NRC
Research Press

ARTICLE

Movement-based methods to infer parturition events in migratory ungulates

Matthew D. Cameron, Kyle Joly, Greg A. Breed, Lincoln S. Parrett, and Knut Kielland

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 iswidely 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 two movement-based methods developed to infer parturition in nonmigratory woodland caribou *(Rangifer tarandus caribou* (Gmelin, 1788)) to 241 reproductive seasons spanning 6 years of GPS data from migratory barren-ground caribou *(Rangifer tarandus granti* J.A. Allen, 1902). 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 interannual variation ranging from 61% to 100%. When we considered instances when the two analytical methods agreed on parturition outcome, the accuracy increased to 89% with an annual range of 73%-100%. Using these methods, we identified marked interannual 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.

Key words: calving, caribou, migration, parturition rate, *Rangifer tarandus,* Western Arctic Herd.

Resume : Les migrations sur de longues distances d'especes d'ongules representent un phenomene nature! menace a l'echelle planetaire, et leur conservation necessite la surveillance d'indices vitaux des populations. Le suivi par telemetrie satellitaire est abondamment utilise pour comprendre la repartition spatiale et les deplacements d'animaux, particulierement ceux d'animaux migrateurs en regions eloignees. Si des methodes analytiques Ont recemment ete mises au point pour inferer les evenements de parturition a partir de donnees sur les deplacements pour differentes especes qui s'isolent pour merue bas, l'utilite de ces methodes n'a pas encore ere validee pour des animaux migrateurs qui se regroupent au moment de la mise bas. Nous avons applique deux methodes basees sur les deplacements developpees pour inferer les parturitions chez les caribous des bois *(Rangifer tarandus caribou* (Gmelin, 1788)), des caribous non migrateurs, a 241 periodes de reproduction couvrant 6 annees de donnees GPS sur des caribous de la toundra *(Rangifertarandus granti* J.A. Allen, 1902) migrateurs. Nous comparons les resultats des deux methodes a des donnees de recensements aeriens de femelles dotees de colliers emetteurs durant la periode de mise bas. Nous constatons que chacune des methodes basees sur les deplacements presente une exactitude globale d'environ 80 % pour ce qui est de detecrer les evenements de mise bas, pour une fourchette de variation interannuelle de 61% a 100 %. En considerant les cas ou les resultats des deux methodes d'analyse concordent, l'exactitude passe a 89 %, pour une fourchette de variation interannuelle de 73 % a 100 %. En utilisant ces methodes, nous observons des differences interannuelles marquees du moment de la pointe des mises bas et des raux de parturition plus eleves que les raux publies par le passe pour ce rroupeau de caribous. L'application concluante de ces analyses a un ongule gregaire migrateur semble elargir l'applicabilite de cette methodologie. [Traduit par la Redaction)

Mots-des : mise bas, caribou, migration, taux de parturition, *Rangifer tarandus,* troupeau de l'ouest de l'Arctique.

Introduction

Long-distance ungulate migrations are 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 spatial and

Received 30 October 2017. Accepted 1 March 2018.

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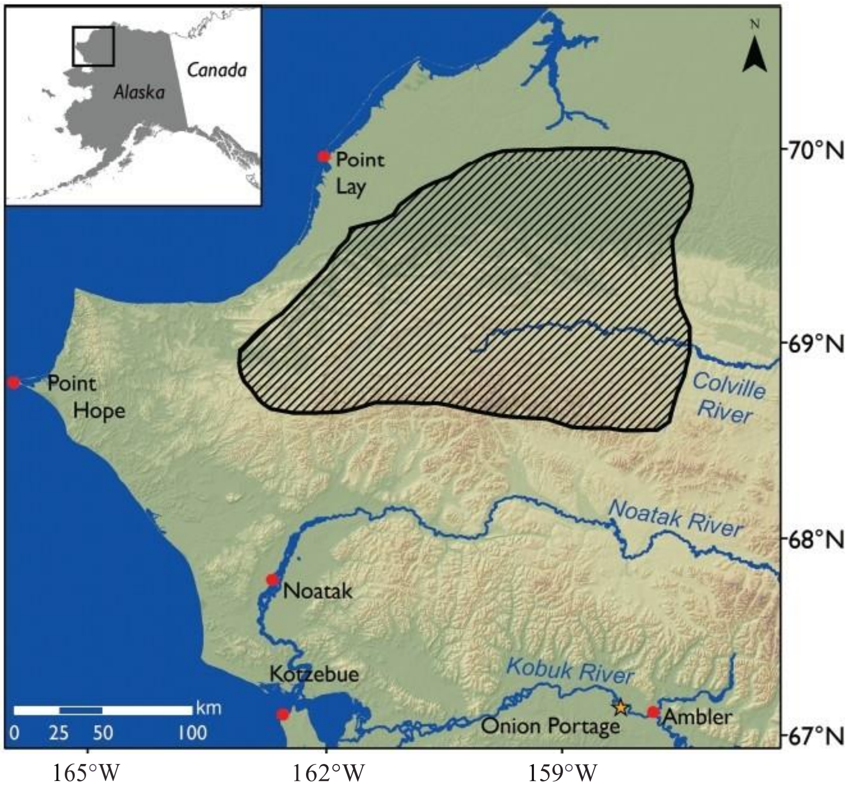
Fig. 1. Historic calving ground (black hatched polygon) delineated from aerial surveys from 1987 to 2016 of Western Arctic Herd barren-ground caribou *(Rangifer tarandus granti)* in Alaska, USA. Spring caribou migrations typically lead to the calving grounds from the south. Red circles (gray circles in print) are villages within the caribou range and the orange star (white star in print) is Onion Portage, where collars were deployed. Color version online.



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* Linnaeus, 1758) (Walsh et al. 2016), migration by moose (Alces alces (Linnaeus, 1758)) (Bunnefeld et al. 2011), and haul outs on sea ice by bearded seals *(Erignathus barbatus* (Erxleben, 1777)) (Mcclintock et al. 2017).

Obtaining estimates of a particular life-history event (parturition) is important for managers as an assessment of range condition, because the probability of parturition is linked to body condition during 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 nonmigratory animals such as moose (~88%; Severud et al. 2015), elk *(Cervus canadensis* Erxleben, 1777) (~93%; Dzialak et al. 2011), and with the highest success for woodland caribou *(Rangifer tarandus caribou* (Gmelin, 1788)) (>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* J.A. Allen, 1902).

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). Nonpregnant females typically migrate later than pregnant females (Pruitt 1960; Joly 2011; Dau 2015), but nonpregnant 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 (i) apply two movement-based models developed for sedentary woodland caribou to GPS data from the Western Arctic Herd (WAH), a migratory barren-ground caribou herd in Alaska, USA; (ii) evaluate the accuracy of each method relative to aerial surveys, as well as to each other; and (iii) compare the estimated rates and timing of parturition derived from these analyses to previously reported results from aerial surveys.

Materials and 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 and 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 (Fig. 1; Lent 1966a). Annual estimates for

Table 1. Aerial calving survey dates, number of collared females each year (reproductive seasons), and number of collared females observed of Western Arctic Herd barren-ground caribou (*Rangifer tarandus granti*) in Alaska, USA.

Year	First date of survey	Last date of survey	Active GPS collars	Collared animals observed	Percentage of individuals with "known" parturition status
2010	5 June	12 June	33	31	73
2011	7 June	10 June	39	28	51
2012	4 June	15 June	37	35	78
2013	5 June	14 June	38	34	61
2014	8 June	14 June	45	43	91
2015	6 June	16 June	49	49	88
Total			241	220	75

Note: 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.

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 multiagency monitoring of the WAH (Davis and Valkenburg 1985; Dau 2005). Starting in 2009, GPS collars (model TGW-4680; Telonics, Mesa, Arizona, USA) have been deployed annually during the fall migration at Onion Portage along the Kobuk River (Fig. 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 h 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 1 July for each reproductive year, totaling 241 reproductive seasons (one individual for one parturition time frame; Table 1). The percentage of females with complete GPS data coverage ranged from 22% to 91% and the number of missing locations per individual each parturition season ranged from 0% to 64% (see Supplementary Table S1).[1]

Annual aerial surveys of calving grounds

Aerial surveys of the calving grounds were conducted annually by Alaska Department of Fish and Game (ADF&G) biologists in a Piper PA-18 airplane (Table 1). Surveys were timed to begin just prior to estimated peak calving (when approximately 50% of calves are born), typically from 9 to 13 June (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 nonparturient, 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 method (IBM) and population-based method (PBM) 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 version 3.3.1 statistical computing program (R Core Team 2017); our R codes are provided in the Supplementary material along with data-file examples (Example_Data.csv and Example_Data_PBM_Threshold_Rates.csv).[1] 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 two a priori models: nonparturition and parturition. The nonparturition model fit a constant mean movement rate across the time series (one 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 (three 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 two 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, respectively) 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 (4 July; Lent 1966b).

The PBM analysis consisted of two 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 mean 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 nine parturient individuals that gave birth between observations and had a parturition date identified

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[1] Supplementary tables and R codes are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjz-2017-0314.

by the IBM between those two observations. Given the requirement that an individual must be first seen without a calf and then subsequently seen with a calf, parturition events that 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 the 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 postcalving 3-day mean 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 mean 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), because we found that 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). 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 1000 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 data set of 241 reproductive seasons from 2010 to 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 mean movement rate to fall below the threshold.

Comparing model results to aerial survey data

Both 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 nonparturient if their calf died before or between aerial observations, we considered parturition unknown for two instances: (1) females with a model-estimated calving date 5 days or more 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 three 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 IBM and PBM, we considered the estimated timing of parturition from movement methods to agree if the two parturition dates were within 3 days. We performed a linear regression with agreement between 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 h GPS relocation data to 16 and 24 h 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 that 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 with the aerial data following the same procedure outlined above.

We investigated the sensitivity of the 3 constraints in the IBM — int and two values (minimum and maximum) 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 reran 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 the new results with the aerial observation data.

Estimating calving phenology and parturition rates

We used a combination of approaches to estimate calving dates for parturition events 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 that 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 (ANOVA) to test for significant interannual variation in parturition timing. To investigate the inference to herd management that 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 with the annual ratio of calves to 100 cows 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., Fig. 2A) was 77% (n = 166; Table 2). We observed interannual variation in support of the IBM to identify calving events ranging from 61% to 94% (Table 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 one step (8 h) early, before the period of decreased movement rate.

Bootstrapping the PBM calving threshold resulted in a bimodal kernel distribution with a maximum at 135 m/h. One individual exhibited a noticeably faster postcalving 3-day mean movement rate (1.5-3 times greater than the other individuals), so we excluded that individual and reran the bootstrap procedure. The

Fig. 2. Detection of calving events based on three different methods for Western Arctic Herd barren-ground caribou *(Rangifer tarandus granti)* from 2010 to 2015 in Alaska, USA. 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 (gray dot-dashed line in print) is the estimated parturition event, and the blue dashed line (gray dashed line in print) is the aerial observation during which a calf was observed. Plot B depicts the application of the population-based method (PBM) to a different individual based on 3-day mean movement rates: the horizontal dashed line is the estimated population threshold, PBM calving date is depicted by the dotted red line (dotted gray line in print), and two aerial observations are depicted by the blue dashed lines (gray dashed lines in print). Plot C depicts the nonparturition IBM model and plot D depicts the nonparturition model result of the PBM with two additional individuals that were estimated to be not parturient by observation of soft antlers (blue dashed lines; gray dashed lines in print). Color version online.

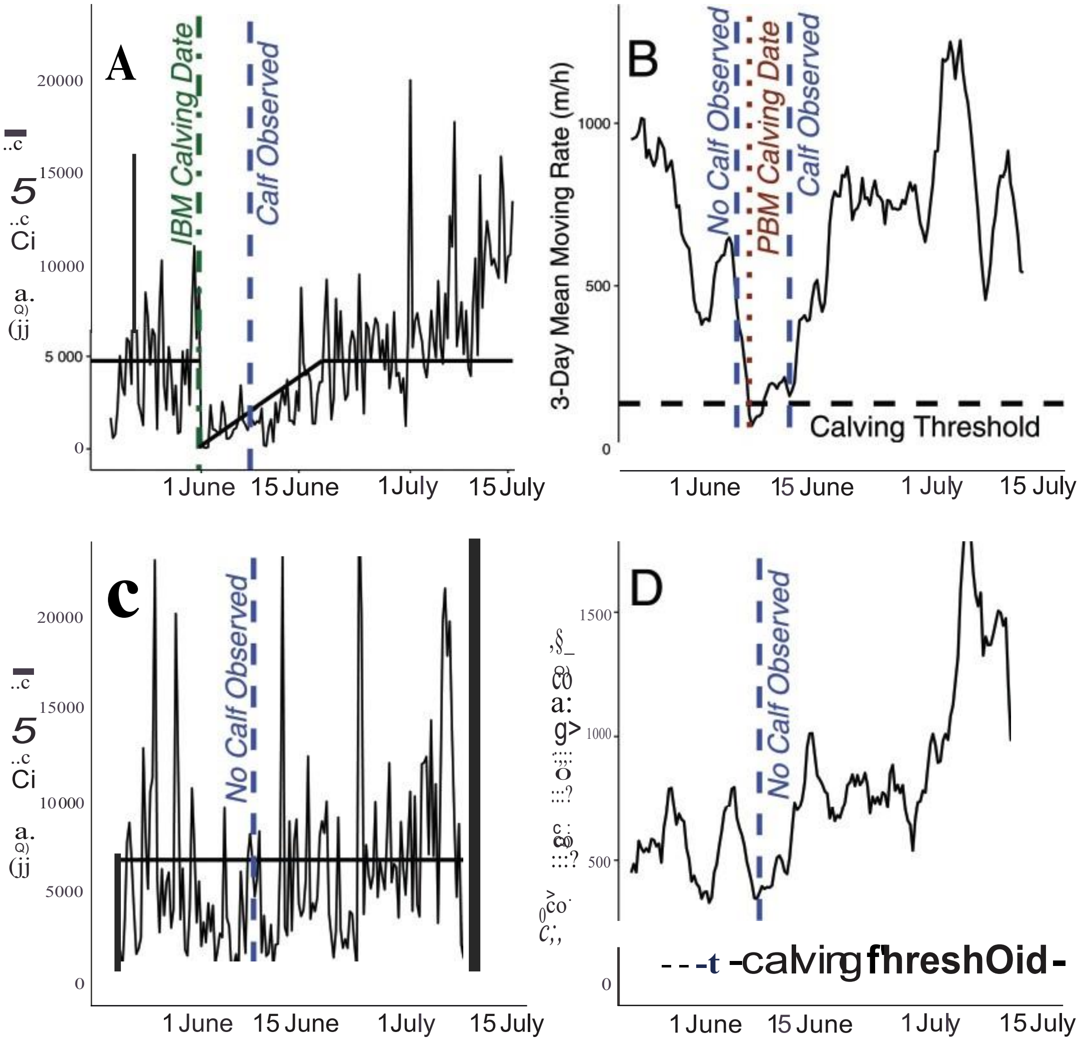

Table 2. Agreement among individual-based method (IBM), population-based method (PBM), and aerial observation method results for Western Arctic Herd barren-ground caribou *(Rangifer tarandus* granti) parturition events in Alaska, USA.

	IBM-aerial		PBM-aerial		IBM-PBM		Consensus-aerial	
Year	Percent agreement	*n*	Percent agreement	*n*	Percent agreement	*n*	Percent 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

Note: 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.

resulting distribution was unimodal with a maximum value at 137 m/h. 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 interannual variation ranging from 68% to 100% (e.g., Fig. 2B, Table 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 reproductive seasons, all of which had extensive periods of missing data (10-58 missing steps).

Agreement in parturition outcome between IBM and PBM methods was 70% (*n* = 232) and ranged annually from 61% to 83% (Table 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 and aerial observations, movement-based results appeared to agree more often when aerial observation detected parturition in contrast to nonparturition (78% and 63%, respectively). When we considered only those cases in which IBM and PBM concurred on parturition outcome, aerial observations suggested an 89% overall accuracy (*n* = 119), with annual variation ranging from 73% to 100% (Table 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 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 of accuracy resulting in an R^2 value of 0.8.

Our subsampled 16 and 24 h fix rate data exhibited similar results as the original data. For the 16 h fix rate, overall concordance was 76% (*n* = 163) for the IBM and 82% (*n* = 154) for the PBM when compared with aerial observations. For the 24 h fix rates, this was 76% (*n* = 167) for the IBM and 83% (*n* = 151) for the PBM when compared with aerial observations. For the consensus approach, support for the movement-based methods was 87% for both 16 h (*n* = 118) and 24 h (*n* = 119) fix rates (Supplementary Table S2).[1] We found the IBM model robust to different values of the three constraints (int and minimum and maximum 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 the original results; agreement with the original results ranged from 95% to 99% and concordance with aerial observations decreased by only 2% at the most (Supplementary Table S3).[1] 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 interannual 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 1 June (2014) to 8 June (2013) (Fig. 3). Peak calving (when the mean middle 50% of calving events occurred) was 2-6 June for our study period and encompassed 4-7 days, with the earliest starting on 31 May (2010 and 2014) and the latest ending on 11 June (2013). We compared the estimated parturition rates from each movement-based method with ratios of observed calf to 100 cows from Dau (2015) and found that both approaches fell below observed ratios for some years (Table 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 of 12% higher than aerial estimates.

Discussion

We set out to examine if the movement-based methods used to identify parturition events for nonmigratory ungulates were applicable for migratory populations. Although 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 data set, with the potential that some of the instances of disagreement were not randomly affiliated with one 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 two methods appeared to function as an index of accuracy, given the R^2 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 with 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. Although 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 with 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 8 June. 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/h) for the WAH was nine times greater than that of the woodland caribou threshold (15.3 m/h) 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/h). 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 Uoly 2005; Prichard et al. 2014). We observed individual variation in postpartum 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 postpartum 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 postpartum movement rates because the herd-level movements are increasing as the herd moves into the faster postcalving movements associated with insect harassment in July (Dau 2015).

Fig. 3. Annual calving phenology for Western Arctic Herd barren-ground caribou (Rangifer *tarandus* granti) from 2010 to 2015 in Alaska, USA. Each histogram indicates the number of estimated parturition events per day for each year. Red vertical dashed lines (gray vertical dashed lines in print) 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-based and population-based methods that were supported by aerial observations, as well as instances where the two movement-based methods agreed on parturition events that lacked aerial observations. Color version online.

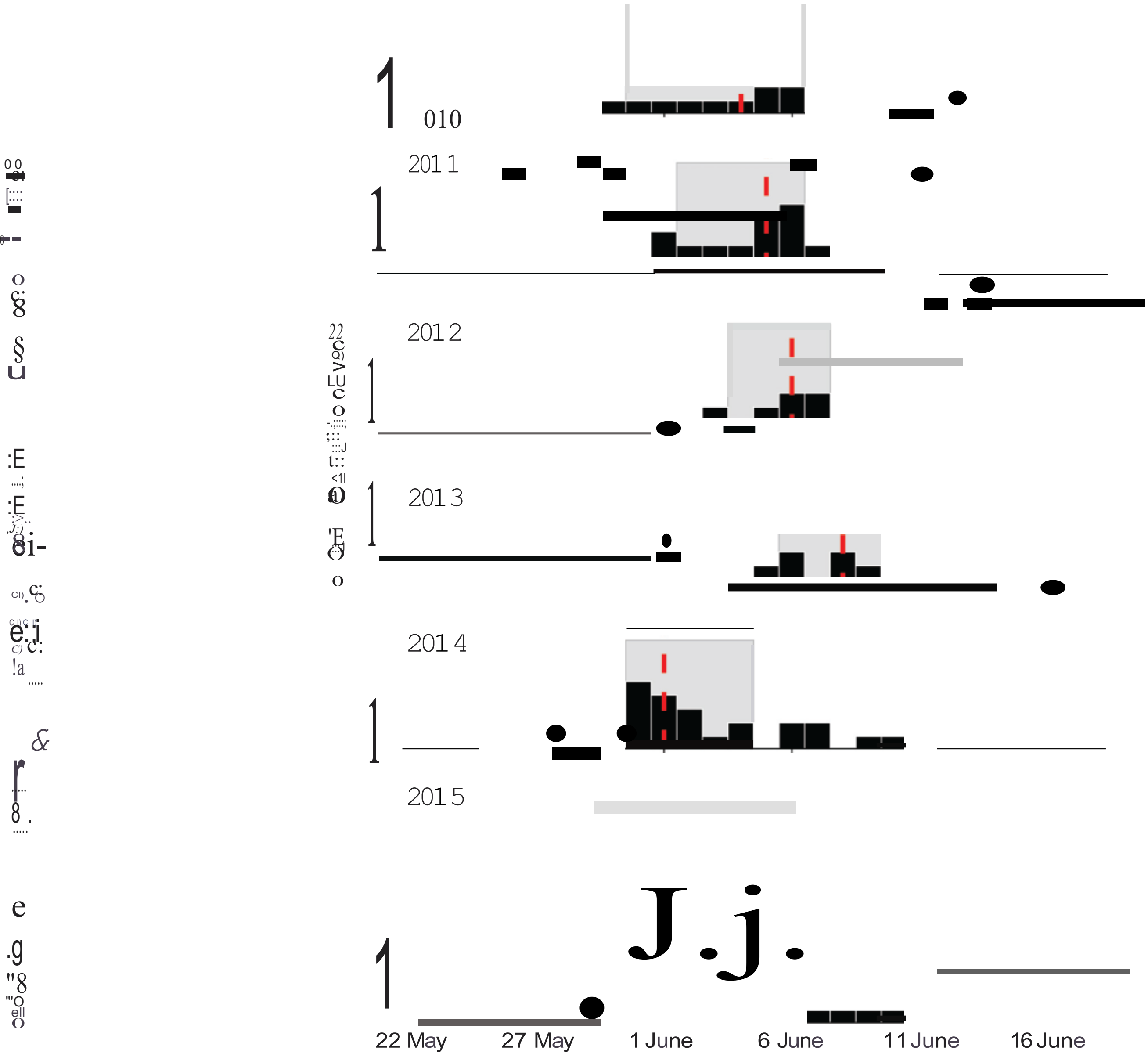

Table 3. Estimates of apparent parturition rates (%) from aerial surveys, individual-based method (IBM), and population-based method (PBM) for Western Arctic Herd barren-ground caribou *(Rangifer tarandus* granti) in Alaska, USA.

	Aerial surveys		IBM only		PBM only		IBM-PBM consensus	
Year	Percent parturition	*n*	Percent parturition	*n*	Percent parturition	*n*	Percent 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 per 100 cows from Dau (2015), which is in contrast to the estimated parturition rates of the movement-based methods.

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/h, well below our PBM threshold, and we attributed some early parturition detections that 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; however, we 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 it 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 Uoly 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 the middle of the time series, followed by a sharp increase in movement rates as the herd transitioned into postcalving movements. As 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 (i.e., 2012) corresponded to the latest spring migration, as noted by the dates of crossing the Noatak River Uoly and Cameron 2017). Although we were unable to test this relationship further, the correlation suggests that detection of p on 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 and 24 h intervals, which contrasts the findings of DeMars et al. {2013} of continual decline in accuracy as the fix rate decreased. We attribute this resilience of sensitivity to the larger magnitude of movement rate changes in migratory animals compared with woodland caribou, and that even a reduced fix rate of one location every 24 h still captured the abrupt change in movement rate associated with parturition. Considering that our analysis was performed using 8 h intervals, we expect that a more frequent relocation schedule during calving could increase the accuracy of these methods, especially for those individuals in which 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 two 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; however, we suspect that a portion of these were indeed pregnant. This means that we were also limited in 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 and 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 three females with hard antlers on the calving grounds having 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 time frame is a reliable indicator of nonparturition.

High neonatal mortality has been reported for neighboring migratory populations such as the Porcupine Herd (8%-25% in the first 48 h; Whitten et al. 1992). Because we lacked daily aerial observations, classifications of nonparturition 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 noncalving 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 — by barren-ground caribou from GPS location data. We recommend the use of both 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 spatial and temporal resolutions in inferring life-history events such as parturition, which can be valuable for future studies that investigate the ecology of migratory animals inhabiting remote environments.

Acknowledgements

We thank J. Dau, C. Westing, B. Dunker, and B. Saito (ADF&G) for conducting annual aerial calving surveys. We thank R. Sarwas of National Park Service (NPS) for his invaluable assistance in data preparation for these analyses, as well as C. Swingley of ABR, Inc. for the many years of managing an immense and complicated data set. We further thank C. DeMars and M. Auger-Methe for their advice and assistance in applying their R script. We thank the NPS and ADF&G for their ongoing support in the long-term monitoring of one of the largest caribou herds on the planet. Lastly, we thank C. Mulder, j. Curl, R. Beltran, and two anonymous reviewers for their helpful feedback that greatly improved the manuscript Funding was provided by NPS.

References

Berger, J. 2004. The last mile: how to sustain long-distance migration in mammals. Conserv. Biol. 18(2): 320-331. doi:10.1111/j.1523-1739.2004.00548.x.

Bergeru<l, A.T., Ferguson. R., and Butler, H.E. 1990. Spring migration and dispersion of woodland caribou at calving. Anim. Behav. 39: 3ro-368. doi:10.1016(S0003-3472(05)8088U.

Bolger, O.T., Newmark, W.O., Morrison, TA., and Doak, D.F. 2008. The need for integrative approaches to understand and conserve migratory ungulates. Ecol. Lett. 11:63-77. doi:10.1111/j.1461-0248.2007.01109.x. PMID: 17897327.

Bowman, J.L, and Jacobson, H.A. 1998. An improved vaginal-implant transmitter for locating white-tailed deer birth sites and fawns. Wildl Soc. Bull. 26(2): 295-298. Available from hnps:/fwwwjstor.org/stable/3784052.

Bree<l, GA., cosra, O.P.• Jonsen, 1.0., Robinson, P.W., and MilJs. FJemming, J. 20U. State-space methods for more completely capturing behavioral dynamics from animal tracks. Ecol. Model. 235-236: 49-58. doi:10.1016/j.ecolmodel. 20U.03.021.

Bunnefeld, N., Borger, L., Van Moorter, B., Rolandsen, C.M., Denki, H., Solberg, E.J., and Ericsson, G. 2011. A model-driven approach to quantify migration panems: individual,regional and yearly differences. J. Anim.Ecol 80(2):466-476. doi:10.1111/j.1365-2656.2010.01776.x. PMID:21105872 .

Burnham, K.P., and Anderson, D.R. 2002. Model selection and multimodel inference: a practical information-theoretic approach Springer, New York.

Calef, GW., DeBock, EA, and Lortie, G.M. 1976. The reaction of barren-ground caribou to aircraft. Arctic, 29(4): 201-212. doi:10.14430/arctic2805.

cameron, R.D., and Whinen, K.R.1979.Seasonal movements and sexual segregation of caribou determined by aerial survey.J. Wildt Manage.43(3): 626-633.doi:10.2307/3808740 .

cameron, R.D., Smith, W.T., Fancy, SG., Gerhart, K.L, and White, R.G. 1993. Calving success of female caribou in relation to body weight. Can.J. ZooL 71(3): 480-486. doi:10.1139/z93-069.

Carroll, G.M., Parren, L.S., George, J.C., and Yokel, D.A. 2005. Calving distribution of the Teshekpuk caribou herd, 1994-2003. Rangifer, 25(16): 27-35. doi: 10.7557/2.25.4.1767.

Chapman, B.B., BrOnmark, C., Nilsson, J.A., and Hansson, LA. 2011. The ecology and evolution of partial migration. Oikos, 120(12): 1764-1775. doi:10.1111/j.1600-0706.2011.20131.X.

Dau, J.R 1997. Units 210, 22A. 228, 23, 24, 26A caribou management report. *In* Caribou management report of survey-inventocy activities, 1July1994-30 June 1996. *Edited* by MV. Hicks. Alaska Department Fish and Game, Juneau. pp. 158-185.Available from http1{wwwad.fg.alaska.gov/staticfhomeflibral}'/pdfs/wildlifefresearch_pdfs/ca_97 _hicks.pdf

Dau, J.R. 2005. Units 210, 22A, 228, 22C, 220, 22E, 23, 24, and 26A caribou management report. *In* Caribou management report of survey and inventory activities, 1July 2002-30 June 2004. *Edited* by C. Brown. Alaska Department of Fish and Game, Juneau. pp. 177-218. Available from httpsI'www.adfgalaska.gov/static/homefhoracy/pdfs/wildlifejmgt_rpts/ca05_wah.pdf

Dau, J.R. 2011. Units 210, 22A. 22B, 22C, 22D, 22E, 23, 24, and 26A caribou management report. *In* Caribou management report of survey and inventory activities, 1July 2008-30 June 2010. *Edited* by P. Harper. Alaska Department of Fish and Game, Juneau. pp. 187-250. Available from httpI'www.adfgalaska.gov/static/homefhoracy/pdfs/wildlifejmgt_rpts{ll_carlOOu.pdf

Dau, J.R. 2015. Units 210, 22A, 228, 22C, 220, 22E, 23, 24, and 26A. *In* Caribou management report of SUtVey and inventory activities, 1July 2012-30June 2014. *EdJted* by P. Harper and LA. McCarthy. Alaska Department of Fish and Game, Juneau. Chapter 14, pp. 14-1 through 14-89. Available from hnp1{www.adfg.alaska.gov/staticf researchfwildlife/speciesmanagementreports/pdfs/caribou_201S_chapter_14_wah.pdf

Davis, J.L, and Valkenburg, P. 1985. alitative and quantitative aspects of natural mortality ofthewestemArctic caribou herd. Final Report FederalAid in Wildlife Restoration Project W-17-11, W-21-2, W-22-1, W-22-2, W-22-3, Job 3.24R Alaska Department of Fish and Game, Juneau, Alaska. Available from hnp:/{www.adfg.alaska.gov/static/homejlibrary/pdfs {wildlife/federal_aid{85_ca_wah_davis_valkenburg.pdf.

DeMars, CA., Auger-Methe, M., Schlllgel, UE., and Boutin, S. 2013. Inferring parturition and neonate survival from movement panems of female ungulates: a case study using woodland caribou. Ecol. Evol. 3(12):4149-4160. doi: 10.1002/ece3.785. PMID:24324866.

de Vos, A. 1960. Behavior of barren ground caribou on their calving grounds. J. Wildt Manage. 24(3):250-258. doi:10.2307/3797511

Dzialak, M.R., Harju, S.M., Osborn, R.G., Wondzell, J.J., Hayden-Wing, LD., Winstead, J.B., and Webb, S.L 2011 Prioritizing conservation of ungulate calving resources in multiple-use landscapes. PLoS ONE, 6(1): e14597. doi:1O.1371/journal.pone.0014597. PMID 21297866.

Fancy, S.G., and Whinen, K.R. 1991. Selection of calving sires by Porcupine herd caribou. *Can. J.* Zoo!. 69(7): 1736-1743. doi:10.1139/z91-242.

Fancy, SG., Pank, LF., Whinen, K.R., and Regelin, W.L. 1989. Seasonal movements of caribou in arctic Alaska as determined by satellite. Can.J. ZooL 67(3): 644-650. doi:10.1139/z89-093.

Franke, A., caelli, T., and Hudson, R.J. 2004. Analysis of movements and behavior of caribou *(Ranglfer* tarandus) using hidden Markov models. Ecol. Model. 173(2-3): 259-270. doi:10.1016/j.ecolmodel.2003.06.004.

Grolemund, G., and Wickham, H. 2011 Dates and times made easy with Jubridate.J. Stat. Softw. 40(3): 1-25. doi: 10.18637/jss.v040.i03.

Gurarie, E., Andrews, R.D., and Laidre, K.L. 2009. A novel method for identifying behavioural changes in animal movement data. Ecol Len. 12(5): 395-408. doi:10.1111/j.1461-0248.2009.01293.x. PMID: 19379134.

Joly, K. 2005. The effects of sampling regime on the analysis of movements of overwintering female caribou in east-central Alaska. Rangifer, 25(2): 67-74. doi:10.7557/2.25.2.254.

Joly, K. 2011. Modeling influences on winter distribution of caribou in northwestern Alaska through use of satellite telemetl}'. Raogifer, 31(2 75-85. doi:10.7557/2.31.2.1992.

Joly, K., and cameron, MD. 2017. Caribou vital sign annual report for the Arctic Network Inventory and Monitoring Program: September 2015-August 2016. Natural Resource Report NPS/ARCN/NRR-2017/1398. National Park Service, Fort Collins, Colo. Available from https1/irma.nps.gov/DataStorejReferencef Profile/2238821

Joly, K., Miller, S.D., and Shults, B.S. 2012. Caribou monitoring protocol for the Arctic Network Inventory and Monitoring Program. Natural Resource Report NPS/ARCN/NRR-2012/564. National Park Service, Fort Collins, Colo. Available from https:lf irma.nps.gov{DataStorejReferencefProfile/2188837.

Kareiva, P.M., and Shigesada, N. 1983. Analyzing insect movement as a correlated random walk. Oecologia, 56(2): 234-238. doi:10.1007/BF00379695. PMID:28310199.

Kelsall, JP. 1968. The migratocy barren-ground caribou of North America. Can Wildt Serv. Monogr. Ser. No.3. Department of Indian Affairs and Northern Development, Ottawa, Ont.

Lent, P.C. 1966a. Calving and related social behavior in the barren-ground caribou. Z. Tierpsychol. 23(6): 701-756. doi:10.1111/j.1439-0310.1966.tb01707.x. PMID:5990062.

Lent, PC. 1966b. The caribou of northwestem Alaska. *In* Environment of the cape Thompson Region, Alaska. *Edited* by N.J. Wilimovsky and J.N. Wolfe. U.S. Atomic Energy Commission, Oak Ridge, Tenn. pp. 481-517.

McClintock, B.T., London, J.M., cameron, MF., and Boveng, P.L. 2017. Bridging thegaps inanimal movement: hidden behaviors and ecological relationships revealed by integrated data streams. Ecosphere, 8(3): e01751. doi:10.1002/ecs2.1751

Mohr, C.O. 1947. Table of equivalent populations of North American small mammals. Am. Midi. Nat. 37(1): 223-249. doi:10.2307/2421652.

Morales, J.M., Haydon, D.T., Frair, J., Holsinger, K.E., and Fryxell, J.M. 2004. Extracting more out of relocation data: building movement models as mixtures of random walks. Ecology, 85(9): 2436-2445. doi:10.1890/03-0269.

Nicholson, K.L., Arthur, S.M., Home, J.S., Garton, E.O., and Del Vecchio, PA 2016. Modeling caribou movements: seasonal ranges and migration routes of the Central Arctic Herd. PLoS ONE, 11(4): e0150333. doi:10.1371/journal.pone.0150333. PMID:27045587.

Person, B.T., Prichard, A.K., carroll, G.M., Yokel, DA., Suydam, R.S., and George, J.C. 2007. Distribution and movements of the Teshekpuk Caribou Herd 1990-2005: prior to oil and gas development. Arctic, 60(3): 238-250. doi:10.14430/arctic216.

Prichard, A.K., Yokel, DA, Rea, C.L., Person, B.T., and Parren, LS. 2014. The effect of frequency of telemetry locations on movement-rate calculations in arctic caribou. Wildt Soc. Bull 38{1): 78-88. doi:10.1002{wsb.357.

Pruitt, W.O., Jr. 1960. Behavior of thebarren-ground caribou. *In* Biological Papers of the University of Alaska. University of Alaska Fairbanks, Institute of Arctic Biology, Fairbanks [originally printed by The Intelligencer Printing Company, Lancaster, Pa.]. Available from http:J/hdl.handle.net/11122/1425.

R Core Team. 2017. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from https1{www.r-project.org/.

Severud, W.J., Del Giudice, G., Obermoller, T.R., Enright, TA., Wright, R.G., and Forester, J.D. 2015. Using GPS collars to determine parturition and cause-specific mortality of moose calves. Wildt Soc. Bull. 39(3): 616-625. doi:1O.1002/wsb.558.

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

Turchin, P.1998. antitative analysis of movement: measuring and modeling population redistribution in plants and animals. Sinauer Associates, Inc., Sunderland, Mass.

Walsh, P.B., Sethi, SA., Lake, B.C., Mangipane, B.A., Nielson, R., and Lowe, S. 2016. Estimating denning date of wolves with daily movement and GPS location fix failure. Wild!. Soc. Bull 40(4): 663-668. doi:10.1002/wsb.703.

Whitten, K.R.1995. Antler Joss and udder distention in relation to parturition in caribou. J. Wildl Manage. 59(2): 273-277. doi:10.2307/3808940.

Whitten, K., Gamer, G., Mauer, F., and Harris, R. 1992. Productivity and early calf survival in the Porcupine caribou herd. J. Wildt Manage. 56(2): 201-212. doi:10.2307/3808814.

Wickham, H. 2007. Reshaping data with the reshape package. J. Stat. Softw. 21(12): 1-20. doi:10.18637/jss.v02Li12.

Worton, B.J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology, 70(1): 164-168. doi:10.2307/1938423.

Zeileis, A., and Grothendieck, G. 2005. zoo: S3 infrastructure for regular and irregular time series. J. Stat. Softw. 14(6): 1-27. doi:10.18637/jss.V014.i06.