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Pronounced Fidelity and Selection for Average Conditions of Calving Area Suggestive of Spatial Memory in a Highly Migratory Ungulate

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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 that result in this pattern are poorly understood. Effective conservation of these species requires reliable delineation of such areas, quantifying the factors that 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 six 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 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.

Keywords: Alaska, calving grounds, caribou, migration, NDVI, *Rangifer tarandus*

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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 two 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). Because 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 hodgsonii*; 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 caused by 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 because 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). Considering that 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 confounded 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 8 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, for calving marks the destination of long-distance migration in the spring for pregnant females, which aggregate around 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 (first scale) comprise an annual calving area (second scale), that in turn constitute a calving ground when considered across numerous years (third scale; **Figure 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.

MATERIALS AND 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**; 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 ($\geq$2years 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

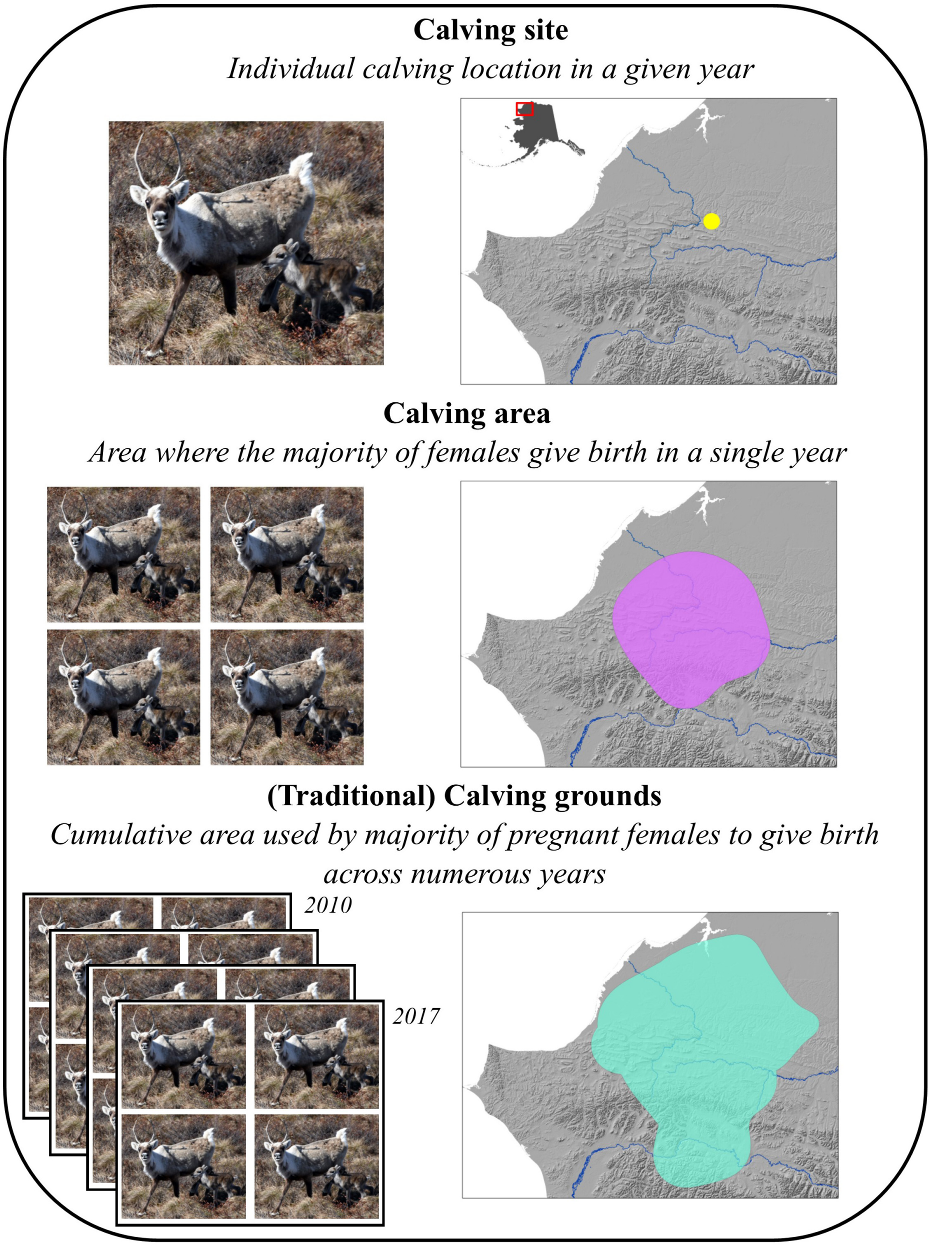

FIGURE 1 | The scales and definitions of calving considered in this analysis of the Western Arctic Herd. The calving location (yellow point) was from an individual in 2010, the calving area (purple polygon) was based on all detected calving events in 2010, and the calving ground (teal polygon) was the extent of all calving areas from 2010–2017 combined. Definitions adapted from Gunn and Miller (1986).

Alaska Institutional Animal Care and Use Committee (IACUC; 0040-2017-40). Collars were programmed to record locations every 8 h 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). Caribou populations are known to fluctuate at decadal time scales, and this is generally linked with large-scale climate patterns (Gunn, 2003; Joly et al., 2011). 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

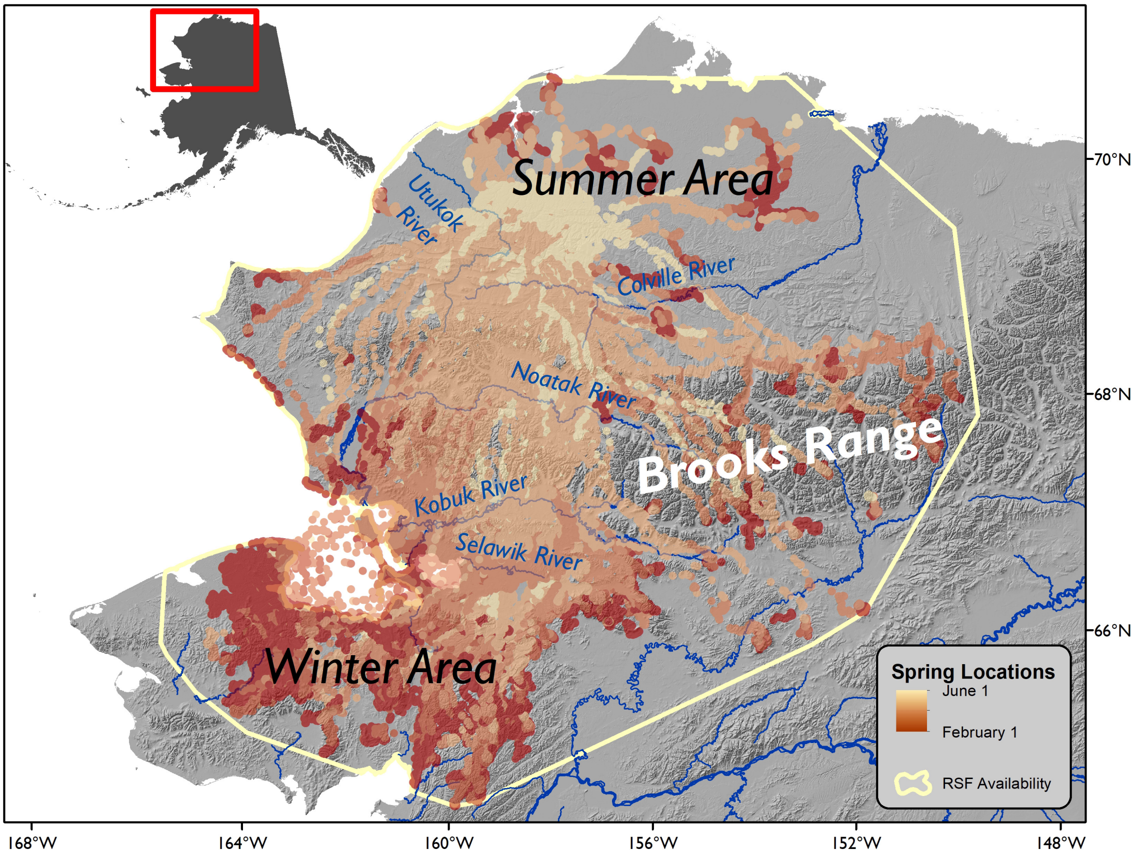

FIGURE 2 | Annual range of Western Arctic Herd caribou, Alaska. All GPS points from February 1 (dark red) to June 1 (yellow) are displayed from 2009–2017. The 100% minimum convex polygon, indicating the extent of the available area for the resource selection function (RSF), is presented as a pale yellow line and was generated using all annual locations in the same span of years.

method established a herd-specific movement rate threshold for calving from known events and then analyzed movement rates for individuals that dropped below the threshold using a 3-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, because there was a record number of non-migratory individuals during the winter of 2016–2017 (Joly and Cameron, 2019) and 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 that 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, because 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 × 500 m 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 2 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 2 years being considered, so that if the observed overlap was smaller than all observed overlap values, the p-value was <0.004 (see **Supplementary Figure 1** for illustration). We performed this analysis for all combinations of annual comparisons, ranging from sequential up to 7-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 the 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 8 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 8 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 15×15 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; **Supplementary Table 1**). We filtered points that 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., 2005a) acquired from the MODIS V6 and compiled into 7-day composites with 250 m 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 (1 week before peak calving, the week of the peak, and the following 3 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 8 years (June 3, see section "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 8 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 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 that remained on the winter range of the Seward Peninsula and three in 2017 for WAH individuals that 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 8 years.

TABLE 1 | Detected calving events based on movement data for the Western Arctic Herd (WAH), 2010–2017, Alaska.

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

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 provide totals for calving events and the average median parturition date and calving area across all 8 years.

Spatial Patterns in Calving Areas

Across the 8 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 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 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**). This trend of significant differentiation among years was evident at all further levels of comparison: at 2-year ($p < 0.05$ for five out of six), 3-year ($p < 0.05$ for four out of five), 4-year ($p < 0.05$ for three out of four), 5-year ($p < 0.05$ for one out of three), 6-year ($p < 0.05$ for one out of two), and 7-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 that was used every year of the study, with calving areas of less frequent use stretching as far away as the Noatak River (**Figure 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 that 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; **Supplementary Table 2**) 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 that indicate selection for intermediate values for both, an interaction between elevation and ΔNDVI.148, and terrain ruggedness (**Supplementary Table 3**). Females strongly selected for sites with high ΔNDVI at the time of peak calving (**Table 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 that 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

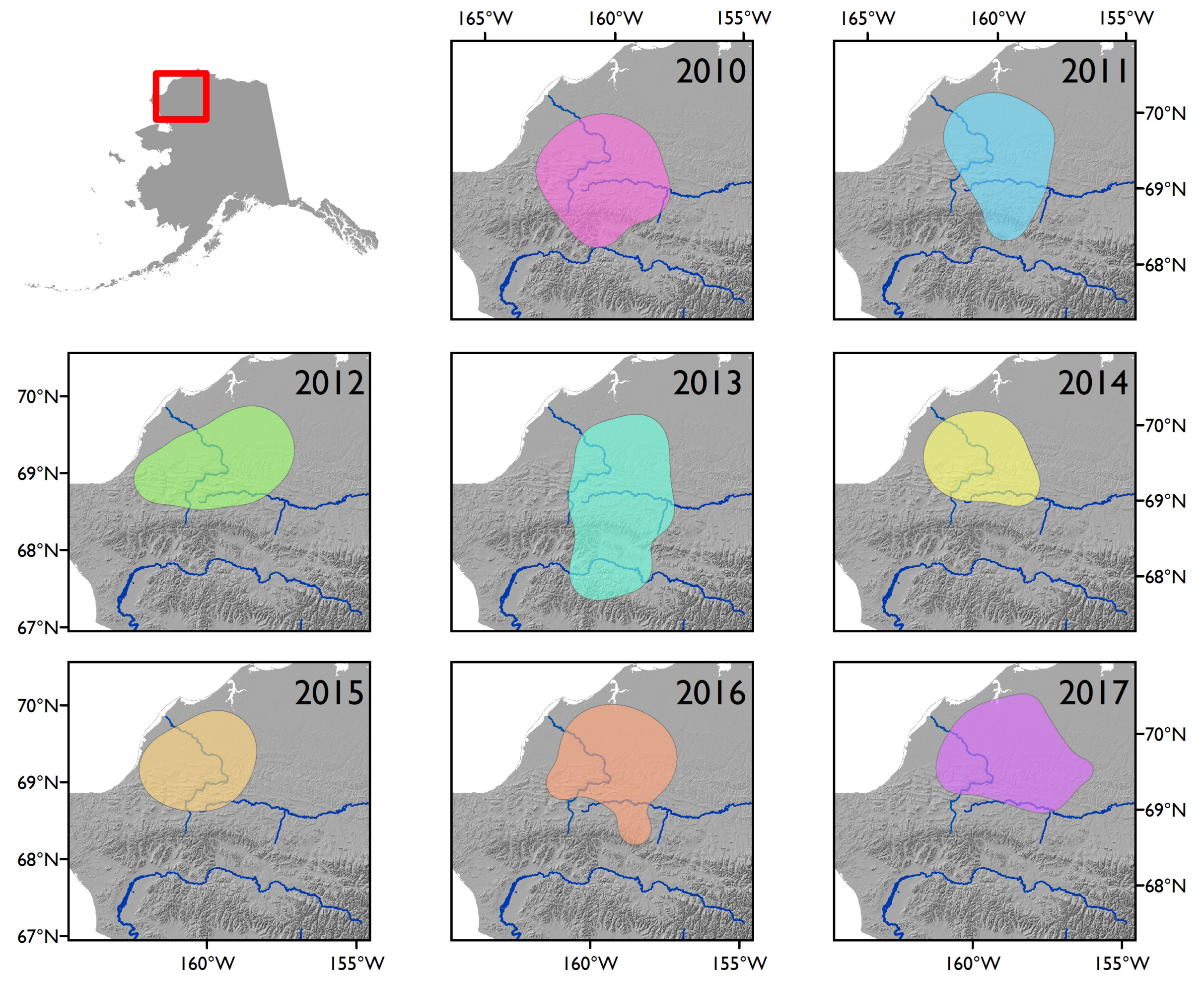

FIGURE 3 | Annual calving areas of the Western Arctic Herd, 2010–2017, Alaska. Calving areas were delineated using the 95% contour of a kernel utilization distribution generated from parturition locations, which were inferred from GPS data.

TABLE 2 | Kernel overlap tests comparing annual calving areas of Western Arctic Herd caribou, 2010–2017, Alaska.

	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

Comparisons were performed for every interval ranging from 1 to 7-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.

cover at calving (**Table 3**). The solar radiation index also exhibited a quadratic relationship for calving site selection (**Table 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 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 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 (**Supplementary Figure 2**).

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).

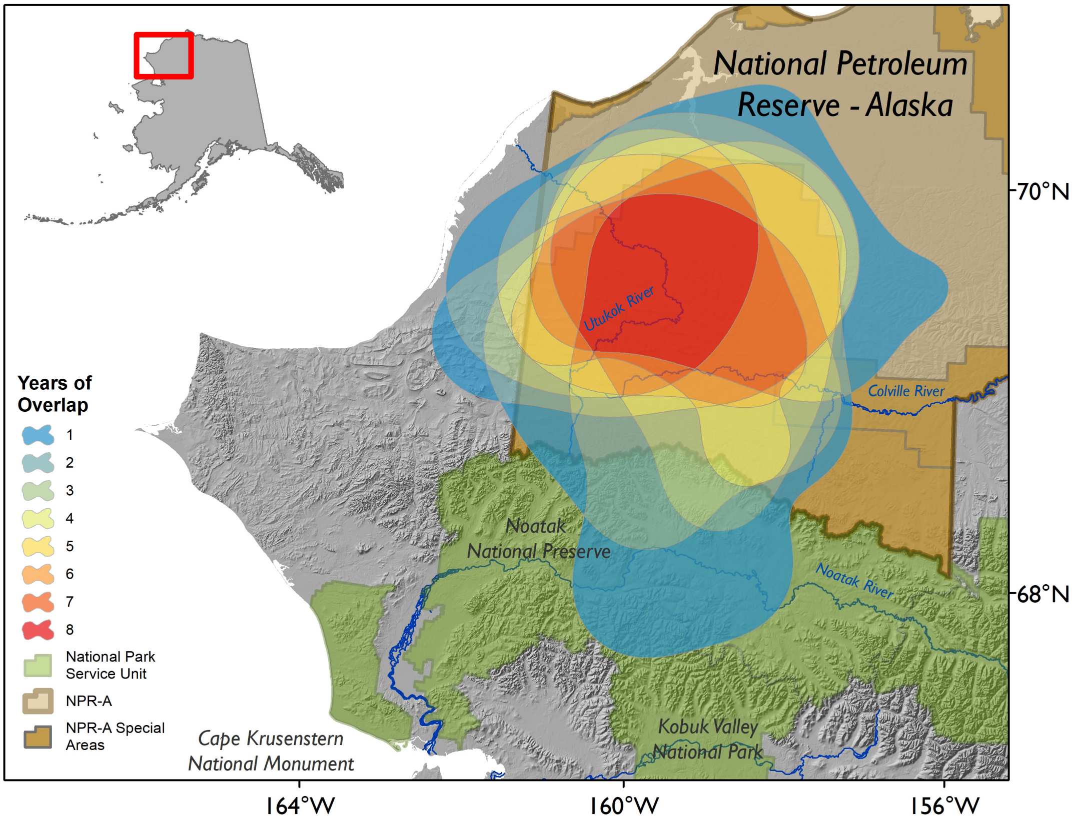

FIGURE 4 | Overlap of all observed annual calving areas for caribou of the Western Arctic Herd, 2010–2017, Alaska. Calving areas were delineated using the 95% contour of a kernel utilization distribution generated from parturition locations, which were inferred from GPS data. Special Areas of the National 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).

TABLE 3 | Coefficient estimates from the top RSF model for female caribou calving site selection, Western Arctic Herd, 2010–2017, Alaska.

	Variable	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

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).

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 (*Loxodonta 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

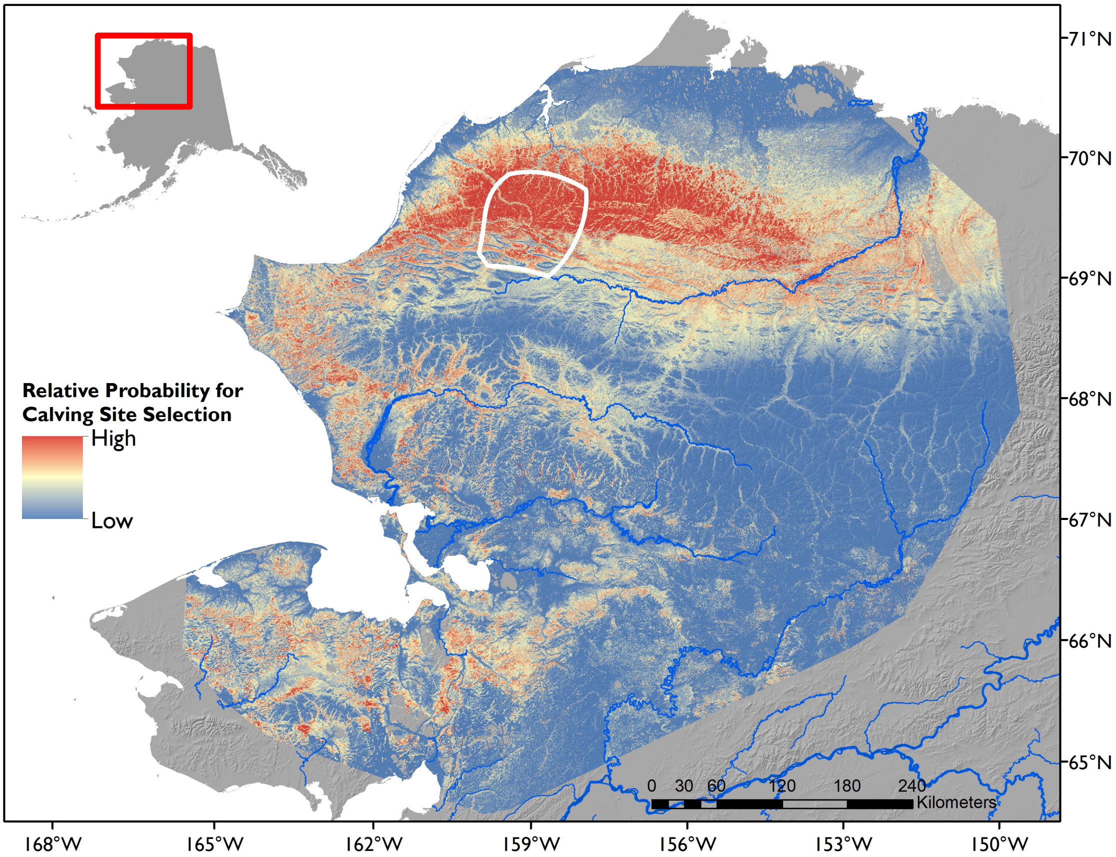

FIGURE 5 | Predictive map of high-quality calving habitat for caribou of the Western Arctic Herd, Alaska. Map was made from the top performing resource selection function model including land cover, elevation, solar radiation, terrain ruggedness, and rate of NDVI increase from the week before to the week of average peak calving. Data for NDVI rate at peak calving were averaged across the 8 years of NDVI composites from the analysis for map generation. White polygon indicates the core area in which calving was detected for all 8 years in the study.

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 preparation), 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 caused by 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 experienced 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 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 that 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 that 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 (*Ursus arctos*), and golden eagles (*Aquila 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 (**Supplementary Table 4**). 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 that 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 suggested 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 at 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 avenues for future research.

Management Implications

Migratory ungulates rely on large expanses of range to maximize fitness (Hebblewhite et al., 2008; Joly et al., 2019) and migration routes of animals that 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 8 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 (**Supplementary Figure 3**; Lent, 1966; Kelleyhouse, 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, for 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.

DATA AVAILABILITY STATEMENT

Movement data used in this manuscript is stored in a public repository called IRMA, but access is restricted due to the sensitivity of a harvestable species' location data. Contact authors for access. https://irma.nps.gov/Datastore/Reference/Profile/2260262.

ETHICS STATEMENT

The animal study was reviewed and approved by the State of Alaska Institutional Animal Care and Use Committee (IACUC; 0040-2017-40).

AUTHOR CONTRIBUTIONS

MC and KJ managed the data. MC, KJ, GB, CM, and KK analyzed and interpreted the data, and contributed to manuscript revision. MC wrote the first draft of the manuscript. All authors read and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2020.564567/full#supplementary-material

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