ESTIMATION OF MOOSE PARTURITION DATES IN COLORADO: INCORPORATING IMPERFECT DETECTIONS

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ABSTRACT: Researchers and managers use productivity surveys to evaluate moose populations for harvest and population management purposes, yet such surveys are prone to bias. We incorporated detection probability estimates (*p*) into spring and summer ground surveys to reduce the influence of observer bias on the estimation of moose parturition dates in Colorado. In our study, the cumulative parturition probability for moose was 0.50 by May 19, and the probability of parturition exceeded 0.9 by May 27. Timing of moose calf parturition in Colorado appears synchronous with parturition in more northern latitudes. Our results can be used to plan ground surveys in a manner that will reduce bias stemming from unobservable and yet-born calves.

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Throughout North America and Europe, researchers and managers use surveys of moose productivity to evaluate populations for harvest management purposes (Boertje et al. 2007, Grøtan et al. 2009, Milner et al. 2013); however, surveys are prone to bias (Williams et al. 2001, White 2005). When surveying for newborn moose calves, one source of bias is associated with the detection probability (*p*) of moose calves-at-heel (Bergman et al. 2020). More specifically, if a calf is observed, then *p* is conceptually 1 for that individual during that occasion. However, if a calf is not observed, then uncertainty about its presence exists (i.e., was the calf simply not observed, or was there no calf to be observed). If surveys are conducted near the peak time of parturition, this bias is confounded by the possibility that cows may have not yet given birth. Calf-at-heel estimates are also prone to bias as calf mortality occurs. However, multiplying monthly (or daily) calf survival rates by calf-at-heel ratios provides a numerical correction for bias stemming from calf mortality (Bergman et al. 2020). No simple multiplicative, numerical correction exists for pre-parturition observations.

Fortunately, accounting and accommodating for many types of bias is possible in both modelling and survey design. First, estimates of *p* can be modelled from repeated observations (Bergman et al. 2020). Once estimated, *p* is used to inflate calf-at-heel or calf:cow ratios to reduce bias in estimates. An example of such an approach was completed by Bergman et al. (2020) who used occupancy modelling and 3 years of ground observation data from radio-collared cow moose to generate a summertime estimate of p = 0.80. We suggest that a supplemental approach to reducing bias stemming from unborn calves is to quickly and efficiently conduct calf-at-heel surveys after the bulk of parturition has occurred.

Under ideal conditions and with modern technology, timing of moose parturition can be estimated with minimal uncertainty. For instance, Vaginal Implant Transmitters (VIT) are used to alert researchers to the timing and location of a birthing event (Patterson et al. 2013, 2016, McLaren et al. 2017). This approach is often used when the objective is to capture and collar newborn calves. However, it requires capturing adult females to assess pregnancy status and to deploy a VIT. The recent development of satellite-based VITs minimizes the previous need for daily ground or aerial monitoring, but the technology remains cost prohibitive for most routine management purposes.

A second and increasingly tractable approach to estimate parturition dates and locations for large herbivores is also tied to satellite technology. Satellite collars now allow researchers to shorten the duration between sequential locations of animals and achieve nearly real-time transmission of data. Movement algorithms, or even close scrutiny of sequential data points can be used to identify clustered locations that are often indicative of birthing events (Severud et al. 2015, McLaren et al. 2017, Cameron et al. 2018). However, neither traditional VHF radio-collars, store-on-board GPS collars, nor early generation satellite collars provide the frequency of locations and the nearly real-time transmission of data necessary to identify birth sites.

Our objectives for this research were twofold. First, using ground observation data, we estimated a parturition date curve for moose in Colorado. Managers in Colorado and elsewhere will benefit from estimates of the timing of parturition made more precise by incorporation of p, such that they can implement recruitment surveys when a threshold (such as >90%) of birthing events is predicted. Our second objective was to correct estimates of parturition timing for p in this modelling process, thereby improving the precision of parturition date estimates. We hypothesized that accounting for p would shift the date of cumulative births to an earlier date, thereby allowing managers to initiate calf surveys at an earlier date without pre-parturition bias.

STUDY AREA

We conducted this research across 3 study areas in Colorado. The 2 most northerly were located in Jackson (North Park) and Larimer (Laramie River) Counties, with the southern study area (San Juan Mountains) in Hinsdale and Mineral Counties (Fig. 1).

North Park was a high elevation (2,400–2,750 m), wide (14–46 km) mountain valley surrounded on the west by the Park Range mountains, on the south by the Rabbit Ears mountain range, and on the east by the Rawah and Never Summer mountain ranges. To the north of the study area was a mix of private and public lands managed primarily for agricultural and open rangeland purposes. Moose habitat in North Park followed small rivers and creeks comprised of a diversity of willow (*Salix* spp.) communities. Moose also used aspen (*Populus tremuloides*), lodgepole pine (*Pinus contorta*), and Englemann spruce (*Picea engelmannii*) forests. Much of the pine and spruce forests in North Park and throughout Colorado experienced mountain pine beetle (*Dendroctonus ponderosae*) outbreaks during the latter part of the 20th and first decade of the 21st century, placing these forests into an array of successional stages (Hayes 2020).

The Laramie River study area was located ~ 40 km northeast of North Park with the Rawah mountain range (3,200–3,840 m) separating them. It was also a high elevation mountain valley (2,470–2,800 m), although the valley floor was not as wide as North Park (3–9 km). Diverse willow stands located along the rivers and creek corridors gave way

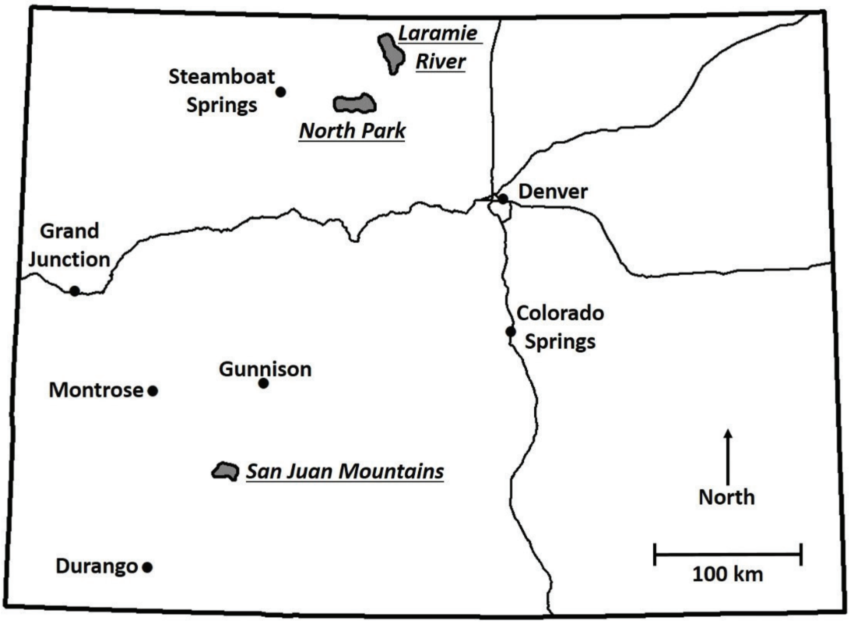

Fig. 1. Map of Colorado, USA (black rectangular perimeter) depicting 3 study areas in relation to nearby cities and communities. Study units are depicted by gray filled polygons.

to more upland aspen, lodgepole pine, and Englemann spruce forests.

The San Juan Mountains study area in southern Colorado at 2,750–3,130 m elevation was higher than the North Park and Laramie River study areas. It was comprised of narrow valleys (0.5–1.5 km wide) with vegetation communities similar to those in the northern study areas.

Management authority of moose belonged to Colorado Parks and Wildlife (CPW) in all 3 study areas, and each sustained limited cow and bull harvest. Predator assemblages were consistent across study areas with black bears (*Ursus americanus*) and mountain lions (*Puma concolor*) the primary predators of moose, although coyotes (*Canis latrans*) could potentially kill newborn moose calves; wolves (*Canis lupus*) and grizzly bears (*Ursus arctos horribilis*) were absent. Predation pressure was considered low in each study area.

METHODS

Field methods

We captured cow moose (>1 year-old) via helicopter darting for 4 winters between mid-December and the end of January, 2015–2018. We sedated moose using one of three different drug combinations: 1) BAM (54.6 mg of butorphanol, 18.2 mg of azaperone, and 21.8 mg of medetomidine) in combination with ketamine (200 mg), 2) carfentanil (3 mg) in combination with xylazine (100 mg), or 3) thiafentanil (10 mg) in combination with xylazine (25 mg). Once sedated, we blindfolded each animal and administered oxygen (via nasal canula) to minimize the risk of adult and fetal hypoxia. We fitted moose with either a VHF radio-collar (Advanced Telemetry Systems, Isanti, Minnesota, USA; USA model: M2520B), a store-on-board GPS/VHF collar ([Advanced Telemetry Systems; USA model: G2110D], or a satellite/VHF telemetry collar

[Vectronics Aerospace GmbH, Berlin, Germany; model: Vertex Plus, and Advanced Telemetry Systems; USA model: G5-2D]). Blood samples were taken to determine pregnancy status using Pregnancy Specific Protein B (PSPB, Wood et al. 1986). After handling, capture drugs were antagonized with naltrexone (100 mg, antagonist for carfentanil and thiafentanil), tolazoline (500 mg, antagonist for azaperone and xylazine), and atipamezole (100–150 mg, antagonist for medetomidine and xylazine). All capture and handling methods were approved by the Institutional Animal Care and Use Committees at Colorado Parks and Wildlife (#08-2013) and the University of Montana (#032-17CBWB-060517).

During the first year, no moose had been previously captured or collared. In subsequent years, previously collared moose were neither targeted nor avoided by the capture crew. As a result, this random process meant that the pregnancy status of some collared moose was unknown.

Each spring and summer we conducted ground surveys to evaluate the calf-at-heel status of each collared cow. We began observations in early May and continued through August. Pregnant moose, based on PSPB results at the time of capture, were prioritized for observation. Once these animals were observed, we completed observations of radio-collared animals with unknown pregnancy status. Typically, ground observations were completed by a single observer by relying on previous known locations and using VHF signals for ground tracking. A second observer was used for individual moose that consistently evaded observation by a single observer. In cases with two observers, one homed in on the moose using the described techniques, with the second observer stationed along the expected exit route with the goal of observing the moose as it passed by. Moose observations typically fell into 2 categories: stationary or moving. Stationary observations were made of moose that were either bedded or standing idly while they foraged. Stationary observations often lasted from 5 to 20 min and ended when a moose stood and moved or foraged out of sight. Moving observations were those of moose displaced by an observer. To be considered a completed observation, observers needed to see the entire moose and the surrounding 2 m of space. Repeat observations were made on animals throughout the summer to increase the detection probability of calves, and to help determine the fate of calves. We recorded date, time, and location of each observation.

Analytical methods

Our objective was to estimate the parturition date for moose in Colorado. Thus, only cow moose that were eventually observed with calves-at-heel were included in analyses. Cow moose that were never observed with a calf helped inform calf-at-heel and calf:cow ratios (Bergman et al. 2020), but did not inform estimates of birth dates. The date of each observation was standardized against the date of the earliest survey (27 April), allowing for simple numerical progression throughout the survey period.

We used a hierarchical Bayesian model to evaluate the probability of parturition during the study period (McCarthy 2007, Gelman et al. 2009). The hierarchical component refers to the multiple levels included in the model, which are ultimately integrated to estimate posterior estimates for each parameter of interest (Gelman et al. 2009).

The base model for parturition probability included an estimate of the probability of detection and followed a logistic regression with a "logit" link. The model had the following form:

$$logit\,(\rho_i) \sim \alpha + (\beta \times \vartheta_i) + \gamma_{\delta_i} + \gamma_{\tau_i},$$

where α is the global intercept, ϑ is the date of observation (with corresponding coefficient β), and random effects (γ) of year (δ) and cow (τ) for each cow, i. The predicted calf presence, ρ, was influenced by an estimated probability of detection 0.8 (Bergman et al. 2020) and followed a Bernoulli distribution, modeled as:

$$Y_i \sim Bern\ (\varphi_i);$$
$$\varphi_i = \mu \times \omega_i;$$
$$\omega_i \sim Bern\ (\rho_i),$$

where the observed calf detections (Y) follow a Bernoulli distribution with probability (φ) informed by the product of the detection probability (μ) and estimated calf detection (ω, per cow i). This is standard practice for including detection probability in Bayesian models (McCarthy 2007).

The random effects were given vague normal priors with uniform precision (inverse of variance):

$$N\left[0,\,\theta\right];\ \theta = \frac{1}{\sigma^2};\ \sigma^2 \sim U\left[0,\,10\right].$$

The global intercept and β coefficient were given vague normal priors:

$$N\,[0,\ 1.0 \times 10^{-6}].$$

We ran the model using the "runjags" package (Denwood 2016) in R (R Core Team 2019) including 3 chains, with 10,000 iterations per sample and a burn-in of 5,000 iterations and a thinning parameter of 5. We determined convergence when R-hat < ~1.1 for monitored parameters (Gelman and Rubin 1992).

RESULTS

We captured 46 individual cow moose that were observed with spring or summer calves-at-heel, providing for 86 unique animal-by-year observations (i.e., some cows were observed multiple years). We made a total of 213 unique observations of these individuals. Within a single year, the minimum number of observations of an individual moose was 1 (when a cow was observed with a calf during the first observation and subsequent observations were not made), and the maximum was 5. We made an average of 1.72 (SD = 0.96) observations of each cow. Our earliest survey was on 27 April 2016 (day 1), and our earliest observation of a calf was on 17 May 2016.

Based on raw observation data, the median annual parturition dates ranged from 8 June through 18 July; however, these dates reflect uncorrected adjustments. As expected, accounting for p shifted dates for the predicted probability of parturition to an earlier period. The cumulative parturition probability for moose was 0.50 by day 22 (19 May, with a 95% credible interval [CI] range from 19 to 20 May). In consideration of cumulative parturition among all moose, without correcting for detection probability, the probability of parturition exceeded 0.90 on day 64 (June 30, 95% CI = 20 June to 19 July; Fig. 2). When detection probability was incorporated into the model, the cumulative probability of parturition exceeded 0.90 by 30 days after 27 April (27 May; 95% CI = 26 May to 28 May; Fig. 2).

DISCUSSION

Evolutionary theory suggests that for many large, northern ungulates, the peak and duration of parturition periods are shaped to occur within a narrow window of time (Rutberg 1987). But because our ground-based field methods to estimate parturition dates were laborious and observation rates low (0–5/day), the date of first observation for many cows extended well into summer. However, analytical adjustments to the estimation of parturition dates

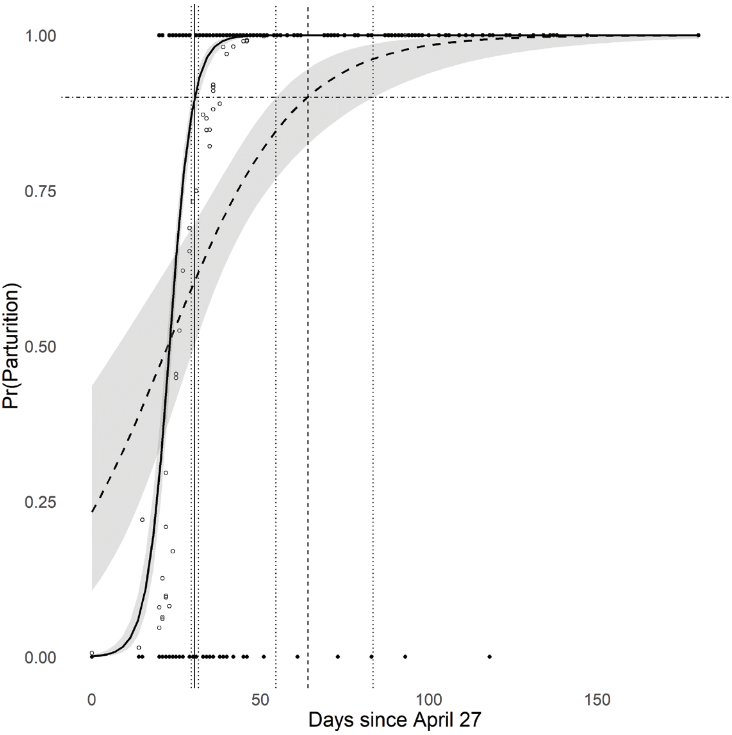

Fig. 2. Predicted probability of parturition by date (shown as days since 27 April), modeled with (solid) and without (dashed) including the probability of detection, Colorado, USA. The horizontal dotted-dashed line indicates a 90% parturition probability. The vertical lines indicate the days on which that 90% parturition probability was estimated to have been achieved for each model (dotted lines represent 95% credible intervals). Raw observational data are depicted as black dots.

(i.e., accounting for *p*) buffered the bias associated with our slower field methods and led to the prediction that 50% of parturition events had occurred by 19–20 May. This 2-day window aligned very closely with the range of median parturition date of 19–22 May reported by Gasaway et al. (1983) and Keech et al. (2000) for the interior of Alaska. Similarly, Bowyer et al. (1998) reported a mean parturition date of 25 May for moose in Denali National Park, and concluded that 95% of births occurred during a 16-day window. The median parturition date for moose calves in southwest Yukon was also 25 May (Larsen et al. 1989). Our results also aligned with parturition dates for moose in the eastern United States and Scandinavia. In New Hampshire, Musante et al. (2010) and Jones et al. (2017) reported a median date of 19 May with 78 and 90% of births occurring between 13 and 27 May, respectively. Parturition dates in Norway were also similar (23 May), but dates were sensitive to the number of mature bulls in the population (Sæther et al. 2003). Finally, Severud et al. (2015) reported a slightly earlier mean parturition date (14 May) for moose in Minnesota, but a 1-month range of parturition (2 May–2 June). This earlier mean parturition date aligned with that reported in Ontario (13 May; Patterson et al. 2016).

We estimated that the cumulative probability of parturition increased from 0.50 to

0.90 between 19 and 27 May, indicating that Colorado has a similarly narrow parturition period as reported across much of moose range. This narrow window may be shaped by the interaction of habitat and season (Rutberg 1987, Bowyer et al. 1998), as well as predation (Bergerud 1975, Testa 2002). Perhaps less intuitive was that Colorado's moose appear to calve in synchrony with moose at more northern latitudes. In comparison, the onset of spring and summer is generally earlier and winter later in Colorado. This variation in seasonality could potentially afford moose in Colorado and other southern populations flexibility from tight parturition patterns identified in northern populations; however, no shifts in parturition date are apparent. While the seasonality of Colorado's southern latitude may be mediated by high elevations, the parturition synchrony within the species across latitudes may prove to be relevant and informative in the face of a generally warming environment. More specifically, moose occupy a wide geographical and latitudinal range, over which seasons are not perfectly synchronous. Yet, they apparently maintain tight synchrony in the timing of parturition across this range. Thus, concerns over the shifting of seasonality due to global warming (i.e., earlier spring and delayed winter) may not intrinsically, or negatively impact the timing of parturition.

From a management perspective, the estimation of parturition dates in Colorado was particularly useful to design field surveys. One goal of refining productivity surveys is to reduce bias, and as noted, one source of bias is *p* and its confounding effects when moose are transitioning between pregnancy and calf-at-heel. Ideally, surveys should be implemented post-parturition, but early enough that neonatal mortality is minimal. After applying the probability of detection at which the probability of parturition reached 90%, we recommend that surveys in Colorado be initiated on 27 May, or 34 days prior to the date predicted without considering probability of detection. In addition, incorporating probability of detection decreased the credible interval (by about 28 days) associated with the predicted date at which 90% of parturition events occurred. While ground surveys cannot fully replicate the results of aerial surveys, managers can use our results to improve and facilitate the timing of ground surveys. For example, a concerted ground survey effort at the end of May, conducted typically on foot or horseback with a large number of volunteers and field personnel, should produce a productivity estimate with minimal bias from pregnant females and calf mortality. Importantly, the narrower credible interval indicates that earlier surveys need not compromise confidence, and applying our refined, optimal date to initiate earlier surveys will produce measurable savings in effort and agency resources.

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