



Original Articles

Using fine-scale movement patterns to infer ungulate parturition

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ABSTRACT

Quantifying a fundamental life history event like parturition for any species is important both for wildlife management and research purposes. Surveys to estimate reproductive success for large mammals are typically done by visual observations on the ground or from the air and are time consuming, expensive and labor intensive particularly when conducted in remote locations. An alternative to visual verification is remote monitoring of animal movement and locations which can identify and link movement behavior to different types of life history events, such as parturition. We used GPS locations of a large ungulate (moose) to identify a specific behavioral change in the movement pattern that would indicate a calving event. From these data we applied three methods, one of which is a novel technique, to search for localized movement patterns that characterize a calving event for female moose in Sweden ($n = 60$ moose-years, ground observations) and Alaska ($n = 49$ moose-years, aerial observations). The three methods include a computerized visual method using Tracking Analyst® (TA), a rolling window minimum convex polygon (rMCP), and behavioral change point analysis (BCPA), all of which provided nearly identical results. BCPA confirmed lack of a parturition date for 100% of the animals that were never observed with a calf, whereas the rMCP method yielded 1 false positive. For Sweden, parturition dates inferred using rMCP agreed exactly or ± 1 day with the dates inferred using BCPA for 98% moose-years whereas TA vs BCPA and rMCP agreed 98% and 100% respectively; for Alaska parturition dates estimated from rMCP and BCPA agreed equally at 94%. In this study we showed that evaluation of wildlife movement patterns from remote monitoring can lead to increased precision and understanding of parturition with minimal bias from neonatal mortality, in addition to understanding spatiotemporal distribution, resource selection, and other behaviors.

1. Introduction

Life history traits are fundamental biological components in wildlife ecology and management that help biologists understand and predict the dynamics of animal populations (McCullough, 1979). They reflect selective pressure on timing of reproduction and include components of maturity, fecundity and senescence. Collection of information regarding life history traits from wild animals usually requires large field efforts, so any method that is more effective, precise, and efficient techniques to gain this knowledge would be valuable.

Reproduction and survival of young are life history traits that are typically monitored by both biologists and managers. Because both these traits are the main limiting factors of population size, their estimates are often used to model population dynamics and set harvest quotas for conservation of harvested populations (e.g., Boertje et al., 2007; Keech et al., 2000; Sand, 1996). For many species, age specific

reproduction and survival rates demonstrate that young individuals are often more vulnerable to factors such as predation, density dependence or disease (Albon et al., 1992; Solberg et al., 2000).

There are several methods for monitoring seasonal reproduction or recruitment rates in animal populations. For instance, recruitment rates for wild populations can be obtained by direct observations (ground or aerial), and fecundity rates can be estimated by examining reproductive organs from females harvested during fall or winter hunts (Lavsund et al., 2003; Sand, 1996). However, many methods are restricted to certain seasons, and these methods do not always provide precise estimates during periods when they would best benefit adaptive management. Reliable and representative estimates of these life history traits requires monitoring reproduction at different stages during the reproductive season, including precise information on when individual females give birth (e.g., Keech et al., 2000). Without this information, parturition estimates are likely biased low due to unobserved neonatal

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mortality, particularly where large carnivores exist.

Species with precocial young like moose (*Alces alces*) exhibit annual variation in parturition (Garel et al., 2009; Solberg et al., 2007), so daily observations over the entire birthing period is the highest standard to avoid bias. For large ungulates such efforts in remote areas often involve aerial telemetry (Keech et al., 2000; Boertje et al., 2007) and are both expensive and impractical for routine monitoring. Therefore, in contrast to direct observation, remote monitoring of animal movement and location can allow biologists to identify and link movement behavior to different types of life history events, such as birth (Millsbaugh et al., 2012). In this perspective, an important challenge for biologists would be to develop tools to identify and link movement behavior to specific life history events. Global positioning systems (GPS) have provided an important tool to meet these challenges by providing fine spatial and temporal resolution of location data that has facilitated the expansion in variety and complexity of movement models (Schick et al., 2008; Smouse et al., 2010) and alleviated the need to routinely seek out the individual to obtain similar data. Identifying behavioral events from remotely collected data has been gaining traction in recent years with expanding analysis options that include correlated random walks (Kareiva and Shigesada, 1983), Lévy flight models, state space models (Anderson-Sprecher and Ledolter, 1991), and fractal analysis (Mårell et al., 2002; Turchin, 1996).

In this study we applied three methods based on GPS locations, one of which is a novel technique, to search for localized movement patterns characteristic of calving female moose for more exact temporal estimates of parturition. We hypothesized that these methods will detect and identify a specific behavioral change in the movement pattern that are indicative of a calving event, given that female movements change considerably close to the time of parturition. We used methodology initially developed for studying GPS-collared female moose in Sweden and tested its applicability using a similar dataset collected in Alaska (USA).

2. Study area

2.1. Sweden

We evaluated moose parturition within Grimsö Wildlife Research Area (140 km²) and the surrounding area (total: 730 km²), located in the boreal zone in south-central Sweden (59°–60° N, 15°–16° E). Elevation ranged between 100 and 150 m. Climate was typical for inland, where temperatures usually range from –20 °C in winter to 25 °C in summer (Vedin, 1995). Mean annual precipitation was 60–70 cm, of which 30% falls as snow and the ground is generally covered by snow from December to late March (Alexandersson and Andersson, 1995). The area consisted of 71% forests, 14% bogs, 8% pastures and 6% lakes and rivers. Intensive forestry practices have created a mosaic of various successional stages with a high production of browse for moose. The moose population is mainly controlled by harvest but since the early 2000s they are also impacted by wolf predation. Moose population densities commonly range between 0.6 and 1.5 moose/km². Established forest stands are dominated by Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*) and birch (*Betula pubescens* and *Betula pendula*) (Månsson et al., 2007), bilberry (*Vaccinium myrtillus*), lingonberry (*Vaccinium vitis-idaea*), dwarf birch (*Betula nana*) and heather (*Calluna vulgaris*) (Månsson unpublished data).

2.2. Alaska

The Alaska study area (3700 km²) was in the floodplains of the Innoko and Yukon Rivers and surrounding uplands (62°–63° N, 159°–161° W). Elevation ranged from 30 m with closed forest composed of spruce (*Picea* spp.), Alaska birch (*Betula neoalaskana*), balsam poplar (*Populus balsamifera*), quaking aspen (*P. tremuloides*), graminoid meadows, and wetlands to 850 m in subalpine mountains with sparse open

forest, shrub communities of alder *Alnus* spp., shrub/dwarf birch (*Betula glandulosa/nana*), and *Salix* spp. and scattered tundra. It is a continental climate with temperatures that range from –45 °C in winter to 30 °C in summer. The winter snow period typically lasts from October through April (Paragi et al., 2017), with average December to April monthly depths of 85 cm during the study period. March and April snow depths often exceeded thresholds affecting moose habitat use (70 cm) and causing high energy expenditure (90 cm) (Coady, 1974). Wildland fire is prevalent but stochastic in spruce (*Picea* spp.) – dominated upland forest (Gabriel and Tande, 1983), whereas flooding is the more common disturbance in the forested lowlands, wetlands, and meadows. These disturbance agents, including ice scouring in the active floodplain during spring break-up, rejuvenate willow shrubs and young deciduous trees that provided concealment cover and winter forage for moose. The study area is comprised of wilderness with four small isolated villages along major rivers. During the study moose abundance was approximately 3 moose/km², and 31–55% of parturient females had twin calves (Paragi et al., 2015). Moose were subject to predation by black bears (*Ursus americanus*), brown bears (*U. arctos*), and wolves (*Canis lupus*), all of which were hunted or trapped, and antlered male moose were harvested in fall (Peirce, 2014).

3. Materials and methods

3.1. Capture – Sweden

Adult female moose were immobilized by aerial darting following the procedures described in Arnemo et al. (2003) in March 2007 (n = 20) and 2010 (n = 10). Individuals were fitted with GPS/Global System for Mobile Communications (GSM) collars (GPS/GSM Plus 4D; Vectronic Aeospace GmbH, Berlin, Germany) set to acquire locations every 2 h. For the analysis, we used GPS locations of parturient females only. Reproductive status was assessed, and continuous daily observation events were performed in spring of each year (12 May – 04 July) until the presence of calves was verified. Additional surveys were also performed in late summer (26 Aug. – 09 Sep.) and at the end of winter the following year (01 Apr. – 29 Apr.) to determine summer and winter survival, respectively.

3.2. Capture – Alaska

During 14–18 March 2010 moose were spotted from Piper PA-18 fixed-wing aircraft and immobilized by darting from a helicopter (see details in Paragi et al., 2017). Moose were fitted with Telonics, Inc. (Mesa, AZ) Generation IV model CLM-340 GPS transmitters which were programmed to collect GPS locations every 4 hrs. We assessed reproductive status/females once each year (26 May – 06 June) during aerial surveys to estimate fecundity rate a few days after assumed median calving date (Boertje et al., 2007). Additional flights occurred in fall (2–3 Nov.) and late winter (12–31 Mar.) to validate the number of calves at heel; these observations could verify a calf missed during the spring when flights were logistically impossible or in rare circumstance a calf born after the first observation event (Appendix B in Paragi et al., 2017). We used reproductive status to corroborate estimates of parturition from movement data that were analyzed using the models developed from Sweden data.

3.3. Estimating parturition from movement rates

We used multiple methods to estimate calving dates from collared female location data. Both datasets of moose GPS locations were screened for positioning errors in program R (R Development Core Team, 2015) following a modified method described in Bjørneraas et al. (2010). The screening consisted in removing all unlikely movements, defined by travel speed, travel distances and turning angles. Locations were removed if they were ≥100 km from the median of a 21-point

moving window, centered on that location, or if the speed of the segments immediately preceding and following that location exceeded 1.5 km/h and the cosine of the turning angle was less than -0.97 . We did not screen locations using the mean of the moving window, as described in Bjørneraas et al. (2010), because this proved to be overly conservative, owing to intervals between occasional successive missed locations. GPS paths with data gaps in excess of 72 h were eliminated from analysis. We used field observations to estimate an approximate calving date based on calf age. GPS data covering this period was then visualized by mapping the spatial patterns or movements through time using Tracking Analyst® (TA) extension in ArcGIS (v. 10.3 ESRI, Redlands CA) on the Sweden dataset.

Female moose begin to localize their movements prior to parturition and reduce the distance they move just after parturition (Poole et al., 2007; Wattles and DeStefano, 2013; Welch et al., 2000) and may remain sedentary for several days postpartum (Bowyer et al., 1999; Cederlund et al., 1987; Chekchak et al., 1998; Stringham, 1974; Testa et al., 2000). Therefore, initially we used TA to visualize and animate the movement data of an individual (see Supplemental Video for example). We assigned parturition to the first localization pattern of sequential moose locations confined to $\leq 100 \text{ m}^2$ (Poole et al., 2007) for a period of ≤ 3 days from mid-May to early June.

The second method we used was behavioral change point analysis [BCPA] (Gurarie et al., 2009) to search for a localized movement pattern characteristic of calving female moose to determine more exact temporal estimates of parturition. We used persistence velocity as the representative movement metric. Persistence velocity (Vp) decomposes an animal's movement into the velocity (V) and turning angle (Ψ) between subsequent locations, defined as:

$$V_p = V * \cos(\Psi)$$

The BCPA is an empirical distillation of movement data (Gurarie et al., 2009) with three algorithm parameters that must be user specified: size of analysis window, sensitivity to change detection, and cluster width. First, we set a moving window of 50 data points (100 h for Sweden and 200 h for Alaska) over which to search for change points. Second, following exploratory analysis on a subset of the data, we settled on a sensitivity parameter for the adjusted Bayesian Information Criterion (K) of 0.3, which produced a reasonable balance between reliably identifying a change point while minimizing spurious structural shifts in the plot of Vp. K is generally conservative with respect to selecting the most parsimonious BCPA; increasing its value increases the sensitivity to detect change in movement pattern; if K is too low, no change points will be identified. If no change point corresponding to the calving period could be identified, we increased K to 0.5 and repeated the analysis. Third, to filter out minor change points we used a 48 h cluster width within which neighboring change points were clustered.

As a complement to BCPA, our method was estimating parturition date based on a rolling minimum convex polygon (rMCP) for adult females. McGraw et al. (2014) described the 'localization' behavior of cow-calf pairs in Minnesota, where cow moose commonly make movements over relatively long distances immediately preceding parturition, followed by a period of very little movement. In their study, the area used following parturition dropped to $1.72 \pm 0.48 \text{ ha}$ for approximately 7 days. To correctly identify a parturition date from the rMCP, we searched for 'localization' behavior immediately preceded by a spike in movement. We initially calculated the area of the rMCP in a moving window. For the Sweden dataset, we used a 12-point moving window, with locations spaced roughly 2 h apart, yielding an approximately 24-hour period. Note that these windows are overlapping, yet they are not the same as daily movement, i.e., the first window consisted of the first 1–12 locations, the second window consisted of locations 2–13, etc. By using a 24-hour rolling window we include daytime and nighttime locations in every window while keeping the interval short enough to detect a change in movement in a relatively

short period. Based on McGraw et al.'s (2014) mean localization area, we identified the earliest date where the mean of the overlapping rMCPs remained $\leq 1.7 \text{ ha}$ for approximately 72 h. The date of the first location in a window that meets this criterion, then, should be indicative of parturition. We used a threshold area of 25 ha for the Sweden dataset to represent the spike in movement prior to localization, after which the search algorithm initialized to identify a 72-hour period where the average of the 24-hour rMCPs did not exceed 1.7 ha.

To keep a consistent time period, we used a 6-point moving window for the rMCP for the Alaska moose. Through our observation of the data and setting thresholds we noted the Alaska moose moved greater distances than those in Sweden, both in general and immediately preceding parturition. Therefore, we increased the threshold area for the search algorithm to 100 ha for the Alaska dataset.

4. Results

4.1. Sweden

We monitored 60 moose-years for parturition in Sweden during 2007–2011. Field observations confirmed that 50 of those moose calved and 10 did not calve during this period. The localization of movement patterns was not evident for the 10 moose-years which were confirmed not to have calved (examples of non-birth moose movement Fig. 1). For the 50 field observations that confirmed that calves were produced (examples of parturition movement Fig. 2), there was one instance where the analytical methods did not indicate calving behavior though a calf was seen in late summer. Additionally, there was one instance where rMCP indicated a parturient moose, though BCPA and field observations did not.

The three methods (TA, BCPA and rMCP) to estimate calving dates, all yielded nearly identical results (Table 1). Parturition dates inferred using rMCP agreed with the dates inferred using BCPA with $< \pm 1$ day for 98% moose-years whereas TA vs BCPA and rMCP agreed 98% and 100% respectively (Table 1). Due to the high level of agreement between TA and the other two analytical methods (98% BCPA; 100% rMCP) in the Sweden dataset, we decided not to use TA on the Alaska moose.

4.2. Alaska

We monitored 49 moose-years for parturition in Alaska during 2010–2013. Field observations indicated that six moose did not produce a calf while 36 did. Neither BCPA nor rMCP indicated a parturition event for the six field observations where no calf was observed (e.g., Fig. 3). Another seven female moose were observed as barren during telemetry flights but had movement patterns indicative of parturition (Table 2). Analysis using either method showed that all these seven barren moose had a spatial movement pattern suggesting that parturition had occurred (example moose 24 Fig. 4).

For the 36 moose-years with confirmed visual observations of calves, parturition dates inferred using rMCP agreed with the dates inferred using BCPA with $< \pm 1$ day for 94% (Table 2; Fig. 4). Of the four where the method disagreed $> \pm 1$ day, one differed by two days, two were ambiguous owing to a secondary localization in movement patterns, and the last had the rMCP search algorithm identify parturition as occurring on 5/10/2012, whereas the actual date from BCPA and field observations was identified as 5/25/2012 (Fig. 5).

Not surprisingly, the ability to conduct additional telemetry flights after a spring survey increases the ability to confirm parturition when ≥ 1 calf survives during the intervening periods. We observed 21 parturient individuals among 29 females we monitored on spring telemetry flights in 2010 and 2011 but validated 27 parturient females when including observations from 1 to 2 subsequent flights those years. In those two years BCPA further suggested another three females reproduced although we did not observe a calf during telemetry flights.

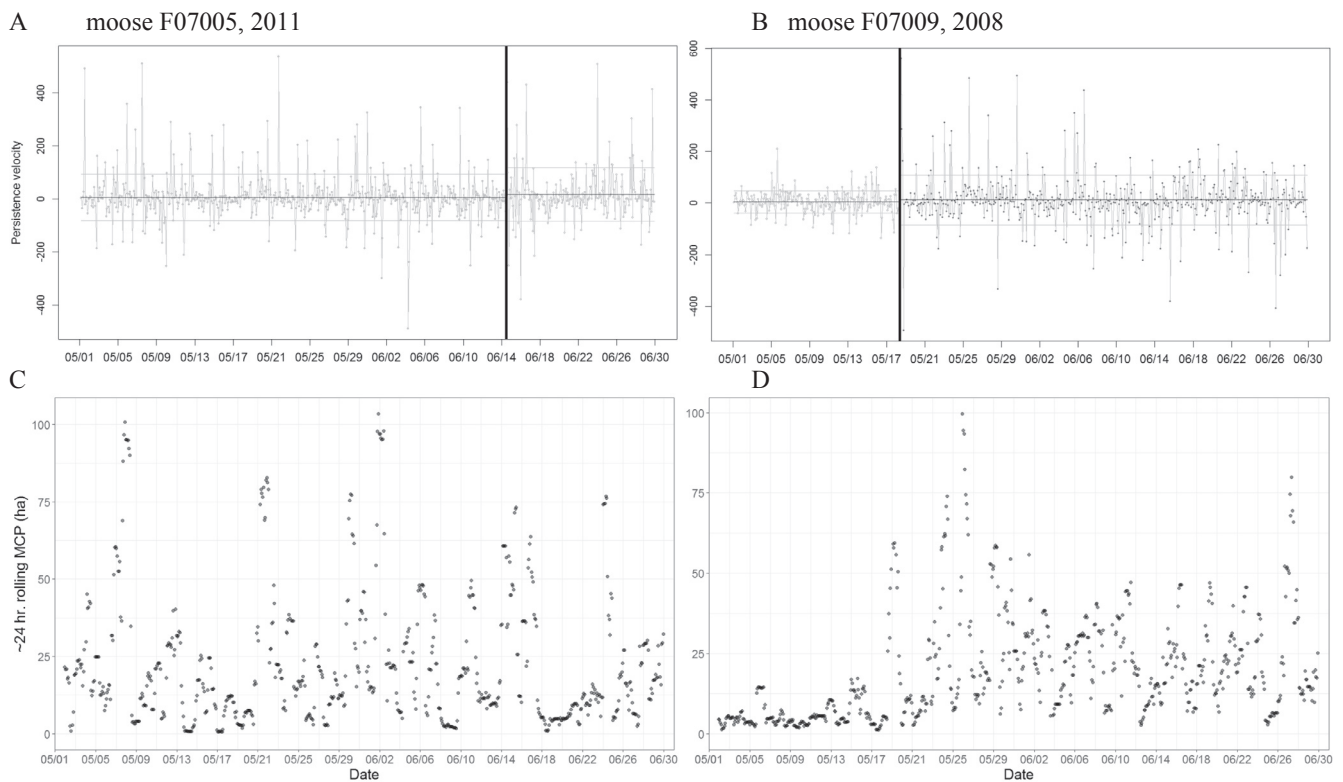


Fig. 1. Example of movement of non-parturient cow moose in Sweden (moose ID F07005 in 2011 and F07009 in 2008) plotted by the BCPA (A, B) and the rMCP methods (C, D). Analysis from GPS locations recorded in a rolling window spanning approximately 24 h. Solid vertical line in BCPA graphs indicates the day at which there was a “change point” in the movement metric.

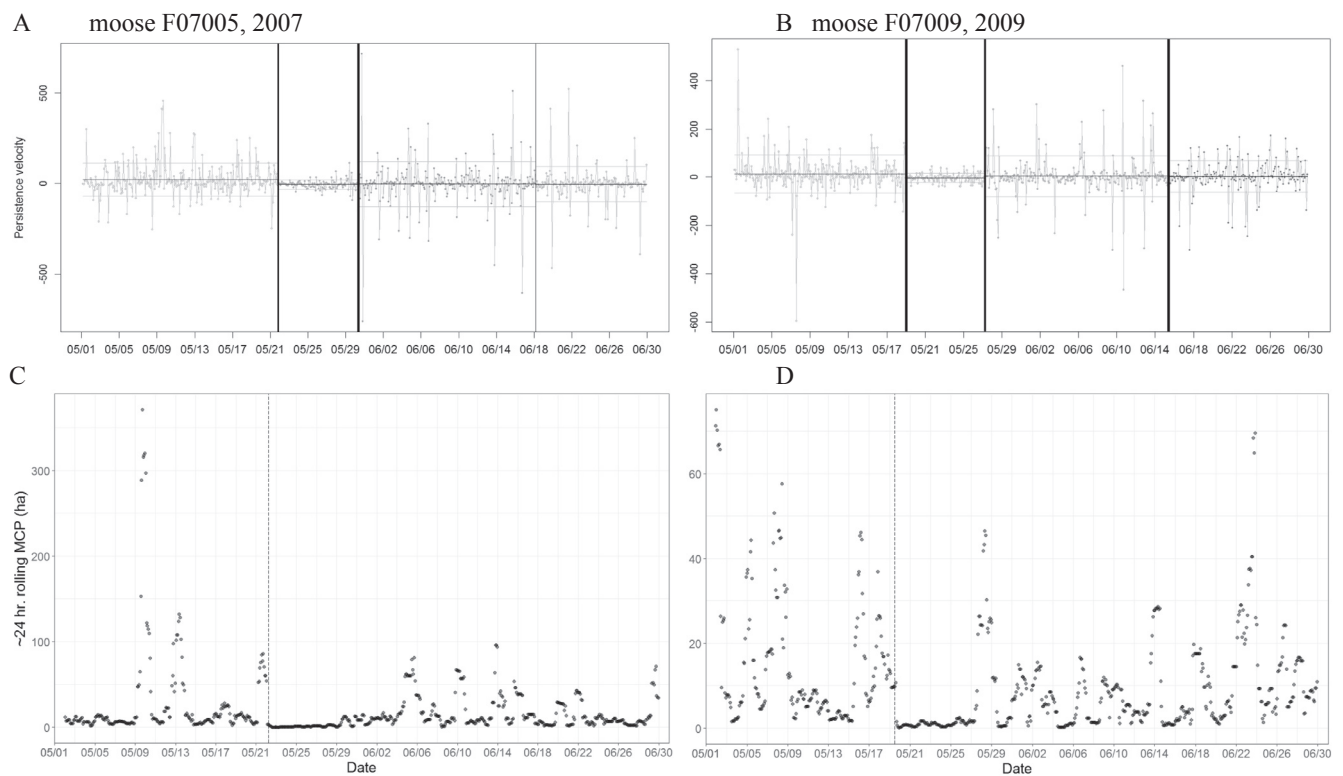


Fig. 2. Example of identification of parturition date for GPS-collared moose in Sweden (moose ID F07005 in 2007 and F07009 in 2009) inferred from the BCPA (A, B) and the rMCP methods (C, D) for GPS locations recorded in a rolling window spanning approximately 24 h. Solid vertical line in BCPA graphs indicates the day at which there was a “change point” in the movement metric. Vertical dash line indicates date of constriction in the rMCP.

Table 1

Difference ($0, \pm 1, > \pm 1$ days) between estimation methods and sample size of estimating calving dates for confirmed parturient moose in Sweden (2007–2011; 60 moose-years). Methods were visual estimation using Tracking Analyst (TA), behavioral change point analysis (BCPA), and rolling minimum convex polygon (rMCP).

Year	# female moose	Observations		TA vs BCPA			TA vs rMCP			BCPA vs rMCP		
		# moose no calf	# moose with calf	0	± 1	$> \pm 1$	0	± 1	$> \pm 1$	0	± 1	$> \pm 1$
2007	14	3	11	10	1	0	10	1	0	9	2	0
2008	13	2	11	8	2	1	9	2	0	8	2	1
2009	12	2	10	8	2	0	6	4	0	8	2	0
2010	13	1	12	8	3	0	6	5	0	7	4	0
2011	8	2	6	6	0	0	4	2	0	4	2	0
Total	60	10	50	40	8	1	35	14	0	36	12	1
				82%	16%	2%	71%	29%	0%	73%	24%	2%

Compared to use of BCPA to identify activity break points indicative of parturition, telemetry observations during 2010–13 underestimated the proportion of parturient females by 16% (7/43; Table 2).

5. Discussion

By using movement information, we were able to identify and confirm calving events for moose in Sweden and Alaska. In only one of the 109 moose-years a calf was born without being detected by either method. BCPA confirmed lack of a parturition date for 100% of the animals that were never observed with a calf, whereas the rMCP method yielded one false positive. Although the TA-method is not analytical, it is a first step in exploring data that permits animating and visualizing movement patterns. In the absence of aerial or ground observations, these methods can be used to gauge if and when to examine collared individual in the field. Furthermore, by comparing the methods we have strong evidence that we can identify the date of calving within ± 1 day.

Quantifying reproductive success is important both for studying

wildlife ecology and population management. Reproductive surveys should be timed to maximize the sample size of parturient females (toward end of calving period) yet minimize exposure of early-born calves to neonatal mortality that will negatively bias estimates of reproduction (Boertje et al., 2007; Bowyer et al., 1999; Testa et al., 2000). Observations of barren females during a single spring survey around the median calving date (but before leaf eruption in shrubs and trees reduces visual detection of calves) may result from neonatal calf predation before the observational flight (Boertje et al., 1988; Keech et al., 2011). Additionally, the presence of newborn calves are sometimes difficult to verify because of remoteness (limited search time), complex habitat structures, and dense vegetation (Addison et al., 1990). These difficulties require multiple surveys at short intervals to confirm presence of a calf at heel (Boertje et al., 2007). Data collected during other seasons is not directly comparable to observations conducted in the spring because of the variable time of exposure to mortality factors. Climate change may affect the phenology of plants or snow cover, which in turn could alter the selection for timing of parturition for herbivores such as moose (Bowyer et al., 1998; Monteith et al., 2011;

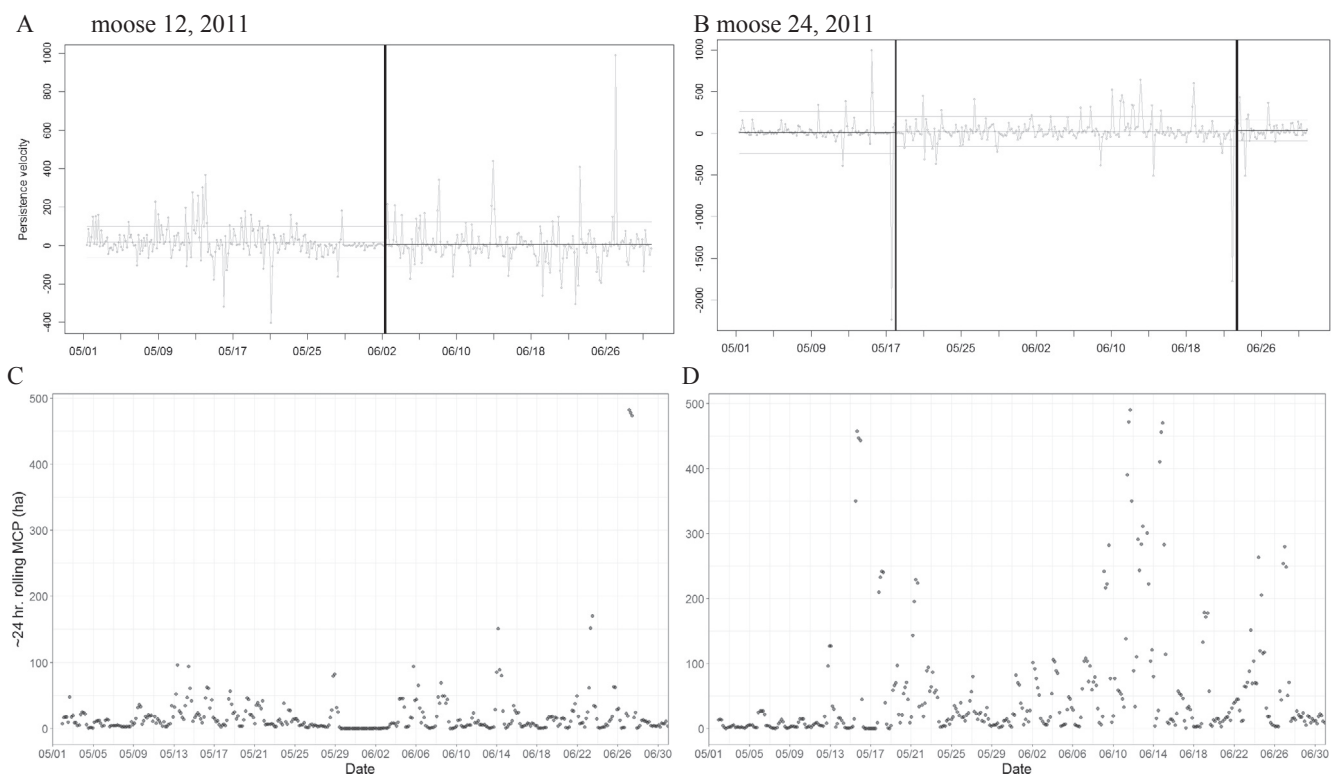


Fig. 3. Example of movement from non-parturient cow moose in Alaska (moose ID 12 and 24 in 2011) plotted by the BCPA (A, B) and the rMCP methods (C, D). Analysis from GPS locations recorded in a rolling window spanning approximately 24 h. Solid vertical line in BCPA graphs indicates the day at which there was a “change point” in the movement metric.

Table 2

Difference ($0, \pm 1, > \pm 1$ days) between estimation methods and sample size of estimating calving dates for confirmed parturient moose in Alaska (2010–2013; 49 moose-years). Analysis indicated suspected moose had calved even though calves were not observed. Analytical methods were behavioral change point analysis (BCPA) and rolling minimum convex polygon (rMCP).

Year	# female moose	Observations		Difference in Date of calving (days) BCPA vs rMCP			# females with no calf but suspected from movements	Difference in date of calving (days) BCPA vs rMCP		
		# females with no calf	# females with calf confirmed	0	± 1	$> \pm 1$		0	± 1	$> \pm 1$
2010	20	2	16	6	10	0	2	1	1	
2011	18	4	13	3	9	1	1	1		
2012	7	0	5	3	1	1	2	1		1
2013	4	0	2	1	1	0	2	1		1
Total	49	6	36	13	21	2	7	4	1	2
				36%	58%	6%		57%	14%	29%

Post and Forchhammer, 2008). In this context, methods that can be used to monitor temporal changes in important life history traits such as parturition dates should be an important tool in assessing effects of climate change in terrestrial ecosystems.

Biological cues, such as changes in movement patterns, can help to focus search efforts and make field observations more cost effective. These cues provide a more appropriate estimate of the number of parturient cows compared with aerial surveys. If aerial surveys had been limited to one flight in the spring for Alaska, we would have assumed only 29 moose calved, whereas the analytical methods of remote monitoring indicated that there were 43. If the objective was to estimate the average number of calves born per female in the population (natality rate; Schwartz, 2007:142) or the proportion of parturient females with twins (Boertje et al., 2007), neither of the two GPS-based methods would have been sufficient because neither can discern litter size. However, the GPS methods allow an estimate of parturition rate (the fraction of females producing offspring) without requiring

repeated flights to monitor marked females until each gave birth. The GPS data acquisition in Alaska was designed for other purposes (Paragi et al., 2017), and for cost efficiency we uploaded collar data once a week; however, real-time analysis during the calving period was possible. As cost of technology decreases and automation (speed) of data download and analysis increases, we expect deployment of GPS collars to monitor other finer-scale animal movements will become more common in wildlife research and management.

An analysis similar to BCPA has been used to identify moose calving locations in Minnesota (McGraw et al., 2014) where they utilized 20 min GPS locations and calculated distance moved per day, focusing on the localization of the movements to identify the birth site. Poole et al. (2007) described moose movement behavior to be localized to 0.8 ha in size and a moose would stay localized on average 6.5 days while giving birth. This method is flexible in that it not only identifies the exact day using 2 or 4-hour intervals within a 3-day window but could also easily be linked to GPS coordinates and pin-point the calving

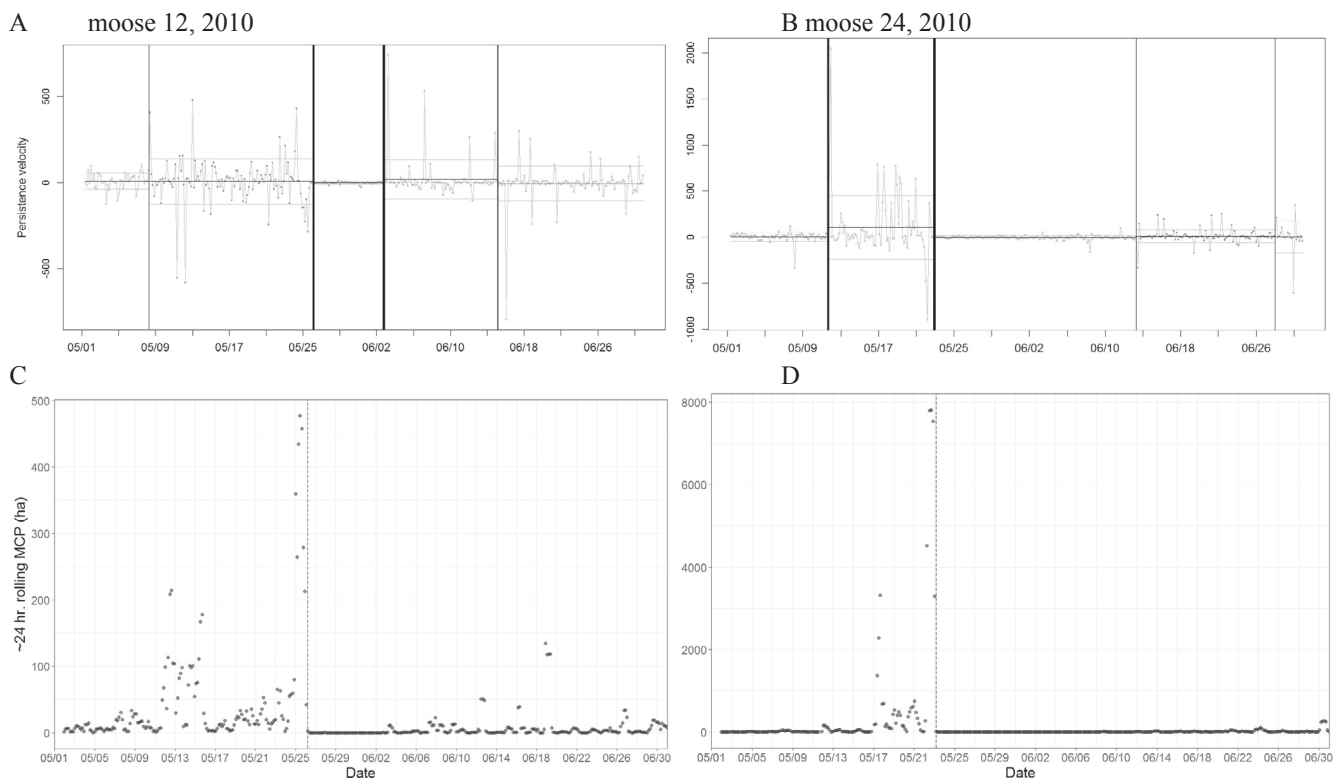


Fig. 4. Example of identification of parturition date for GPS-collared moose in Alaska (moose ID 12 and 24 in 2010) inferred from the BCPA (A, B) and the rMCP methods (C, D) for GPS locations recorded in a rolling window spanning approximately 24 h. Solid vertical line in BCPA graphs indicates the day at which there was a “change point” in the movement metric. Vertical dash line indicates date of constriction in the rMCP.

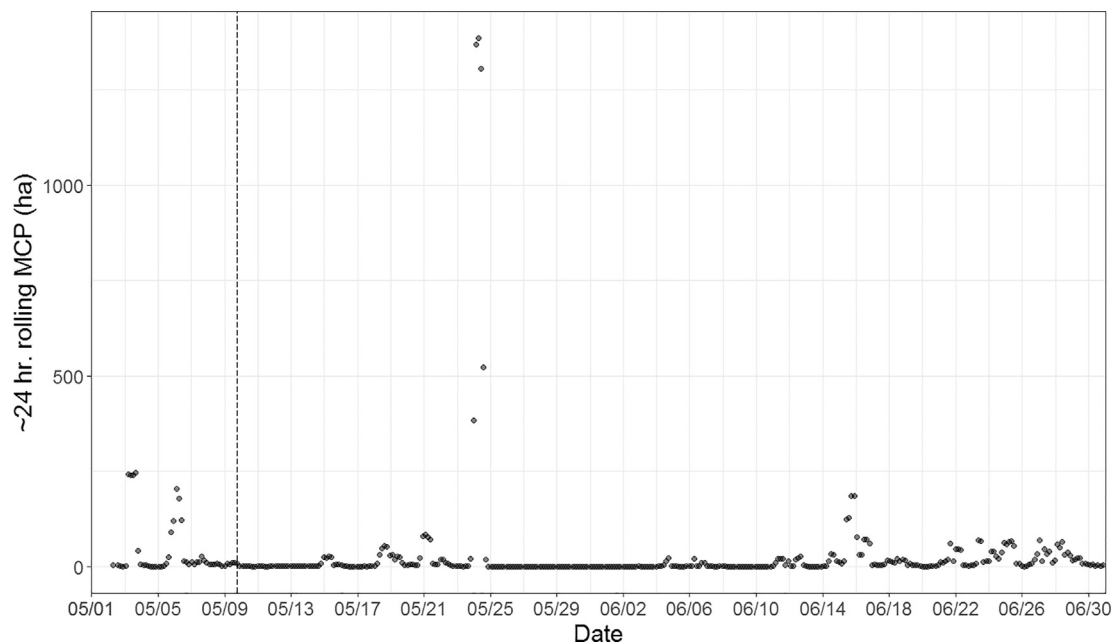


Fig. 5. Parturition date (vertical dashed line) identified by a search algorithm for a GPS-collared moose in western Alaska inferred from the contraction in area of the rMCP for GPS locations recorded in a rolling window spanning approximately 24 h. This date is almost certainly a false positive; the actual date appears to be closer to 5/25/2012.

location for additional studies of habitat related birth sites. BCPA also provides an unbiased estimate of percent parturient females. For example, not all Alaska calves were spotted on the first flight as weather or mechanical problems prevented some surveys to be conducted as planned. Recently BCPA has been used in a variety of manners such as separating out foraging vs. traveling movements (Gurarie, 2008; Gurarie et al., 2009) or identifying calving sites for caribou (*Rangifer tarandus*) and survival of neonates (e.g., DeMars et al., 2013). Although our study was not designed to estimate survival of neonates, it is possible through carefully monitoring of parturient cows that BCPA and rMCP could be used to identify females that lose their calves after parturition.

Using MCPs in wildlife studies has been around for > 50 years (e.g., Mohr, 1947). Over this time, modifications and alternative uses relying on the fundamental concept have arisen to calculate home ranges, delineating core habitat, or areas of high use (Long and Nelson, 2011; Lyons et al., 2013). Our use of MCPs are not intended to map space use such as with local nearest-neighbor convex-hull (Getz and Wilmers, 2004), we are using MCPs to determine the point in time when a behavior changed based only on the time between locations. Thus, to our knowledge, using a moving window MCP to identify behavioural movement changes related to calving is a novel modification. Whereas rMCP is a measure of area used, BCPA is a measure of the movement pattern, albeit requiring the fit 3 of empirical parameters of positional change. Both methods are based on the same GPS locations and are empirical techniques that require optimization of short-term movement sensitivity to discern known behavioral stages associated with parturition. However, rMCP requires a sampling frequency sufficient to capture changes in movement behavior. Thus, it may not be accurate in all instances and should preferably be used as a starting point for identifying parturition, rather than a certainty. rMCP is conceptually intuitive, is less subjective than interpreting output from other tools (e.g., TA in ArcGIS), and objectively identifies movement localization as a complement to BCPA.

We used moose as a model species, but these methods may be widely applicable given feasible technology (e.g., appropriate transmitter size and weight) and species-specific adjustments in parameter fitting. Having confirmation of exact timing of birth for wild forest-

dwelling animals is rare and difficult to get. On the ground visual observation of birth and age estimation of juveniles are typical protocols for many studies but the estimation of the exact date of birth for moose can become tricky after an age of > 3 days. In addition, visual age estimation (thus date of parturition) is likely to be greatly affected by the experience of the observer, the duration of the observation, the proximity to the animal to recognize age characteristics, and the number of days after birth. Therefore, we chose to not include nor treat the estimated dates of birth from field observations as the truth to compare with the analytical results from movement pattern. Instead, this study searched for abrupt changes in the movement behavior of females' indicative of reproduction and evaluated how this corresponded between the analytical methods used. These methods confirmed parturition through remote monitoring. Additionally, the agreement between the methods (± 1 day – 97% agreement), the confirmatory support from field observations, and the high performance in distinguishing cows with and without calves, is strong indication that the estimate of parturition is at or close to the true dates.

Because equipping animals with GPS collars can be an expensive undertaking, it is possible that reducing the resolution of locations obtained per day would increase the battery life of the collar. In this study we were able to detect the movement pattern for parturition using 2- or 4- hour intervals of GPS locations in < 3 days. A finer time scale may require finessing the sensitivity of the input parameters, particularly the cluster width, to ensure the detection of a single localization period, if parturition did occur. Additionally, the finer time scale for any method becomes an inefficient use of battery life of the collar which may be providing more detail than is necessary for the algorithm to define the parturition behaviour. Though we did not specifically assess the method's ability to recognize the parturition pattern at coarser resolutions (i.e., 6- or 8-hour intervals), they are still likely to work given that moose in this study localized for around 3 days at a minimum, and for 6–7 days in British Columbia and Minnesota (Poole et al., 2007; McGraw et al., 2014). At time scales > 8 h, the methods may fail to capture biologically meaningful movements.

When GPS telemetry is used for monitoring wild free-ranging ungulates, the minimal extra effort to obtain data on parturition provides an opportunity to gather additional real-time demographic and

behavioral data that can be relevant to research and management. These analytical methods are non-intrusive compared with the expense of implant transmitters or potential disturbance from repeated close observations around the date of parturition, and GPS telemetry is more cost efficient than repeated observations in remote areas requiring observations from aircraft. With prior planning managers can incorporate this technique as part of operational protocols to increase efficiency and sample size. For instance, managers could design a twinning survey that by deploying GPS transmitters would eliminate or reduce the necessity for the daily direct parturition observations on those individuals. If utilized in conjunction with additional less expensive VHF collars, managers could effectively reduce the number of individuals that require intensive surveys.

Movement patterns can differ during certain life history events such as mating, migration, or parturition, all of which influence reproductive success. In this study we showed that evaluation of wildlife movement patterns from remote monitoring, in addition to improving our understanding of spatiotemporal distribution and resource selection and other ecologically important behaviors, can also lead to increased understanding of reproductive behaviors and outcomes. With continued refinement of these techniques, it may be possible to distinguish between females that have twins from those with single calves. Similarly, calf mortality may be detected as DeMars et al. (2013) has estimated for caribou. These movement cues may be used to increase the accuracy of estimates for parturition and survival in moose and other ungulates and thereby also to better understand and predict the dynamics of the populations.

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Author contributions

KLN, HS, and JM conceived the ideas and designed methodology; TP, HS, and JM collected the data; CR, KLN, and MJW analyzed the data; KLN led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2019.01.004>.

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