (HRSA) which summarized the migration process at the most ecologically relevant level (in this case: the herd-year). The methodological innovation was necessary due to the extremely large number of observations for multiple populations which were collected using diverse technology and sampling rates across several decades. The set of parameters that are estimated by the HRSA includes a great deal of information that we did not analyze closely here, including population-level range sizes and locations, migration distances, and the population-level variability in each of the parameters. The extent of variability among individuals in arrival timing at calving grounds can be an indirect measure of birth synchrony. The HRSA can also be readily applied to

other complex and large-scale caribou movement, for example, the shift from calving ranges to summering ranges and the subsequent fall migration to widely dispersed wintering grounds. As an ancillary benefit, migration parameters are also estimated for each individual, which can be used for further analysis; for example, to compare the arrival time at calving grounds to individual specific calving dates, whether observed or estimated from movement data (DeMars et al. 2013, Cameron et al. 2018). As the quantity of individually tracked movement data increases, hierarchical approaches to movement modeling will be increasingly relevant. By making the code available, we hope to encourage the adoption, further development, and refinement of hierarchical movement modeling to address population-level questions.

Conclusions

A central, novel conclusion of our work is that migration timing—and in particular arrival timing at calving grounds—might be a useful proxy for the physical condition of pregnant females. Late migration arrival timing may be associated with lower parturition rates and possibly lower calf survival. This relationship must be confirmed with more specific analyses that compare migration timing, for example, with observed female calf ratios collected via aerial surveys or from movement-derived estimates of parturition timing (DeMars et al. 2013, Cameron et al. 2018) and parturition success. If this relationship holds, remotely tracked animal movement data could be used as an indicator of female body condition—and perhaps reproductive potential—on a large scale. As the number of satellite-tracked animals grows in tandem with improvements in remotely sensed environmental data, large-scale analyses of this type will be increasingly important for making mechanistic links between global-scaled phenomena to processes that affect animal populations. Finally, these large- and long-scaled observations can point toward the adaptive benefits of collective migratory behavior.

Acknowledgments

The authors acknowledge first and foremost the field workers, collaborators, and local community members that engaged in the capture and collaring of the caribou. Funding for capture and collaring was provided by the Alaska Department of Fish and Game, US National Park Service, Government of Northwest Territories and Yukon Territorial Government. The data collation, analysis, and writing were funded primarily by NASA ABoVE Animals on the Move (grants NNX15AU20A and NNX15AW71A) to NB, MH, EG, SD. EG was further supported with a National Park Services CESU (grant P18AC00229), and EG and WF were partially funded by US National Science Foundation (grant ABI-1458748 and DBI-1915347). SD was also supported by NASA grant NNX15AT91A. The authors declare no conflicts of interest.

Literature Cited

Adamczewski, J., J. Boulanger, H. Sayine-Crawford, J. Nishi, D. Cluff, J. Williams, and L.-M. LeClerc. 2019. Estimates of breeding females & adult herd size and analyses of demographics for the Bathurst herd of barren-ground caribou: 2018 calving ground photographic survey. Manuscript Report 279. Government of Northwest Territories, Yellowknife, Northwest Territories, Canada.

Adamczewski, J., A. Gunn, K. G. Poole, A. Hall, J. Nishi, and J. Boulanger. 2015. What happened to the Beverly Caribou herd after 1994? Arctic 68:407–421.

Adams, L. G., and B. W. Dale. 1998. Timing and synchrony of parturition in Alaskan caribou. Journal of Mammalogy 79:287–294.

Aikens, E. O., M. J. Kauffman, J. A. Merkle, S. P. H. Dwinnell, G. L. Fralick, and K. L. Monteith. 2017. The greenscape shapes surfing of resource waves in a large migratory herbivore. Ecology Letters 20:741–750.

Albon, S. D., et al. 2017. Contrasting effects of summer and winter warming on body mass explain population dynamics in a food-limited Arctic herbivore. Global Change Biology 23:1374–1389.

Ambaum, M. H. P., B. J. Hoskins, and D. B. Stephenson. 2001. Arctic oscillation or North Atlantic oscillation? Journal of Climate 14:3495–3507.

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.

Barrett, R. T. 2011. Recent response to climate change among migrant birds in northern Norway. Ringing & Migration 26:83–93.

Barton, K. 2018. MuMIn: Multi-Model Inference. R package version 1.40.4. https://CRAN.R-project.org/package=MuMIn

Bastille-Rousseau, G., C. B. Yackulic, J. P. Gibbs, J. L. Frair, F. Cabrera, and S. Blake. 2019. Migration triggers in a large herbivore: Galápagos giant tortoises navigating resource gradients on volcanoes. Ecology 100:e02658.

Berger, J. 2004. The last mile: How to sustain long-distance migration in mammals. Conservation Biology 18:320–331.

Bergerud, A. T. 1996. Evolving perspectives on caribou population dynamics, have we got it right yet? Rangifer 16:95–116.

Bichet, O., A. Dupuch, C. Hébert, H. Le Borgne, and D. Fortin. 2016. Maintaining animal assemblages through single-species management: The case of threatened caribou in boreal forest. Ecological Applications 26:612–623.

Bischof, R., L. E. Loe, E. L. Meisingset, B. Zimmermann, B. Van Moorter, and A. Mysterud. 2012. A migratory northern ungulate in the pursuit of spring: jumping or surfing the green wave? American Naturalist 180:407–424.

Boelman, N., et al. 2019. Integrating snow science and wildlife ecology in Arctic-boreal North America. Environmental Research Letters 14: 010401.

Boisvert, L., and J. Stroeve. 2015. The Arctic is becoming warmer and wetter as revealed by the Atmospheric Infrared Sounder. Geophysical Research Letters 42:4439–4446.

Börger, L., and J. Fryxell. 2012. Quantifying individual differences in dispersal using net squared displacement. Pages 222–228 *in* J. Clobert, M. Baguette, T. Benton, and J. Bullock, editors. Dispersal ecology and evolution. Oxford University Press, Oxford, UK.

Both, C., C. A. Van Turnhout, R. G. Bijlsma, H. Siepel, A. J. Van Strien, and R. P. Foppen. 2009. 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.

Boulanger, J., A. Gunn, J. Adamczewski, and B. Croft. 2011. A data-driven demographic model to explore the decline of the Bathurst caribou herd. Journal of Wildlife Management 75:883–896.

Boulanger, J., K. G. Poole, A. Gunn, and J. Wierzchowski. 2012. Estimating the zone of influence of industrial developments on wildlife: a migratory caribou *Rangifer tarandus groenlandicus* and diamond mine case study. Wildlife Biology 18:164–179.

Bracis, C., and T. Mueller. 2017. Memory, not just perception, plays an important role in terrestrial mammalian migration. Proceedings of the Royal Society B 284:20170449.

Bråthen, K. A., V. T. Ravolainen, A. Stien, T. Tveraa, and R. A. Ims. 2017. Rangifer management controls a climate-sensitive tundra state transition. Ecological Applications 27:2416–2427.

Bryant, J. P., K. Joly, F. S. Chapin III, D. L. DeAngelis, and K. Kielland. 2014. Can antibrowsing defense regulate the spread of woody vegetation in arctic tundra? Ecography 37:204–211.

Burch, E. S. 1972. The caribou/wild reindeer as a human resource. American Antiquity 37:339–368.

Burnham, K. P., and D. R. Anderson. 2004. Multimodel inference: Understanding AIC and BIC in model selection. Sociological Methods & Research 33:261–304.

Buus-Hinkler, J., B. U. Hansen, M. P. Tamstorf, and S. B. Pedersen. 2006. Snowvegetation relations in a High Arctic ecosystem: Inter-annual variability inferred from new monitoring and modeling concepts. Remote Sensing of Environment 105:237–247.

Cagnacci, F., et al. 2016. How many routes lead to migration? Comparison of methods to assess and characterize migratory movements. Journal of Animal Ecology 85:54–68.

Caikoski, J. R. 2018. Porcupine caribou herd grows to record high numbers. State of Alaska press release. Department of Fish and Game, Division of Wildlife Conservation (Northwest), Fairbanks, Alaska, USA.

Calabrese, J. M., C. H. Fleming, W. F. Fagan, M. Rimmler, P. Kaczensky, S. Bewick, P. Leimgruber, and T. Mueller. 2018. Disentangling social interactions and environmental drivers in multi-individual wildlife tracking data. Philosophical Transactions of the Royal Society B 373:20170007.

Calenge, C. 2006. The package adehabitat for the R software: tool for the analysis of space and habitat use by animals. Ecological Modelling 197:1035.

Cameron, M. D., K. Joly, G. A. Breed, L. S. Parrett, and K. Kielland. 2018. Movement-based methods to infer parturition events in migratory ungulates. Canadian Journal of Zoology 96:1187–1195.

Cameron, R. D., W. T. Smith, S. G. Fancy, K. L. Gerhart, and R. G. White. 1993. Calving success of female caribou in relation to body weight. Canadian Journal of Zoology 71:480–486.

Cameron, R. D., and J. M. Ver Hoef. 1994. Predicting parturition rate of caribou from autumn body mass. Journal of Wildlife Management 58:674–679.

Carpenter, B., A. Gelman, M. D. Hoffman, D. Lee, B. Goodrich, M. Betancourt, M. Brubaker, J. Guo, P. Li, and A. Riddell. 2017. Stan: a probabilistic programming language. Journal of Statistical Software 76:1.

Collins, W. B., and T. S. Smith. 1991. Effects of wind-hardened snow on foraging by reindeer (*Rangifer tarandus*). Arctic 44:217–222.

Cook, J. G., B. K. Johnson, R. C. Cook, R. A. Riggs, T. I. M. Delcurto, L. D. Bryant, and L. L. Irwin. 2004. Effects of summer-autumn nutrition and parturition date on reproduction and survival of elk. Wildlife Monographs 155:1–61.

COSEWIC. 2016. COSEWIC assessment and status report on the Caribou Rangifer tarandus, Barrenground population, in Canada. Technical Report. Committee on the Status of Endangered Wildlife in Canada, Ottawa, Ontario, Canada.

Cotton, P. A. 2003. Avian migration phenology and global climate change. Proceedings of the National Academy of Sciences USA 100:12219–12222.

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.

Crête, M., and J. Huot. 1993. Regulation of a large herd of migratory caribou: Summer nutrition affects calf growth and body reserves of dams. Canadian Journal of Zoology 71:2291–2296.

Crête, M., J. Huot, R. Nault, and R. Patenaude. 1993. Reproduction, growth and body composition of Rivière George caribou in captivity. Arctic 46:189–196.

Dalziel, B. D., M. L. Corre, S. D. Côté, and S. P. Ellner. 2016. Detecting collective behaviour in animal relocation data, with application to migrating caribou. Methods in Ecology and Evolution 7:30–41.

Dauphiné Jr, T. C., and R. L. McClure. 1974. Synchronous mating in Canadian barren-ground caribou. Journal of Wildlife Management 38:54–66.

de Groot, W. J., M. D. Flannigan, and A. S. Cantin. 2013. Climate change impacts on future boreal fire regimes. Forest Ecology and Management 294:35–44.

DeMars, C. A., M. Auger-Méthé, U. E. Schlägel, and S. Boutin. 2013. Inferring parturition and neonate survival from movement patterns of female ungulates: a case study using woodland caribou. Ecology and Evolution 3:4149–4160.

Denryter, K. A., R. C. Cook, J. G. Cook, and K. L. Parker. 2017. Straight from the caribou's (*Rangifer tarandus*) mouth: Detailed observations of tame caribou reveal new insights into summer–autumn diets. Canadian Journal of Zoology 95:81–94.

Descamps, S., J. Aars, E. Fuglei, K. M. Kovacs, C. Lydersen, O. Pavlova, Å. Ø. Pedersen, V. Ravolainen, and H. Strøm. 2017. Climate change impacts on wildlife in a High Arctic archipelago–Svalbard, Norway. Global Change Biology 23:490–502.

Doiron, M., G. Gauthier, and E. Lévesque. 2015. Trophic mismatch and its effects on the growth of young in an Arctic herbivore. Global Change Biology 21:4364–4376.

Douglas, D. C., R. Weinzierl, S. C. Davidson, R. Kays, M. Wikelski, and G. Bohrer. 2012. Moderating Argos location errors in animal tracking data. Methods in Ecology and Evolution 3:999–1007.

Ellebjerg, S. M., M. P. Tamstorf, L. Illeris, A. Michelsen, and B. U. Hansen. 2008. Inter-annual variability and controls of plant phenology and productivity at Zackenberg. Advances in Ecological Research 40:249–273.

Flannigan, M., A. S. Cantin, W. J. De Groot, M. Wotton, A. Newbery, and L. M. Gowman. 2013. Global wildland fire season severity in the 21st century. Forest Ecology and Management 294:54–61.

Flydal, K., and E. Reimers. 2002. Relationship between calving time and physical condition in three wild reindeer *Rangifer tarandus* populations in southern Norway. Wildlife Biology 8:145–151.

Forbes, B. C., et al. 2016. Sea ice, rain-on-snow and tundra reindeer nomadism in Arctic Russia. Biology Letters 12:20160466.

Forchhammer, M. C., E. Post, N. C. Stenseth, and D. M. Boertmann. 2002. Long-term responses in arctic ungulate dynamics to changes in climatic and trophic processes. Population Ecology 44:113–120.

Gerhart, K., D. Ruussell, D. V. D. Wetering, R. White, and R. Cameron. 1997*a*. Pregnancy of adult caribou (*Rangifer tarandus*): evidence for lactational infertility. Journal of Zoology 242:17–30.

Gerhart, K., R. White, R. Cameron, D. Russell, and D. Van de Wetering. 1997*b*. Pregnancy rate as an indicator of nutritional status in Rangifer. implications of lactational infertility. Rangifer 17:21–24.

Gorelick, N., M. Hancher, M. Dixon, S. Ilyushchenko, D. Thau, and R. Moore. 2017. Google Earth Engine: Planetary-scale geospatial analysis for everyone. Remote Sensing of Environment 202:18–27.

Gunn, A. 2003. Voles, lemmings and caribou-population cycles revisited? Rangifer 23:105–111.

Gunn, A., and K. Poole. 2009. Environmental trends across the range of the Barhurst Caribou Herd and timing of arrival of cows on their calving ground 1996–2009. Report. Environment and Natural Resources, Yellowknife, Northwest Territories, Canada.

Gurarie, E., F. Cagnacci, W. Peters, C. H. Fleming, J. M. Calabrese, T. Mueller, and W. F. Fagan. 2017. A framework for modelling range shifts and migrations: asking when, whither, whether and will it return. Journal of Animal Ecology 86:943–959.

Heard, D. C., T. M. Williams, and D. A. Melton. 1996. The relationship between food intake and predation risk in migratory caribou and implications to caribou and wolf population dynamics. Rangifer 16:37–44.

Hebblewhite, M., M. Hurley, P. Lukacs, and J. Nowak. 2018. Satellite remote sensing for conservation action: case studies from aquatic and terrestrial ecosystems. Pages 194–228 *in* A. K. Leidner and G. M. Buchanan, editors. Chap. Predicting mule deer harvests in real time. Cambridge University Press, Cambridge, UK.

Hegel, T. M., A. Mysterud, T. Ergon, L. E. Loe, F. Huettmann, and N. C. Stenseth. 2010. Seasonal effects of Pacific-based climate on recruitment in a predator-limited large herbivore. Journal of Animal Ecology 79:471–482.

Helle, T., and I. Kojola. 1994. Body mass variation in semidomesticated reindeer. Canadian Journal of Zoology 72:681–688.

Helle, T., and L. Tarvainen. 1984. Effects of insect harassment on weight gain and survival in reindeer calves. Rangifer 4:24–27.

Henshaw, J. 1968. The activities of the wintering caribou in northwestern Alaska in relation to weather and snow conditions. International Journal of Biometeorology 12:21–27.

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.

Huete, A., K. Didan, T. Miura, E. P. Rodriguez, X. Gao, and L. G. Ferreira. 2002. Overview of the radiometric and biophysical performance of the MODIS vegetation indices. Remote Sensing of Environment 83:195–213.

Hummel, M., and J. C. Ray. 2008. Caribou and the North: a shared future. 288 pp. Dundurn Press, Toronto, Ontario, Canada.

Hurley, M. A., M. Hebblewhite, P. M. Lukacs, J. J. Nowak, J.-M. Gaillard, and C. Bonenfant. 2017. Regional-scale models for predicting overwinter survival of juvenile ungulates. Journal of Wildlife Management 81:364–378.

Johnson, C. J., M. S. Boyce, R. L. Case, H. D. Cluff, R. J. Gau, A. Gunn, and R. Mulders. 2005. Cumulative effects of human developments on arctic wildlife. Wildlife Monographs 160:1–36.

Joly, K., E. Gurarie, M. S. Sorum, P. Kaczensky, M. D. Cameron, A. F. Jakes, B. L. Borg, D. Nandintsetseg, J. G. C. Hopcraft, B. Buuveibaatar, P. F. Jones, T. Mueller, C. Walzer, K. A. Olson, J. C. Payne, A. Yadamsuren, M. Hebblewhite. 2019. Longest terrestrial migrations and movements around the world. Scientific Reports 9(1)

Johnson, H. E., D. D. Gustine, T. S. Golden, L. G. Adams, L. S. Parrett, E. A. Lenart, and P. S. Barboza. 2018. NDVI exhibits mixed success in predicting spatiotemporal variation in caribou summer forage quality and quantity. Ecosphere 9: e02461.

Joly, K., F. S. Chapin, and D. R. Klein. 2010. Winter habitat selection by caribouin relation to lichen abundance, wildfires, grazing, and landscape characteristics in northwest Alaska. Ecoscience 17:321–333.

Joly, K., M. J. Cole, and R. R. Jandt. 2007. Diets of overwintering caribou, *Rangifer tarandus*, track decadal changes in Arctic tundra vegetation. Canadian Field-Naturalist 121:379–383.

Joly, K., R. R. Jandt, and D. R. Klein. 2009. Decrease of lichens in Arctic ecosystems: the role of wildfire, caribou, reindeer, competition and climate in northwestern Alaska. Polar Research 28:433–442.

Joly, K., D. R. Klein, D. L. Verbyla, T. S. Rupp, and F. S. Chapin III. 2011. Linkages between large-scale climate patterns and the dynamics of Arctic caribou populations. Ecography 34:345–352.

Klein, D. R. 1991*a*. Caribou in the changing North. Applied Animal Behaviour Science 29:279–291.

Klein, D. R. 1991*b*. Limiting factors in caribou population ecology. Rangifer 11:30–35.

Klein, D. R. 2000. Arctic grazing systems and industrial development: Can we minimize conflicts? Polar Research 19:91–98.

Koenig, W. D. 2002. Global patterns of environmental synchrony and the Moran effect. Ecography 25:283–288.

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 Corre, M., C. Dussault, and S. D. Côté. 2017. Weather conditions and variation in timing of spring and fall migrations of migratory caribou. Journal of Mammalogy 98:260–271.

Legagneux, P., et al. 2014. Arctic ecosystem structure and functioning shaped by climate and herbivore body size. Nature Climate Change 4:379.

Lent, P. C. 1968. Calving and related social behaviour in the barren-ground Caribou. Dissertation. University of Alberta, Edmonton, Alberta, Canada.

Macander, M. J., C. S. Swingley, K. Joly, and M. K. Raynolds. 2015. Landsat based snow persistence map for northwest Alaska. Remote Sensing of Environment 163:23–31.

Mahoney, P. J., et al. 2018. Navigating snowscapes: scale-dependent responses of mountain sheep to snowpack properties. Ecological Applications 28:1715–1729.

Mallory, C. D., and M. S. Boyce. 2017. Observed and predicted effects of climate change on Arctic

caribou and reindeer. Environmental Reviews 999:1–13.

Mallory, C. D., M. W. Campbell, and M. S. Boyce. 2018. Climate influences body condition and synchrony of barren-ground caribou abundance in Northern Canada. Polar Biology 41:855–864.

Marra, P. P., C. M. Francis, R. S. Mulvihill, and F. R. Moore. 2005. The influence of climate on the timing and rate of spring bird migration. Oecologia 142:307–315.

Merkle, J. A., K. L. Monteith, E. O. Aikens, M. M. Hayes, K. R. Hersey, A. D. Middleton, B. A. Oates, H. Sawyer, B. M. Scurlock, and M. J. Kauffman. 2016. Large herbivores surf waves of green-up during spring. Proceedings of the Royal Society B 283:20160456.

Miller, F. L. 2003. Wild mammals of North America: biology, management, and conservation. Pages 965–997 *in* G. A. Feldhamer, B. C. Thompson, and J. A. Chapman, editors. Chap. Caribou. Johns Hopkins University Press, Baltimore, Maryland, USA.

Miller, F. L., and S. J. Barry. 2009. Long-term control of Peary caribou numbers by unpredictable, exceptionally severe snow or ice conditions in a nonequilibrium grazing system. Arctic 62:175–189.

Mochizuki, T., et al. 2010. Pacific decadal oscillation hindcasts relevant to near-term climate prediction. Proceedings of the National Academy of Sciences USA 107:1833–1837.

Møller, A. P., W. Fiedler, and P. Berthold. 2010. Effects of climate change on birds. Oxford University Press, Oxford, UK.

Monteith, K. L., T. R. Stephenson, V. C. Bleich, M. M. Conner, B. M. Pierce, and R. T. Bowyer. 2013. Risk-sensitive allocation in seasonal dynamics of fat and protein reserves in a long-lived mammal. Journal of Animal Ecology 82:377–388.

Morales, J. M., P. R. Moorcroft, J. Matthiopoulos, J. L. Frair, J. G. Kie, R. A. Powell, E. H. Merrill, and D. T. Haydon. 2010. Building the bridge between animal movement and population dynamics. Philosophical Transactions of the Royal Society B: Biological Sciences 365:2289–2301.

Moran, P. 1953. The statistical analysis of the Canadian lynx cycle. Australian Journal of Zoology 1:291–298.

Moritz, R. E., C. M. Bitz, and E. J. Steig. 2002. Dynamics of recent climate change in the Arctic. Science 297:1497–1502.

Moyes, K., D. H. Nussey, M. N. Clements, F. E. Guinness, A. Morris, S. Morris, J. M. Pemberton, L. E. B. Kruuk, and T. H. Clutton-Brock. 2011. Advancing breeding phenology in response to environmental change in a wild red deer population. Global Change Biology 17:2455–2469.

Nagy, J. A., D. L. Johnson, N. C. Larter, M. W. Campbell, A. E. Derocher, A. Kelly, M. Dumond, D. Allaire, and B. Croft. 2011. Subpopulation structure of caribou (*Rangifer tarandus* L.) in arctic and subarctic Canada. Ecological Applications 21:2334–2348.

Nakagawa, S., and H. Schielzeth. 2013. A general and simple method for obtaining R^2 from generalized linear mixed-effects models. Methods in Ecology and Evolution 4:133–142.

Pan, C. G., P. B. Kirchner, J. S. Kimball, Y. Kim, and J. Du. 2018. Rain-on-snow events in Alaska, their frequency and distribution from satellite observations. Environmental Research Letters 13:075004.

Park, T., S. Ganguly, H. Tømmervik, E. S. Euskirchen, K.-A. Høgda, S. R. Karlsen, V. Brovkin, R. R. Nemani, and R. B. Myneni. 2016. Changes in growing season duration and productivity of northern vegetation inferred from long-term remote sensing data. Environmental Research Letters 11:084001.

Parker, K. L., P. S. Barboza, and M. P. Gillingham. 2009. Nutrition integrates environmental responses of ungulates. Functional Ecology 23:57–69.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. Annual Review of Ecology, Evolution, and Systematics 37:637–669.

Pearson, R. G., S. J. Phillips, M. M. Loranty, P. S. A. Beck, T. Damoulas, S. J. Knight, and S. J. Goetz. 2013. Shifts in Arctic vegetation and associated feedbacks under climate change. Nature Climate Change 3:673–677.

Pettorelli, N. 2013. The normalized difference vegetation index. Oxford University Press, Oxford, UK.

Pettorelli, N., F. Pelletier, A. von Hardenberg, M. Festa-Bianchet, and S. D. Côté. 2007. Early onset of vegetation growth vs. rapid green-up: impacts on juvenile mountain ungulates. Ecology 88:381–390.

Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar and R Core Team. 2017. nlme: Linear and nonlinear mixed effects models. R package version 3.1-131.

Plard, F., J.-M. Gaillard, T. Coulson, A. J. M. Hewison, D. Delorme, C. Warnant, and C. Bonenfant. 2014. Mismatch between birth date and vegetation phenology slows the demography of roe deer. PLoS Biology 12:e1001828.

Post, E. 2013. Ecology of climate change: the importance of biotic interactions. Princeton University Press, Princeton, New Jersey, USA.

Post, E., U. Bhatt, C. Bitz, J. Brodie, T. Fulton, M. Hebblewhite, J. Kerby, S. Kutz, I. Stirling, and D. Walker. 2013. Ecological consequences of sea-ice decline. Science 341:519.

Post, E., and M. C. Forchhammer. 2002. Synchronization of animal population dynamics by large-scale climate. Nature 420:168–171.

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 B: Biological Sciences 363:2367–2373.

Post, E., et al. 2009. Ecological dynamics across the Arctic associated with recent climate change. Science 325:1355–1358.

Pruitt, W. O. 2005. Why and how to study a snow-cover. Canadian Field-Naturalist 119:118–128.

R Core Team. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rennert, K. J., G. Roe, J. Putkonen, and C. M. Bitz. 2009. Soil thermal and ecological impacts of rain on snow events in the circumpolar Arctic. Journal of Climate 22:2302–2315.

Reynolds, H. V., G. W. Garner, and H. V. Reynolds. 1987. Patterns of grizzly bear predation on caribou in northern Alaska. Bears: Their Biology and Management 7:59–67.

Rickbeil, G. J. M., N. C. Coops, and J. Adamczewski. 2015. The grazing impacts of four barren ground caribou herds (*Rangifer tarandus groenlandicus*) on their summer ranges: An application of archived remotely sensed vegetation productivity data. Remote Sensing of Environment 164: 314–323.

Rodell, M., et al. 2004. The global land data assimilation system. Bulletin of the American Meteorological Society 85:381–394.

Rowell, J. E., and M. P. Shipka. 2009. Variation in gestation length among captive reindeer (*Rangifer tarandus tarandus*). Theriogenology 72:190–197.

Rozylowicz, L., F. P. Bodescu, C. M. Ciocanea, A. A. Gavrilidis, S. Manolache, M. L. Matache, I. V. Miu, I. C. Moale, A. Nita, and V. D. Popescu. 2019. Empirical analysis and modeling of Argos Doppler location errors in Romania. PeerJ 7:e6362.

Rubolini, D., A. P. Møller, K. Rainio, and E. Lehikoinen. 2007. Intraspecific consistency and geographic variability in temporal trends of spring migration phenology among European bird species. Climate Research 35:135–146.

Russell, D. E., A. M. Martell, and W. A. Nixon. 1993. Range ecology of the Porcupine caribou herd in Canada. Rangifer 13:1–168.

Rutberg, A. T. 1987. Adaptive hypotheses of birth synchrony in ruminants: an interspecific test. American Naturalist 130:692–710.

Schmitz, O. J., C. C. Wilmers, S. J. Leroux, C. E. Doughty, T. B. Atwood, M. Galetti, A. B. Davies, and S. J. Goetz. 2018. Animals and the zoogeochemistry of the carbon cycle. Science 362: eaar3213.

Skarin, A., Ö. Danell, R. Bergström, and J. Moen. 2008. Summer habitat preferences of GPS-collared reindeer *Rangifer tarandus tarandus*. Wildlife Biology 14:1–15.

Skogland, T. 1986. Sex ratio variation in relation to maternal condition and parental investment in wild reindeer *Rangifer t. tarandus*. Oikos 46:417–419.

Skoog, R. O. 1968. Ecology of the caribou (Rangifer tarandus granti) in Alaska. Dissertation. University of California, Berkeley, Berkeley, California, USA.

Spitz, D. B., M. Hebblewhite, and T. R. Stephenson. 2017. MigrateR: Extending model-driven methods for classifying and quantifying animal movement behavior. Ecography 40:788–799.

Stan Development Team. 2018. RStan: the R interface to Stan. R package version 2.17.3.

Tamstorf, M. P., L. Illeris, B. U. Hansen, and M. Wisz. 2007. Spectral measures and mixed models as valuable tools for investigating controls on land surface phenology in high arctic Greenland. BMC Ecology 7:9.

Telfer, E. S., and J. P. Kelsall. 1984. Adaptation of some large North American mammals for survival in snow. Ecology 65:1828–1834.

Thornton, P., M. Thornton, B. Mayer, Y. Wei, R. Devarakonda, R. Vose and R. Cook. 2017. Daymet: Daily surface weather data on a 1-km grid for North America, Version 3. Technical Report. ORNL DAAC, Oak Ridge, Tennessee, USA. https://doi.org/10.3334/ORNLDAAC/1328

Tyler, N. J. 2010. Climate, snow, ice, crashes, and declines in populations of reindeer and caribou (*Rangifer tarandus* L.). Ecological Monographs 80:197–219.

Väisänen, M., H. Ylänne, E. Kaarlejärvi, S. Sjögersten, J. Olofsson, N. Crout, and S. Stark. 2014. Consequences of warming on tundra carbon balance determined by reindeer grazing history. Nature Climate Change 4:384.

Veiberg, V., L. E. Loe, S. D. Albon, R. J. Irvine, T. Tveraa, E. Ropstad, and A. Stien. 2017. Maternal winter body mass and not spring phenology determine annual calf production in an Arctic herbivore. Oikos 126:980–987.

Vors, L. S., and M. S. Boyce. 2009. Global declines of caribou and reindeer. Global Change Biology 15:2626–2633.

Walsh, N. E., S. G. Fancy, T. R. McCabe, and L. F. Pank. 1992. Habitat use by the Porcupine caribou herd during predicted insect harassment. Journal of wildlife management 56:465–473.

Walther, G.-R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. Beebee, J.-M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. Nature 416:389.

Ward, D. H., J. Helmericks, J. W. Hupp, L. McManus, M. Budde, D. C. Douglas, and K. D. Tape. 2016. Multi-decadal trends in spring arrival of avian migrants to the central Arctic coast of Alaska: effects of environmental and ecological factors. Journal of Avian Biology 47:197–207.

Weckworth, B. V., M. Musiani, A. D. McDevitt, M. Hebblewhite, and S. Mariani. 2012. Reconstruction of caribou evolutionary history in Western North America and its implications for conservation. Molecular Ecology 21:3610–3624.

Weladji, R. B., Ø. Holand, and T. Almøy. 2003. Use of climatic data to assess the effect of insect harassment on the autumn weight of reindeer (*Rangifer tarandus*) calves. Journal of Zoology 260:79–85.

Wheeler, B., and M. Torchiano. 2016. lmPerm: Permutation tests for linear models. R package version 2.1.0.

Whitman, E., M.-A. Parisien, D. T. Price, M.-H. St-Laurent, C. J. Johnson, E. R. DeLancey, D. Arseneault, and M. D. Flannigan. 2017. A framework for modeling habitat quality in disturbance-prone areas demonstrated with woodland caribou and wildfire. Ecosphere 8:e01787.

Witter, L. A., C. J. Johnson, B. Croft, A. Gunn, and M. P. Gillingham. 2012*b*. Behavioural trade-offs in response to external stimuli: Time allocation of an Arctic ungulate during varying intensities of harassment by parasitic flies. Journal of Animal Ecology 81:284–295.

Witter, L. A., C. J. Johnson, B. Croft, A. Gunn, and L. M. Poirier. 2012*a*. Gauging climate change effects at local scales: Weather-based indices to monitor insect harassment in caribou. Ecological Applications 22:1838–1851.

Wolfe, R. J., and R. J. Walker. 1987. Subsistence economies in Alaska: productivity, geography, and development impacts. Arctic Anthropology 24:56–81.

Young, D. D., and T. R. McCabe. 1997. Grizzly bear predation rates on caribou calves in northeastern Alaska. Journal of Wildlife Management 61:1056–1066.

Zamin, T. J., S. D. Côté, J.-P. Tremblay, and P. Grogana. 2017. Experimental warming alters migratory caribou forage quality. Ecological Applications 27:2061–2073.

Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2971/full