DRIVERS AND MECHANISMS OF MIGRATION IN AN ARCTIC CARIBOU HERD

By

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Abstract

Migration is one of the world's great natural wonders and the scale of some migratory journeys is astounding. Yet migration is globally imperiled and effective conservation of the remaining migrations will require a thorough understanding of the drivers and mechanisms underlying how migrants complete such journeys. In this dissertation, I present three chapters that sought to better understand spring and autumn migration for the Western Arctic Herd, a population of barren-ground caribou (*Rangifer tarandus*) that complete some of the longest terrestrial migrations on the planet. In the first chapter, I applied and validated an analytical method to infer parturition events from GPS data with robust statistical confidence. In the second chapter, I examined the parturition events detected with these methods to better understand the drivers and mechanisms of spring migration because the calving grounds are the destination for pregnant females in spring. I quantified annual spatial patterns of calving and assessed what environmental factors influenced calving site selection by caribou through time. I found evidence of both memory and perception influencing spring migration, such that caribou use memory to return to an area of generally high-quality forage at the time of calving, and consequently adjust calving sites each year based on experienced conditions. In the third chapter, I sought to understand the environmental cues caribou respond to in deciding when to migrate in autumn. I found that decreasing temperatures and the timing of first snowfall events of the season had the greatest influence on migratory movements, but notably, caribou re-assessed decisions throughout the migration period as the conditions they experience changed. I also found that the cues caribou used are similar across individuals despite the herd being broadly dispersed in late summer, and the variability in migration timing observed each year is likely due to variability in environmental conditions experienced across the range. These findings pertaining to the drivers and mechanisms of migratory behavior, and broader aspects of movements by caribou, are

highly relevant for conservation and management of the species across the circumpolar North. Moreover, the observation that caribou movement exhibits strong responses to particular climate phenomena, such as temperature and precipitation, have important implications for how caribou might respond as the climate of the Arctic continues to change.

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Introduction

Migration is one of the great wonders of the natural world. The scale of migratory journeys varies widely by taxa: there are the small diel migrations of zooplankton (Gliwicz 1986), the annual journeys of the monarch butterflies *(Danaus plexippus*) that require multiple generations to complete (Reppert and de Roode 2018), and the globe-spanning migrations of the Arctic tern (*Sterna paradisaea*; Egevang et al. 2010). Regardless of scale, migration is an adaptation to seasonal fluctuations of resources, environmental conditions, and predation pressure (Alerstam et al. 2003). This behavioral adaptation can have landscape-level ecological consequences, as migratory populations can achieve greater numbers than resident conspecifics (Fryxell et al. 1988). Migrants also can shape ecosystem communities through transport and trophic effects (Bauer and Hoye 2014), such as influencing primary productivity (McNaughton 1985) and nutrient redistribution (Naiman et al. 2002). Yet many traditional migratory patterns around the globe have disappeared or are threatened due to overhunting, habitat loss, and/or loss of habitat connectivity of migration routes (Berger 2004, Harris et al. 2009). In order to conserve remaining migrations around the world, we need a thorough understanding of the drivers and mechanisms underlying these notable movements.

To better understand migration, I – along with my coauthors – employed GPS collar data from female caribou (*Rangifer tarandus*) of the Western Arctic Herd (WAH), which range across northwest Alaska. Caribou are an iconic species of the Arctic and complete some of the longest-distance terrestrial migrations on the planet (Joly et al. 2019). These animals have defined cultural traditions of Indigenous people of the area and have been an integral component of subsistence for over 10,000 years (Anderson 1988). In the three research chapters presented here, my goal was to improve our understanding of the relationships between environmental variables that influence why, where, and when caribou migrate in the spring and autumn.

In the first chapter, I addressed a methodological question of how to remotely detect parturition, which can be envisioned as the end-point of spring migration. My goal was to validate an analytical approach to detect parturition based on GPS data – essentially detecting when a female slowed down enough to deliver a calf – by comparing the modeled parturition result to aerial observation data. At the time of this research, similar work had been done with moose (*Alces alces*; Severud et al. 2015), elk (*Cervus canadensis*; Dzialak et al. 2011), and two techniques had been developed for woodland caribou in Canada (*Rangifer tarandus caribou*; DeMars et al. 2013). Female woodland caribou spatially isolate themselves at the time of calving (Bergerud et al. 1990) and these methods had proven to be remarkably accurate, but they were assumed to not apply to barren-ground caribou. This is because barren-ground caribou (*Rangifer tarandus granti*) are known for aggregating at the time of parturition (Kelsall 1968) and were thought to not meet assumptions of individual independence of movement (DeMars et al. 2013). Our work was the first to directly test the efficacy of these methods and we found that they were more applicable than previously thought (Cameron et al. 2018). This insight paved the way for the next project: understanding the drivers of spring migration.

In the second chapter, I set out to understand the patterns and processes of spring migration's terminus by quantifying the spatial patterns of calving areas each year and investigating environmental characteristics of these areas. Barren-ground caribou are known for returning to historical calving grounds in spring and these areas are used to define herds (Skoog 1968, Gunn and Miller 1986). Yet annual variation of calving areas is characteristic for many herds and for some, this variation can be pronounced when considering broader time scales

(Taillon et al. 2012). For the WAH, I used the data obtained from the previous chapter, locations of parturition events, and derived annual delineations of calving areas each year from 2010-2017. To quantify variability across the time period, I tested for patterns of overlap across various combinations of years. To understand why caribou select this area, I used remotely-sensed environmental metrics that characterized the forage conditions and physical attributes of calving sites and compared these with the broader range of the herd. I compared these delineations with historical maps dating back 5 decades, interpreted our findings in relation to navigation mechanisms for how caribou reach this area, and provided management recommendations regarding this critical life history event (Cameron et al. 2020).

In the last chapter, I set out to understand the mechanism for how caribou decide when to migrate in autumn. At the time of this research, autumn migration in ungulates had received but a fraction of the attention that spring migration had received (Gallinat et al. 2015), despite being highly relevant to harvest management and understanding the contemporary variability in, and potential impact to future, migration patterns. To understand how WAH caribou decide when to migrate in autumn, I paired GPS collar data with environmental covariate data to characterize the environmental conditions individuals experienced throughout their journey. I used these data sources with recently-developed analytical methods that relate an individual’s movement with the environmental conditions experienced at that specific time and place. In this framework, I was able to infer what environmental stimuli act as the impetus to migrate in autumn and compare the herd-level responses across nine years (Cameron et al. 2021). The insights gained from this work have implications for how arctic caribou are likely to respond to ongoing changes in the climate.

As I have learned is the case with science during my time in this program, while each of these projects furthered our collective understanding of caribou and migration ecology, they also revealed many more questions about how these animals inhabit the vast landscape of the Arctic. My hope is that the information presented here will stimulate further ideas and a deeper appreciation of this iconic species and migration in general.

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Chapter 1: Movement-based methods to infer parturition events in migratory ungulates[1]

Abstract

Long-distance migrations by ungulate species are a globally-imperiled natural phenomenon and conservation of them requires monitoring population vital rates. Satellite telemetry tracking is widely used for understanding the spatial distribution and movement of animals, especially migratory animals in remote environments. Recently, analytical methods have been developed to infer parturition events from movement data in multiple species that calve in isolation, but to date such methods have not been tested on animals that both migrate and spatially aggregate during calving. We applied 2 movement-based methods developed to infer parturition in non-migratory woodland caribou (*Rangifer tarandus caribou*) to 241 reproductive seasons spanning 6 years of GPS data from migratory barren-ground caribou (*Rangifer tarandus granti*). We compared results from both methods to data from aerial surveys of collared females during the calving period. We found that each movement-based method had ~ 80% overall accuracy to identify calving events, with inter-annual variation ranging from 61-100%. When we considered instances when the 2 analytical methods agreed on parturition outcome, the accuracy increased to 89% with an annual range of 73-100%. Using these methods, we identified marked inter-annual differences in peak calving dates and higher parturition rates than previously reported for this caribou herd. The successful application of these analyses to a migratory, gregarious ungulate suggests a broader applicability of the methodology.

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[1] Cameron, M.D., Joly, K., Breed, G.A., Parrett, L.S., and Kielland, K. 2018. Movement-based methods to infer parturition events in migratory ungulates. Can. J. Zool. **96**: 1187–1195. doi:dx.doi.org/10.1139/cjz-2017-0314.

Introduction

Long-distance ungulate migrations are an awe-inspiring natural phenomena, though the world has lost many of the migratory populations (Berger 2004). Successful conservation of those remaining migratory populations will be aided by monitoring demographic parameters using the best methodology available (Bolger et al. 2008). GPS tracking technology has become the standard tool for monitoring wildlife populations, particularly those that inhabit remote environments for which direct observation is logistically difficult or costly. Analyses of location data have traditionally focused on the spatial distribution (Mohr 1947, Worton 1989) and movement patterns of study species (Kareiva and Shigesada 1983, Turchin 1998). The advent of GPS tracking technology introduced increased resolution in both the spatial and temporal scales of location data, and methods to classify the underlying behavior from such data are becoming common in movement analyses (Franke et al. 2004, Morales et al. 2004, Gurarie et al. 2009, Breed et al. 2012). Such methods have primarily provided insights into how animals use the environment, but changes in movement characteristics have also been used to identify important life-history events such as denning in wolves (*Canis lupus*; Walsh et al. 2016), migration by moose (*Alces alces;* Bunnefeld et al. 2011), and haul outs on sea ice by bearded seals (*Erignathus barbatus;* McClintock et al. 2017).

Obtaining estimates of a particular life-history event, parturition, is important for managers as an assessment of range condition, since the probability of parturition is linked to body condition the previous autumn (Cameron et al. 1993), and also as a proxy for some important vital rates in population monitoring. Estimating annual parturition rates is typically accomplished via aircraft or observations from the ground of the study animals during the birthing season (such as Lent 1966b; Cameron and Whitten 1979). In ungulates, different analyses of movement characteristics from GPS location data have been used to infer parturition with varying degrees of accuracy for non-migratory animals such as moose (~88%; Severud et al. 2015), elk (*Cervus canadensis*; ~93%; Dzialak et al. 2011), and with the highest success for woodland caribou (*Rangifer tarandus caribou*; >97%; DeMars et al. 2013). Woodland caribou disperse and calve in isolation (Bergerud et al. 1990), and DeMars et al. (2013) assumed that their methods would not be applicable to species that aggregate during the parturition season, such as migratory barren-ground caribou (*Rangifer tarandus granti*).

Barren-ground caribou exhibit some of the longest migrations of any terrestrial mammal (Fancy et al. 1989). Females migrate in the spring to annual calving grounds and tend to spatially aggregate during calving (Kelsall 1968; Skoog 1968). Non-pregnant females typically migrate later than pregnant females (Pruitt 1960, Joly 2011, Dau 2015), but non-pregnant females have also been observed in the area during calving (Lent 1966a). Previous studies have indicated depressed movement rates for parturient females in migratory herds after calving (Lent 1966a, Fancy et al. 1989, Fancy and Whitten 1991, Carroll et al. 2005), suggesting that movement characteristics can be used to detect calving.

Here, we examined the efficacy of movement-based analyses for detecting parturition events in migratory caribou. We hypothesized that despite spatially aggregating, parturition is an individual-specific event which can be detected through analyses of movement data. Our primary objectives were to: 1) apply two movement-based models developed for sedentary woodland caribou to GPS data from the Western Arctic Herd (WAH), a migratory caribou herd in Alaska; 2) evaluate the accuracy of each method relative to aerial surveys as well as to each other; 3) and compare the estimated rates and timing of parturition derived from these analyses to previously reported results from aerial surveys.

Methods

Caribou data

The WAH is among the largest migratory barren-ground caribou herds in Alaska, with a population that has historically fluctuated between 75,000-490,000 individuals and ranges over 350,000 km^2 (Dau 2015). Calving grounds for the WAH are in the Utukok River uplands at the headwaters of the Colville River in northwestern Alaska (Figure 1.1; Lent 1966a). Annual estimates for parturition are obtained from aerial surveys of the calving grounds, currently requiring approximately 300 km of roundtrip travel (not including the survey work). Peak calving has been estimated from these surveys to occur between 9 and 13 June (Dau 2015), but detailed, daily observations of parturition timing have not been recorded since 1961 (Lent 1966a).

Caribou location data were obtained from ongoing multi-agency monitoring of the WAH (Davis and Valkenburg 1985, Dau 2005). Starting in 2009, GPS collars (model TGW-4680, Telonics, Mesa, AZ) have been deployed annually during the fall migration at Onion Portage along the Kobuk River (Figure 1.1; Joly et al. 2012). Captures were conducted by hand from motorboats using procedures approved by the State of Alaska Institutional Animal Care and Use Committee (IACUC; 2012-031R). We deployed collars primarily on mature (≥2 years old) female caribou using capture and monitoring techniques described in Dau (1997), Joly et al. (2012), and Dau (2015). Collar locations were acquired every 8 hours and downloaded via a satellite network. From 2009 to 2015, 140 GPS collars were deployed (Joly and Cameron 2017). We only included females with GPS data through July 1 for each reproductive year, totaling 241 reproductive seasons (1 individual for 1 parturition timeframe, Table 1.1). The percentage of females with complete GPS data coverage ranged from 22 - 91% and the number of missing locations per individual each parturition season ranged from 0 - 64% (See Appendix 1A.1).

Annual aerial surveys of calving grounds

Aerial surveys of the calving grounds were conducted annually by Alaska Department of Fish and Game biologists in a Piper PA-18 airplane (Table 1.1). Surveys were timed to begin just prior to estimated peak calving (when approximately 50% of calves are born), typically from June 9 to 13 (Dau 2015). Collared individuals were identified using VHF frequencies, and antler status and calf presence were recorded for each individual. We used antler status to infer parturition status for females without a calf following Whitten (1995): females with ≥ 5 cm of new antlers ("soft antlers", i.e., in velvet) were assumed non-parturient, 1-2 hard antlers were likely pre-parturient, and no antlers were unknown. Udder status was not recorded. Attempts were made to revisit individuals of unknown or pre-parturition status (i.e., no new antlers or calf).

Application of movement-based methods

We used the individual-based and population-based methods (hereafter IBM and PBM, respectively) described in DeMars et al. (2013) to analyze movement data of individual females during each parturition season from 2010 to 2015. Both methods comprised elements to estimate neonate mortality; however, since the temporal intensity and duration of our aerial surveys were inadequate to detect neonate mortality events, we focused only on identifying parturition events. Analyses were conducted using the packages 'lubridate' (Grolemund and Wickham 2011), 'zoo' (Zeileis and Grothendieck 2005), and 'reshape' (Wickham 2007) in the R 3.3.1 statistical computing program (R Core Team 2017) and our code is provided in Appendix 1B and

Appendix 1C. We describe the general approach of both methods, but for greater details see DeMars et al. (2013).

The IBM was used to fit the movement data to 2 *a priori* models: non-parturition and parturition. The non-parturition model fit a constant mean movement rate across the time-series (1 parameter to estimate). The parturition model fit a breakpoint in the movement rate (interpreted as the calving event), followed by a mean linear increase until the movement rate returned to the female's prior mean movement rate (3 parameters to estimate – mean movement rate, calving breakpoint, and time for cow/calf pair to return to mean movement rate). Both models assumed an exponential distribution for step lengths. An approximation of maximum likelihood estimation was used to estimate the parameters for both models and model selection was based on Akaike's Information Criterion values (Burnham and Anderson 2002) for each reproductive season.

We stipulated 2 sets of constraints to perform the IBM: 1) the minimum number of sequential locations (hereafter referred to as steps) in the series before and after a breakpoint could be assigned ("int") and 2) the minimum and maximum number of steps it takes a female/calf pair to return to the pre-parturition step rate ("kcons"). We set "int" to 9 steps (3 days) and chose 15 and 63 steps (5 and 21 days) as the minimum and maximum, respectively, for "kcons" based on previous observations of calf development for the WAH (Lent 1966a). We analyzed movement data spanning 19 May – 15 July for each animal in each year to cover the earliest calving event documented (22 May, 1960) as well as the latest (July 4; Lent 1966b).

The PBM analysis consisted of 2 stages: 1) calculating a population-specific 'calving threshold' (maximum movement rate consistent with parturition) from a subset of individuals with known calving events (see below) using the movement data from the 3 days following parturition; 2) performing a 3-day average movement rate analysis for the first movement rate to fall below the predefined threshold for each individual. To generate the calving threshold for the PBM, we needed the calving dates for a subset of individuals that were confirmed parturient. From the aerial data, we identified 9 parturient individuals that gave birth between observations and had a parturition date identified by the IBM between those 2 observations. Given the requirement that an individual must be first seen without a calf and then subsequently seen with a calf, parturition events which occurred before the beginning of aerial observations were likely underrepresented in this sample. To alleviate this underrepresentation of early parturition events, we also included in our analysis 15 individuals that had been observed with hard antlers and a calf, which indicates a recent calving event (typically within 7 days; Whitten 1995), and were identified as parturient near the time of observation by the IBM. Because the aerial observations were infrequent and not intensive at the individual level, we used the IBM-estimated calving date (plus a step – see IBM section of Results) for these 24 individuals. Despite incorporating some dependence on the IBM, the inclusion of these individuals by evaluating antler status allowed for minimization of bias that may have resulted from our methods.

The calving threshold was calculated using the post-calving 3-day average movement rates from 10 individuals. A distribution of individual rates was used to draw a kernel density estimate using the ‘density’ function in R (R Core Team 2017) and integrated to generate a cumulative distribution for the proportion of individuals at or below each 3-day average movement rate (DeMars et al. 2013). The calving threshold from this process was interpreted as the 98th percentile of this distribution, which differs from the original 99th percentile used by DeMars et al. (2013), as we found 98% worked better for our population which has an overall faster movement rate than the more sedentary woodland caribou analyzed by DeMars et al. (2013). In order to address the variation of possible calving thresholds within our population, we bootstrapped the calving threshold estimation by randomly selecting (with replacement) the movement data of 10 individuals from the sample of 24 individuals and generated a calving threshold from this subset. We repeated this threshold calculation 1,000 times and applied a kernel density estimate to the histogram of bootstrapped values. We used the maximum of the kernel density to identify the most common value and selected this as the calving threshold. With this threshold, we ran the PBM analysis on the full dataset of 241 reproductive seasons from 2010 – 2015. Because the PBM did not require a 3-day initiation period before it could detect a calving event, we began the analysis on 22 May to match the IBM (which we began on 19 May) and ended it on 15 July. We assigned the parturition date to be the first step in the 3-day average movement rate to fall below the threshold.

Comparing model results to aerial survey data

Both the PBM and IBM models resulted in parturition classifications (calved or not calved) and, for those determined parturient, an estimated date for the event. We compared the parturition classification produced by each method to aerial observations for each reproductive season. Comparisons between movement models and aerial observations were considered to agree if the parturition classifications were the same and the estimated parturition date was supported by the aerial observations. To avoid misclassifying individuals as non-parturient if their calf died before or between aerial observations, we considered parturition unknown for 2 instances: 1) females with a model-estimated calving date 5 or more days before being noted with soft antlers during an aerial observation; and 2) if neither a calf nor soft antlers were observed. These exceptions were due to observations of 3 individuals from 2015, which were first noted with hard antlers and subsequently observed 4 or 5 days later with soft antlers but without a calf. We considered these probable calf mortalities given the high percentage (99%) of parturition events for females with hard antlers reported by Whitten (1995). From these observations, we inferred that a female could shed hard antlers and grow enough new antler material to be categorized with 'soft antlers' in 5 days. Thus, we only categorized females as parturient if they were observed with a calf. To account for methodological differences in estimating parturition dates between the IBM and PBM, we considered the estimated timing of parturition from movement methods to agree if the 2 parturition dates were within 3 days. We performed a linear regression with agreement between the IBM and PBM as the predictor and estimated accuracy from the aerial surveys as the response to evaluate the how well model agreement indicated accuracy.

Simulating longer GPS intervals and IBM sensitivity analysis

To investigate the effects of location intervals on the estimates from these movement-based methods, we downsampled our 8-hour GPS relocation data to 16-hour and 24-hour intervals. We recalculated the distance between subsequent locations (step lengths) and completed the IBM and PBM analyses on these lower-resolution data. We adjusted the specifications for both analyses to reflect the biological constraints we outlined above: parturition events for the IBM were constrained between 5 and 21 days, and the parturition threshold for the PBM was recalculated for each interval using the same dates as the original analysis. The results were compared to the aerial data following the same procedure outlined above.

We investigated the sensitivity of the 3 constraints in the IBM – "int" and 2 values (min/max) of "kcons" – by performing the analysis while adjusting each constraint individually.

We tested “int” values of 1, 2, 4, and 5 days, minimum values for “kcons” of 3, 4, 6, and 7 days, and maximum values for “kcons” of 12, 15, 18, and 24 days. We re-ran the analysis with each new constraint value, holding the other two constraints at the original levels, and compared the new results with the original results as well as compared new results to aerial observation data.

Estimating calving phenology and parturition rates

We used a combination of approaches to estimate calving dates for parturition events in order to maximize our sample size. When a calf was detected on an aerial survey and the IBM and PBM agreed, we used the PBM parturition date. For instances in which the models did not agree and a calf was observed on an aerial survey, the estimated date which corroborated aerial observations and antler status was used. For individuals that were not observed or the parturition outcome was unknown from aerial observations, only instances of IBM and PBM agreement were used. We performed an analysis of variance to test for significant inter-annual variation in parturition timing. To investigate the inference to herd management these movement-based methodologies offer, we compared the estimated annual parturition rate when using the IBM or PBM on their own, as well as the consensus approach, and compared these to the annual calves per 100 cows ratios from aerial surveys reported in Dau (2015).

Results

Based on parturition outcomes between models and aerial observations, the overall concordance for the IBM (e.g., Figure 1.2A) was 77% (n = 166; Table 1.2). We observed inter-annual variation in support for the IBM to identify calving events ranging from 61-94% (Table 1.2). Of the 39 designations made by the IBM that were not in concordance with aerial observations, 12 were false positives (aerial observations did not support a modeled parturition event), 16 were false negatives (model failed to detect a calf when aerial observation detected one), and 11 were instances in which the estimated parturition date was inconsistent with aerial observations. Visualizations of the fitted model to the data from each female suggested that the IBM consistently estimated the calving date 1 step (8 hours) early, before the period of decreased movement rate.

Bootstrapping the PBM calving threshold resulted in a bimodal kernel distribution with a maximum at 135 meters (m)•hr^{-1}. One individual exhibited a noticeably faster post-calving 3-day average movement rate (1.5-3 times greater than the other individuals), so we excluded that individual and re-ran the bootstrap procedure. The resulting distribution was unimodal with a maximum value at 137 m•hr^{-1}, and we used this threshold value for the second stage of the analysis. The PBM returned similar results to the IBM in that 81% (n = 161) of overall events were confirmed by aerial surveys with inter-annual variation ranging from 68-100% (e.g., Figure 1.2B; Table 1.2). Of the 31 parturition designations in disagreement, 7 were false positives, 13 were false negatives, and 11 were instances in which the estimated parturition date was not supported by aerial observations. The PBM did not run for 9 reproductive seasons out of the 241 total, all of which had extensive periods of missing data (10-58 missing steps).

Agreement in parturition outcome between the IBM and PBM methods was 70% (n=232) and ranged annually from 61-83% (Table 1.2). Of the 69 instances of disagreement, 54 were when the methods resulted in different parturition designations and 15 occurred when the estimated parturition dates were greater than 3 days apart. In comparing the concordance between movement-based methods to aerial observations, movement-based results appeared to agree more often when aerial observation detected parturition in contrast to non-parturition (78%

and 63%, respectively). When we considered only those cases in which the IBM and PBM concurred on parturition outcome, aerial observations suggested an 89% overall accuracy (n=119), with annual variation ranging from 73-100% (Table 1.2). Of the 13 incorrect model outcomes, 4 were false positives, 4 were false negatives, and 5 were instances where the estimated parturition date was inconsistent with aerial observations. We identified a subset of 13 reproductive seasons in which a female was observed both before and after she had a calf, and had matching IBM/PBM parturition designations. Ten of the 13 estimated parturition dates occurred between aerial observations and the 3 incorrect dates occurred before the actual parturition event. Agreement between movement-based methods appeared to predict accuracy, with the linear regression of model agreement as a predictor for accuracy resulting in an R-squared value of 0.8.

Our subsampled 16-hour and 24-hour fix rate data exhibited similar results as the original data. For the 16-hour fix rate, overall concordance was 76% (n=163) for the IBM and 82% (n=154) for the PBM when compared to aerial observations. For the 24-hour fix rates, this was 76% (n=167) for the IBM and 83% (n=151) for the PBM when compared to aerial observations. For the consensus approach, support for the movement-based methods was 87% for both the 16-hour (n=118) and the 24-hour fix rates (n=119; Appendix 1A.2). We found the IBM model robust to different values of the 3 constraints ("int" and min/max for "kcons,"). Using values of up to 2 days in either direction for "int" and the minimum of "kcons" marginally affected inference, and results broadly agreed with original results; agreement with original results ranged from 95-99% and concordance with aerial observations decreased by only 2% at the most (Appendix 1A.3). A range of 12-24 days for the maximum value of "kcons" resulted in 93-99%

agreement with original results and only a 1% decrease in concordance with aerial observations for the lowest value.

We found significant inter-annual variation in parturition timing (ANOVA, F (5, 125) = 9.5, $p < 0.01$) and the median calving date for each year of monitoring ranged from June 1 (2014) and June 8 (2013; Figure 1.3). Peak calving (when the average middle 50% of calving events occurred) was June 2-6 for our study period and encompassed 4 – 7 days; with the earliest starting on May 31 (2010 and 2014) and the latest ending on June 11 (2013). We compared the estimated parturition rates from each movement-based method to observed calf:100 cows ratios from Dau (2015) and found that both approaches fell below observed ratios for some years (Table 1.3), but both resulted in 4-5% higher overall rate estimates. When we compared estimated parturition rates from the IBM and PBM consensus approach, we found consistently higher parturition rates each year and an overall rate 12% higher than aerial estimates.

Discussion

We set out to examine if the movement-based methods used to identify parturition events for non-migratory ungulates were applicable for migratory populations. While each method independently exhibited limitations in accuracy (approximately 80% each), and had higher false negative rates in which the methods failed to detect a calving event, we found that aerial observations suggested we were ~90% accurate by adopting a consensus approach in which we only considered the movement-based results when the two models agreed. The disadvantage of this approach is that we were unable to make inferences for 30% of the possible reproductive events in our dataset, with the potential that some of the instances of disagreement were not randomly affiliated with 1 outcome or another. However, the benefit is that for the remaining 70% we increased our confidence in the validity of the identified parturition events. Agreement between the 2 methods appeared to function as an index of accuracy, given the R-squared value of 0.8, with the years of lowest agreement achieving the lowest accuracy. Our estimated accuracy of the PBM/IBM consensus approach is less than the 97% reported for woodland caribou (DeMars et al. 2013), but comparable to other results using mixtures of direct observation of GPS data and relatively simple movement models reported for moose (~88%; Severud et al. 2015) and elk (~93%; Dzialak et al. 2011).

Traditional methods to detect parturition rely on invasive techniques such as vaginal implants (Bowman and Jacobson 1998) which are logistically challenging to deploy in remote areas, or on frequent and repeated observations of the study animal (such as Whitten et al. 1992) which can be costly to achieve fine-scale temporal resolution. While still requiring the capture and collaring of an adult individual to perform these movement-based analyses, this approach to remotely monitor parturition offers reduced disturbance across the lifetime of the animal. Comparing our analytical results to aerial observations suggests that these methods provide an alternative with increased confidence in estimated timing and location of parturition, if not overall rate, for migratory ungulates and could be useful to managers seeking to limit aerial flights during a time of year when animals are susceptible to disturbance (de Vos 1960, Calef et al. 1976). Using the results from our analysis, we found that peak calving for the WAH varied throughout the first 11 days of June and usually occurred before June 8. These observed differences in parturition timing have management implications for this herd and future work should investigate the environmental and physiological influences behind this pattern.

We note that our estimated PBM calving threshold (137 m•hr^{-1}) for the WAH was 9 times greater than that of the woodland caribou threshold (15.3 m•hr^{-1}) estimated in DeMars et al. (2013), highlighting the differences in movement strategies between these disparate populations. The WAH calving threshold is similar to movement rates of parturient females reported for the nearby migratory Teshekpuk Herd (162 m•hr^{-1}), although their reported rates were based on daily VHF collar relocations (Carroll et al. 2005) and longer relocation intervals lead to lower estimated movement rates (Joly 2005, Prichard et al. 2014). We observed individual variation in post-partum movement rates, as illustrated by the bimodal distribution of the first bootstrapped calving threshold. In future applications of this methodology, we suggest further evaluation of variation in post-partum movement rates and whether it correlates with timing of parturition in relation to the herd, migration timing, or is variation inherent to the individual and, thus, annually consistent. Possibly, late parturition events are marked by faster post-partum movement rates because the herd-level movements are increasing as the herd moves into the faster post-calving movements associated with insect harassment in July (Dau 2015).

Variation in seasonal movement patterns appeared to influence the efficacy of these methods. Dau (2015) reported median daily rates of travel from GPS data for WAH caribou during winter as less than 100 m/hour, well below our PBM threshold, and we attributed some early parturition detections which were not supported by aerial observations to localized, pre-migration movement patterns. We based the decision on when to initiate the analysis on the earliest reported calving event for the study population, but noticed that migration appeared to start later than this date in some reproductive years. One potential improvement for future applications of this method would be to start the movement time series being analyzed at the onset of migration at the individual level, which would be derived from a separate analysis. Such an improvement would increase the complexity of the analysis for the user, but would likely reduce false positive detections at the beginning of the time series.

Partial migration, in which a migratory population is composed of migrants and residents (Chapman et al. 2011), has occurred sporadically for individuals in the WAH (Joly and Cameron 2017), and appears to be much more common in other herds (Person et al. 2007, Nicholson et al. 2016). For those WAH individuals overwintering closer to the calving grounds, movement was characterized by low rates from the beginning to middle of the time series, followed by a sharp increase in movement rates as the herd transitioned into post-calving movements. Since the parturition model of the IBM assumes a mean movement rate that is similar before and after the calving event, we suspect that this method is ill-suited for individuals exhibiting disparate pre- and post-calving movement patterns. We recommend careful inspection of variation in migratory strategies when applying this method to other migratory ungulates and ensuring that the general movement patterns fit the assumptions of the models being applied. Interestingly, the year with the highest agreement between models and with aerial data, 2012, corresponded to the latest spring migration, as noted by the dates of crossing the Noatak River (Joly and Cameron 2017). While we were unable to test this relationship further, the correlation suggests that detection of parturition is more effective when the interval between the end of migration and the onset of parturition is short.

We found in this study that reducing the fix rate resulted in only a 3% decrease in accuracy for methods when using 16-hour and 24-hour intervals, which contrasts to the findings of DeMars et al. (2013) of continual decline in accuracy as fix rate decreased. We attribute this resilience of sensitivity to the larger magnitude of movement rate changes in migratory animals compared to woodland caribou, and that even a reduced fix rate of 1 location every 24-hours still captured the abrupt change in movement rate associated with parturition. Considering that our analysis was performed using 8-hr intervals, we expect that a more frequent relocation schedule during calving could increase the accuracy of these methods, especially for those individuals in which the IBM and PBM disagreed, and result in fewer unclassified reproductive years.

We recognize that our ability to validate movement-based methods was likely influenced by 2 factors within our study: 1) our relatively poor temporal resolution and sparsity in aerial observations, and 2) potentially high neonatal mortality on the calving grounds that we were unable to quantify. Because we only considered females parturient if they were observed with a calf, our designations of parturition events from the aerial data were likely conservative given the high rate of eventual parturition observed in females with hard antlers (Whitten 1995). Of our 220 observations of individuals across 6 years, 9% were females observed without a calf and never observed with antlers, were only observed with hard antlers, or were observed with hard antlers and then observed with soft antlers. We categorized these individuals as “unknown” in an effort to minimize uncertainty, but suspect that a portion of these were indeed pregnant. This means that we were also limited to detecting parturition events only up to the last aerial observation. Our methodology differs from previous reports of WAH parturition rate (Dau 1997, 2011), which used calf presence as well as hard antler status to indicate parturition. Other studies to validate movement-based approaches to infer parturition have analyzed blood samples taken at capture for progesterone to classify pregnant females (Dzialak et al. 2011, DeMars et al. 2013, Severud et al. 2015). Lacking this detailed data, we interpreted the aerial observation data and comparisons with the movement-based methods conservatively. Our observations of 3 females with hard antlers on the calving grounds that each initiated growth of new antlers within 5 days of calving is a potentially novel observation and an exception to Whitten’s (1995) findings that growth of new antlers by females during the parturition timeframe is a reliable indicator of non-parturition.

High neonatal mortality has been reported for neighboring migratory populations such as the Porcupine Herd (8-25% in the first 48 hours; Whitten et al., 1992). Because we lacked daily aerial observations, classifications of non-parturition from our aerial data were inherently more uncertain than for parturition due to the potential of neonatal mortality. Overall parturition rate estimates from each of the individual methods (IBM and PBM) was 4-5% higher than those reported from only aerial observations, and the overall estimate from the consensus approach was 12% higher. Both results suggest that neonatal mortality is a factor for the WAH and highlights the importance of considering the timing of aerial surveys in relation to peak calving when interpreting results from spring parturition surveys. However, we recommend further validation of these methods using more consistent aerial observation data to better understand inconsistencies between IBM and PBM predictions, the overall increase in estimated rates when comparing movement based methods to aerial observations, and the potential for calving events to be easier for movement models to detect than instances of non-calving or neonatal mortality.

Our results suggest a broader applicability of these movement-based methods to migratory animals. Despite the strategy of spatial aggregation during calving, we were able to identify an abrupt behavioral change – parturition – for barren-ground caribou from GPS location data. We recommend the use of both the IBM and PBM in conjunction and placing the highest confidence in results when both methods concur to identify parturition events. Movement-based methods such as these offer an improvement in the spatial and temporal resolution for inferring life-history events such as parturition, which can be valuable for further studies to investigate the ecology of migratory animals inhabiting remote environments.

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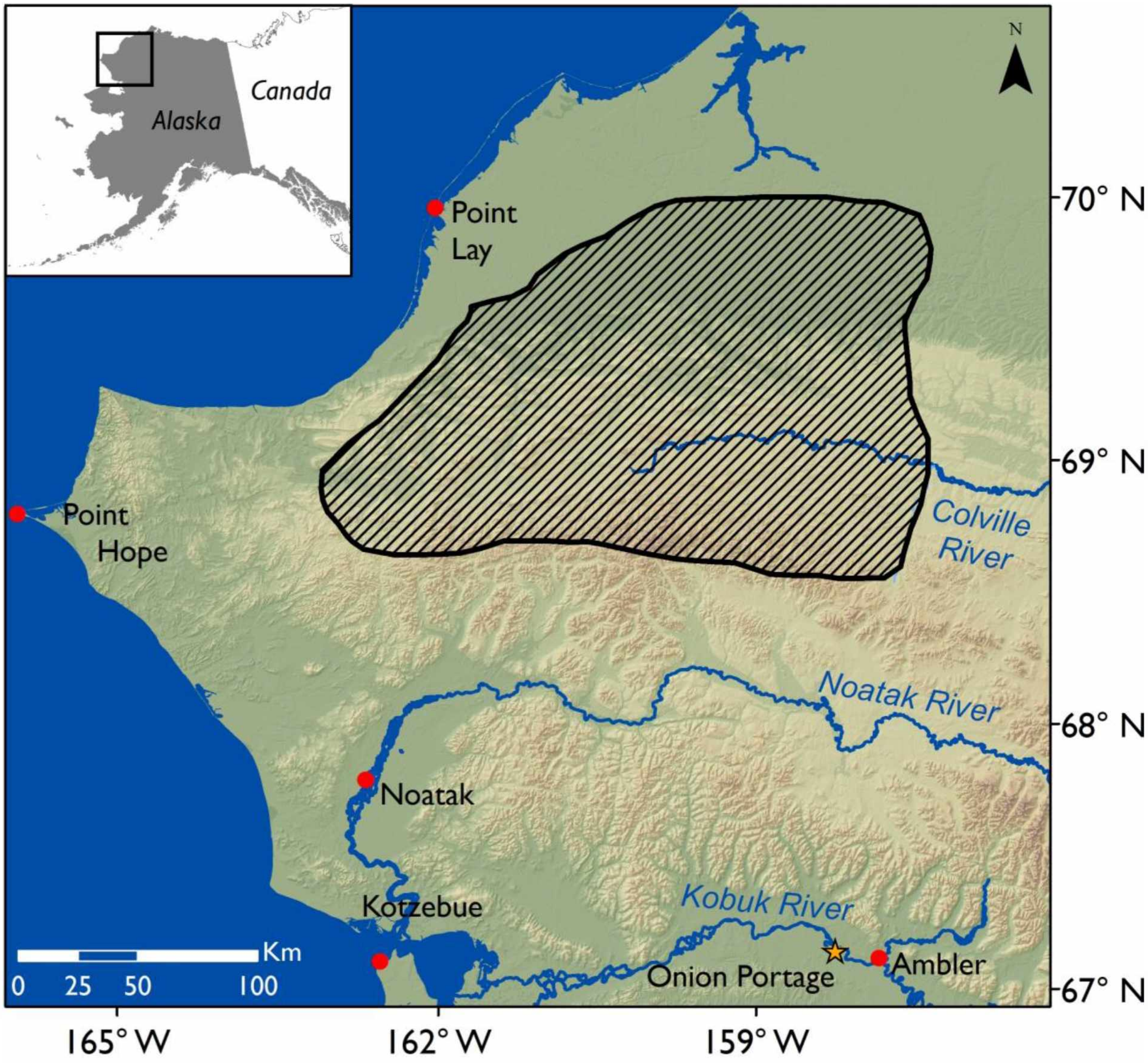

Figure 1.1: Historic calving ground (black hatched polygon) delineated from aerial surveys from 1987-2016 of Western Arctic Herd caribou (*Rangifer tarandus granti*), Alaska. Spring caribou migrations typically lead to the calving grounds from the south. Red circles are villages within the caribou range and the orange star is Onion Portage, where collars were deployed.

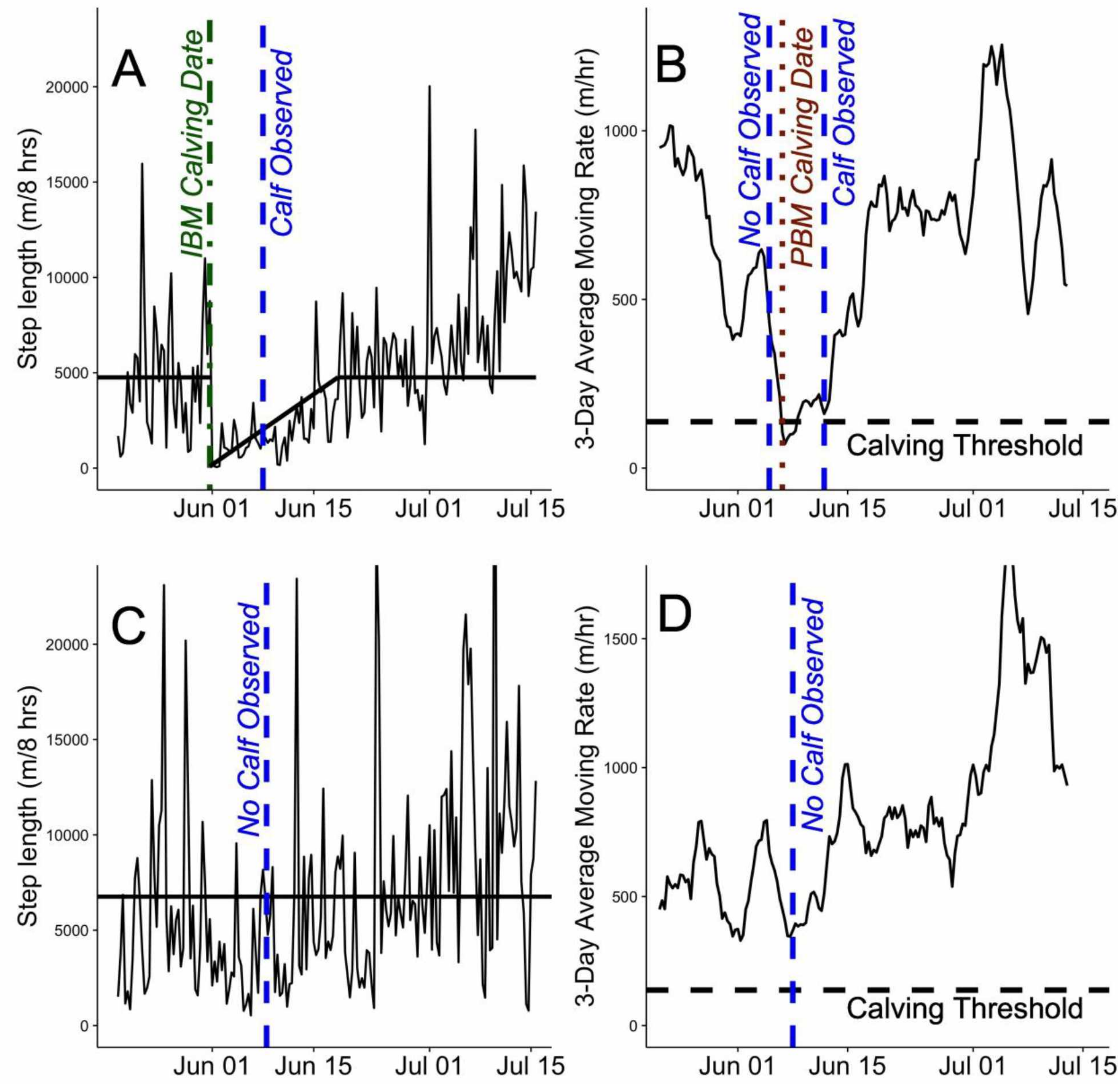

Figure 1.2: Detection of calving events based on 3 different methods for Western Arctic Herd caribou (*Rangifer tarandus granti*) from 2010-2015, Alaska. Plot A depicts the application of the individual-based method (IBM): the parturition model (solid black line) is plotted over step lengths on the y-axis, the green dot-dashed line is the estimated parturition event, and blue dashed line is the aerial observation during which a calf was observed. Plot B depicts to application of the population-based method (PBM) to a different individual based on 3-day average movement rates: the horizontal dashed line is the estimated population threshold, PBM calving date is depicted by the dotted red line, and 2 aerial observations are depicted in blue dashed lines. Plot C depicts the non-parturition IBM model and plot D depicts the non-parturition model result of the PBM to 2 additional individuals which were estimated to be not parturient by observation of soft antlers (blue dashed lines).

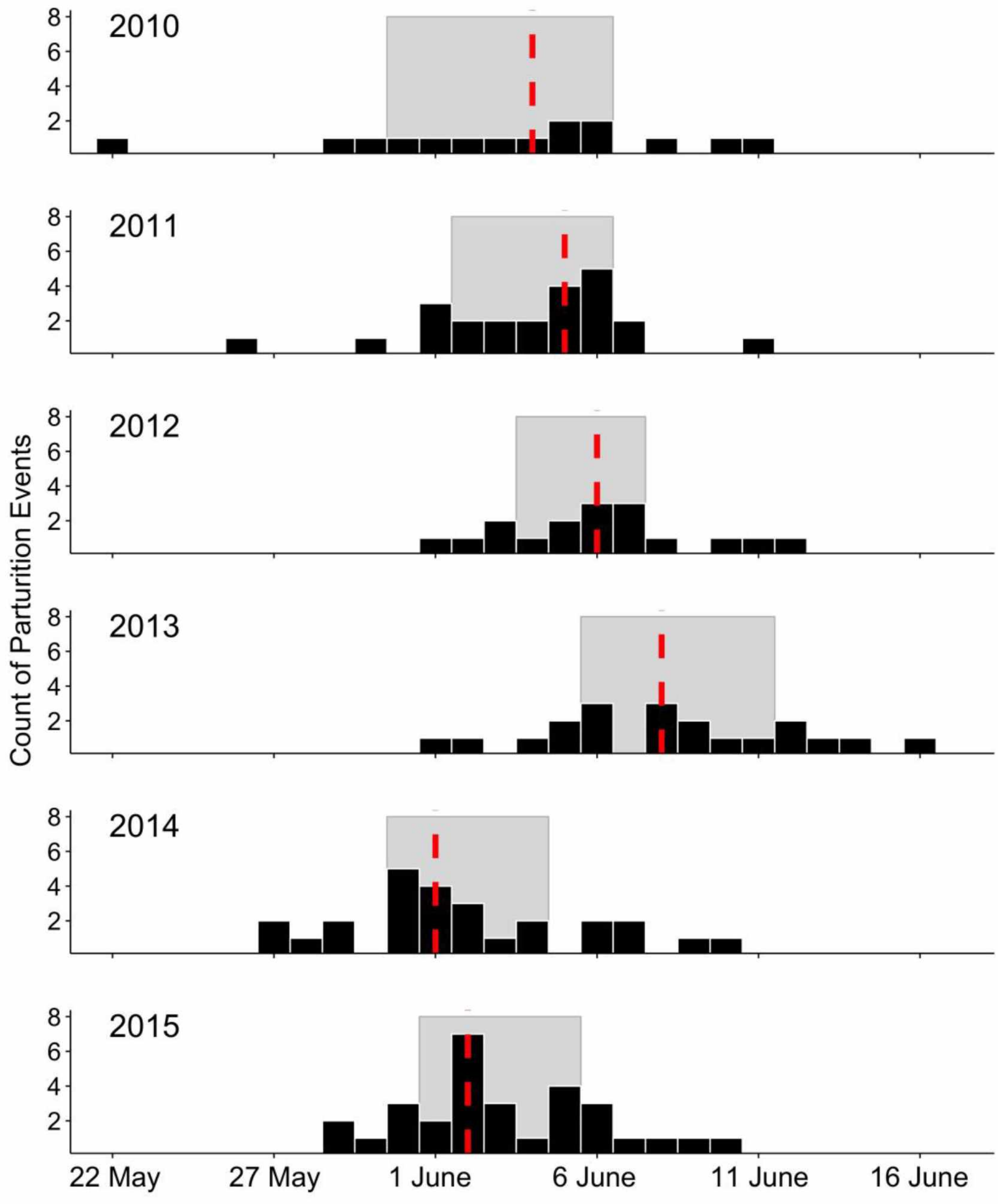

Figure 1.3: Annual calving phenology for Western Arctic Herd caribou (*Rangifer tarandus granti*) from 2010-2015, Alaska. Each histogram indicates the number of estimated parturition events per day for each year. Red vertical dashed lines indicate the median calving date and the gray box indicates the middle 50% quantile (peak calving) for each year. Parturition events were identified from the individual and population-based methods which were supported by aerial observations, and instances where the 2 movement-based methods agreed on parturition events which lacked aerial observations.

Table 1.1: Aerial calving survey dates, number of collared females each year (reproductive seasons), and number of collared females observed of Western Arctic Herd caribou (*Rangifer tarandus granti*), Alaska. Biologists observed antler status and calf presence for collared females. Individuals for which parturition status was deemed "known" included only those females observed with a calf or growing soft antlers on the first observation.

Year	First Date Of Survey	Last Date Of Survey	Active GPS Collars	Collared Animals Observed	% of Individuals with "Known" Parturition Status
2010	June 5	June 12	33	31	73%
2011	June 7	June 10	39	28	51%
2012	June 4	June 15	37	35	78%
2013	June 5	June 14	38	34	61%
2014	June 8	June 14	45	43	91%
2015	June 6	June 16	49	49	88%
Total			241	220	75%

Table 1.2: Agreement among individual-based method (IBM), population-based method (PBM), and aerial observation method results for Western Arctic Herd caribou (*Rangifer tarandus granti*) parturition events in Alaska. Movement-based methods were considered to agree with aerial observations if the parturition result (calved versus did not calve) and estimated parturition date were supported. Comparisons between IBM and PBM results were considered to agree if the parturition result was the same and estimated dates were within 3 days. Consensus indicates a subset of results from movement-based approaches in which the IBM and PBM agreed.

	IBM/Aerial	PBM/Aerial	IBM/PBM	Consensus/Aerial
Year	*% Agreement (n)*	*% Agreement (n)*	*% Agreement (n)*	*% Agreement (n)*
2010	63 (24)	71 (21)	64 (33)	73 (15)
2011	94 (18)	85 (20)	72 (39)	94 (17)
2012	92 (25)	100 (25)	83 (36)	100 (22)
2013	75 (24)	68 (22)	68 (37)	87 (15)
2014	87 (31)	91 (32)	74 (43)	96 (25)
2015	61 (44)	71 (41)	61 (44)	80 (25)
Overall	77 (166)	81 (161)	70 (232)	89 (119)

Table 1.3: Estimates of apparent parturition rates (%) from aerial surveys and movement-based methods for Western Arctic Herd caribou (*Rangifer tarandus granti*), Alaska. Sample size is denoted in parentheses for each method in each year.

	Aerial Surveys	IBM Only	PBM Only	IBM/PBM Consensus
Year	*% Parturition (n)*	*% Parturition (n)*	*% Parturition (n)*	*% Parturition (n)*
2010	73 (80)	67 (33)	70 (33)	76 (21)
2011	77 (74)	87 (39)	79 (39)	93 (28)
2012	62 (71)	68 (37)	58 (36)	67 (30)
2013	63 (71)	79 (38)	68 (37)	80 (25)
2014	69 (68)	84 (45)	81 (43)	91 (32)
2015	78 (68)	65 (49)	84 (44)	81 (27)
Overall	70 (432)	75 (241)	74 (232)	82 (163)

[*] Note: Results from aerial surveys were reported as number of calves:100 cows from Dau (2015), in contrast to the estimated parturition rates of the movement-based methods.

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Appendix 1A: Chapter 1 supplemental tables

Appendix 1A.1: Numbers of collared female caribou (*Rangifer tarandus granti*) and individuals with missing GPS locations per calving season for the Western Arctic Herd from 2010 – 2015, Alaska. For individuals with some missing location data, mean and standard deviation of the percentage of locations missing are presented. Collars in the early years were mostly retrieved and downloaded, ensuring greater data coverage compared to newer collars which depended on satellite network uploads.

	2010	2011	2012	2013	2014	2015	Total
Collars active per calving season	33	39	37	38	45	49	241
Individuals with missing locations	3	4	7	19	18	38	89
Mean % of locations missing per individual (± SD)	1 ± 0	1 ± 0	4 ± 10	4 ± 6	14 ± 15	22 ± 14	-

Appendix 1A.2: Comparisons of a subset of parturition results, which included only individuals for which the individual-based method (IBM) and population-based method (PBM) agreed, with aerial observations results for Western Arctic Herd caribou (*Rangifer tarandus granti*) in Alaska. Methods were considered to agree if the parturition result (calved versus did not calve) was the same and the estimated date was supported by aerial observation.

	8-hour Interval	**16-hour Interval**	**24-hour Interval**
Year	*% Agreement (n)*	*% Agreement (n)*	*% Agreement (n)*
2010	73 (15)	58 (12)	71 (14)
2011	94 (17)	94 (18)	94 (18)
2012	100 (22)	100 (22)	100 (22)
2013	87 (15)	79 (14)	74 (19)
2014	96 (25)	96 (25)	100 (23)
2015	80 (25)	81(27)	78 (23)
Overall	89 (119)	87 (118)	87 (119)

Appendix 1A.3: Results of the sensitivity analysis for the 3 specified constraints of the Individual-based Method (IBM) performed on data from collared female caribou (*Rangifer tarandus granti*) of the Western Arctic Herd from 2010 – 2015, Alaska. The original, reference-level values for each constraint are in bold and highlighted. Constraint values are the number of sequential GPS locations, "Agree with Reference (%)" quantifies the overall agreement between the tested value and the original value model results, and "Agree with Aerial (%)" indicates proportion of results which were supported by aerial observations, i.e. when parturition result (calved versus did not calve) and estimated parturition date were supported by observations.

int	Agree with Reference (%)	Agree with Aerial (%)
3	95	75
6	99	76
9	—	**77**
12	99	76
15	98	77

kcons - min	Agree with Reference (%)	Agree with Aerial (%)
9	97	75
12	98	75
15	—	**77**
18	98	77
21	96	77

kcons - max	Agree with Reference (%)	Agree with Aerial (%)
36	93	76
45	96	77
54	98	77
63	—	**77**
72	99	77

Appendix 1B: Chapter 1 R code for applying Individual-based Model

R script to run the Individual-based Model (IBM) on movement data. This code uses the IBM previously published in Demars et al. (2013) and iteratively runs the analysis for all individuals in the provided data. The principle additions in this code is to output one file containing all of the individual results, as well as to generate plots of the fitted models to data for visual inspection. See provided data (“Example Data.csv”) for example of movement data for IBM analysis.

Literature cited

DeMars, C. A., Auger-Méthé, M., Schlägel, U. E., & Boutin, S. (2013). Inferring parturition and neonate survival from movement patterns of female ungulates: a case study using woodland caribou. *Ecology and Evolution*, *3*(12), 4149–4160. https://doi.org/10.1002/ece3.785

```
## "Movement-based methods used to infer parturition events for migratory ungulates"
## By Matthew D. Cameron, Kyle Joly, Greg A. Breed, Lincoln S. Parrett, and Knut Kielland
## For this analysis, the time-series window is May 19 - July 15
## If you use this code, please cite our paper and also cite:
#   DeMars, C., M. Auger-Methe, U. Schlaegel, S. Boutin, (Published online)
#   Inferring Parturition and Neonate Survival from Movement Patterns of Female Ungulates.
#   Ecology and Evolution. DOI: 10.1002/ece3.785

library(lubridate)
library(ggplot2)
library(zoo)
library(modeest)

setwd()  # Set working directory to folder which includes original "IBM.R" file
# Download this from: http://onlinelibrary.wiley.com/doi/10.1002/ece3.785/full

## Note: running this code will make a .csv file in your working directory to hold the model results, and save the plot of the model fit as a .jpeg if "draw=T" on the function
```

```
###################################################################################
################# Make a function to run IBM and plot the model results w/ data
###################################################################################
# Note: this function will loop through each column of data (each individual) in the data set.

run.IBM <- function(database, min.adult, max.adult, int, draw=T) {

  source("IBM.R")  # Load the code for the IBM from DeMars et al. 2013 paper. Ensure that this is in the working directory

  for(i in 2:length(database)){
    print(names(database)[[i]]) #Print ID
    id=names(database)[[i]] #saves animal ID for graph titles
    num.missed.fix=sum(is.na(database[[i]])) #How many missed fixes for that animal
    fix.time=database$LocalFixTime
    step.length=database[,i]
    step.num=as.vector(1:length(database[,1]))  ##How many fixes
    bou.df=data.frame(fix.time,step.length,step.num)
    ## We set up the above dataframe in order to prepare data for
    # analysis by moving null values to fix.time as described in DeMars et al. 2013

    hold=is.na(bou.df$step.length)
    bou.df$fix.time[hold]=NA
    bou.df$step.num[hold]=NA
    SL=bou.df$step.length[!is.na(bou.df$step.length)]
    ti=bou.df$step.num[!is.na(bou.df$step.num)]
    tp=bou.df$fix.time
    int=int  #The numbers of steps before calving is a possibility
    kcons=as.vector(c(min.adult,max.adult)) #Min and Max time (in steps) a calf can reach travel maturity
```

```
  results=mnll3M(SL, ti, tp, int, kcons)
  print(results)

print(paste("##############################################################"))

  year.hold=year(tp) # makes vector of year for all fixes
  yr=year.hold[!is.na(year.hold)][1] # Saves the year being analyzed for graph titles

  ###### Saving results from IBM as csv ####
  AICS=data.frame(id,
                  results$resCA[1,8],
                  as.numeric(results$resCA[1,5]),
                  as.numeric(results$resCA[1,6]),
                  as.numeric(results$resCA[1,7]),
                  as.POSIXct(results$BPs[1,1]),
                  as.POSIXct(results$BPs[1,2]),
                  as.POSIXct(results$BPs[1,3]),
                  num.missed.fix,
                  yr)
  write.table(AICS,"IBM output.csv",sep=",",
              col.names=FALSE, row.names = FALSE,append=TRUE)



  ####### Making plots of results ##########
  if(draw==T){
   if (results$resCA[1,8]==0) {   #if the best model is the "didn't calve model", plot a flat line

     no.calf.plot <- ggplot(database,aes(LocalFixTime,database[,i],group=1)) +
      geom_line() +
```

```
      theme(panel.background=element_blank()) +  #Sets background to white
      geom_hline(yintercept=results$mpar[1,1],colour="dark grey") +
      labs(x="Date",y="Step length (m)",title=paste("No parturition model for",id,"in ",yr)) +
      theme(axis.line.x=element_line(size=.5,colour = "black",linetype = "solid")) + #add axis lines
      theme(axis.line.y=element_line(size=.5,colour = "black",linetype = "solid")) + #add axis lines
      theme(plot.title=element_text(size=20,face="bold",margin = margin(10,0,10,0))) +
      ylim(c(0,22000))

    ggsave(filename=paste(id," plot for ",yr," no calving.jpeg",sep=""),plot=no.calf.plot,width = 8,height = 4)
  }



  if (results$resCA[1,8]==1){   #if the best model is the "calved model", plot a single break point
    ## Settings for line commands ##
    calve=as.POSIXct(results$BPs[1,1])
    k1=as.numeric(results$mpar[1,4])
    b1=as.numeric(results$mpar[1,2])
    maturity.steps=as.numeric(results$BPs[4]+k1)
    maturity.date=database[maturity.steps,1]
    last=database[max(ti),1]


    ## Plotting ##
    calved.plot = ggplot(database,aes(LocalFixTime,database[,i],group=1)) +
      geom_line() +
      theme(panel.background=element_blank()) +  #Sets background to white
      geom_vline(xintercept=as.numeric(calve),linetype=4,colour="black") + #break point at calving event
```

```
geom_text(aes(x=(calve+ddays(1)),label=calve,y=10000),angle=90,size=4,fontface="italic") +
#Labels the calving line with calving date

        geom_segment(x=0,y=b1,xend=as.numeric(calve),yend=b1,colour="dark gray") + ##plots
mean movement rate before calving event


geom_segment(x=as.numeric(calve),y=(b1/k1),xend=as.numeric(maturity.date),yend=b1,colour
="dark grey") + #plots increasing calving movement rate


geom_segment(x=as.numeric(maturity.date),y=b1,xend=as.numeric(last),yend=b1,colour="dark
grey") + #plots mature motion rates

        labs(x="Date",y="Step length (m)",title=paste("Parturition model for",id,"in",yr,sep = " "
)) +

        theme(axis.line.x=element_line(size=.5,colour = "black",linetype = "solid")) + #add axis
lines

        theme(axis.line.y=element_line(size=.5,colour = "black",linetype = "solid")) + #add axis
lines

        theme(plot.title=element_text(size=20,face="bold",margin = margin(10,0,10,0))) +

        ylim(c(0,22000))


      ggsave(filename=paste(id," plot for ",yr," Calved.jpeg",sep=""),plot=calved.plot,width =
8,height = 4)

    }



    if (results$resCA[1,8]==2){  #if the best model is the "calved then calf lost" model, plot 2
breakpoints

      ## Settings for line commands ##

      calve=as.POSIXct(results$BPs[1,2])

      calf.loss=as.POSIXct(results$BPs[1,3])

      k2=round(results$mpar[1,5])

      b2=round(results$mpar[1,3])

      last=database[max(ti),1]
```

```
      ## Plotting ##
      calf.mort.plot <- ggplot(database,aes(LocalFixTime,database[,i],group=1)) +
        geom_line() +
        theme(panel.background=element_blank()) +  #Sets background to white
        geom_vline(xintercept=as.numeric(calve),linetype=4,colour="black") + #break point at calving event

geom_text(aes(x=(calve+ddays(1)),label=calve,y=10000),angle=90,size=4,fontface="italic") + #Labels calving event
        geom_vline(xintercept=as.numeric(calf.loss),linetype=4,colour="black") + #break point at calf loss event
        geom_text(aes(x=(calf.loss-ddays(1)),label=calf.loss,y=10000),angle=90,size=4,fontface="italic") + #Labels calf loss
        geom_segment(x=0,y=b2,xend=as.numeric(calve),yend=b2,colour="dark gray") + ##plots mean movement rate before calving event

geom_segment(x=as.numeric(calve),y=(b2/k2),xend=as.numeric(calf.loss),yend=b2,colour="dark grey") + #plots increasing calving movement rate

geom_segment(x=as.numeric(calf.loss),y=b2,xend=as.numeric(last),yend=b2,colour="dark grey") + #plots mature motion rates
        labs(x="Date",y="Step length (m)",title=paste("Calf mortality model for",id,"in",yr,sep = " " )) +
        theme(axis.line.x=element_line(size=.5,colour = "black",linetype = "solid")) + #add axis lines
        theme(axis.line.y=element_line(size=.5,colour = "black",linetype = "solid")) + #add axis lines
        theme(plot.title=element_text(size=20,face="bold",margin = margin(10,0,10,0))) +
        ylim(c(0,22000))


      ggsave(filename=paste(id," plot for ",yr," Calf loss.jpeg",sep=""),plot=calf.mort.plot,width = 8,height = 4)
     } # End last if statement
    } # End draw == T if
  } # End for loop for each individual in database
```

```
} # End function

###########################################################################
########################## Run the function for your data ########################
###########################################################################

## Make a dataframe and csv for the output results
output=data.frame("ID", "Best Model","M0 AIC","M1 AIC","M2 AIC","M1 Calving Date","M2
Calving Date","M2 Mort Date","Missed Fixes","Year")
write.table(output,"IBM output.csv",sep=",",
        col.names=FALSE, row.names = FALSE,append=TRUE)  # This is only here to make
the shell of the .csv file, in which the results will be saved.
# By making it here, it will have headers.

## Ensure that the Date/Time column is in the right format in your data for Lubridate to read
## Format: mm/dd/yy hh:mm (ex: 05/21/2015 08:00)

### Example Data ###
Distance.2010 <- read.csv("Example Data.csv",na.strings="NULL",stringsAsFactors = FALSE)
Distance.2010$LocalFixTime=mdy_hm(Distance.2010$LocalFixTime,tz="US/Alaska")
short.2010 <- with(Distance.2010, Distance.2010[ LocalFixTime >= "2010-05-19 00:00:00
AKDT",]) # This is so you can adjust the beginning of the time series
run.IBM(short.2010, min.adult = 15, max.adult = 63, int = 9, draw = T)  # Perform analysis
```

Appendix 1C: Chapter 1 R code for applying Population-based Model

R script to run the Population-based Model (PBM) on movement data. This code modifies the PBM previously published in Demars et al. (2013) to only analyze for parturition and iteratively runs the analysis for all individuals in the provided data. The principle additions in this code are to bootstrap the calving threshold generation from more than 10 individuals, output one file containing all of the individual results, and generate plots of the fitted models to data for visual inspection. See provided data (“Example Data PBM Threshold Rates.csv”) for example of data to generate the calving threshold and (“Example Data.csv”) for example of movement data used in the calving analysis.

Literature cited

DeMars, C. A., Auger-Méthé, M., Schlägel, U. E., & Boutin, S. (2013). Inferring parturition and neonate survival from movement patterns of female ungulates: a case study using woodland caribou. *Ecology and Evolution*, *3*(12), 4149–4160. https://doi.org/10.1002/ece3.785

```
## "Movement-based methods used to infer parturition events for migratory ungulates"
## By Matthew D. Cameron, Kyle Joly, Greg A. Breed, Lincoln S. Parrett, and Knut Kielland
## For this analysis, the time-series window is May 22 - July 15
## If you use this code, please cite our paper and also cite:
#   DeMars, C., M. Auger-Methe, U. Schlaegel, S. Boutin, (Published online)
#   Inferring Parturition and Neonate Survival from Movement Patterns of Female Ungulates.
#   Ecology and Evolution. DOI: 10.1002/ece3.785

library(lubridate)
library(ggplot2)
library(zoo)
library(reshape)

setwd() # Set working directory which has your data/included example data.

## Note: running this code will make a .csv file in your working directory to hold the model results, and save the plot of the model fit as a .jpeg if "draw=T" on the function
```

```
## Load the movement data for animals with high confidence of calving date
## This is the step length data for the 3 days after the calving date as specified by the IBM.
## These began one step after the IBM identified date for the WAH analysis.
thresh.ind <- read.csv("Example Data PBM Threshold Rates.csv")

### This is the function from DeMars et al 2013 to generate the PBM threshold. ##
### The quantile of the CDF was modified to be 0.98; because the WAH data exhibited such a greater scale of movement rates, 0.99 didn't work.
makeThresh <- function(moveRates, timeInt, rare=F, draw=F){
 if (rare==T){
  rarIndex <- apply(moveRates, 2, function(x)   quantile(x, probs=0.99, na.rm=T))
  for (i in 1:ncol(moveRates)) moveRates[moveRates[,i]    > rarIndex[i],i] <- NA
 }
 rollAverage <- rollapply(moveRates, 3*24/timeInt, mean, na.rm=T, by.column=T)
 rollPool <- as.vector(rollAverage)
 rollDensity <- density(rollPool)
 densityFun <- approxfun(rollDensity$x, rollDensity$y, yleft=0, yright=0)
 y <- seq(1, max(rollPool)+20, 0.1)
 rollCumu <- rep(NA, length(y))
 for (i in 1:length(y)) rollCumu[i] <- integrate(densityFun, -Inf, y[i], stop.on.error=F)$value
 quant <- 0.981  ## Changed from the original 0.999
 threshold <- y[which(rollCumu >= quant)[1]]
 if (draw==T){
  hist(rollPool, 50, freq=F, xlim=c(0,threshold+10), xlab="TDAM mean movement rates", main="Histogram, Density and Threshold")
  lines(rollDensity, col='red', lwd=2)
  abline(v=threshold, lwd=2, col='blue')
 }
 return(threshold)
```

```
}


############# Bootstrapping the threshold value ###########################


set.seed(1)
thresh.bootstrapped <- data.frame(Run=1:1000,Threshold=rep(0,1000))
for(i in 1:1000){
  calved.sample <- sample(thresh.ind,size = 10,replace=TRUE)
  rndm.rates <- as.matrix(calved.sample/8)
  threshCalf <- makeThresh(rndm.rates, timeInt = 8, rare=F, draw=F)
  thresh.bootstrapped[i,2] <- threshCalf
}


den <- density(thresh.bootstrapped$Threshold,na.rm = TRUE)
example.thresh <- den$x[den$y==max(den$y)]  ## This is the peak of the density line of the histogram
example.thresh


hist(thresh.bootstrapped$Threshold,prob=TRUE,breaks=33,
        main = "Bootstrapped Threshold Values", xlab = "TDAM threshold value (m/hr)", ylab= "Frequency") ## Plot the histogram
lines(density(thresh.bootstrapped$Threshold,na.rm = TRUE))
abline(v = example.thresh, col = "red",lwd=3)



#########   Making the function for running PBM   #######################


## Modifying original code  -- The following is from DeMars et al. 2013
## The calf loss section has been removed (see methods section). The following function only returns the calving date.
getStatus <- function(movF, threshCalf){
```

```
  meanMR <- rollapply(movF$MR, 3*24/movF$interval, mean, na.rm=T)
  calved <- any(meanMR < threshCalf)
  calfIndex <- which(meanMR < threshCalf)[1]  ## Note: originally 17 was added here to the
first date of calving. As it is now, the first day that the TDAM rate falls below the threshold is
returned as the calving date.
  calfDate <- movF$tp[calfIndex]


  results <- data.frame(Calved = calved, CalvingDate = calfDate)
  return(results)
}



##########################
## Function to run the PBM analysis and save a plot of each reproductive season. Loops through
columns of dataset.


run.PBM <- function(database, interval, threshCalf, draw=T){ # database is the data.frame of the
step lengths for each animal (as columns), interval is the
  # hourly time between GPS locations


  for(i in 2:length(database)){
    tp <- database$LocalFixTime
    id <- names(database)[[i]] #saves animal ID for graph titles
    num.missed.fix <- sum(is.na(database[[i]])) #How many missed fixes for that animal
    MR <- database[[i]]/8
    movF <- data.frame(MR, tp, interval = rep(interval,length(tp))) # The repeat command here is
repeating the interval, which is defined in the run command
    result <- getStatus(movF,threshCalf)
    print(names(database)[[i]]) #Print ID
    print(result)
    print("##########################")
```

```
###### Saving results from PBM model as csv ####
year.hold=year(tp) # makes vector of year for all fixes
yr=year.hold[!is.na(year.hold)][1] # Saves the year being analyzed for graph titles
tab <- data.frame(id,
                 result[1,1],
                 result[1,2],
                 num.missed.fix,
                 yr)
write.table(tab,paste("PBM output.csv"),sep=",",
            col.names=FALSE, row.names = FALSE,append=TRUE)

####### Generate a dataframe of the 3 day movement rates for the graph ##########
meanMR <- rollapply(MR, 3*24/interval, mean, na.rm=T)
pbm.plot <- data.frame(
  tp[1:(length(tp)-8)],
  meanMR)
colnames(pbm.plot) <- c("fix.times","MR")

####### Making plots of results ##########

if (draw==T) {
  if (is.na(result[1,1])=="FALSE"){ # For the successful model analyses, do the following:
    if (result[1,1]=="FALSE") {   #if the best model is the "didn't calve model", plot a flat line

      no.calf.plot <- ggplot(pbm.plot,aes(fix.times,MR,group=1)) +
        geom_line() +
        theme(panel.background=element_blank()) +  #Sets background to white
        geom_hline(yintercept = threshCalf,linetype = "dashed") +
```

```
        labs(x="Date",y="3-Day Average Moving Rate (m/hr)",title=paste("No parturition PBM model for",id,"in ",yr)) +
        theme(axis.line.x=element_line(size=.5,colour = "black",linetype = "solid")) + #add axis lines
        theme(axis.line.y=element_line(size=.5,colour = "black",linetype = "solid")) + #add axis lines
        theme(plot.title=element_text(size=20,face="bold",margin = margin(10,0,10,0))) +
        ylim(c(0,3000))


      ggsave(filename=paste("PBM ",id," plot for ",yr," No Calving.jpeg",sep=""),plot=no.calf.plot,width = 8,height = 4)
    } # End of ggplot False



    if (result[1,1]=="TRUE"){   #if the best model is the "calved model", plot a single break point
      ## Settings for line commands ##
      calve=result[1,2]
      ## Plotting ##
      calved.plot = ggplot(pbm.plot,aes(fix.times,MR,group=1)) +
        geom_line() +
        theme(panel.background=element_blank()) +  #Sets background to white
        geom_hline(yintercept = threshCalf,linetype = "dashed") +
        labs(x="Date",y="3-Day Average Moving Rate (m/hr)",title=paste("Parturition PBM model for",id,"in",yr,sep = " " )) +
        geom_vline(xintercept=as.numeric(calve),linetype=4,colour="black") + #break point at calving event

geom_text(aes(x=(calve+ddays(1)),label=calve,y=1200),angle=90,size=4,fontface="italic") + #Labels the calving line with calving date
        theme(axis.line.x=element_line(size=.5,colour = "black",linetype = "solid")) + #add axis lines
        theme(axis.line.y=element_line(size=.5,colour = "black",linetype = "solid")) + #add axis lines
```

```
          theme(plot.title=element_text(size=20,face="bold",margin = margin(10,0,10,0))) +
          ylim(c(0,3000))


        ggsave(filename=paste("PBM ",id," plot for ",yr,"
Calved.jpeg",sep=""),plot=calved.plot,width = 8,height = 4)
       } # End of ggplot True


      } # End of "if result is not NA"
      if (is.na(result[1,1]=="TRUE")){  ## If the model CAN'T RUN:
        null.plot <- ggplot(pbm.plot,aes(fix.times,MR,group=1)) +
         geom_line() +
         theme(panel.background=element_blank()) +  #Sets background to white
         geom_hline(yintercept = threshCalf,linetype = "dashed") +
         labs(x="Date",y="3-Day Average Moving Rate (m/hr)",title=paste("NULL PBM model
for",id,"in ",yr)) +
         theme(axis.line.x=element_line(size=.5,colour = "black",linetype = "solid")) + #add axis
lines
         theme(axis.line.y=element_line(size=.5,colour = "black",linetype = "solid")) + #add axis
lines
         theme(plot.title=element_text(size=20,face="bold",margin = margin(10,0,10,0))) +
         ylim(c(0,3000))


        ggsave(filename=paste("PBM ",id," plot for ",yr," NULL
MODEL.jpeg",sep=""),plot=null.plot,width = 8,height = 4)


      } #End of graphing NA
    } # End of graphing all results
  } # End of all animals loop
} # End of function


#################  Perform the PBM analysis with the WAH caribou data  ###########
```

```
## Generate file for the output

output=data.frame("ID", "Calved?","Calving Date","Missing Locations","Year")

write.table(output,"PBM output.csv",sep=",",

        col.names=FALSE, row.names = FALSE,append=TRUE)


## Ensure that the Date/Time column is in the right format.

## Format: mm/dd/yy hh:mm (ex: 05/21/2014 08:00)


## Run for example data: ###

## The following subsets the data to being May 22th; this was done to match with the IBM date
window. The IBM started on May 19, and the earliest the IBM could ID an event was on May
22, so this accounts for the difference

Distance.2010 <- read.csv("Example Data.csv",na.strings="NULL",stringsAsFactors = FALSE)

Distance.2010$LocalFixTime=mdy_hm(Distance.2010$LocalFixTime,tz="US/Alaska")

short.2010 <- with(Distance.2010, Distance.2010[ LocalFixTime >= "2010-05-22 00:00:00
AKDT",])  # Allows for easy editing of the beginning of the time series being analyzed

run.PBM(short.2010,interval = 8,threshCalf = 137.0731, draw=T)  # Note, this is the reported
WAH threshold, not one from the example dataset
```

Chapter 2: Pronounced fidelity and selection for average conditions of calving area suggestive of spatial memory in a highly migratory ungulate[2]

Abstract

A distinguishing characteristic of many migratory animals is their annual return to distinct calving (birthing) areas in the spring, yet the navigational mechanisms employed during migration which result in this pattern are poorly understood. Effective conservation of these species requires reliable delineation of such areas, quantifying the factors which influence their selection, and understanding the underlying mechanisms resulting in use of calving areas. We used barren-ground caribou (*Rangifer tarandus granti*) as a study species and identified calving sites of the Western Arctic Herd in Alaska using GPS collar data from 2010 – 2017. We assessed variability in calving areas by comparing spatial delineations across all combinations of years. To understand calving area selection at a landscape scale, we performed a resource selection analysis comparing calving sites to available locations across the herd's range and incorporated time-varying, remotely-sensed metrics of vegetation quality and quantity. We found that whereas calving areas varied from year to year, this annual variation was centered on an area of recurring attraction consistent with previous studies covering the last 6 decades. Calving sites were characterized by high-quality forage at the average time of calving, but not peak calving that year, and by a narrow range of distinct physiographic factors. Each year, calving sites were

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[2] Cameron, M.D., Joly, K., Breed, G.A., Mulder, C.P.H., and Kielland, K. 2020. Pronounced fidelity and selection for average conditions of calving area suggestive of spatial memory in a highly migratory ungulate. Front. Ecol. Evol. 8: 564567. doi:10.3389/fevo.2020.564567.

located on areas of above-average conditions based on our predictive model. Our findings indicate that the pattern of spring migration for pregnant females was to migrate to areas that consistently provide high-quality forage when averaged across years, and then upon arriving at this calving ground, refine selection using their perception of annually-varying conditions that are driven by environmental stochasticity. We suggest that the well-documented and widespread pattern of fidelity to calving grounds by caribou is supportive of a navigational mechanism based on spatial memory at a broad scale to optimize foraging and energy acquisition at a critical life-history stage. The extent to which migrants depend on memory to reach their spring destinations has implications for the adaptability of populations to changing climate and human impacts.

Introduction

Migration is a behavioral adaptation to seasonal environmental conditions and resource availability (Alerstam et al., 2003; Avgar et al., 2014). How animal movement relates to resource conditions is scale dependent (Bailey et al., 1996), such that movements within patches of resources (MacArthur and Pianka, 1966; Charnov, 1976) can scale up to landscape-scale use patterns and can result in the dramatic movements characteristic of migratory animals (Shaw and Couzin, 2013). A current challenge in the field of animal ecology is to understand the influence of the navigational mechanisms responsible for large-scale movements such as migration. These mechanisms broadly fall into 2 domains: perception-based movements, where animals follow immediately-perceived resource gradients to track high-quality resources as they arise, or memory-based movements, where animals use previous experience to direct their movements to areas of high-quality resources outside of the immediately perceptible zone (Avgar et al., 2013; Fagan et al., 2013). Examples of perception-based movement include animals ‘surfing a green wave' of high-quality forage as it moves across a spatial gradient (van der Graaf et al., 2006; Merkle et al., 2016; Aikens et al., 2017), whereas memory-based movements are characterized by animals moving independently of proximal resource gradients and moving to distant areas of high-quality resources (Howery et al., 1999; Polansky et al., 2015; Bracis and Mueller, 2017). Since these navigational processes cannot be directly measured in wild animals, inferring their relative influence from movement data requires integrating empirical observations with theoretical and experimental findings (Fagan et al., 2013).

Spring migration of females in many migratory ungulate species culminates with parturition (hereafter calving), with females often aggregating on calving areas. Such species include blue wildebeest (*Connochaetes taurinus;* Estes, 1976), Tibetan antelope (*Pantholops hodgsoni;* Schaller et al., 2006), Saiga antelope (*Saiga tatarica*; Bekenov et al., 1998) and barren-ground caribou (*Rangifer tarandus*; Kelsall, 1968). Calving begins a period of heightened nutritional demand for pregnant females due to the high energetic cost of lactation (Chan-McLeod et al., 1994). Owing to this demand, females are hypothesized to synchronize calving with periods of high vegetative quality (Oftedal, 1985; Miller-Rushing et al., 2010) and, indeed, selection for calving areas has been linked to vegetative productivity for some species (Tibetan antelope, Ganzorig et al., 2011; Mongolian gazelle (*Procapra gutturosa*), Leimgruber et al., 2001). Spring vegetative productivity has also been positively associated with offspring condition (Pettorelli et al., 2005b, 2006). An alternative explanation for calving area selection is that females attempt to space away from predators (Bergerud, 1996; Creel et al., 2005), but testing the influence of these two hypotheses is often difficult.

Calving aggregations are typically highly vulnerable to human disturbance since a large percentage of the population is concentrated in relatively small areas at calving and anthropogenic influences can strongly alter female behavior (Nellemann and Cameron, 1998; Joly et al., 2004; Singh et al., 2010). Survival of neonates is a critical factor in population dynamics (Gaillard et al., 2000) and lactation performance directly affects offspring growth (White, 1992; Crête and Huot, 1993), meaning conservation of calving areas is likely a key component to managing these populations (Taillon et al., 2012). Since calving areas typically exhibit some level of annual variability (Lent, 1966; Skoog, 1968; Griffith et al., 2002), documenting annual use at decadal scales and understanding the mechanistic processes driving selection of these areas are critical for effective, long-term conservation (Singh and Milner-Gulland, 2011; Wilson et al., 2012). Understanding these processes before anthropogenic development has taken place is essential; inferences about calving selection after development has taken place will likely be contaminated by risk effects and avoidance behavior, introducing potentially large and unknown biases to calving site selection (Harju et al., 2011).

To address these issues in a unified approach, we used migratory barren-ground caribou as a study species and investigated the use of calving areas across eight years for the Western Arctic Herd (WAH) in Alaska, one of the largest caribou herds in the world. Barren-ground caribou are an excellent study species for this approach, since calving marks the destination of long-distance migration in the spring for pregnant females, which aggregate at calving and generally exhibit inter-annual fidelity to their calving grounds (Kelsall, 1968). We defined three scales of calving: individual calving sites in a given year comprise an annual calving area, which in turn constitute a calving ground when considered across numerous years (Figure 2.1; Gunn and Miller, 1986). Our goals were to 1) document spatial trends in the calving areas of the WAH, 2) investigate the landscape-level factors influencing selection for calving sites to better understand the emergent spatial patterns of calving areas, and 3) interpret our findings to better understand what navigational mechanisms could explain the phenomenon of fidelity of caribou to their calving grounds. We hypothesized that if females exhibited primarily perception-based selection, calving sites would be characterized by low interannual consistency and track high-quality vegetation for each year. Alternatively, if selection were primarily memory-based, calving sites would be characterized by high interannual consistency and high-quality vegetation, as averaged across the study period, but not necessarily the best site in any given year.

Methods

Study species

The WAH utilizes over 350,000 km^2 of northwestern Alaska, typically migrating from wintering areas in the south, which vary by year and individual, to the calving ground and summer range in the north (Figure 2.2; Lent, 1966, Dau, 2015, Joly and Cameron, 2019). Calving generally occurs May 31 – June 13 (Cameron et al., 2018). Beginning in 2009, GPS collars (Telonics, Mesa, AZ) were deployed annually on adult female caribou (≥ 2 years old) as they swam across the Kobuk River during fall migration (Dau, 1997; Joly et al., 2012). Captures were conducted using procedures approved by the State of Alaska Institutional Animal Care and Use Committee (IACUC; 0040-2017-40). Collars were programmed to record locations every eight hours and by 2017, 203 collars had been deployed. From 2003 to 2016, the herd decreased from a high of 490,000 to 201,000 caribou and then increased to 244,000 in 2019 (Alaska Department of Fish and Game, 2019). The northeast extent of the WAH range overlaps with the neighboring Teshekpuk Herd, and individuals between the two herds have been known to mix (Mager et al., 2013; Prichard et al. 2020).

Identifying calving events

We applied two different approaches to infer calving events from the 2010-2017 GPS data: an individual-based method and a population-based method (DeMars et al., 2013; Cameron et al., 2018). The former fit two a-priori movement models (parturient and non-parturient) to movement rate data and model fit was evaluated using information criteria. The second method established a herd-specific movement rate threshold for calving from known events and then analyzed movement rates for individuals which dropped below the threshold using a three-day smoothing parameter (DeMars et al., 2013). Using instances when the two methods agreed resulted in accurately classifying calving events 89% of the time (n=119) when compared to aerial observation data (Cameron et al., 2018).

For data spanning 2010-2015, we used the calving events as reported in Cameron et al. (2018), in which aerial data were used to validate identified calving events from the movement-based approaches. For the data spanning the calving period of 2016-2017, we followed the procedures outlined in Cameron et al. (2018) to identify calving events without relying on supporting aerial data. However, due to a record number of non-migratory individuals during the winter of 2016-2017 (Joly and Cameron, 2019) and since the individual-based method is ill-suited for individuals not exhibiting migration movements prior to calving (Cameron et al., 2018), we incorporated a designation of migratory and non-migratory for each individual and adjusted the analysis as follows. For individuals that migrated (identified as crossing at least one of the three major rivers separating summer and wintering areas), we used the calving events from instances of method agreement. For individuals that did not migrate to a southern wintering area that year and for which the two model results disagreed, we used calving events identified by the population-based method. For calving sites, we used the GPS location that corresponded with the identified calving event from the population-based method, since the individual-based method appeared to label events one GPS-interval early (Cameron et al., 2018).

Spatial patterns in calving areas

To address our first goal of spatial trends in calving areas, we defined an annual calving area as the area used by the majority (>80%) of individuals for calving in the herd in a given year (Gunn and Miller, 1986). We calculated a kernel utilization distribution (Worton, 1989) based on the calving sites for each year using the package “adehabitatHR” version 0.4.14 (Calenge, 2006) in the R statistical program version 3.4.3 (R Core Team, 2017). In this approach, a bivariate normal probability distribution is centered over each calving site in a given year and averaged together, resulting in one distribution (the kernel) for each year. Kernels were generated using a 500 x 500m grid in an Albers equal area projection which minimizes distortion along the latitudinal gradient given the relatively high latitude of our study area and ensured valid comparisons between years (Snyder, 1987). All kernels were generated using the same bandwidth smoothing parameter ($h = 25{,}000$) and we used the 95% contour as they resulted in unbroken range delineations for all years (Hooten et al., 2017). This approach, which is based on the explicit calving sites, minimizes potential bias in delineating calving areas that can be introduced by mismatches between calving timing and aerial observation timing during traditional surveys (Gunn and Miller, 1986).

To test the null hypothesis that the spatial distribution of annual calving areas did not vary by year, we employed a kernel randomization analysis outlined by Breed et al. (2006). For comparisons between two years, we randomly assigned (without replacement) a year designation to each calving site. Then, kernels for both years were generated using the same grid and smoothing parameters as outlined above. The area of both randomized kernels was then computed, as well as the area of overlap between the two kernels. Last, we calculated the test statistic as the area of the kernel overlap divided by the largest area of the two kernel regions. We repeated this process 250 times without duplicating any random year assignments. The *p*-value was calculated as the proportion of random overlaps smaller than the observed overlap for the two years being considered, so that if the observed overlap was smaller than all observed overlap values, the *p*-value was < 0.004 (see Appendix 2A.1 for illustration). We performed this analysis for all combinations of annual comparisons, ranging from sequential up to seven-year intervals, and considered our alpha level as 0.05 for a one-tailed test.

Range-wide calving site selection

Our other goals were to understand the biotic and abiotic factors driving caribou calving site selection at the landscape level and what navigational mechanisms caribou employ to arrive there. We performed a resource-selection function analysis (RSF; Manly et al., 2002) using the calving sites each year and compared them with random locations from the herd's range, representing the third-order of selection (Johnson, 1980). To define range-wide availability, we drew a 100% minimum-convex polygon, constrained to the coastal boundary, around all GPS locations during the study period. Defining availability is a particular challenge for resource selection studies, with the implicit assumption that available points are unused and available to all individuals (Keating and Cherry, 2004; Aarts et al., 2008). We focused on a range-wide scale for this analysis because individuals in the herd used the polygon area throughout the eight years of study and we detected calving events at the extreme southwestern and northeastern extent of the range, far outside of the traditionally defined calving area. For each of the eight years from 2010 to 2017, we created 10,000 random locations within the polygon, for a total of 80,000 available points.

We attributed both used and available points with a combination of physiographic attributes and annually varying environmental indices. We attributed elevation values from a 5 m resolution digital terrain model derived from the Interferometric Synthetic Aperture Radar (U.S. Geological Survey, 2017) and calculated a solar radiation index (Keating et al., 2007) for each point using slope and aspect derived from the terrain model. This index ranges from -1 to 1, with low index values corresponding to north-facing steep slopes, high values south-facing steep slopes, and flatter slopes around 0.35. We calculated a vector ruggedness measure (VRM) (Sappington et al., 2007), which is a measure of the ruggedness of the terrain, for each point using the digital terrain model and a 15 x 15 m swath. We used a land cover classification map (Boggs et al., 2016) to attribute all points with land cover type and reduced the classifications into four categories from the original 20 based on diet categories of the predominant vegetation (forest, shrub, herbaceous, and lichen/sparse; Appendix 2A.2). We filtered points which occurred in pixels originally categorized as bare ground, fire scar, ice/snow, and water.

For environmental indices, we attributed the annual snow off date (day of year) specific to that year for each point as determined from Moderate Resolution Imaging Spectroradiometer (MODIS) data (Macander et al., 2015). We included two measures of primary productivity at multiple time intervals using the normalized difference vegetative index (NDVI, for review see Pettorelli et al., 2005) acquired from the MODIS V6 and compiled into 7-day composites with 250m resolution (data available from the U.S. Geological Survey; Jenkerson et al., 2010). For an index of forage quantity, we used the raw NDVI value at a weekly temporal resolution and as an index of forage quality we calculated the change in NDVI values between sequential NDVI composites (NDVI rate) for the same time period by calculating the difference between sequential coverages (denoted “ΔNDVI”). ΔNDVI has been used in prior studies as an index for forage quality, including in Africa (Boone et al., 2006) and Alaska (Griffith et al., 2002), and also used to calculate a similar measure, the Instantaneous Rate of Green-up (Bischof et al., 2012). For arctic vegetation, a positive change in NDVI during spring corresponds with phenological periods of high nutrient concentrations and rapid vegetation growth (Finstad, 2008; Gustine et al., 2017).

We included five temporal windows (one week before peak calving, the week of the peak, and the following three weeks after peak calving) for both NDVI metrics to assess at what temporal scale caribou may be responding to vegetation signals. To evaluate support for perception-based selection, we assigned the five temporal windows for both NDVI metrics relative to peak calving for that specific year, with the effect that the week of peak calving NDVI values differed between years and corresponded to the timing of calving observed the given year (perception of current conditions). To evaluate the potential for memory-based selection, we assigned these temporal windows relative to the herd's average peak calving across all eight years (June 3, see Results), such that regardless of when peak calving was in a given year, both NDVI metrics represented consistent weeks across years (average conditions). This framework is similar to work assessing the influence of perception and memory in zebra (*Equus burchelli*) migration (Bracis and Mueller, 2017)

We tested the influence of these biotic and abiotic factors on caribou calving site selection using mixed-effects logistic regression, with use of a calving site as the response. We log-transformed elevation and VRM to approximate a normal distribution and standardized continuous covariates (mean centered and divided by the standard deviation) for model fitting. Correlation coefficients among physiographic attributes were under 0.5, and they all were under 0.2 when compared with environmental variables. We included a random intercept term for year to account for sampling across time and considered random slope terms for the environmental variables to account for stochastic annual variability (Gillies et al., 2006). We performed model selection at two stages – the first to select a random effect structure and the second to select fixed effect variables and structures (Bolker et al., 2009) using model selection based on Akaike's Information Criterion corrected for small sample sizes (AICc; Hurvich and Tsai, 1989; Burnham and Anderson, 2002). For all NDVI, ΔNDVI, and snow-free variables, we fitted full fixed-effects models with a random slope term for each environmental covariate (including a random intercept for year) and compared performance with an intercept-only random effects model. In the second stage of model selection, we proceeded with fixed-effects selection using the top-performing random effect structure from the previous stage and included all biologically justifiable interactions and combinations. All analyses were performed in the R statistical program using the package 'lme4' (Bates et al., 2015). We used our top model to generate a predictive map for calving sites by averaging the selected environmental covariate raster across the eight years, as well as generated year-specific predictive maps with the corresponding environmental data for that year. We calculated the average of the year-specific predictive values within each annual calving area and compared these with the calving site values for the given year.

Results

Identifying calving events

From 2010 to 2017, we detected 214 total calving events, ranging from 15 to 52 in a given year, and the average calving date was June 3 (Table 2.1). We identified calving in one non-migratory individual in 2016 and 14 in 2017 for which we used results from only the population-based model. We detected four calving events outside of the historical calving grounds: one in 2012 for an individual which remained on the winter range of the Seward Peninsula and three in 2017 for WAH individuals which calved in the Teshekpuk Herd calving area to the east. For the subsequent analyses of calving area trends and selection, we excluded these four events because they greatly skewed calving distribution estimates, leaving us with 210 total calving events across eight years.

Spatial patterns in calving areas

Across the eight years we analyzed, the WAH calving areas exhibited variation at the annual scale, but the general area was characterized by remarkable fidelity. The average extent of the calving area for the herd in a given year was 24,772 km^2 (Table 2.1). Calving areas exhibited both latitudinal and longitudinal variation across years, with calving occurring in the Brooks Range and as far south as the Noatak River in some years (Figure 2.3). On an annual basis, calving areas had significantly less overlap than expected by chance three out of seven times ($p < 0.05$; Table 2.2). This trend of significant differentiation among years was evident at all further levels of comparison: at two-year ($p < 0.05$ for five out of six), three-year ($p < 0.05$ for four out of five), four-year ($p < 0.05$ for three out of four), five-year ($p < 0.05$ for one out of three), six-year ($p < 0.05$ for one out of two) and seven-year intervals ($p < 0.05$ for the one comparison). When considered across years, the calving area of WAH females always shared a 7,281 km^2 core area of overlapping extent which was used every year of the study, with calving areas of less frequent use stretching as far away as the Noatak River (Figure 2.4) for a total calving ground extent of 53,330 km^2.

Range-wide calving site selection

The selection of calving sites was characterized by mostly flat tundra within a band of elevation that was greening up at the time of average calving for the herd across all years of the study. The environmental covariate which explained the most variance in calving site selection was ΔNDVI at the average peak calving date for the study ("ΔNDVI.148"), from May 21 – 27 to May 28 – June 3 every year (day of year 141-147 to 148-154; Appendix 2A.3) and substantially outperformed the next best model in random effect selection, which included a random slope for ΔNDVI at peak calving specific to each year (ΔNDVI.Calve; Δ AICc = 29.2). In model selection for fixed effects, the top performing model included terms for land cover, quadratic terms for elevation and solar radiation which indicate selection for intermediate values for both, an interaction between elevation and ΔNDVI.148, and terrain ruggedness (Appendix 2A.4). Females strongly selected for sites with high ΔNDVI at the time of peak calving (Table 2.3).

Calving sites were associated with a band of low elevation areas, indicating selection of elevations between approximately 50 – 600 m above sea level. Elevation and ΔNDVI exhibited an interactive effect, with females most strongly selecting for elevations approximately 100-175 m which were experiencing the fastest green-up at the time of peak calving. Of the four land cover classes we considered, we did not detect calving in any forested sites and found the strongest selection for herbaceous cover at calving (Table 2.3). The solar radiation index also exhibited a quadratic relationship for calving site selection (Table 2.3), indicating selection of sites with a positive index ranging from approximately 0.15 to 0.5, which correspond to lower angle slopes and encompass nearly all aspects. The negative linear coefficient for terrain ruggedness supported this result, indicating that females selected for less rugged terrain (Table 2.3). Our predictive map of calving habitat indicates that calving for the WAH occurs in the largest, continuous expanse of habitat characterized by these unique factors within their range, and that the attributes associated with calving sites extend to the east beyond documented calving areas (Figure 2.5). Importantly, calving occurred on sites with higher predicted value from the top model compared to the average of the calving area in the given year (Appendix 2A.5).

Discussion

Mounting evidence indicates that animals use memory to make movement decisions that improve resource acquisition in a heterogeneous landscape (Bailey et al., 1996; Fagan et al., 2013; Bracis et al., 2015; Abrahms et al., 2019, Merkle et al. 2019). For example, bison (*Bison bison*) base foraging on their memory of patch location and quality that result in observed home-range spatial patterns (Merkle et al., 2014). Elephants (*Loxodanta africana*) rely on spatial memory to minimize long-distance travel to perennial waterholes in an arid environment (Polansky et al., 2015). In an explicit test of the relative importance of memory versus perception using zebras, simulations of migration paths based on memory mechanisms reached the actual migration destination more accurately than simulations based on perception mechanisms, even when the perceptual range was increased to omniscience (Bracis and Mueller, 2017). Considering that less productive regions are associated with longer annual movements of large terrestrial mammals (Joly et al., 2019), the extreme variability of arctic conditions could conceivably promote an adaptation for memory-based capabilities in caribou.

Our results highlight the strong fidelity of a highly migratory ungulate to its calving ground within an extensive range across the nearly decade-long study period. Notably, pregnant females selected calving sites that were characterized by high-quality forage at the average time of peak calving. High fidelity is particularly impressive considering the highly variable winter ranges of individuals in this (Joly and Cameron, 2019) and other herds (Schaefer et al., 2000; Faille et al., 2010; Peignier et al., 2019), and thus females must routinely travel different routes between winter ranges and the calving area (Kelsall, 1968; Nicholson et al., 2016; Baltensperger and Joly, 2019). Spring migration routes for pregnant females are typically snow covered (Boelman et al., 2019; Gurarie et al., 2019), so these segments of the migration occur well before green-up and are unlikely to be a product of perception-based movement along the way used by other ungulates (e.g., Merkle et al., 2016). Considering the spatial consistency of use and selection for average conditions, we suggest that the fidelity of caribou to their calving grounds is supportive of memory-based movement at the landscape scale.

The use of perception-based versus memory-based movement are not necessarily mutually exclusive and may depend on the scale being considered (Bailey et al., 1996). Trial studies with sheep (*Ovis* spp.) revealed that individuals can remember the locations of resources between trials and use spatial memory to improve foraging efficiency. Impressively, sheep could also associate a cue with resource locations, such that when a resource patch was moved between trials, the sheep went to the original location first, then directed movement to the cue (and thus the resource; Edwards et al., 1996). Spatial consistency in calving areas for the WAH did not appear to be driven exclusively by memory of a specific place – calving sites for individuals were approximately 55 km apart across years on average (Joly et al., *In Prep*), which is similar to findings for other herds (Fancy and Whitten, 1991; Schaefer et al., 2000). Our finding that specific calving sites had higher forage quality than the overall average for that year's calving area suggests that females refine calving site selection based on updated information perceived after arriving on the calving ground. In other words, our results suggest that memory guides pregnant female caribou to the general calving grounds during spring migration but then the individual's perception of local, contemporary conditions each year refines their movement, resulting in the annual variability in calving sites and thus the characteristic annual variability of the calving areas of many herds.

Weather conditions, such as precipitation (Le Corre et al., 2017), can influence spring arrival timing, and deeper snow increases the cost of movement for caribou (Fancy and White, 1987) and is hypothesized to delay migration in other arctic caribou herds (Duquette, 1988; Gurarie et al., 2019). We suspect some of the southerly calving sites reported here were due to such snowy spring conditions impeding migratory movement and delaying arrival to the main calving ground, which resulted in birth en route. The spring of 2013 had unusually cold temperatures and heavy late spring snowfall (Sousanes and Hill, 2013), as well as the most southerly calving sites of our study. Such snow-related delays have occurred before: some calves were born south of the Brooks Range during the unseasonably late spring of 1962 (Lent, 1966), and late snowmelt has correlated with southerly calving events in the nearby Teshekpuk Herd (Carroll et al., 2005). Based on the influence of forage quality to calving sites we detected, we attribute the observed east-west spatial variation to caribou adjusting their calving sites to annual vegetative conditions they found upon arriving to the calving ground. Variability in the annual calving area has been linked to variation in forage quality for the Porcupine Herd (Griffith et al., 2002), as well as variation in snow conditions (Fancy and Whitten, 1991). Considered cumulatively, WAH caribou utilized an area seven times larger than the core calving area across nearly a decade, likely responding to perceived annual environmental stochasticity.

Our finding of selection for an index of vegetation phenology (NDVI rate from weekly composites) supports previous studies documenting selection for ΔNDVI after calving (Kelleyhouse, 2001; Griffith et al., 2002) and aligns with recent work suggesting that raw NDVI is a poor metric of forage nutrients (Johnson et al., 2018). For many ungulates, calving and subsequent lactation are the most energetically-demanding periods of the year (Clutton-Brock et al., 1989; Barboza and Parker, 2008). Female caribou exhibit a strong preference for immature floral heads of cottongrass (*Eriophorum vaginatum)* at calving (Kuropat and Bryant, 1980; Thompson and McCourt, 1981; Griffith et al., 2002), which offers one of the greatest sources of digestible nitrogen and protein at the beginning of the arctic growing season (Kuropat and Bryant, 1980; Johnstone et al., 2002; Cebrian et al., 2008; Gustine et al., 2017). Cottongrass is adapted to early spring growth relative to other tundra plant communities (Chapin et al., 1979), with initiation of the floral heads the autumn before allowing elongation to resume shortly after snow ablation (Wein, 1973; Cebrian et al., 2008). Considering the dominance of tussock-tundra communities (of which cottongrass is the primary component) in the foothills north of the Brooks Range (Boggs et al., 2016), we posit that the forage quality signal we identified in calving site selection by the WAH is largely influenced by cottongrass flowering, though early leaf flush of deciduous shrubs such as willow species (such as *Salix pulchra*) may also occur during the calving period (Borner et al., 2008). The absence of calving in the large area of predicted high-quality habitat to the east of the calving ground (Figure 2.5) is notable. One explanation is that following calving, the herd reliably moves to the southwest and toward the coast to avoid insect harassment, an activity which exerts large energetic costs as well as lost foraging opportunities (Witter et al., 2012; Dau, 2015; Joly and Cameron, 2019; Joly et al., 2020). Potentially, the selection of calving sites balances the nutritional need for access to high-quality resources at calving with distance to insect relief areas which will be critical in July. If so, this would suggest that selection of calving sites can also be influenced by the expectation of conditions to come after calves are born.

Another possible interpretation for our results of calving area consistency, and the most widely-accepted alternative explanation for migratory ungulates to synchronously give birth in distinct calving areas, is to escape predation (Bergerud, 1974, 1996; Estes, 1976; Fancy and Whitten, 1991). The principal predators for caribou calves are wolves (*Canis lupus*), brown bears (*Ursos arctos*), and golden eagles (*Aguila chrysaetos*; Whitten et al., 1992). If predation risk primarily motivates selection of the calving area, then we would expect calving to occur in areas of the lowest predator densities across the range. Indeed, coarse estimates indicate that densities of wolves and brown bears are higher south of the Brooks Range compared to the north. However, in the northern portion of the herd's range, densities for both predators are greater in the Brooks Range foothills, where WAH calving is centered, compared to the coastal plain to the north (Appendix 2A.6). Thus, the location of the core WAH calving ground is not consistent with predation risk as the primary driver of calving site selection. Our findings support the alternative hypothesis that migratory species match the increased metabolic demands of calving with favorable foraging conditions (Baker, 1938), and fit within a growing body of literature which links bottom-up signals to calving area selection by migratory ungulates. In Mongolia, calving areas for Mongolian gazelles exhibited higher NDVI values than the rest of the range at the time of use (Leimgruber et al., 2001). In Kazakhstan, Saiga antelope calving was found to be synchronized with peak productivity based on NDVI, and calving areas were characterized by low variability, and thus high reliability, of vegetative productivity (Singh et al., 2010). A preliminary study on the Tibetan Plateau suggests that Tibetan antelopes synchronize use of calving areas with peaks in primary productivity as well (Ganzorig et al., 2011). Whereas none of these studies directly tested for predator avoidance effects, there is mounting evidence from around the globe that bottom-up forces influence calving site selection for ungulates and that the motivation of selection cannot be simplified without considering scale and the potential that predation risk plays a lesser role than has been previously suggested (Fancy and Whitten, 1991; Bergerud, 1996).

Recent studies indicate that animal movement is strongly affected by social interactions when animals are in groups, termed collective movement (Westley et al., 2018). In a collective movement framework, individual group members may hold different levels of information about the environment (Couzin et al., 2005) and more informed individuals can act as group leaders in movement processes (Huse et al., 2002; Couzin et al., 2005; Guttal and Couzin, 2010; Berdahl et al., 2018). Given that caribou migrate in the spring in groups, we speculate that collective movement processes are likely at play (Duquette and Klein, 1987). This concept has a long history with local indigenous knowledge about caribou, which recommends "let the leaders pass" during migration (Padilla and Kofinas, 2014). If so, determining what level information is held in caribou groups (such as age classes) and what proportion of informed individuals are necessary to result in the observed calving patterns, are promising avenue for future research.

Management implications

Migratory ungulates rely on large expanses of range in order to maximize fitness (Hebblewhite et al., 2008; Joly et al., 2019) and migration routes of animals which rely on spatial memory are more susceptible to disturbance as they are likely more inflexible (Bracis and Mueller, 2017). Once lost, migratory patterns can take many generations for a population to learn and re-establish (Jesmer et al., 2018). Previous studies recommend that to fully conserve calving grounds for species such as caribou, managers should consider the full extent of calving at a decadal scale as the goal (Carroll et al., 2005; Taillon et al., 2012). Across eight years of study, the WAH used an approximately 7,000 km^2 core area along the Utukok River for calving and a broader area of 53,330 km^2 to respond to environmental variability experienced each year on the calving ground. Comparing our findings with previous studies of the WAH up to six decades prior highlights the remarkable fidelity of this herd to its general calving ground (Appendix 2A.7; Lent 1966; Kellyhouse 2001) and local indigenous knowledge suggests this pattern extends before the 20th century (Lent, 1966; Burch, 2012). We recommend managers adopt the extent of the calving ground as the management goal for migratory caribou herds such as the WAH to ensure adequate space to respond to the annual environmental variability faced by caribou populations. We expect this recommendation has immediate utility for WAH management, since the area where the majority of calving occurs is on the National Petroleum Reserve – Alaska and specifically within the Utukok River Special Area. The Bureau of Land Management is currently revising the Integrated Activity Plan, which will designate conservation areas within the Reserve and stipulations on development in the greater area, and decisions made now have the potential to impact the WAH calving grounds for decades.

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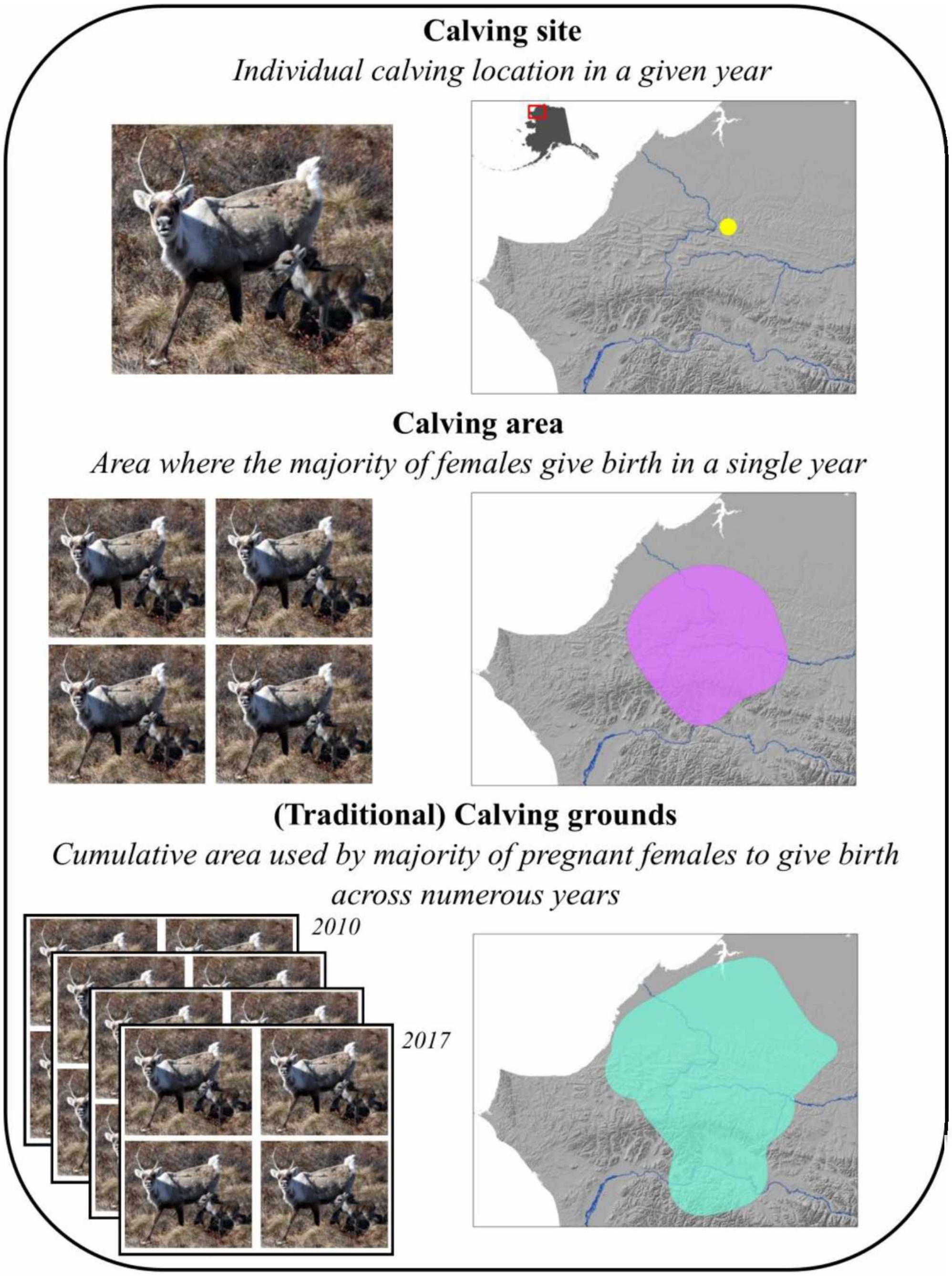

Figure 2.1: The scales and definitions of calving considered in this analysis of the Western Arctic Herd. The calving location (yellow point) was from an individual in 2010, the calving area (purple polygon) was based on all detected calving events in 2010, and the calving ground (teal polygon) was the extent of all calving areas from 2010-2017 combined. Adapted from (Gunn and Miller, 1986).

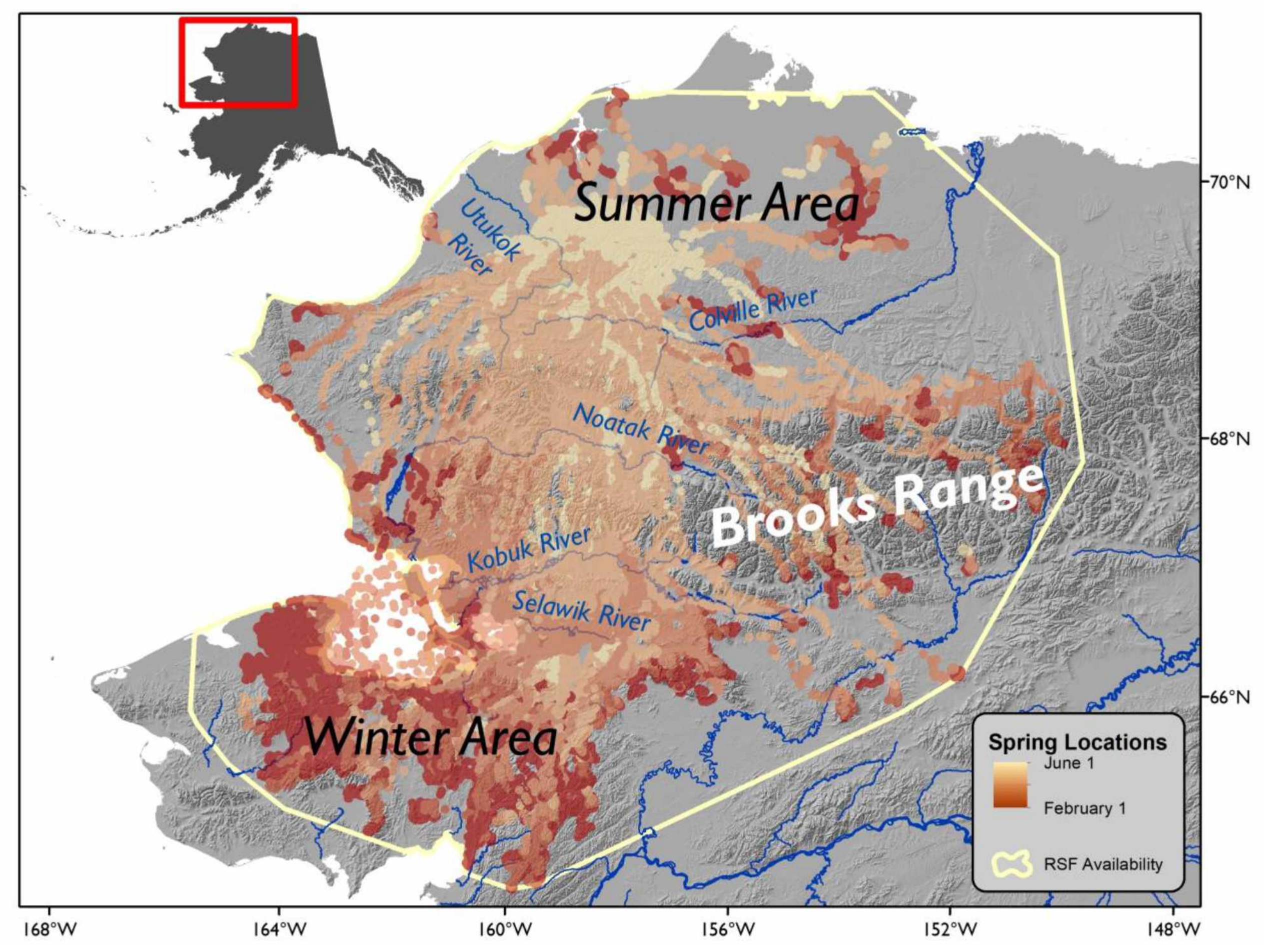

Figure 2.2: Annual range of Western Arctic Herd caribou, Alaska. All GPS points from February 1 (dark red) to June 1 (yellow) are displayed from 2009-2017. The 100% minimum convex polygon, indicating the extent of the available area for the RSF, is presented as pale yellow line and was generated using all annual locations in the same time span.

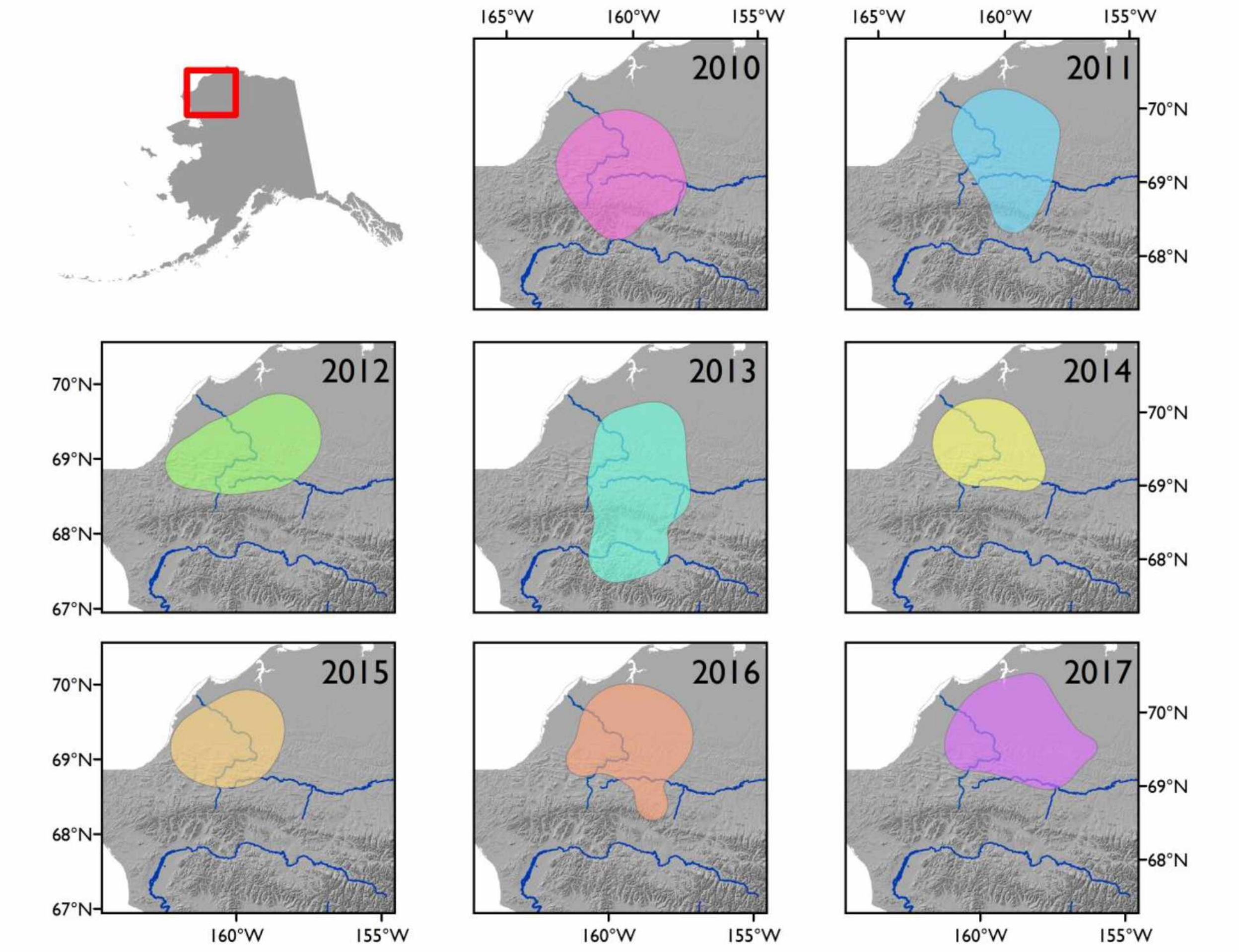

Figure 2.3: Annual calving areas of the Western Arctic Herd, 2010 – 2017, Alaska. Calving areas were delineated using the 95% contour of a kernel utilization distribution generated from parturition locations, which were inferred from GPS data.

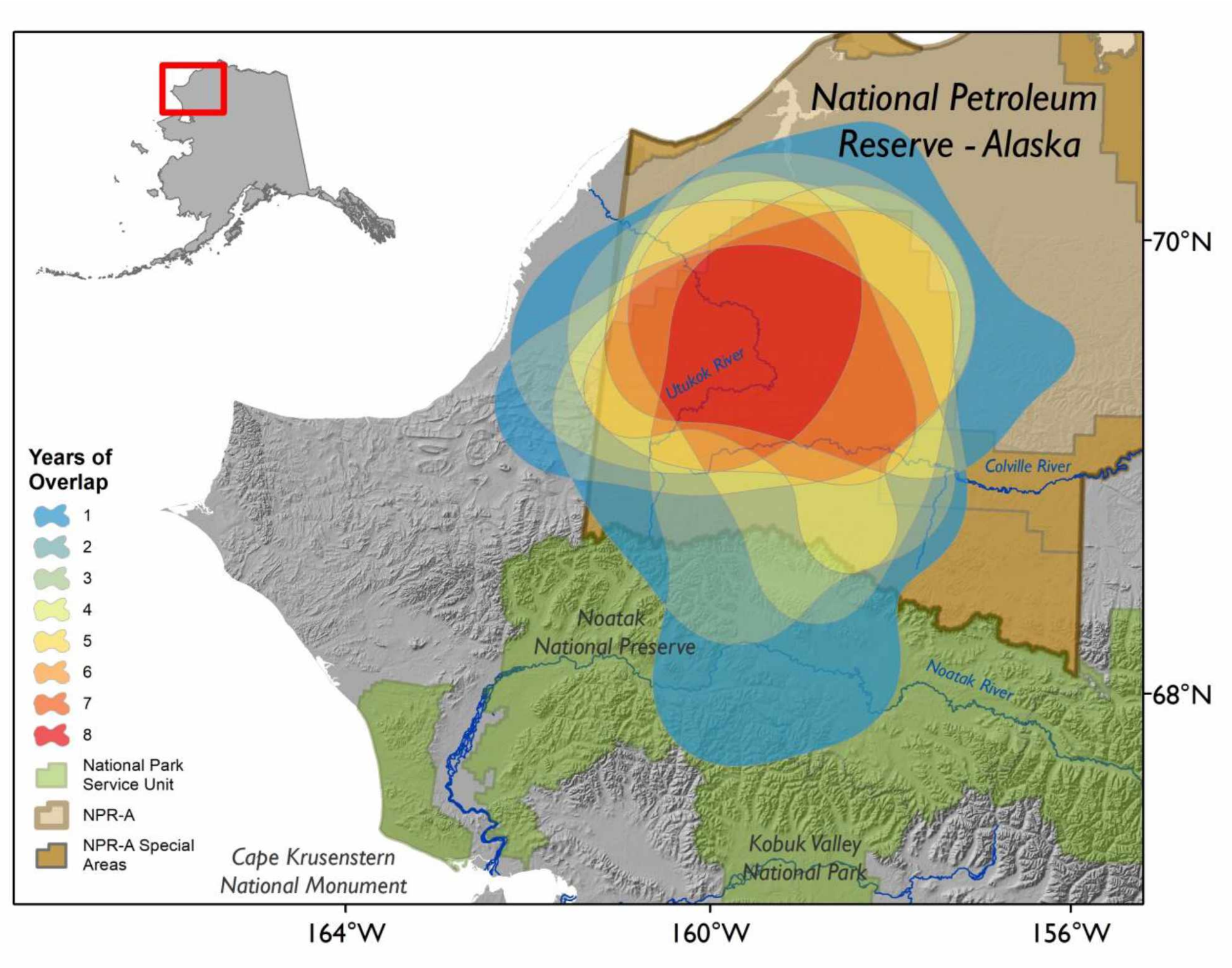

Figure 2.4: Overlap of all observed annual calving areas for caribou of the Western Arctic Herd, 2010-2017, Alaska. Calving areas were delineated using the 95% contour of a kernel utilization distribution generated from parturition locations, which were inferred from GPS data. Special Areas of the National Petroleum Reserve – Alaska (NPR-A; brown) include the Utukok River Uplands and Colville River Special Areas, as defined in the 2013 Integrated Activity Plan (BLM, 2012).

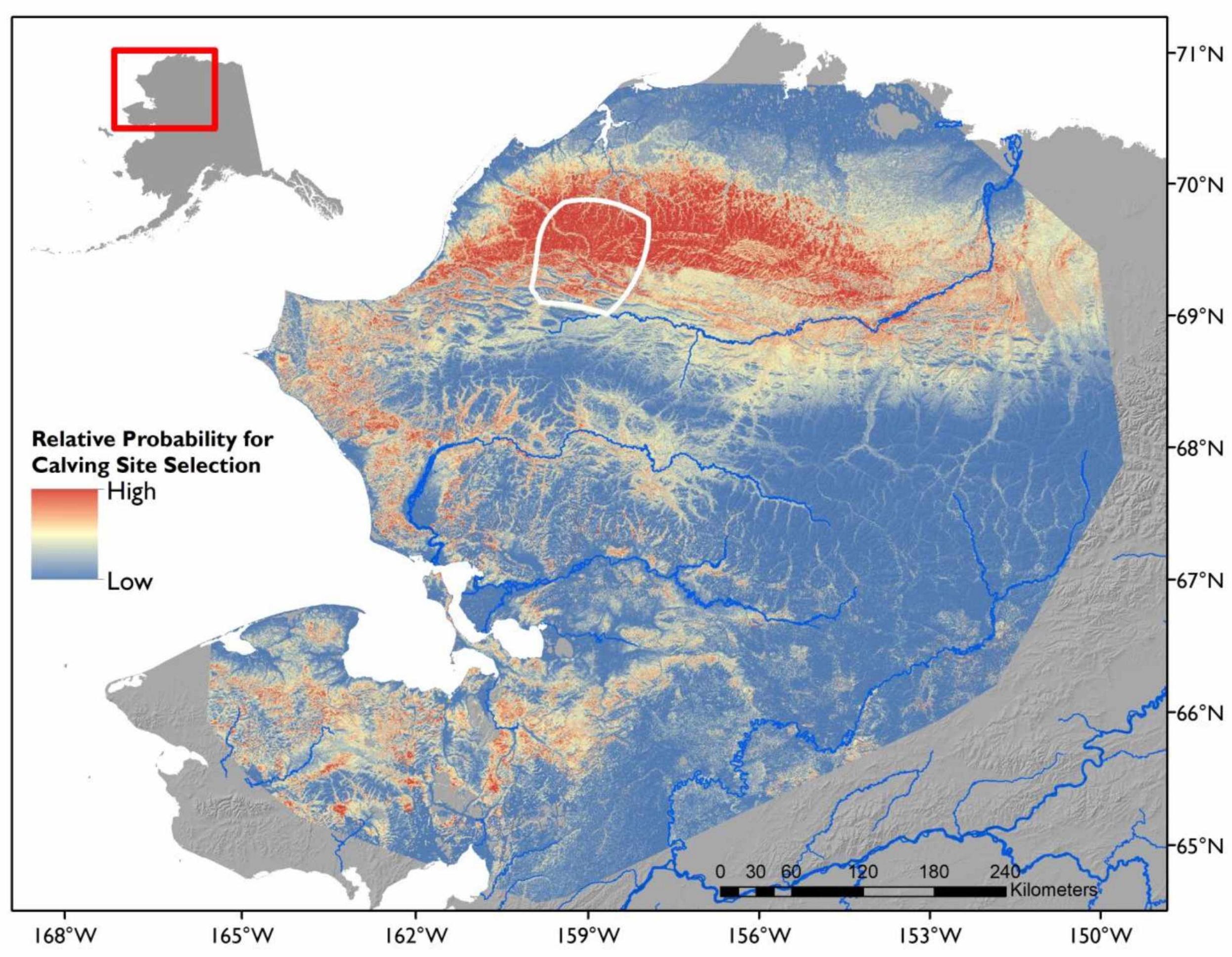

Figure 2.5: Predictive map of high-quality calving habitat for caribou of the Western Arctic Herd, Alaska. Map was made from the top performing resource selection function model including land cover, elevation, solar radiation, terrain ruggedness, and rate of NDVI increase from the week before to the week of average peak calving. Data for NDVI rate at peak calving were averaged across the eight years of NDVI composites from the analysis for map generation. White polygon indicates the core area in which calving was detected for all eight years in the study.

Table 2.1: Detected calving events based on movement data for the Western Arctic Herd (WAH), 2010 – 2017, Alaska. We excluded four events from the subsequent analyses (used 'WAH Only') because they were far outside of the typical calving area. Area of annual calving areas was determined from kernel densities generated from detected calving events. The bottom rows provides totals for calving events and the average median parturition date and calving area across all eight years.

Year	Calving Events	WAH Only	Median Calving Date	Calving Area (km^2)
2010	15	15	4-Jun	27,313
2011	23	23	5-Jun	24,261
2012	17	16	6-Jun	24,913
2013	20	20	8-Jun	33,487
2014	26	26	1-Jun	18,196
2015	30	30	3-Jun	19,110
2016	31	31	30-May	24,269
2017	52	49	3-Jun	26,630
	214	210	3-Jun	24,772

Table 2.2: Kernel overlap tests comparing annual calving areas of Western Arctic Herd caribou, 2010-2017, Alaska. Comparisons were performed for every interval ranging from one to seven-years apart, and the results for each interval can be read along the diagonal. A significant result ($p < 0.05$, one-tailed test; bold text) indicates less overlap than expected by random chance.

	2011	2012	2013	2014	2015	2016	2017
2010	0.096	0.064	0.160	**0.004**	**< 0.004**	**0.008**	**< 0.004**
2011		0.340	**0.048**	**< 0.004**	**< 0.004**	0.612	0.08
2012			**0.008**	**0.004**	**< 0.004**	0.556	0.136
2013				**< 0.004**	**< 0.004**	**< 0.004**	**0.004**
2014					0.112	**0.004**	**< 0.004**
2015						**< 0.004**	**< 0.004**
2016							0.608

Table 2.3: Coefficient estimates from the top RSF model for female caribou calving site selection, Western Arctic Herd, 2010 – 2017, Alaska. Elevation and terrain ruggedness were log transformed and all continuous variables were standardized (mean = 0; SD = 1). 'SRI' is the solar radiation index, 'VRM' is the vector ruggedness measure, and 'ΔNDVI.148' is the difference in NDVI values from the week prior to and the week of average peak calving for the study (May 21 – June 3). Coefficients presented in logit- space and from a no-intercept model (no reference class).

	Coefficient	β	**SE**
Land cover	Forest	-21.78	53.40
	Herbaceous	-4.99	0.21
	Shrub	-6.19	0.30
	Sparse	-5.57	1.02
	Elevation	-0.44	0.16
	Elevation^2	-1.58	0.20
	SRI	-1.96	0.33
	SRI^2	-1.55	0.43
	VRM	-0.17	0.10
	ΔNDVI.148	0.47	0.20
	Elevation: ΔNDVI.148	-0.43	0.12

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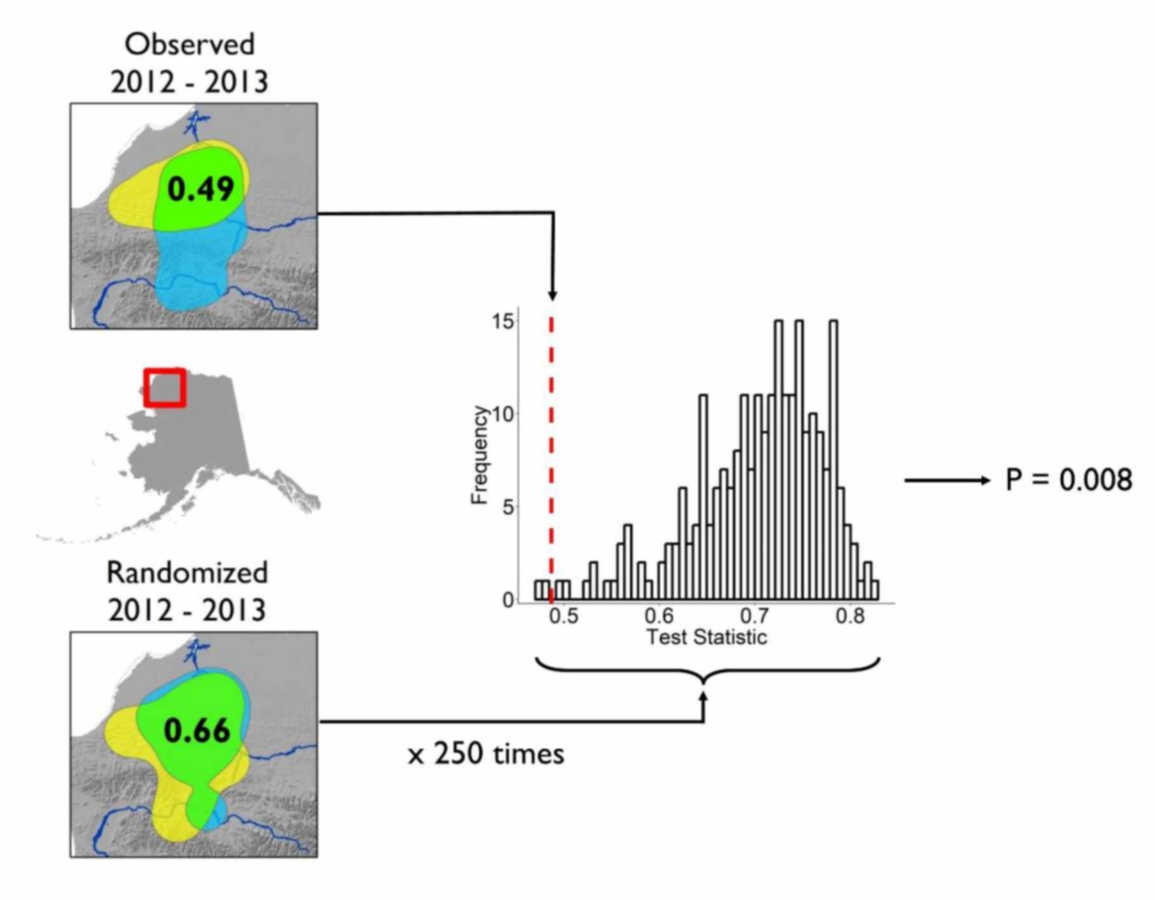
Appendix 2A: Chapter 2 supplemental tables and figures



Appendix 2A.1: Overview of kernel randomization process. For two years being compared, the year of calving is randomly assigned to the calving sites without replacement, 95% kernel utilization distributions are drawn and the area of the overlap divided by the larger of the two kernel areas is calculated. Repeated 250 times, this generates a distribution of the test statistic. The observed overlap is compared to this distribution, and the p-value is calculated as the proportion of random values which are less than the observed value (Breed et al. 2006). For 2012-2013, two random iterations of overlap were smaller than the observed overlap, indicating a p-value of 0.008 and significantly different calving areas between the two years.

Appendix 2A.2: Simplified land cover classification categories from Boggs et al. (2016) used in the resource selection analysis for Western Arctic Herd caribou calving areas, Alaska, 2010-2017, Alaska.

Category	Description	Count
Forest	Predominantly deciduous and spruce forest: *Betula papyrifera, Picea spp.*	11091
Herbaceous	Predominantly herbaceous cover, such as *Carex spp.* and *Eriophorum spp.*	35985
Shrub	Predominantly shrub cover: *Salix spp.*, low *Betula nana,*	24210
Sparse Vegetation	Predominantly lichen or limited vegetation	3324
Removed	Water, ice and snow, fire scar, bare ground, and flooded aquatic plant classification	5604
	Total	80214

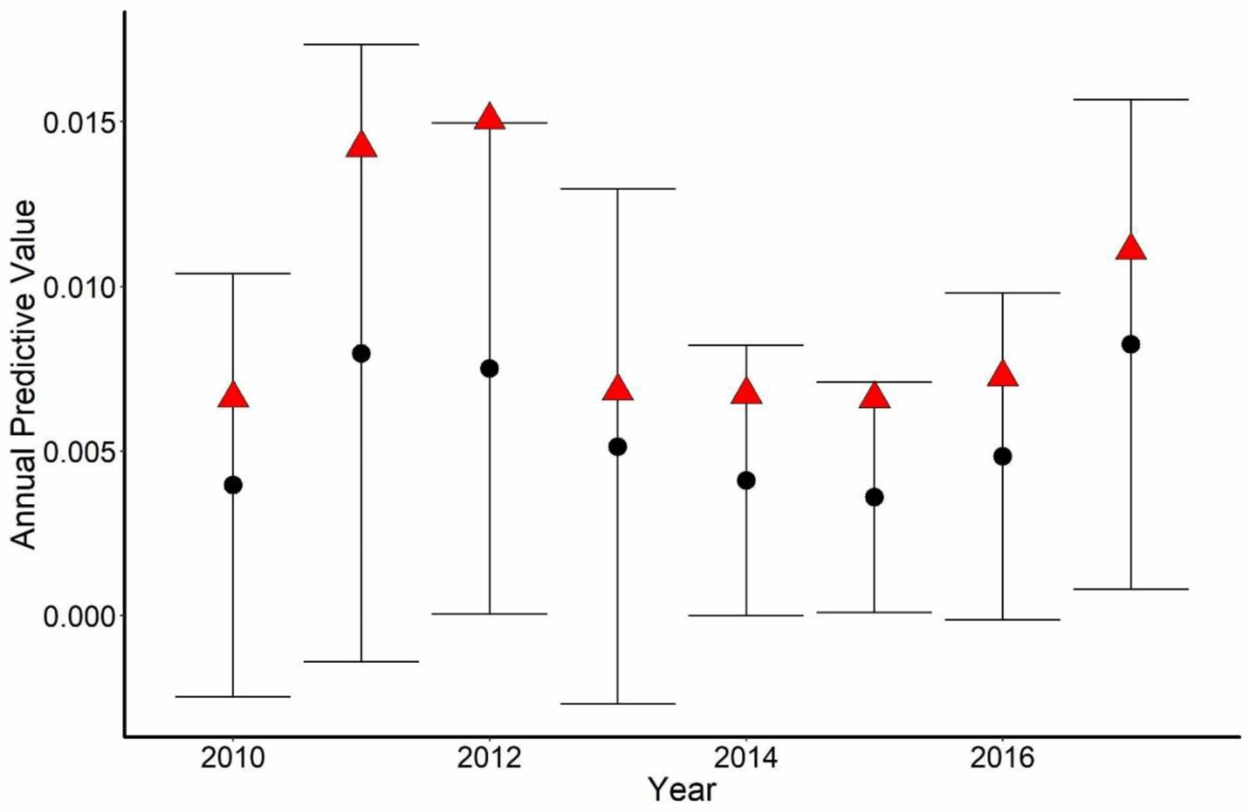
Appendix 2A.3: Generalized linear mixed-effects models used in testing the random effect structure of environmental covariates for selection for calving sites by female caribou of the Western Arctic Herd, 2010-2017, Alaska. Used calving sites (versus random locations) are the response and fixed effects include additive effects of landcover, quadratic terms for elevation and solar radiation index, and terrain ruggedness. 'NDVI' indicates the Normalized Difference Vegetative Index (NDVI) values for the specified 7-day composite across all years (NDVI.141 represents NDVI from day of year 141-147). 'Δ NDVI' indicates the difference in NDVI values between sequential NDVI composites, coded by the first day of the second composite (Δ NDVI.141 indicates the difference between the NDVI composites from day of year 141-147 and 134-140). NDVI metrics were also adjusted to match temporal coverage relative to peak calving that year, with "Pre.Calve", "Calve", etc. referring to the week specified that specific year. 'Snowfree' is the day-of-year a pixel was determined to be snow free in a given year.

Model Equation	K	AIC$_c$	Δ_i	w_i
Use ~ Fixed Effects + (Δ NDVI.148|Year)	12	2357.8	0.0	1.0
Use ~ Fixed Effects + (Δ NDVI.Calve|Year)	12	2387.0	29.2	0
Use ~ Fixed Effects + (NDVI.Pre Calve|Year)	12	2400.9	43.1	0
Use ~ Fixed Effects + (Δ NDVI.Pre Calve|Year)	12	2401.6	43.8	0
Use ~ Fixed Effects + (NDVI.141|Year)	12	2405.1	47.3	0
Use ~ Fixed Effects + (Δ NDVI.162|Year)	12	2409.0	51.3	0
Use ~ Fixed Effects + (Snowfree Date|Year)	12	2409.8	52.0	0
Use ~ Fixed Effects + (NDVI.148|Year)	12	2412.0	54.3	0
Use ~ Fixed Effects + (Δ NDVI.2wk Post Calve|Year)	12	2412.5	54.7	0
Use ~ Fixed Effects + (Δ NDVI.3wk Post Calve|Year)	12	2416.1	58.3	0
Use ~ Fixed Effects + (NDVI.Calve|Year)	12	2419.2	61.4	0
Use ~ Fixed Effects + (Δ NDVI.169|Year)	12	2419.4	61.6	0
Use ~ Fixed Effects + (Δ NDVI.155|Year)	12	2420.0	62.2	0
Use ~ Fixed Effects + (Δ NDVI.1wk Post Calve|Year)	12	2421.0	63.3	0
Use ~ Fixed Effects + (NDVI.169|Year)	12	2426.1	68.3	0
Use ~ Fixed Effects + (NDVI.3wk Post Calve|Year)	12	2426.1	68.3	0
Use ~ Fixed Effects + (NDVI.155|Year)	12	2428.6	70.9	0
Use ~ Fixed Effects + (1|Year)	10	2430.0	72.2	0
Use ~ Fixed Effects + (Δ NDVI.141|Year)	12	2430.1	72.3	0
Use ~ Fixed Effects + (NDVI.1wk Post Calve|Year)	12	2430.4	72.6	0
Use ~ Fixed Effects + (NDVI. 2wk Post Calve|Year)	12	2431.9	74.1	0
Use ~ Fixed Effects + (NDVI.162|Year)	12	2432.2	74.5	0

Appendix 2A.4: Generalized linear mixed-effects models used in testing for the fixed-effects structure for selection for calving sites by female caribou of the Western Arctic Herd, 2010-2017, Alaska. Used calving sites (versus random locations) are the response and all models include the random effects structure of a random slope for Δ NDVI.148 (difference between NDVI composites from day-of-year 148-154 and 141-147) and a random intercept of year. ‘Landcover’ is the four-level habitat classification (‘Forest’, ‘Herbasic’, ‘Shrub’, ‘Sparse Veg.’), ‘SRI’ is the solar radiation index, ‘VRM’ is the vector ruggedness measure, and ‘Snowfree Date’ is the day-of-year a pixel was determined to be snow free. Elevation and VRM were log transformed and all continuous covariates were standardized.

Appendix 2A.4: Continued

Model Equation	K	AICc	Δ_i	w_i
Use ~ Landcover + Elevation + Elevation^2 + Δ NDVI.148 + Elevation: Δ NDVI.148 + SRI + SRI^2 + VRM	14	2344.2	0	0.99
Use ~ Landcover + Elevation + Elevation^2 + SRI + SRI^2 + VRM + Δ NDVI.148	13	2354.5	10.3	0.01
Use ~ Landcover + Elevation + Elevation^2 + SRI + SRI^2 + Δ NDVI.148 + SRI: Δ NDVI.148 + VRM	14	2356.5	12.3	0
Use ~ Landcover + Elevation + Elevation^2 + Δ NDVI.148 + Elevation: Δ NDVI.148 + SRI + VRM	13	2378.7	34.5	0
Use ~ Landcover + Elevation + Elevation^2 + Δ NDVI.148 + Elevation: Δ NDVI.148 + SRI	12	2384.9	40.7	0
Use ~ Landcover + Elevation + Elevation^2 + SRI + VRM + Δ NDVI.148	12	2389.5	45.3	0
Use ~ Landcover + Elevation + Elevation^2 + SRI + Δ NDVI.148 + SRI: Δ NDVI.148	12	2398.3	54.0	0
Use ~ Landcover + Elevation + Elevation^2 + Δ NDVI.148 + Elevation: Δ NDVI.148	11	2402.7	58.5	0
Use ~ Landcover + Elevation + Δ NDVI.148 + Elevation: Δ NDVI.148 + SRI + SRI^2 + VRM	13	2455.2	111.0	0
Use ~ Landcover + Elevation + SRI + SRI^2 + VRM + Δ NDVI.148	12	2465.9	121.7	0
Use ~ Landcover + Elevation + SRI + SRI^2 + Δ NDVI.148 + SRI: Δ NDVI.148 + VRM	13	2467.8	123.6	0
Use ~ Landcover + Elevation + SRI + SRI^2 + VRM + Δ NDVI.148 + VRM: Δ NDVI.148	13	2467.9	123.7	0
Use ~ Landcover + Elevation + SRI + SRI^2 + Δ NDVI.148	11	2469.7	125.5	0
Use ~ Landcover + SRI + SRI^2 + VRM + Δ NDVI.148	11	2469.8	125.6	0
Use ~ Landcover + SRI + SRI^2 + Δ NDVI.148	10	2471.2	126.9	0
Use ~ Landcover + Elevation + SRI + VRM + SRI:VRM + Δ NDVI.148	12	2500.3	156.1	0
Use ~ Landcover + Elevation + SRI + Elevation:SRI + VRM + Δ NDVI.148	12	2505.7	161.5	0
Use ~ Landcover + Elevation + VRM + Elevation:VRM + Δ NDVI.148	11	2510.7	166.5	0
Use ~ Landcover + Elevation + SRI + VRM + Δ NDVI.148 + snowfree	12	2512.7	168.5	0
Use ~ Landcover + Δ NDVI.148 + Landcover: Δ NDVI.148 + Elevation + SRI + VRM	14	2518.3	174.1	0



Appendix 2A.5. Average predictive value for Western Arctic Herd calving sites by year (red triangles) from the top-performing model for calving site selection solved for each year. Average values of all pixels within the observed calving area for each year (black circles) are presented with one standard deviation (error bars), 2010-2017 Alaska.

Appendix 2A.6: Approximate estimates for wolf (*Canis lupus*) and brown bear (*Ursos arctos*) densities in the Western Arctic Herd range, Alaska.

Species	Area	Approx. Estimated Spring Density (wolf/1,000 km2)	Year	Method	Reference
Wolf	Coastal Plain	2	1977	Aerial Survey	Stephenson and James 1982
	Brooks Range Foothills	3	1977	Aerial Survey	Stephenson and James 1982
	Colville River (Eastern Foothills)	1 - 6	1992, 1994, 1998, 2008	Aerial Survey	Carroll 2012
	Kobuk River - South of Brooks Range	2 - 4	1987-1991	Aerial Survey	Ballard et al. 1997
	Gates of the Arctic National Park & Pres.	5	1987-1991	Aerial Survey	Adams et al. 2008

	Area	Approx. Estimated Density (adult bear/1,000 km2)	Year	Method	Reference
Brown Bear	Coastal Plain	1 - 2	1995	Meta-analysis	Carroll 1995
	Brooks Range Foothills	10 - 30	1995	Meta-analysis	Carroll 1995
	Brooks Range	10 - 20	1995	Meta-analysis	Carroll 1995
	Lower Noatak (Southern Brooks Range)	29 - 33	2008	Aerial Survey	Westing 2013

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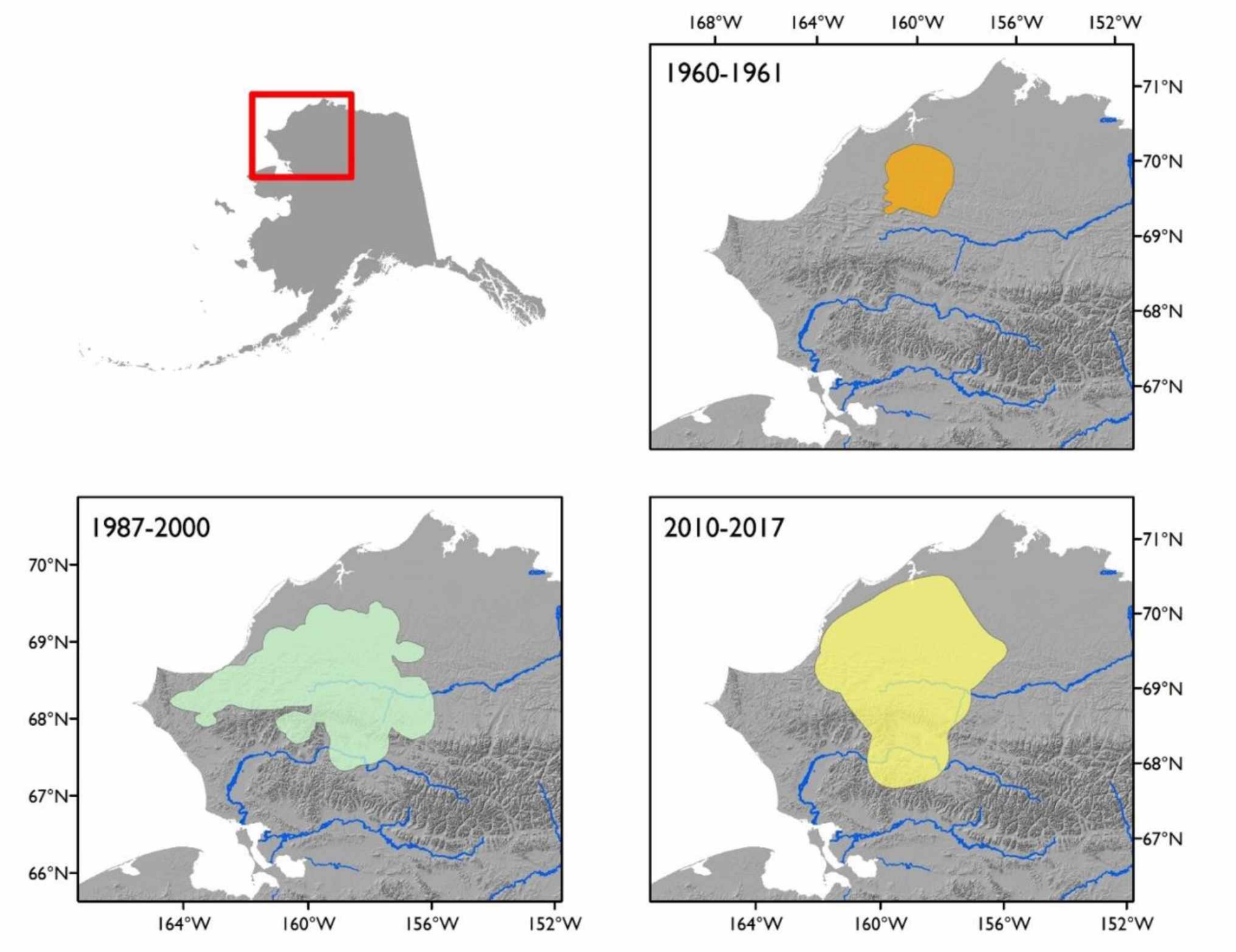

Appendix 2A.7: Maps of documented calving grounds of the Western Arctic Herd using different methodologies spanning the last 60 years, Alaska. 1960-61 was based on field observations from the ground by Lent (1966). 1987-2000 depicts the full extent of calving areas delineated using kernel techniques based on aerial surveys of tagged female caribou (Kellyhouse 2001). 2010-2017 depicts the full extent of calving areas from this study.

Chapter 3: Mechanistic movement models identify continuously updated autumn migration cues in Arctic caribou[3]

Abstract

Migrations in temperate systems typically have two migratory phases, spring and autumn, and many migratory ungulates track the pulse of spring vegetation growth during a synchronized spring migration. In contrast, autumn migrations are generally less synchronous and the cues driving them remain understudied. Our goal was to identify the cues that migrants use in deciding when to initiate migration and how this is updated while *en route*. To do so, we analyzed autumn migrations of Arctic barren-ground caribou (*Rangifer tarandus)* as a series of persistent and directional movements and assessed the influence of a suite of environmental factors. We fitted a dynamic-parameter movement model at the individual-level and estimated annual population-level parameters for weather covariates on 389 individual-seasons across 9 years. Our results revealed strong, consistent effects of decreasing temperature and increasing snow depth on migratory movements, indicating that caribou continuously update their migratory decision based on dynamic environmental conditions. This suggests that individuals pace their migration along gradients of these environmental variables. Whereas temperature and snow appeared to be the most consistent cues for migration, we also found interannual variability for the effect of wind, NDVI, and barometric pressure. The dispersed distribution of individuals in

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[3] Cameron, M.D., Eisaguirre, J.M., Breed, G.A., Joly, K., Kielland, K. 2021. Mechanistic movement models identify continuously updated autumn migration cues in Arctic caribou. Movement Ecology. **9**(54). doi: 10.1186/s40462-021-00288-0.

autumn resulted in diverse environmental conditions experienced by individual caribou and thus pronounced variability in migratory patterns. By analyzing autumn migration as a continuous process across the entire migration period, we found that caribou migration was largely related to temperature and snow conditions experienced throughout the journey. This mechanism of pacing autumn migration based on indicators of the approaching winter is analogous to the more widely researched mechanism of spring migration, when many migrants pace migration with a resource wave. Such a similarity in mechanisms highlights the different environmental stimuli to which migrants have adapted their movements throughout their annual cycle. These insights have implications for how long-distance migratory patterns may change as the Arctic climate continues to warm.

Introduction

"*A heavy fall of snow appears to be the signal for the start [of autumn migration]; if, however, it is followed by a prolonged spell of good weather, the animals either remain scattered about the flat country near Sandy Lake, or they continue slowly and in a very irregular way towards their winter quarters. With the advent of cold or snows the movement invariably becomes more or less general, and is extremely precipitate when the cold is intense or the snowfall unusually heavy.*"

— *A. Radclyffe Dugmore, 1913*

Movement is a fundamental adaptation by animals and migration is a prime example thereof to improve fitness in environments characterized by seasonally predictable spatiotemporal fluctuations in conditions (Fryxell and Sinclair 1988, Dingle and Drake 2007, Martin et al. 2018). The spatial scale of migration can vary drastically among or even within taxa. Regardless of distance, however, a complete migration trajectory is composed of a series of persistent and directional movements that emerge from a complex suite of physiological and behavioral adaptations (Dingle 1996, Åkesson and Hedenström 2007). An integral component for understanding how migratory patterns arise is to identify the cues that migrants use in deciding when to initiate migration and how to move while *en route*.

For many species, spring migrations are tightly linked to seasonal resource pulses (Merkle et al. 2016, Rivrud et al. 2016b, Aikens et al. 2017, 2020, Middleton et al. 2018). Under the Green Wave Hypothesis, migrants track fronts of emergent, high-quality vegetation to increase nutrient intake as spring progresses along the migratory route (van der Graaf et al. 2006, Bischof et al. 2012). Implicit to this paradigm of spring migration is that herbivores track these emergent vegetative fronts based on the perception of proximate resource quality, permitting migrants to move with resource gradients along the migration route. This is applicable to both temperate migrants in spring and tropical migrants at the beginning of the wet season (Boone et al. 2006, Holdo et al. 2009, Hopcraft et al. 2014). It does not, however, explain fall migrations in temperate migrants, some Arctic migrants in spring, nor the transition to the dry season for tropical migrants [e.g., 16]. Learning can influence migration and some migrants use their memory more than perception of proximal cues to navigate to distant destinations (Bracis and Mueller 2017, Abrahms et al. 2019, Merkle et al. 2019, Cameron et al. 2020). Regardless of the relative influence of reactive (perception-based) and proactive (learned) mechanisms in driving migration behavior, birthing generally coincides with peak resource quality (Dingle 1996, Newton 2008), and this likely constrains variability and enhances synchronization of spring migration timing and pace (Monteith et al. 2011, Debeffe et al. 2019, Gurarie et al. 2019).

In contrast to spring migration, autumn migration has been less studied and lacks a common, driving life history event (i.e. birthing) across taxa. Unlike the distinct pulse of vegetation green-up of spring, senescence of vegetation in autumn is prolonged and marked by a gradual decline of forage quality (Chapin et al. 1975). Perhaps owing to the greater observed variability in autumn phenology patterns during this time, factors influencing autumn migration have received but a fraction of the attention in research on spring migration (Gallinat et al. 2015) and autumn migration research still lacks a consistent theoretical framework across taxa.

For temperate ungulate species, vegetative productivity, snow, and temperature influence autumn migration to varying degrees. For example, autumn migrations in roe deer (*Capreolus capreolus*) and red deer (*Cervus elaphus*) populations across Europe were influenced by decreased vegetation productivity but not snow events (Peters et al. 2019). For red deer in Norway, most individuals left the summer range before the first snowfall, but snow appeared to trigger autumn migration for those that remained (Rivrud et al. 2016a). Moreover, migration initiation was associated with decreasing temperatures for females (Rivrud et al. 2016a) but not with vegetation senescence for either sex (Debeffe et al. 2019). Snow interacts with decreasing temperature in white-tailed deer (*Odocoileus virginianus*) autumn migrations, such that the first snow to occur in colder temperatures greatly increased the likelihood of migration (Nelson 1995). Snow and temperature have similar effects on the timing of autumn migration for mule deer (Brinkman et al. 2005, Monteith et al. 2011, Rittenhouse et al. 2015). These studies were all conducted for short-distance migrants and it is unclear if these relationships hold for long-distance migrants.

Populations of barren-ground caribou exhibit the longest terrestrial, non-volant migrations on the planet, for which round-trip distances between seasonal ranges can reach 1,350 km (Joly et al. 2019). Despite a long history of interest in the drivers of autumn migration in caribou, contemporary research on the topic is surprisingly sparse. In 1913, the early naturalist

Arthur Dugmore (Dugmore 1913) speculated that the winter's first heavy snowfall and cold temperatures initiated autumn migration for Newfoundland caribou based on local observations. Early fieldwork in Canada drew a connection between the first snowfall and autumn migration (Kelsall 1968) and later work in Newfoundland suggested that the first snowfall of 5 – 10 cm initiated autumn migrations (Bergerud 1974). Anecdotally, autumn migration for the Porcupine Herd in Alaska and far western Canada was once observed to begin following an early season (August) snowstorm (Whitten et al. 1986). Many of these early field observations also note that autumn migrations slow down or pause altogether if the weather turns mild after such snow events, but resumed when temperatures decreased or snow began to accumulate again (Dugmore 1913, Bergerud 1974, Whitten et al. 1986). More recently, temporal variation in autumn migration for the George River and Leaf River Herds in northern Canada was linked to conditions *en route*, with earlier arrival at the winter range associated with deeper snow at the destination (Le Corre et al. 2017). A promising avenue of migration research is to precisely determine how long-distance terrestrial migrants, such as caribou, respond to experienced environmental conditions throughout migration, given inherent annual environmental variability and the dispersed nature of caribou groups in autumn (Kelsall 1968).

Previous studies have typically treated autumn migration, and the initiation of it, as a single discrete event, and applied analyses designed to relate environmental covariates to the timing of the start and end of migrations [e.g., 23,27,37,38]. This approach explicitly assumes that once initiated, migration continues to its completion. Yet, many long-distance avian migrants (Newton 2008), as well as migratory ungulates such as mule deer (Sawyer and Kauffman 2011), red deer (Debeffe et al. 2019), and elk (*Cervus canadensis*) (Paton et al. 2017), use stopovers (pauses along the migration route) to replenish reserves, sometimes for many weeks. A promising new concept that incorporates variability in movement along a complete migration trajectory is “migratory pacing,” in which an individual continuously adjusts its behavior based on environmental conditions experienced *en route* (Eisaguirre et al. 2019). Migratory pacing incorporates stopover behavior as an example of a distinct change in migration behavior in response to resources, while also incorporating more subtle changes in movement such as different movement rates. Green wave surfing in spring is an example of this behavior in ungulates, in which migrants pace migration to match the wave of spring resource quality (Rivrud et al. 2016b, Aikens et al. 2020). In contrast, how this concept applies to autumn migration in ungulates remains largely unexplored despite a long history of field observations and anecdotes suggesting a similar pacing-type pattern in many taxa. Recent developments in statistical movement models permit characterizing behavioral indices from GPS location data (Hooten et al. 2017) and enables relating these behavioral states to experienced environmental conditions (Eisaguirre et al. 2019, Jonsen et al. 2019).

We propose that a complete seasonal migration consists of a series of persistent, directional movements (hereafter simply “migratory movements”), that may or may not be interspersed with bouts of non-oriented movement (akin to stopovers) occurring at the individual level (Dingle 1996, Dingle and Drake 2007). We test for effects of continuously varying environmental characteristics on autumn migratory movements evaluated as dynamic parameters of a correlated random walk movement model. We examine these metrics in the Western Arctic Herd, a population of migratory, barren-ground caribou in northwest Alaska. We combine recently developed methods to test for effects at the individual level and scale these insights up for population-level inference (Hooten et al. 2016, Eisaguirre et al. 2019). We hypothesized that 1) autumn migratory movements for caribou are a function of contemporaneous, experienced environmental conditions, 2) migration is paced based on a continuous decision-making process, such that if conditions change, movements are accelerated, adjusted, or paused, and 3) these responses are highly consistent throughout the population and across the study period despite the widely disaggregated nature of caribou in autumn. As we show, environmental conditions that are strongly affected by climate change alter migratory behavior, and we discuss our findings in relation to the potential for a continued change to alter long-distance terrestrial migrations in the Arctic.

Methods

Study population

We analyzed data from 175 individual collared caribou from the Western Arctic Herd in northwest Alaska, which annually range from approximately 65° to 71° N and 166° to 150° W. In autumn, the herd generally migrates from the arctic tundra of Alaska's North Slope, through the rugged Brooks Range with peaks over 2,000 meters, to lichen-rich uplands and boreal forests south of the mountain range where they spend the winter. Wintering areas vary by year and the herd is typically broadly dispersed at this time (Joly and Cameron 2020, Joly et al. 2021). Autumn migration timing varies by year as well, with a trend toward later migration in recent years and proportions of the population not fully migrating south (Dau 2015, Joly and Cameron 2020). From 2009 - 2018, GPS collars (Telonics, Mesa, AZ) were deployed on adult females using procedures approved by the State of Alaska Institutional Animal Care and Use Committee (permits 2012-031R and 0040–2017-40). Deployments occurred during autumn migration as caribou crossed the Kobuk River in Kobuk Valley National Park. Methods for collar deployment are described elsewhere (Dau 1997, Joly et al. 2012). Most collars were set to record locations every 8 hours, but some more recently deployed collars recorded locations every 2 or 4 hours. For our analysis, the data were subsampled to 8-hour location intervals for consistency across all individuals and years. During the study period, the herd size decreased from 355,000 animals in 2009 (Dau 2015) to 244,000 in 2019 (Alaska Department of Fish and Game 2019).

We analyzed GPS data between August 15 and December 31 for 2010 – 2018, resulting in nine autumn migration periods. We used 389 individual-season datasets across these 9 years, ranging from 28 in 2010 to 66 in 2016 (Appendix 3A.1). Movement rates associated with insect avoidance in mid-summer are the greatest of the year (Dau 2015, Joly et al. 2020); consequently, we used August 15th as the beginning date for the analysis period based on preliminary investigations of the data which suggested that insect harassment season could extend to mid-August. Winter is characterized by the slowest and most localized movements of the year, and migration is complete by the end of the year (Dau 2015, Joly et al. 2020), so, we ended the analysis period at the end of December. We only used data for which the collar was active for the entire period, and thus excluded individual-seasons where the individual died, was collared during the migratory period, or for which the individual had less than half of the expected GPS locations due to missing collar data (often due to poor satellite network connectivity).

Movement model

To characterize the behavior of each caribou along its GPS movement track and understand how it was related to contemporaneous environmental factors the individual experienced, we fit a continuous-time movement model with a dynamic behavioral parameter similar to that of Eisaguirre et al. (Eisaguirre et al. 2019). The movement process for the jth individual is given by:

$$\mathbf{x}_{j,i}|\mathbf{x}_{j,i-1},\mathbf{x}_{j,i-2} \sim \mathcal{N}\left(\mathbf{x}_{j,i-1} + \gamma_{j,i}\frac{\Delta t_{j,i}}{\Delta t_{j,i-1}}(\mathbf{x}_{j,i-1} - \mathbf{x}_{j,i-2}),\ \Delta t_{j,i}\sigma^2_{x,j}\mathbf{I}\right), \quad (1)$$

where $\mathbf{x}_{j,i}$ is a cartesian coordinate vector of the individual's location at time $t_{j,i}$ and **I** is the identity matrix**.** The model estimates a continuous, time-varying latent variable $\gamma_{j,i} \in [0,1]$. Higher values of $\gamma_{j,i}$ indicate persistent, directional movements and reduced values indicate tortuous, encamped movements (Breed et al. 2012, Auger-Méthé et al. 2017, Eisaguirre et al. 2019, Jonsen et al. 2019). We can therefore interpret higher estimated values of $\gamma_{j,i}$ as an indicator of the degree of migratory behavior expressed along the trajectory. Within the model, $\gamma_{j,i}$ is specified as a linear combination of environmental covariates associated with each location:

$$\text{logit}(\gamma_{j,i}) \sim \mathcal{N}(\mathbf{Z}^T_{j,i}\boldsymbol{\beta}_j,\ \Delta t^2_{j,i}\sigma^2_{\nu,j}), \quad (2)$$

representing the effect of the environment on the animal's movement pattern. Here, $\mathbf{Z}_{j,i}$ is a vector that contains the environmental covariates associated with each $\mathbf{x}_{j,i}$, and $\boldsymbol{\beta}_j$ is a vector that weights the effects of those covariates on $\gamma_{j,i}$. Full model statement and details are provided in Appendix 3B.

We estimated individual model parameters in a Bayesian framework with Hamiltonian Monte Carlo (HMC) using Stan version 2.19.1 (Carpenter et al. 2017), program R version 3.6.2 (R Core Team 2019), and the package "RStan" version 2.19.3 (Stan Development Team 2020). The model was fit to each individual season with 3 chains of 100,000 HMC iterations, including 50,000 for burn-in, and thinned by 10 (see Appendix 3C for implementation). Since the initial stage of our analysis was based at the individual level, we scaled our inference up to the annual population level with recursive Bayesian computation using a second stage Markov chain Monte Carlo (MCMC) algorithm (Lunn et al. 2013, Hooten et al. 2016, 2019, Hooten and Hefley 2019). We modeled the population-level coefficient $\beta_{p,k}$ for the kth covariate as:

$$\beta_{j,k} \sim \mathcal{N}(\beta_{p,k}, \sigma^2_{\beta,k}). \tag{3}$$

We assigned an informative prior centered on zero to each $\beta_{p,k}$ to ensure that any apparent effects of environmental covariates detected were relatively strong (see full model statement in Appendix 3B). To ensure that our results were not heavily weighted by over-representing winter movements in the dataset (that is, movements that were made after migrations had ended), we repeated the analysis and fit models to a truncated movement time-series (August 15 to November 15) and compared these to the original results.

Environmental data

We attributed environmental variables to the caribou location data using the track annotation service Env-DATA (Dodge et al. 2013) on Movebank (www.movebank.org). For each location, we obtained time-specific point estimates for air temperature (°C), snow accumulation (meters), wind speed (m $\sec^{-1}$), and standardized atmospheric pressure (Pa). These were derived from the North American Regional Reanalysis (Commerce 2005) and are produced at 3-hour intervals and 0.3 degree spatial resolution. We also included an index of vegetation greenness, the Normalized Difference Vegetation Index (NDVI), as measured from the MODIS satellite platform for each location with a 250-meter resolution (Didan 2015). NDVI was derived from 16-day composites and the best image within that time span was used as the value. We set NDVI values to 0 for all locations which had measured snow accumulation, because changes in snow cover drives a large part of the seasonal NDVI patterns in Arctic environments (Swanson

2021). Bilinear interpolation was used for all attributes in Env-DATA and weather reanalysis data have been found to have good agreement with weather station data collected in the area of the herd (Lindsay et al. 2014, Lader et al. 2016). Correlations between environmental variables were all less than 0.7 and all variables were standardized to mean zero and unit variance prior to model fit.

To test our hypothesis that migratory behavior is a function of experienced environmental covariates, we fit one model that included the main effects for each environmental covariate. We included an interaction between temperature and snow depth to test for potential additional effects of snow at a given temperature (Nelson 1995). The expected value of movement persistence was thus modeled as:

$$\begin{aligned} E(\mathrm{logit}(\gamma_{j,i})) = \boldsymbol{Z}_{j,i}^{T}\boldsymbol{\beta}_j &= \beta_0 + \beta_1 \cdot \mathrm{Temp}(x_{j,i}) + \beta_2 \cdot \mathrm{Snow}(x_{j,i}) \\ &+\beta_3 \cdot \mathrm{Temp}(x_{j,i}) \cdot \mathrm{Snow}(x_{j,i}) + \beta_4 \cdot \mathrm{Wind}(x_{j,i}) \\ &+\beta_5 \cdot \mathrm{NDVI}(x_{j,i}) + \beta_6 \cdot \mathrm{Pressure}(x_{j,i}). \end{aligned} \tag{4}$$

We interpreted multiple years of 90% credible intervals that did not overlap zero for each year of the population-level model to indicate effects of the environmental covariate (Gelman and Carlin 2014, Kruschke 2015). To visualize our results at the landscape scale, we downloaded environmental rasters of these given covariates at three characteristic periods (early-, middle-, and late-autumn) in 2010. We then mapped expected movement patterns over the landscape using the equation $\hat{\gamma}_i = logit^{-1}(\boldsymbol{Z}_i{}^{\boldsymbol{T}}\hat{\boldsymbol{\beta}}_p)$, where $\hat{\boldsymbol{\beta}}_p$ represents the posterior mean for the population-level coefficients and $\boldsymbol{Z}_i{}^{\boldsymbol{T}}$ the vector of observed environmental conditions in each pixel at a representative date and time . Stan and R code used to implement our approach are provided in Appendices 3B, 3C, and 3D.

Results

Across all 9 years, the combination of snow and temperature had the strongest influence on autumn migratory movements, with estimated coefficients of the interaction term and 90% credible intervals (CI) that were consistently above zero (Figure 3.1). Chain mixing and potential scale reduction statistics ($\hat{R}$) less than 1.01 for all 389 individual season models indicated convergence to the posterior distribution (Carpenter et al. 2017).

Interpretation of the main effects of temperature and snow on migratory movement was nuanced due to the consistently significant interaction term (Figure 3.1, Appendix 3A.2) and was best interpreted through comparing the effect to migratory movement across a range of both temperature and snow values (Figure 3.2). When snow was absent, decreasing temperatures alone resulted in increased migratory movement for all but one year, suggested by higher $\gamma_{j,i}$ at low temperatures (Figure 3.2). Accumulating snow depth modulated this relationship between temperature and migratory movement, such that snow accumulation at relatively warmer temperatures in autumn resulted in higher $\gamma_{j,i}$. This was pronounced for the first snow event and early accumulation of snow depth, which were consistently associated with elevated $\gamma_{j,i}$, such that individuals typically exhibited more persistent movements within 10 days of early season snow events (Figure 3.3; Appendix 3A.3). Notably, migratory movements were clearly altered as environmental conditions moderated in the days following such events, and animals often exhibited more localized, slower movements (decreased $\gamma_{j,i}$) after reaching snow-free areas farther south (e.g., Figure 3.3; Appendix 3A.4). Snow appeared to become a hindrance to movement as it accumulated, such that deep snow (e.g., more than 40 cm) and cold temperatures (such as -20 to -30°C) were associated with the most encamped movement behaviors (Figure 3.2;

Figure 3.3). For 8 of 9 years, the relationship between temperature and $\gamma_{j,i}$ inverted at an average depth of 12 cm (range 2 [2010] – 21 cm [2017]).

Wind, NDVI, and air pressure had less pronounced and more variable effects on migratory movements. Windy conditions were generally associated with increased migratory movements, as the estimated coefficient was positive for 7 out of 9 years (2010 and 2012-2017). However, evidence was weak as of those, only two had 90% CIs that did not include zero (Figure 3.1; Appendix 3A.5). Increased migratory movements were generally associated with decreasing NDVI values, with negative coefficients in 6 years (90% CI below zero for 3 years; Figure 3.1; Appendix 3A.5). Barometric pressure exhibited a generally positive but again weak effect on migratory movements, with 6 years of positive coefficients and of those, two with a 90% CI that did not include 0 (Figure 3.1; Appendix 3A.5). These patterns among environmental variables and migratory movement were consistent, albeit less pronounced, when models were fitted to the truncated timeseries data that ended Nov. 15 (Appendices 3A.6 & 3A.7).

When visualizing the spatiotemporally explicit movement patterns predicted from our model, the result was extremely heterogenous expected migratory movements that were highly dependent upon where animals were located on the landscape and were temporally dynamic (Figure 3.4). The degree of expected migratory movement at a given time and place was a function of the entire suite of environmental factors experienced by individuals. Once snow depth increased to mid-winter depths, movements were predicted to become encamped and homogeneous in the majority of the range regardless of how far south individuals were (Figure 3.4) as individuals ceased migration and entered an overwinter movement regime.

Discussion

More than a century after Dugmore (Dugmore 1913) postulated that accumulating snow, decreasing temperatures, and changes in weather affected autumn migration in caribou, we used modern technology and statistical approaches to quantify the dynamic response by caribou to localized snow and temperature conditions and determined that migration is continuously reassessed throughout the migratory period. Whereas the response to these variables scaled to a consistent population-level pattern (Figure 3.1, Figure 3.2), the dispersion of individuals across a wide geographic area resulted in notable variation in migratory behavior among individuals for any given time due to differences in conditions across the region (Figure 3.4). Our findings suggest that autumn migration can be envisioned as the recently introduced concept of migratory pacing, in which individuals continuously adjust migratory behavior based on experienced *in situ* environmental conditions (Eisaguirre et al. 2019), rather than a single discrete action (i.e. "on/off"). Migratory pacing can include stopover behavior and unifies a set of ideas describing migration patterns across the spring and autumn legs of the complete migratory cycle. While many temperate migrants pace spring migration with the flush of resource quality across the landscape (i.e. 'green wave surfing'; Merkle et al. 2016, Rivrud et al. 2016b, Aikens et al. 2017, 2020, Middleton et al. 2018), senescence in autumn is a gradual and protracted decline of vegetation quality that largely ends when snow accumulates (Swanson 2021). In contrast to spring migration, our results indicate that migrants largely pace autumn migration with respect to indicators of the approaching winter, similar to the 'frost wave' suggested by Xu and Si (Xu and Si 2019). For caribou, these findings are congruent with early field observations which speculated such a mechanism (Dugmore 1913, Bergerud 1974, Whitten et al. 1986).

Our findings have two important implications for the migratory patterns of populations. The first is that experienced environmental conditions across a population prior to and during migration may exhibit a wide range depending on the spatial distribution of individuals. This is pronounced in caribou, as they are typically dispersed in late summer (Kelsall 1968, Russell et al. 1992, Person et al. 2007), and this is especially true for the Western Arctic Herd (Dau 2015, Joly and Cameron 2020; Figure 3.4). Secondly, individuals respond to proximate environmental cues in a common manner despite this widespread spatial dispersion of groups. This finding is similar to that for golden eagles (*Aquila chrysaetos*), which use thermal uplift as a flight subsidy along a variety of autumn (and spring) migration routes (Eisaguirre et al. 2019), as well as elk herds in the Greater Yellowstone Ecosystem, which rely on similar environmental cues for migration timing despite ranges being spatially distinct (Rickbeil et al. 2019). Our findings indicate that caribou generally exhibit a common behavioral response to similar proximate weather conditions (snow and temperature) they experience. One notable commonality was elevated movement persistence after the first snowfall event of the season (such as the individual depicted in Figure 3.3), which appeared to be representative of the general response we found in our population-level results. The dispersed distribution of the herd in late summer results in individuals experiencing different environmental conditions which, in turn, leads to different individual-level migratory decisions. These then scale up to the observed variability and asynchrony in migratory patterns (this study) observed at the population level (Dau 2015, Joly and Cameron 2020). More generally, the consistent population-level responses to environmental cues that we detected suggests that variability in environmental conditions experienced across a population's distribution in a given year can explain why autumn migrations can exhibit such wide variability in timing across many taxa (Cagnacci et al. 2011, Monteith et al. 2011, Debeffe et al. 2019).

Assessing the influence of the environment along the entire migration trajectory provides a mechanistic link between broad-scale weather patterns and migration, suggesting that changes in the prevailing climate may result in changes to migratory patterns. In the range of the Western Arctic Herd, the climatic trend has been for warmer autumns (Walsh and Brettschneider 2019) and has coincided with progressively later autumn migrations over multiple decades (Dau 2007, 2015, Joly and Cameron 2020). Shifts in autumn migration timing have been linked to environmental trends in other species as well, such as for Chukchi Sea Beluga whales (*Delphinapterus leucas*) that now migrate later as seasonal sea-ice formation has become delayed (Hauser et al. 2017). Timing of elk autumn migration in the Greater Yellowstone Ecosystem was found to be highly plastic from 2001 to 2017 and corresponded to changes in snow patterns for many of the herds (Rickbeil et al. 2019). Understanding how climate influences migration behavior is important for predicting how long-distance migrant populations may or may not respond adaptively to future climate change (Shaw 2016). This is especially pertinent for rural Arctic subsistence communities, whose cultural identity and way of life date back to at least 10,000 years and rely on harvesting caribou during migration (Anderson 1988). Given the rapid changes currently being observed in the Arctic and even greater ones predicted with climate change (Hinzman et al. 2005, IPCC 2014), our results indicate that caribou migrating long-distances, and perhaps other long-distance migrants, are highly plastic in their decision of when and at what pace to migrate, and that further migration delays could occur if the warming trend continues.

In the later part of the season we analyzed (i.e., late November – December), we found that movement persistence consistently reached its lowest levels as winter conditions set in, which were characterized by deep snow levels and cold temperatures. This aligns with documented increased costs of winter movements, given that the energy expenditure to move through snow increases exponentially with increased sinking depth (and thus snow depth; Fancy and White 1987). Winter movement rates progressively diminish throughout winter (Joly et al. 2020) and concurrently, metabolic rates and energy requirements in caribou decrease (Boertje 1985). These are some of the numerous adaptations by northern species to survive the long winter months (White et al. 1987) and highlight the importance of incorporating snow metrics in studies of animal movements in northern ecosystems (Pruitt 1959, Boelman et al. 2019).

Our primary finding that migratory movements are a response to dynamic and localized temperature and snow patterns is consistent with previous research for species exhibiting shorter and less demanding migrations, such as mule deer (Brinkman et al. 2005, Monteith et al. 2011, Rittenhouse et al. 2015), white-tailed deer (Nelson 1995, Sabine et al. 2002), elk (Rickbeil et al. 2019), and red deer (Rivrud et al. 2016a). We also found evidence that vegetation and meteorological conditions can influence migratory movements to lesser degrees. For most years observed, we found a negative relationship between NDVI and migratory movements, indicating caribou travelled more persistently as vegetation senesced and, conversely, were more localized when animals encountered greener vegetation (Figure 3.1; Appendix 3A.5). This relationship was not likely to have been driven by snow accumulation (when NDVI values became zero) given the variability in response across years we observed. Our finding that autumn migration timing is related to fall senescence is similar to European populations of roe and red deer, for which migration timing is linked to decreasing plant productivity, as measured by NDVI (Peters et al. 2019). Under the migratory pacing concept, individuals may delay not only the start of autumn migrations but also slow down or pause migration *en route* (stopover) if they encounter improved foraging conditions. This is similar to mule deer, for which stopover sites have higher NDVI values than neighboring migration corridors (Sawyer and Kauffman 2011). Such a tactic could prolong access to good foraging conditions before winter sets in and reduce competition on the winter range by delaying arrival as long as possible. We also found that migratory movements were more persistent on windy, high pressure days in some years, suggesting that migration speed may be modulated by fair weather conditions. Other, less predictable meteorological conditions not considered here, such as rain on snow events, are known to influence caribou movements as well (Bieniek et al. 2018). Autumn migration has been observed during warm weather in the past (Dau 1997), similar to an anomalous year in our data, and this highlights the need for further research into autumn migration.

Conclusions

By treating migration as a series of directional and persistent migratory movements and classifying these as a continuous metric, we show that decreasing temperature and increasing snow depth influence when and how caribou migrate in autumn. These quantitative findings align with the early observations of naturalists and field biologists that have accrued over the last century. Because individuals of this caribou herd are dispersed across a large spatial extent in autumn, variability in experienced conditions resulted in a wide range of observed migration patterns. This mechanism of pacing autumn migration based on indicators of the approaching winter is analogous to the more widely researched mechanism of spring migration, when many migrants pace migration with a resource wave, and highlights the different environmental stimuli migrants have adapted to respond to throughout their annual cycle.

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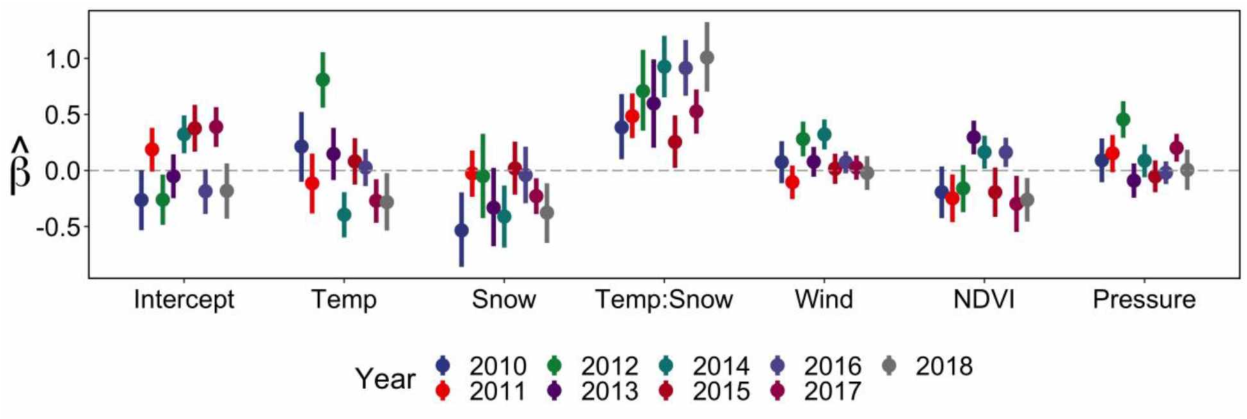

Figure 3.1: Annual estimated population-level coefficients (points) and 90% credible intervals (bars) for the effect of environmental variables on migratory movements ($\hat{\gamma}_i$) from the dynamic-parameter correlated random walk model. Environmental variables were standardized and the model was fitted to individual tracks of caribou data from the Western Arctic Herd, Alaska, 2010-2018.

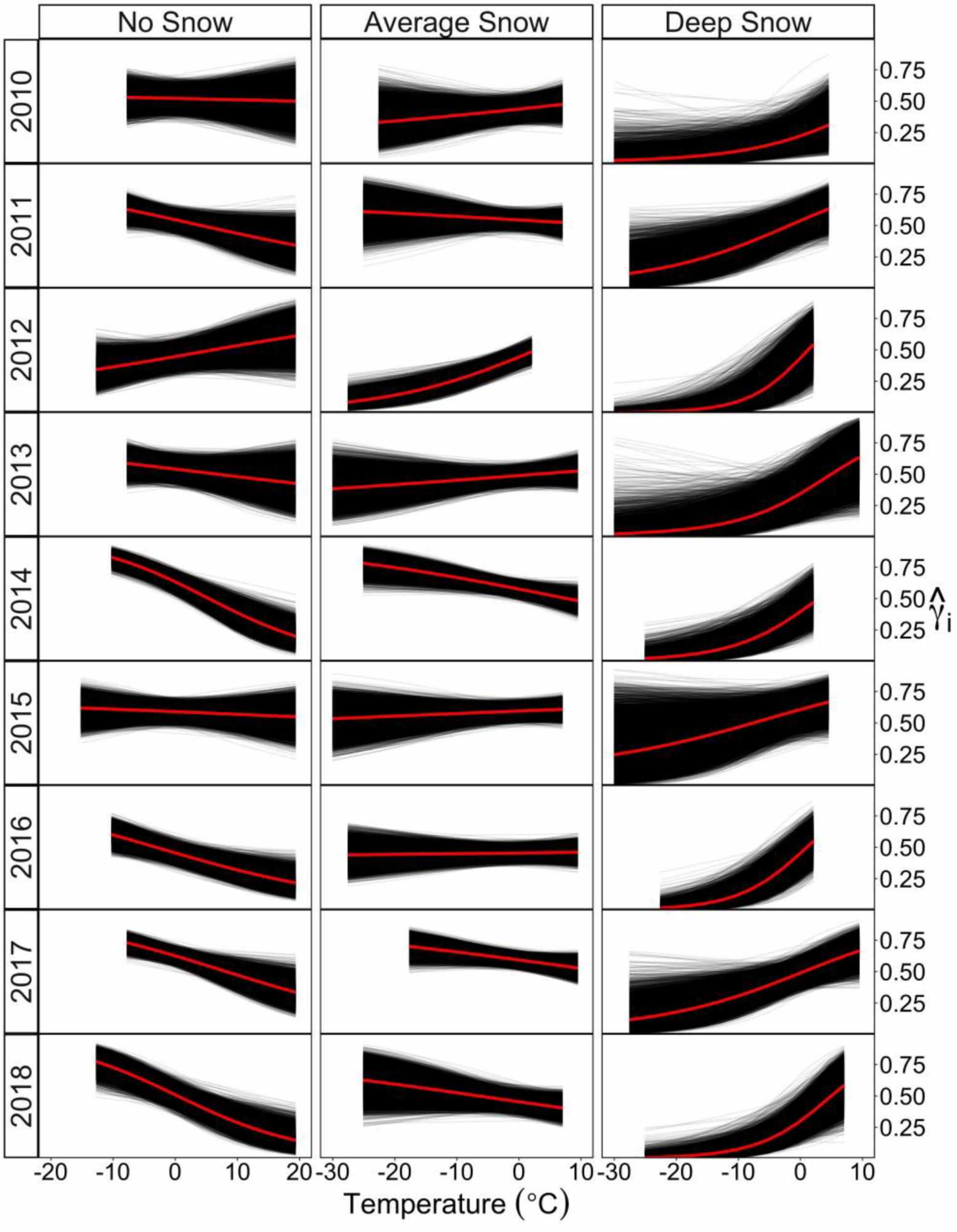

Figure 3.2: The effect of temperature at three different snow depth levels for each year from the population-level fit of the dynamic-parameter correlated random walk movement model fitted to caribou location data of the Western Arctic Herd, Alaska, 2010-2018. For each year, the predicted effect of temperature (x-axis) on the movement parameter ($\hat{\gamma}_i$; y-axis) is plotted across 3 levels of snow depth (no snow = 0 cm, average snow = 11 cm, and deep snow = 46 cm). Each black curve is given by the equation $\hat{\gamma}_i^{(l)} = logit^{-1}(\boldsymbol{Z_i}^{\boldsymbol{T}}\hat{\boldsymbol{\beta}}_{\boldsymbol{p}}^{(l)})$ for the lth Markov-Chain Monte Carlo iteration (termed posterior realizations), and the red line indicates the mean. Annual plots are cut off to the observed range of values for each year.

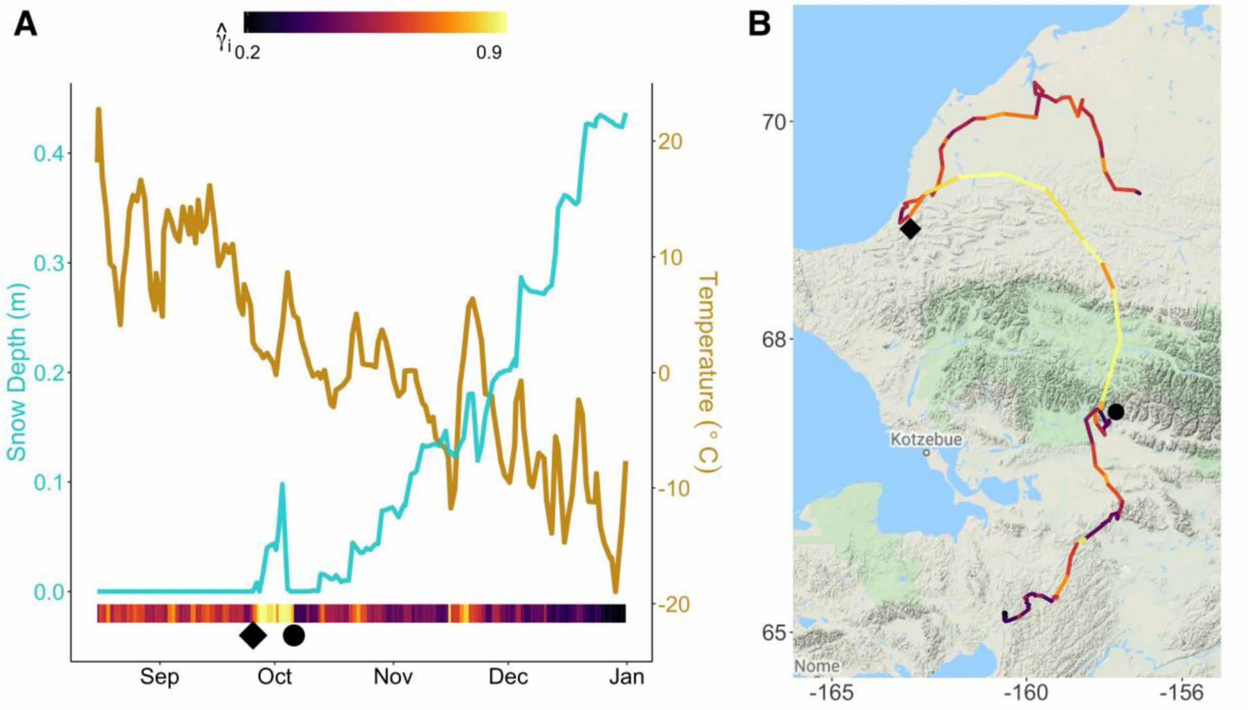

Figure 3.3: Environmental conditions experienced by an individual caribou of the Western Arctic Herd (A) and movement track from Aug 15 – Jan 1, 2010 (B). Panel A indicates the snow depth (blue) and temperature (gold) at each location as extrapolated from the North American Reanalysis Model (National Centers for Environmental Prediction 2005). Estimated migratory movement ($\hat{\gamma}_i$) for the individual is illustrated in the bottom bar from dark blue (low persistence and localized movements) to yellow (high persistence and directional movements). Panel B illustrates the measured caribou movements for the same time period and are colored by the same color scheme for migratory movement as in panel A. The diamond and circle indicate the start and end, respectively, of the longest migratory movement in both panels.

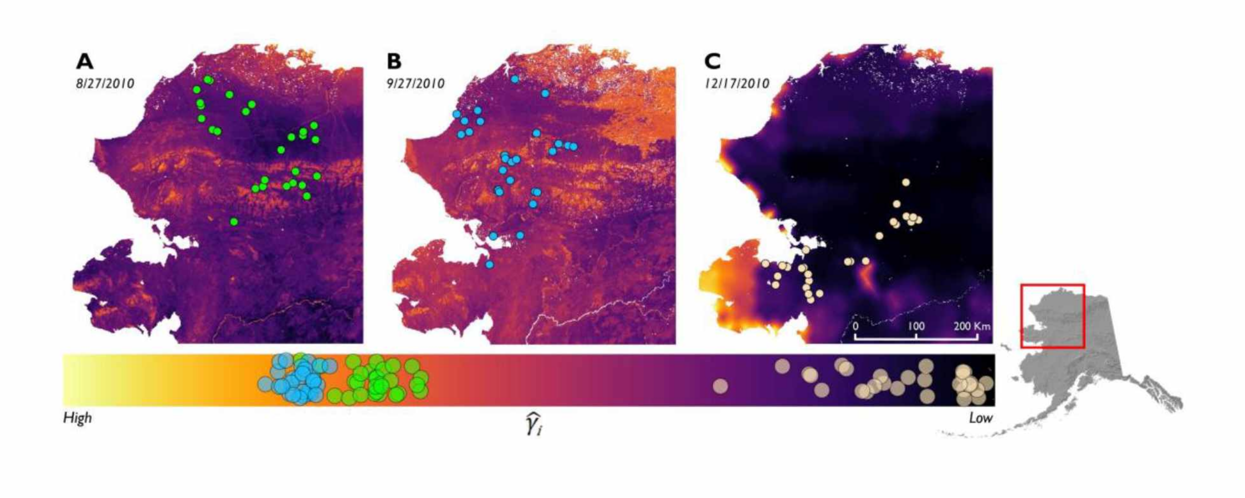

Figure 3.4: Predicted migratory movement ($\hat{\gamma}_i$) for the range of the Western Arctic Herd given the environmental conditions at three time periods – 8/27 (A), 9/27 (B), and 12/17 (C) – and corresponding population-level model results for individuals in 2010. Dark colors indicate reduced movement persistence (low $\hat{\gamma}_i$) and yellow indicate persistent movement (high $\hat{\gamma}_i$). Caribou locations are displayed in each panel and colored by day, and the legend bar along the bottom indicates the range of $\hat{\gamma}_i$ and the corresponding values at the observed caribou locations.

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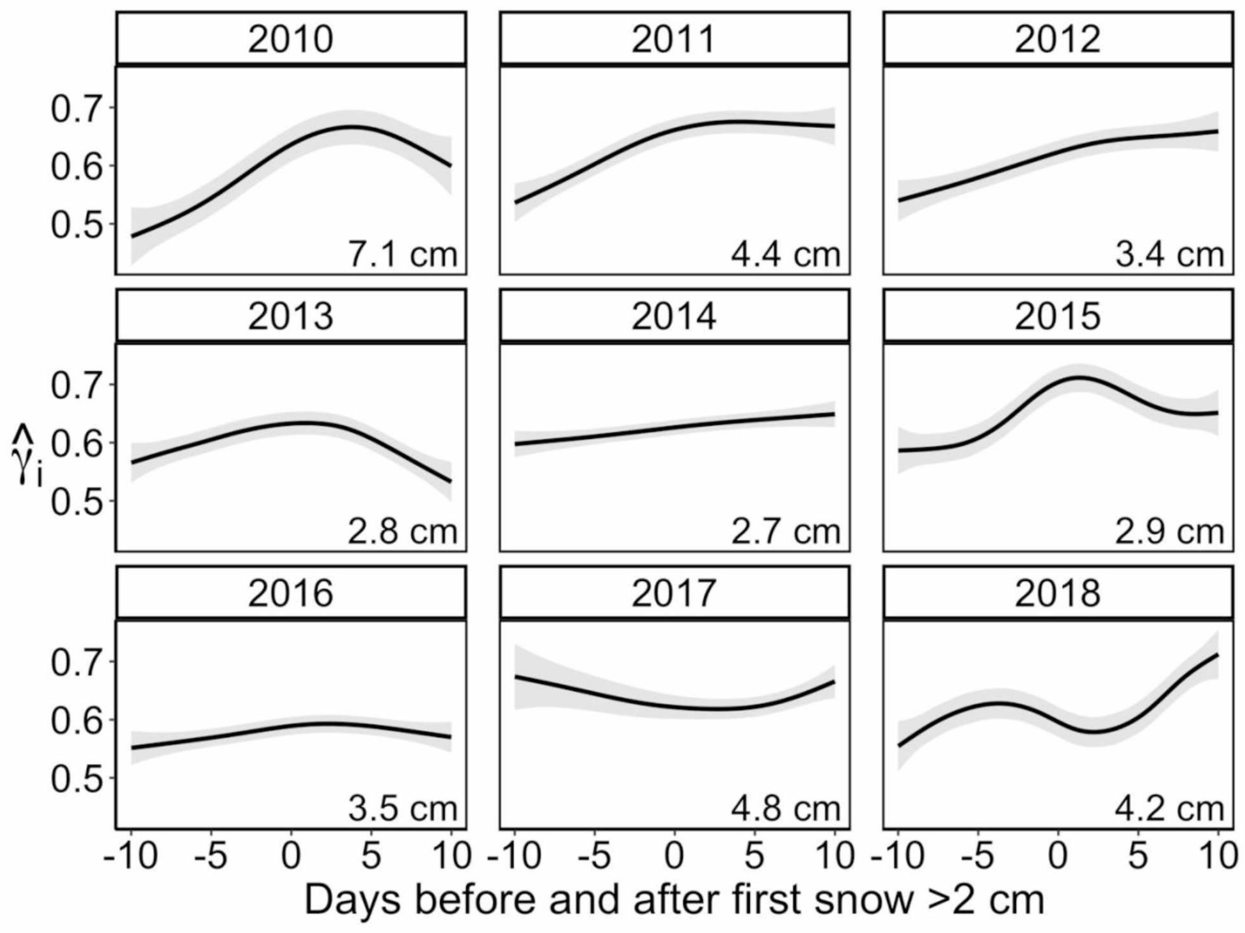
Appendix 3A: Chapter 3 supplemental figures and tables

Appendix 3A.1: Number of individual seasons in each year of analysis for autumn migration of Western Arctic Herd caribou, Alaska.

Year	Individual Seasons
2010	28
2011	38
2012	33
2013	35
2014	42
2015	42
2016	66
2017	62
2018	43

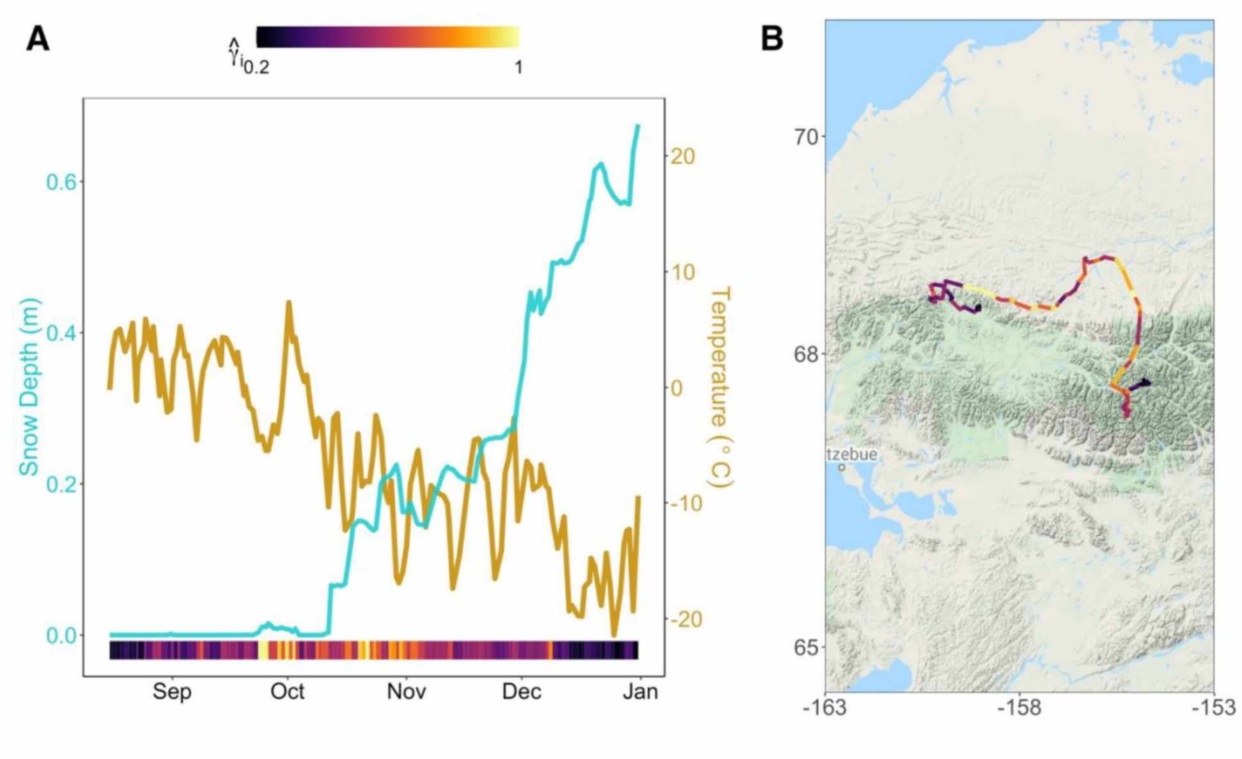
Appendix 3A.2: Probabilities of each parameter estimate being different from zero (either positive or negative coefficient) from the fitted correlated random walk movement model for caribou data of the Western Arctic Herd, Alaska. Probabilities estimated by applying Monte Carlo integration to the marginal posteriors of the population-level parameters

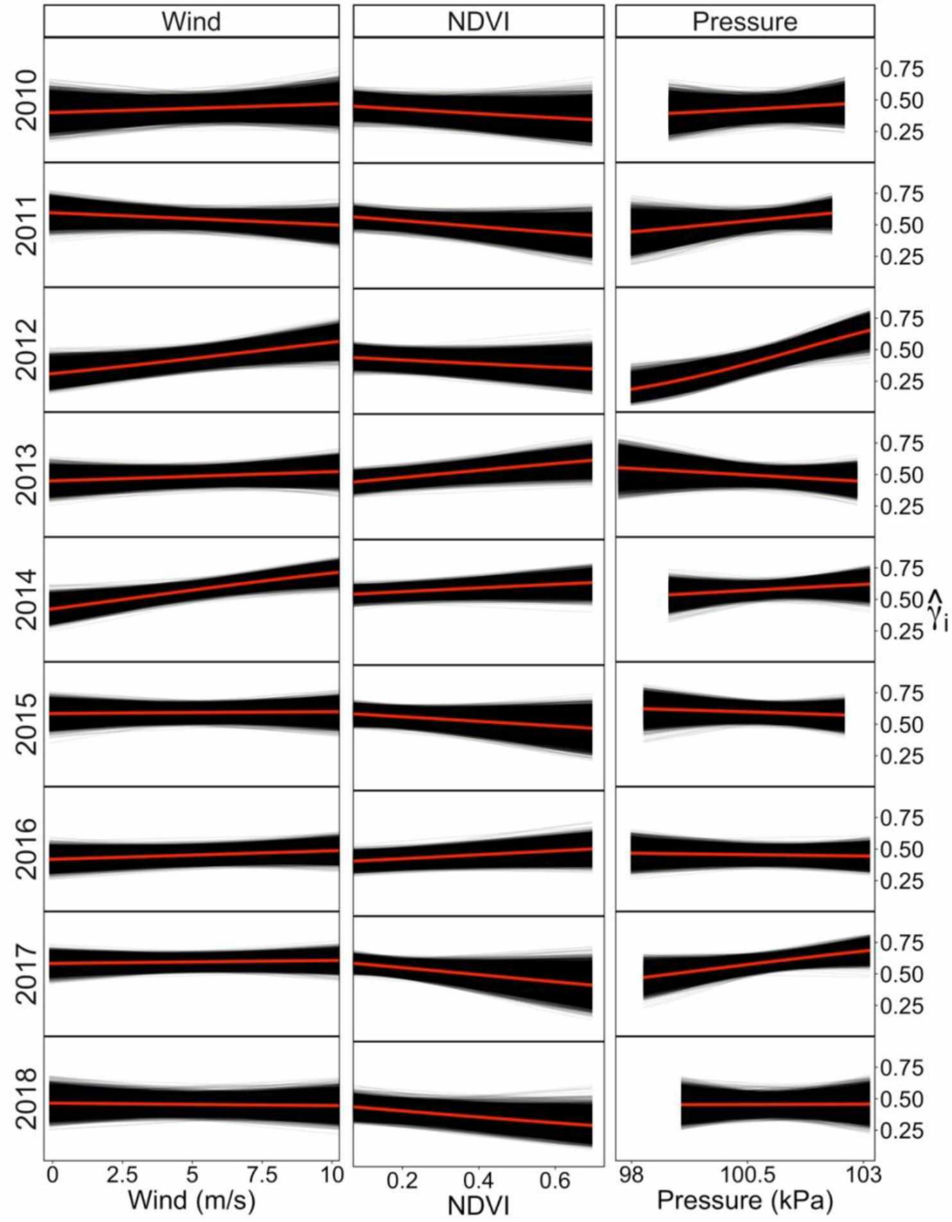
	Probability of β estimates differing from zero								
Parameter	2010	2011	2012	2013	2014	2015	2016	2017	2018
Intercept	0.95	0.94	0.97	0.67	1.00	1.00	0.94	1.00	0.89
Temp	0.87	0.76	1.00	0.85	1.00	0.74	0.60	0.99	0.96
Snow	0.99	0.58	0.59	0.94	0.99	0.55	0.61	0.99	0.99
Temp x Snow	0.99	1.00	1.00	1.00	1.00	0.97	1.00	1.00	1.00
Wind	0.74	0.88	1.00	0.83	1.00	0.57	0.89	0.65	0.59
NDVI	0.92	0.97	0.89	1.00	0.97	0.93	0.98	0.98	0.99
Pressure	0.78	0.93	1.00	0.84	0.84	0.73	0.62	1.00	0.51



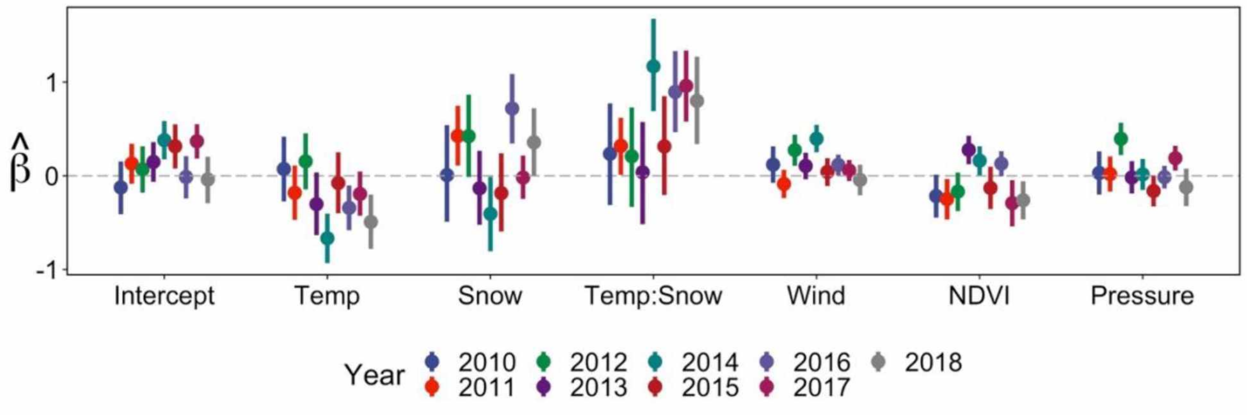
Appendix 3A.3: Fitted $\hat{\gamma}_i$ (y-axis) by year (black lines) smoothed across individuals in relation to the 10 days preceding and following the first appreciable snowfall (> 2 cm) experienced by individual collared caribou of the Western Arctic Herd, Alaska, from 2010-2018. Fitted lines and 95% confidence intervals were generated from a generalized additive model fit with a cubic regression spline for the smoothing parameter for each year using the posterior means of the correlated random walk movement model. Snow data was obtained from the National Centers for Environmental Prediction (2005) and are specific to the time and place of the caribou GPS location. The average snow depth (cm) on day zero for each year is presented in the bottom right of each plot. In general, caribou exhibited elevated $\hat{\gamma}_i$ values (more persistent migratory movement) after the first appreciable snowfall, although this relationship was complicated by the temperature, realized snow depth after the storm, and caribou movement in the days following the event.

Appendix 3A.4: Environmental conditions experienced by an individual caribou of the Western Arctic Herd (A) and movement track from Aug 15 – Jan 1, 2018 (B). Panel A indicates the snow depth (blue) and temperature (gold) at each location as extrapolated from the North American Reanalysis Model (National Centers for Environmental Prediction 2005). Estimated migratory movement ($\widehat{\gamma}_i$) for the individual is illustrated in the bottom bar from dark blue (low persistence and localized movements) to yellow (high persistence and directional movements). Panel B illustrates the measured caribou movements for the same time period and are colored by the same color scheme for migratory movement as in panel A.

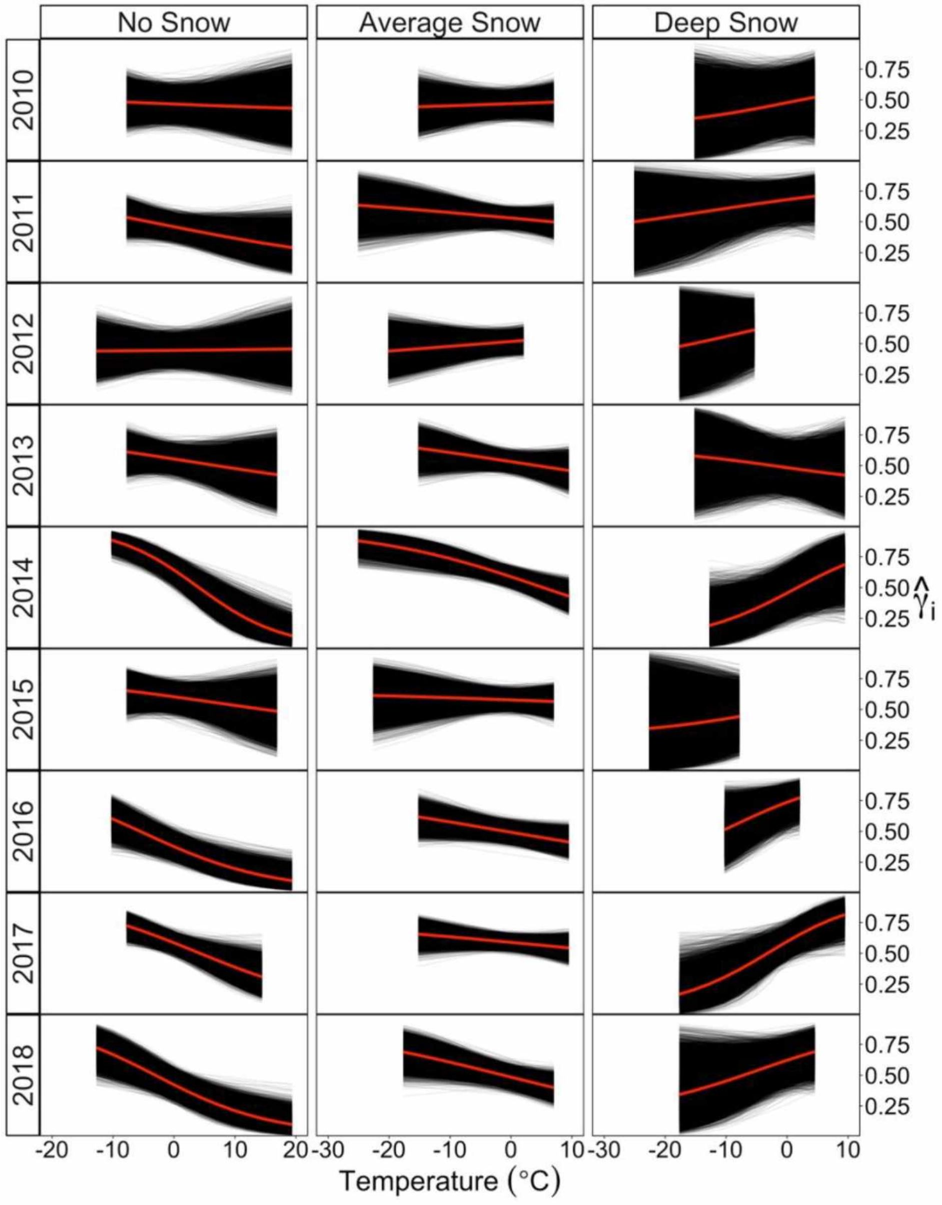




Appendix 3A.5: The effect of wind, NDVI, and standardized air pressure for each year from the population-level fit of the dynamic-parameter correlated random walk movement model fit to caribou location data of the Western Arctic Herd, Alaska, 2010-2018. For each year, the predicted effect of the respective covariate (x-axis) on the movement parameter ($\hat{\gamma}_i$; y-axis) is plotted. Each black curve is given by the equation $\hat{\gamma}_i^{(k)} = logit^{-1}(\boldsymbol{Z_i}^T\hat{\boldsymbol{\beta}}_{\boldsymbol{p}}{}^{(k)})$ for the kth Markov-Chain Monte Carlo iteration (termed posterior realizations), and the red line indicates the mean.



Appendix 3A.6: Annual estimated population-level coefficients (points) and 95% Credible Intervals (bars) for the effect of environmental variables on migratory movements ($\hat{\gamma}_i$) from the dynamic-parameter correlated random walk model. Model was fit to individual tracks of caribou data from the Western Arctic Herd, Alaska, 2010-2018 and the timeseries was restricted to data spanning August 15 – November 15 (rather than the August 15 – December 31 used in Figure 3.1) to assess the impact of the end of the migratory period.



Appendix 3A.7: The effect of temperature at three different snow depth levels for each year from the population-level fit of the dynamic-parameter correlated random walk movement model fit to caribou location data of the Western Arctic Herd, Alaska, 2010-2018. For each year, the predicted effect of temperature (x-axis) on the movement parameter ($\hat{\gamma}_i$; y-axis) is plotted across 3 levels of snow depth (no snow = 0 cm, average snow = 11 cm, and deep snow = 37 cm). Each black curve is given by the equation $\hat{\gamma}_i^{(k)} = logit^{-1}(\boldsymbol{Z_i}^T\hat{\boldsymbol{\beta}}_{\boldsymbol{p}}^{(k)})$ for the kth Markov-Chain Monte Carlo iteration (termed posterior realizations), and the red line indicates the mean. Annual plots are cut off to the observed range of values for each year. The timeseries considered was reduced to data from August 15 to November 15 each year (rather than the August 15 – December 31 used in Figure 3.2) to assess the impact of the end of the migratory period.

Appendix 3B: Chapter 3 Stan model details

Full model statement for the hierarchical, continuous-time movement model with a dynamic behavioral parameter:

$$
\begin{aligned}
\textbf{Individual movement process:}\quad & \mathbf{x}_{j,i}|\mathbf{x}_{j,i-1},\mathbf{x}_{j,i-2} \sim \mathcal{N}\left(\mathbf{x}_{j,i-1}+\gamma_{j,i}\frac{\Delta t_{j,i}}{\Delta t_{j,i-1}}(\mathbf{x}_{j,i-1}-\mathbf{x}_{j,i-2}),\ \Delta t_{j,i}^2\sigma_{x,j}^2\mathbf{I}\right)\\
\textbf{Individual behavioral process:}\quad & \mathrm{logit}(\gamma_{j,i}) \sim \mathcal{N}\left(\mathbf{Z}_{j,i}^T\boldsymbol{\beta}_j,\ \Delta t_{j,i}^2\sigma_{\nu,j}^2\right)\\
\textbf{Population-level process:}\quad & \beta_{j,k} \sim \mathcal{N}\left(\beta_{p,k},\ \sigma_{\beta,k}^2\right)\\
& \sigma_{x,j}^2 \sim \mathcal{N}^+\left(\sigma_{p,x}^2,\ \sigma_{\sigma_x}^2\right)\\
& \sigma_{\nu,j}^2 \sim \mathcal{N}^+\left(\sigma_{p,\nu}^2,\ \sigma_{\sigma_\nu}^2\right)\\
\textbf{Priors:}\quad & \boldsymbol{\beta}_p \sim \mathcal{N}(\mathbf{0},\mathbf{I})\\
& \sigma_{p,x}^2 \sim \mathcal{N}^+(3,3^2)\\
& \sigma_{p,\nu}^2 \sim \mathcal{N}^+(3,3^2)\\
& \sigma_{\beta,k}^2 \sim \mathrm{IG}(2,1)\\
& \sigma_{\sigma_x}^2 \sim \mathrm{IG}(2,1)\\
& \sigma_{\sigma_\nu}^2 \sim \mathrm{IG}(2,1)
\end{aligned}
$$

Stan code for the continuous time, dynamic parameter correlated random walk movement model:

```
data {
  int N; // # of fixes in track
  vector[N] x; // x coordinates
  vector[N] y; // y coordinates
  vector[N] dt; // time intervals

  vector[N] cov_1; // covariates
  vector[N] cov_2;
  vector[N] cov_3;
  vector[N] cov_4;
  vector[N] cov_5;
```

```
}

parameters {

  vector[N] gamma_raw;                // logit behavior parameter -- time-varying, correlates steps
  real<lower=0> sigmax;               // movement process noise in x
  real<lower=0> sigmav;               // behavior process noise
  vector[7] beta;                     // covariate coefficients

}

transformed parameters{

  // Introduce the logit link on the behavior parameter
  vector<lower=0,upper=1>[N] gamma;

  for(j in 1:N){
    gamma[j] = inv_logit( gamma_raw[j] );

  }
}

model {

   // Prior on behavior process noise -- assume there is variability in behavior
  sigmav ~ inv_gamma( 2 , 5 );
```

```
 // Priors on movement process noise -- close to zero
 sigmax ~ inv_gamma( 3 , 1 );


 // Priors on coefficients -- null model is no effect of covariates on behavior
 beta ~ normal( 0 , 1 );


 for (i in 3:N) {


   // Behavior is a linear combination of covariates
   gamma_raw[i] ~ normal( beta[1] + beta[2] * cov_1[i] + beta[3] * cov_2[i] + beta[4] *
cov_1[i]*cov_2[i] + beta[5] * cov_3[i] + beta[6] * cov_4[i] + beta[7] * cov_5[i], dt[i] *
sqrt(sigmav) );


   // Movement process is independent in x and y
   x[i] ~ normal( x[i-1] + gamma[i] * ( dt[i] / dt[i-1] ) * ( x[i-1] - x[i-2] ) , dt[i] * sqrt(sigmax) );
   y[i] ~ normal( y[i-1] + gamma[i] * ( dt[i] / dt[i-1] ) * ( y[i-1] - y[i-2] ) , dt[i] * sqrt(sigmax) );


 }
}
```

Appendix 3C: Chapter 3 Individual-level model implementation

Example code to implement the continuous time, dynamic parameter correlated random walk movement model:

```
library(rstan)
library(dplyr)
library(lubridate)

wah.fall <- read.csv("Data/Data for CRW model - 2020-02-21.csv")

wah.fall$timestamp <- ymd_hms(wah.fall$timestamp)
wah.fall <- subset(wah.fall, yday(timestamp) >= 227)  # Start timeseries on Aug 15

#################
## Run as a loop through all individuals
#################
## Make a file for the parameter estimates:
output=data.frame("param","mean", "se_mean","sd","x2.5.","x25.","x50.","x75.","x97.5.","n_eff","Rhat","id","year")
write.table(output,"Summary of stan models.csv",sep=",", col.names=FALSE, row.names = FALSE)

uniq.ids <- as.character(unique(wah.fall$ID))

for (i in 1:length(uniq.ids)){

  this.id <- uniq.ids[i]
  hold.dat <- subset(wah.fall,ID==this.id)
```

```
  # Calculate dt then toss the first point since it was used to calculate dt

  hold.dat$diff <- as.double(hold.dat$timestamp - dplyr::lag(hold.dat$timestamp)) # calculates the time step for points.

  hold.dat <- hold.dat[-1,]

  hold.dat$diff <- hold.dat$diff/8  # sets dt to equal 1 for a scheduled interval (8 hrs) and 2 for a missed fix, etc.


  # Number of points in track

  N = as.integer(nrow(hold.dat))


  # Assign covariates to model variables

  cov_1 = hold.dat$temp # vectors of length N

  cov_2 = hold.dat$snow.depth

  cov_3 = hold.dat$wind # vectors of length N

  cov_4 = hold.dat$ndvi # vectors of length N

  cov_5 = hold.dat$pressure



  x=hold.dat$x.km  # x coords; vector of length N

  y=hold.dat$y.km  # y coords


  dt= hold.dat$diff # time intervals in hours; vector of length N


  df=list(x=x,y=y,N=N,dt=dt, cov_1=cov_1, cov_2=cov_2, cov_3 = cov_3, cov_4 = cov_4,cov_5 = cov_5) # Saving data for model this way got around a bug when passing stan() a list


  # Fit model in Bayesian framework in Stan
```

```
  stan.fit = stan("R Code/crw_stan.stan",
                  data = df,
                  chains = 3,
                  iter = 100000,
                  thin=10,  # thinning 3 chains of 100,000 by 10 will give you 30,000 samples to
approximate posterior (adjust if needed for memory)
                  cores = 3,
                  control = list(adapt_delta = 0.9))



  ## Save the stanfit object
  save(stan.fit,file=paste0("Output/",this.id,".RData"))


  ## This section will save the summary output as a csv to check things later
  iter.rhat <- data.frame(summary(stan.fit, par=c('beta', 'sigmav', 'sigmax'))$summary)
  iter.rhat$id <- rep(this.id,9)
  iter.rhat$year <- rep(year(hold.dat$timestamp[1]),9)
  write.table(iter.rhat,file = "Summary of stan models.csv",append = TRUE,row.names =
TRUE,sep=",",col.names = FALSE)


}
```

Appendix 3D: Chapter 3 population-level model implementation

Example code to implement the population-level inference for the continuous time, dynamic parameter correlated random walk movement model:

```
############################################################################
###### Second stage MCMC of Bayesian Hierarchical dynamic CRW model ##############
########################### by: Joe Eisaguirre ##################################
####################### last updated: 3 March 2020 ###############################
############################################################################
## In this second stage, we are gaining inference of population-level
##     effects of covariates, beta[i] for the ith covariate.  That is,
##     beta[i,k] ~ Normal(beta[i], s2[i]) for individual k.  We also gain
##     inference of population-level variances, as well.  That is,
##     sigmav[k] ~ Normal+(sv, sv2) and sigmax[k] ~ Normal+(sx, sx2).
#############################################################################



library(rstan)
library(truncnorm)
library(ggplot2)
library(arm)  # for inverse logit


setwd()  # Set to folder of stanfit objects


#### ===========================
#### MCMC algorithm
#### ============================
```

```
mcmc.fun = function(bj.mat.all,
                    sxj.mat,
                    svj.mat,
                    n.iter,
                    J){

  ##
  ## Containers
  ##

  mu.save=matrix(,nrow=length(bj.mat.all),ncol = n.iter)
  bj.save=array(,dim=c(nrow(bj.mat.all[[1]]),length(bj.mat.all),n.iter))
  sxj.save=matrix(,nrow(bj.mat.all[[1]]),n.iter)
  svj.save=matrix(,nrow(bj.mat.all[[1]]),n.iter)
  sv.save=0
  sx.save=0
  sv2.save=0
  sx2.save=0
  s2.save=matrix(,nrow=length(bj.mat.all),ncol = n.iter)



  ##
  ## priors and starting values
  ##

  ## priors
```

```
# IG(2,1) on s2, sv2, sx2
q=2
r=1
# N(0,1) on betas (and bates[k])
mu.0=0
s2.0=1
# N+(3,3^2) on sv, sx
ss.0=3
ss2.0=3^2
# IG(3,1) on sigmax[k] (same as stan model)
qx=3
rx=1
# IG(2,5) on sigmav[k] (same as stan model)
qv=2
rv=5

## starting values
mu=0
s2=1
bj=matrix(,nrow = nrow(bj.mat.all[[1]]), ncol=length(bj.mat.all))
for(i in 1:length(bj.mat.all)){
  bj[,i]=apply(bj.mat.all[[i]],1,mean)
  mu[i]=mean(bj.mat.all[[i]])
}
svj=apply(svj.mat,1,mean)
sv=mean(svj.mat)
sv2=1
```

```
sxj=apply(sxj.mat,1,mean)
sx=mean(sxj.mat)
sx2=1

###
### MCMC loop
###

for(k in 1:n.iter){

  ##
  ## Sample s2 (Gibbs updates)
  ##

  for(i in 1:length(mu)){
    q.tmp=J/2+q
    r.tmp=1/(sum((bj[,i]-mu[i])^2)/2+1/r)
    s2[i]=1/rgamma(1,q.tmp,,r.tmp)
  }

  ##
  ## Sample sv2 (Gibbs updates)
  ##

  q.tmp=J/2+q
  r.tmp=1/(sum((svj-sv)^2)/2+1/r)
  sv2=1/rgamma(1,q.tmp,,r.tmp)
```

```
##
## Sample sx2 (Gibbs updates)
##

q.tmp=J/2+q
r.tmp=1/(sum((sxj-sx)^2)/2+1/r)
sx2=1/rgamma(1,q.tmp,,r.tmp)


##
## Sample betas (Gibbs updates)
##

for(i in 1:length(mu)){
  tmp.var=1/(J/s2[i]+1/s2.0)
  tmp.mn=tmp.var*(sum(bj[,i])/s2[i]+mu.0/s2.0)
  mu[i]=rnorm(1,tmp.mn,sqrt(tmp.var))
}


##
## Sample sv (Gibbs updates)
##

tmp.var=1/(J/sv2+1/ss2.0)
```

```
tmp.mn=tmp.var*(sum(svj)/sv2+ss.0/ss2.0)
sv=rtruncnorm(1,a=0,,tmp.mn,sqrt(tmp.var))

##
## Sample sx (Gibbs updates)
##

tmp.var=1/(J/sx2+1/ss2.0)
tmp.mn=tmp.var*(sum(sxj)/sx2+ss.0/ss2.0)
sx=rtruncnorm(1,a=0,,tmp.mn,sqrt(tmp.var))



##
## Sample individ-level betas (Metropolis steps)
##

for(i in 1:length(mu)){
  bj.star=bj.mat.all[[i]][,k]
  mh.1=dnorm(bj.star,mu[i],sqrt(s2[i]),log=TRUE)+
    dnorm(bj[,i],mu.0,sqrt(s2.0),log=TRUE)
  mh.2=dnorm(bj[,i],mu[i],sqrt(s2[i]),log=TRUE)+
    dnorm(bj.star,mu.0,sqrt(s2.0),log=TRUE)
  keep.idx=exp(mh.1-mh.2)>runif(J)
  bj[,i][keep.idx]=bj.star[keep.idx]
}
```

```
##
## Sample individ-level sv's (Metropolis steps)
##

svj.star=svj.mat[,k]
for(i in 1:J){
 mh.1[i]=log(dtruncnorm(svj.star[i],a=0,,sv,sqrt(sv2)))+
  #log(dtruncnorm(svj[i],a=0,,ss.0,sqrt(ss2.0)))
  dgamma(1/svj[i],qv,,1/rv,log=TRUE)
 mh.2[i]=log(dtruncnorm(svj[i],a=0,,sv,sqrt(sv2)))+
  #log(dtruncnorm(svj.star[i],a=0,,ss.0,sqrt(ss2.0)))
  dgamma(1/svj.star[i],qv,,1/rv,log=TRUE)
}
keep.idx=exp(mh.1-mh.2)>runif(J)
svj[keep.idx]=svj.star[keep.idx]


##
## Sample individ-level sx's (Metropolis steps)
##

sxj.star=sxj.mat[,k]
for(i in 1:J){
 mh.1[i]=log(dtruncnorm(sxj.star[i],a=0,,sx,sqrt(sx2)))+
  #log(dtruncnorm(sxj[i],a=0,,ss.0,sqrt(ss2.0)))
  dgamma(1/sxj[i],qx,,1/rx,log=TRUE)
 mh.2[i]=log(dtruncnorm(sxj[i],a=0,,sx,sqrt(sx2)))+
```

```
      #log(dtruncnorm(sxj.star[i],a=0,,ss.0,sqrt(ss2.0)))
      dgamma(1/sxj.star[i],qx,,1/rx,log=TRUE)
    }
    keep.idx=exp(mh.1-mh.2)>runif(J)
    sxj[keep.idx]=sxj.star[keep.idx]



    ##
    ## Save samples
    ##

    mu.save[,k]=mu
    s2.save[,k]=s2
    bj.save[,,k]=bj
    sxj.save[,k]=sxj
    svj.save[,k]=svj
    sv2.save[k]=sv2
    sx2.save[k]=sx2
    sv.save[k]=sv
    sx.save[k]=sx
  }
  list(mu=mu.save,s2=s2.save,bj=bj.save,
      sxj=sxj.save,svj=svj.save,
      sx=sx.save,sv=sv.save,
      sv2=sv2.save,sx2=sx2.save)
}
#### ============================
```

```
#### end of the algorthim
#### ==============================


####
#### Load samples - This code assumes the file naming convention is year + id (ex: 2010901).
####


files = list.files(getwd(),full.names = T)
load(files[1])
samps = extract(stan.fit, pars=c('beta','sigmav','sigmax'))
samps$id = as.integer(rep(substr(list.files(getwd(),full.names = F)[1], 5, 7),
                          nrow(samps$beta)))
samps$yr = as.integer(rep(substr(list.files(getwd(),full.names = F)[1], 1, 4),
                          nrow(samps$beta)))
tmp=0
tmp.id=0
tmp.yr=0
for(i in 2:length(files)){
  load(files[i])
  tmp=extract(stan.fit, pars=c('beta','sigmav','sigmax'))
  tmp.id = as.integer(rep(substr(list.files(getwd(),full.names = F)[i], 5, 7),
                          nrow(tmp$beta)))
  tmp.yr = as.integer(rep(substr(list.files(getwd(),full.names = F)[i], 1, 4),
                          nrow(tmp$beta)))
  samps$beta=rbind(samps$beta,tmp$beta)
  samps$sigmav=c(samps$sigmav,tmp$sigmav)
  samps$sigmax=c(samps$sigmax,tmp$sigmax)
```

```
  samps$id=c(samps$id,tmp.id)
  samps$yr=c(samps$yr,tmp.yr)
}

####
#### Set up the samples from individual fits
####

# number of iterations for second stage
# (same as first stage, if thinned)
n.iter=nrow(tmp$beta)

# list of individual-level beta MCMC samples
bj.mat.all=vector('list',ncol(samps$beta))
bj.mat=matrix(,nrow = length(unique(samps$id)), ncol = n.iter)
for(j in 1:length(bj.mat.all)){
  for(i in 1:nrow(bj.mat)){
    bj.mat[i,]=samps$beta[,j][samps$id==unique(samps$id)[i]]
  }
  bj.mat.all[[j]]=bj.mat
}

# matrix of individual-level sigmav MCMC samples
svj.mat=matrix(,nrow=length(unique(samps$id)), ncol = n.iter)
for(i in 1:nrow(bj.mat)){
  svj.mat[i,]=samps$sigmav[samps$id==unique(samps$id)[i]]
}
```

```
# matrix of individual-level sigmax MCMC samples
sxj.mat=matrix(,nrow=length(unique(samps$id)), ncol = n.iter)
for(i in 1:nrow(bj.mat)){
  sxj.mat[i,]=samps$sigmax[samps$id==unique(samps$id)[i]]
}

# number of individuals
J=dim(bj.mat)[1]


###
#### Run for data  ###################
###

output.caribou = mcmc.fun(bj.mat.all,
                sxj.mat,
                svj.mat,
                n.iter,
                J)


## Summarize Betas
output.summary.df <- data.frame()
for(i in 1:7){
  hold.df <- data.frame(parameter = paste("Beta",i),
                     type = "Beta",
```

```
                    est = mean(output.caribou$mu[i,]),
                    lower = as.numeric(quantile(output.caribou$mu[i,], c(0.05, 0.95))[1]),
                    upper = as.numeric(quantile(output.caribou$mu[i,], c(0.05, 0.95))[2]),
                    year = 2010)
  output.summary.df <- rbind(output.summary.df,hold.df)
}
```

Conclusions

By applying developments in analytical techniques to a large caribou GPS database and remotely-sensed products, I have shown that the insights on how and why animals migrate can be surprising and profound. In the first chapter, I found that GPS data can be used to infer parturition, which occurs at the destination of spring migration for females. Then, I showed how memory and perception work in tandem to result in the observed patterns of calving site selection across eight years. Lastly, I provide evidence to the hypothesis that autumn migration is driven by an individual's perception of environmental conditions throughout the journey and by continuously updating migratory decisions based on the conditions experienced.

The findings of the first chapter, that parturition events can be inferred from GPS data in barren-ground caribou, suggests that individuals are more independent at the time of calving than once assumed. This aligns with direct observations made on the calving ground of this herd from previous studies, in which "more often the cow stops to commence labor and is left behind by the moving group" (Lent 1966). As the calf develops and becomes more mobile, however, the pair join nursery bands composed of other cow and calf pairs (Pruitt 1960) and the degree to which the cow/calf pair act independently within that group is less certain. After the publication of this work, I was fortunate to have the opportunity to participate in caribou neonate collaring efforts on the Western Arctic Herd (WAH) calving area. What I observed further reinforced the concept of independence at parturition: mothers with newborn calves were commonly found separated from others while mothers with calves that were a few days old (and thus more mobile) were found in nursery bands. While flying through the calving ground, I was struck by how big the area is and how spread out individuals were. Often, you could not see any other caribou from where we caught a neonate; hardly the 'dense aggregation' that is so classically attributed to barren-ground caribou calving grounds. I have since wondered if the distinction between woodland caribou calving in isolation in the forest and barren-ground caribou aggregating at calving on the tundra is a function of the scale being considered. Whereas the WAH's calving ground may appear like a constrained area on a range map, it is still massive (over 53,000 km^2) and only looks small relative to the enormous overall range. A potentially interesting line of inquiry would be to compare the density of woodland caribou during calving to those estimated from annual calving areas of barren-ground caribou (such as those estimated in the second chapter).

Since publication of this work, these methods have been applied to other barren-ground caribou herds in North America. I had the pleasure to work with Joelle Hepler on her UAF Master's thesis to apply these methods to GPS data from the Porcupine and the Fortymile Herds. She found similar success for these methods to detect calving in barren-ground caribou, despite these two herds exhibiting different scales of annual movement patterns (Hepler 2019). Of particular note is that by using higher-frequency location data, she found that she could increase the precision of the Population-Based Method (PBM) by reducing the temporal window of the smoothing parameter from three days to one. This increased specificity not only promises an improvement in the methodology, but the insight that newborn caribou can move over 2 km in the first day of life highlights the incredibly rapid development of these ungulates and how remarkably adapted they are to life on the move (Cameron et al. 2021).

Further insights gained from applying these methods in later years of monitoring highlighted that efficacy of these methods depended on herd movement patterns matching the Individual-Based Method (IBM) model assumptions – one of which was for a similar movement rate before and after calf birth and development. For the years considered in the first chapter, this assumption was generally met. After 2015, however, some caribou of the WAH had shorter autumn migrations in which they wintered further north than those analyzed in Cameron et al. (2018). Subsequently, spring migrations before calving were shorter and less pronounced for these individuals and the assumption of similar movement rates before parturition and after calf development did not appear to be met for the IBM. To address this, I developed a modified methodology that incorporated a step of defining migratory status the winter prior to parturition and only used the PBM results for these individuals (since the PBM did not have this same assumption; Cameron et al. 2020). This serves as a cautionary note in further applications of the IBM to barren-ground caribou and highlights the importance of checking model assumptions with specific herd movement patterns. Another assumption is movement independence and this potentially breaks down as females join nursery bands after parturition; since the IBM can incorporate movements for up to 21 days after calving (the "kcons" parameters within the model), this assumption is potentially less and less valid with longer calf development periods. At this time, my thinking is that the PBM as modified by Hepler (2019) to use higher-frequency data (2-hour interval) and a narrower smoothing window (such as a 1-day moving average) holds the greatest promise for specificity in inferring parturition in barren-ground caribou. However, whichever approach a researcher implements will be dependent on the inference objective, and for conservatively identifying where and when females deliver a calf, the consensus approach of Cameron et al. (2018) provided compelling results. I hope that these methods continue to be a useful tool with which to understand caribou ecology and that further refinements are made with future applications.

In the second chapter, I documented both the variability and consistency in spring migration's destination for caribou: calving areas. The consistency of this area is impressive considering that documented use dates back over 60 years (Lent 1966, Kelleyhouse 2001) and local Indigenous Knowledge suggests that use extends back hundreds of years (Burch 2012). The start of spring migration for arctic caribou is tactical, in that they initiate migration based on immediate environmental conditions (Gurarie et al. 2019) and conditions experienced along the way can influence the timing of arrival (Duquette 1988, Le Corre et al. 2017). My findings pertaining to resource selection in this chapter suggest an evolutionary strategy in which caribou have adapted the timing and place of spring migration's destination to an area of high-quality resources at the time of calving (Cameron et al. 2020). My results also indirectly implicate a navigation mechanism during spring migration: whereas many other migratory ungulates have been found to use perception to track a resource wave of high-quality forage conditions during spring migration (termed 'green-wave surfing'; van der Graaf et al. 2006, Merkle et al. 2016, Aikens et al. 2017), the selection for average conditions that I found suggests that caribou use memory to navigate to an area of consistently high-quality forage, similar to jumping ahead of the green wave (Bischof et al. 2012). Memory and perception are not mutually exclusive, however, and I suggest that once caribou have arrived on the calving ground, perception of immediate conditions guides movement decisions. I posit that this hierarchy of navigation mechanisms gives rise to the spatial patterns of calving areas that I document (Cameron et al. 2020).

Many questions about spring migration remain after this work. How caribou use spatial memory and how they actively navigate during spring migration remains a mystery. Yearling caribou are observed on the calving ground (Lent 1966) and this likely promotes learning, be it from mothers or unrelated individuals. Females often begin spring migration from different wintering areas each year (Joly et al. 2021) and as such, the routes females must traverse to reach the calving ground can differ widely from year to year. This suggests that spatial memory is not solely remembering a specific route or specific markers. Which animals within the herd remember the way also remains a mystery, yet traditional Indigenous Knowledge suggests that there are leaders, typically older females, within caribou groups (Padilla and Kofinas 2014). Research into collective movement (in which individual movement decisions are influenced by other members of the group; Westley et al. 2018) suggests that not all individuals within a group need to know where to go and a small number of informed individuals that act as leaders can give rise to synchronized population-level patterns (Huse et al. 2002, Couzin et al. 2005, Guttal and Couzin 2010, Berdahl et al. 2018). Female caribou migrate in large groups in the spring and group navigation may also improve navigation accuracy (Simons 2004). These and the many other unanswered questions highlight that migration of this species is truly a marvel.

In the third chapter, I set out to understand the controls over autumn migration for the WAH. In contrast to my work on spring migration, where memory heavily influenced the destination, autumn migration appears to be strongly influenced by perception. I found that caribou respond to immediate environmental conditions during autumn, in that indicators of winter conditions such as decreasing temperatures and the first snowfall events of the season corresponded with pronounced migratory movements. Whereas this result may seem intuitive, two aspects of this relationship were notable; one is that the relationship between migratory movements and the environment was consistent across individuals each year despite caribou being spatially dispersed across the summer range. This suggests that how individual caribou decide when to migrate is similar and that the pronounced variability in autumn migration timing for the WAH (Joly and Cameron 2020) is largely due to variability in conditions experienced (stemming from the dispersed distribution in autumn). The second notable insight is that the decision to migrate is continuously updated throughout the journey based on conditions experienced. In other words, as caribou migrate, the conditions that they encounter may change (either due to reaching an area of different weather or the weather changes where they are) and they adjust their migration accordingly. In this chapter, I presented an illustrative example of a female that clearly began migration after the first snowfall on the North Slope but slowed down her movements after reaching snow-free areas south of the mountains (Cameron et al. 2021). These results illustrate the complex relationship between movement behavior and the environment for these animals and I hope this work will serve as a turning point in our collective ability to understand these relationships given improvements in animal-borne technology, remote sensing products, and statistical approaches.

In this third chapter I focused on the decision of when to migrate, yet an important distinction is the decision of not only whether to migrate, but where to migrate to. Partial migration, in which a proportion of a migratory population does not migrate in a given year, is well documented in numerous species (Chapman et al. 2011, Berg et al. 2019). WAH caribou exhibit low fidelity to winter areas (Valkenburg et al. 1983, Joly et al. 2021) and individuals are known to occasionally overwinter in the northern portion of their range (Davis et al. 1982, Joly and Cameron 2020). Recently, increasing proportions of the herd have remained on the northern (i.e. summer) portion of the range, which can be interpreted as non-migration (Joly and Cameron 2020). Notably, many of these ‘non-migratory’ caribou exhibited migratory movements during the migratory period, albeit for much shorter durations, which suggests that these caribou may be migrating but at a different scale. The question of where a caribou decides to migrate, and when this decision is made, remains unanswered. In this work, I was not able to discern whether migrants stopped once they reached their pre-selected winter ranges or stopped when adverse conditions, such as deep snow, halted their progress. This remains a promising avenue for future research with implications for adaptability of Arctic populations. The pattern of low fidelity to winter ranges but high fidelity to spring/summer areas which have been documented in the herd aligns more with the patterns of a partially nomadic rather than a traditional migratory population (Teitelbaum and Mueller 2019) and this classification of nomadic has a long history in the literature for barren-ground caribou (Dugmore 1913, Banfield 1954, Skoog 1968).

A detailed understanding of how climate influences migration behavior is important for predicting how long-distance migrant populations will adapt to future climate change (Shaw 2016). This is especially pertinent for subsistence communities whose cultural identity and way of life rely on harvest during migration, such as the communities in the WAH range. Given the rapid changes currently observed and further expected with climate change in the Arctic (Hinzman et al. 2005, IPCC 2014), the insights from this work can help inform expectations of future migratory patterns. Already, autumn temperatures in the herd's range have warmed in the last seven decades (Walsh and Brettschneider 2019), and this has corresponded with later autumn migrations in the same time period (Dau 2007, 2015, Joly and Cameron 2020). In light of the mechanisms I identified in this work, I expect the trend of later migrations to persist as the climate continues to warm.

Whereas the three chapters presented here represent improvements in our collective understanding of caribou and migration ecology more broadly, much remains to be learned. In future work, I hope to address the fundamental question of *why* migration occurs by quantifying the actual fitness trade-offs among migration strategies. Lichen is the primary resource caribou rely on during the winter, yet our ability to quantify available lichen resources across the range and relate this to winter habitat use is limited to temporally and spatially coarse remotely-sensed products. Quantifying temporal trends in migration patterns is an important step as well. Ultimately, incorporating all of these into understanding the cumulative impacts of potential development within the range and relating this to the herd's outlook is needed.

In closing, the studies I presented here fit within a growing body of literature that highlights how animals are much more cognitively complex than some once gave them credit for. Migration entails numerous adaptions such as navigation (Åkesson and Hedenström 2007), cognitive functions such as memory (Bracis and Mueller 2017, Abrahms et al. 2019), learning (Mueller et al. 2013), and collective behavior (Berdahl et al. 2016, Westley et al. 2018). Animal culture is defined as information or behaviors shared within a population that is learned, and the evidence and appreciation for animal culture and cognition is steadily growing (Brakes et al. 2021, Kashetsky et al. 2021, Whiten 2021). This has conservation implications, for once knowledge of migration patterns is lost within a population, it can take generations to reestablish (Jesmer et al. 2018). A holistic understanding of the patterns, mechanisms, and ecosystem effects of migration will ultimately require an integrated approach that brings together metrics of the environment, species interactions, and cognition. My hope is that my work here has helped advance the field toward this goal in a small way.

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