



Moose calf detection probabilities: quantification and evaluation of a ground-based survey technique

Authors: Bergman, Eric J., Hayes, Forest P., Lukacs, Paul M., and Bishop, Chad J.

Source: Wildlife Biology, 2020(2)

Published By: Nordic Board for Wildlife Research

URL: <https://doi.org/10.2981/wlb.00599>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.



Moose calf detection probabilities: quantification and evaluation of a ground-based survey technique

Eric J. Bergman, Forest P. Hayes, Paul M. Lukacs and Chad J. Bishop

E. J. Bergman (<https://orcid.org/0000-0003-4298-0732>) ✉ (eric.bergman@state.co.us), Mammals Research Group, Colorado Parks and Wildlife, Fort Collins, CO 80526, USA. – F. P. Hayes, P. M. Lukacs and C. J. Bishop, Wildlife Biology Program, Dept of Ecosystem and Conservation Sciences, W.A. Franke College of Forestry and Conservation, Univ. of Montana, Missoula, MT, USA.

Survey data improve population management, yet those data often have associated bias. We quantified one source of bias in moose survey data (observer detection probability, p), by using repeated ground-observations of calves-at-heel of radio-collared moose in Colorado, USA. Detection probabilities, which varied both spatially and temporally, were estimated using an occupancy-modelling framework. We provide an efficient offset for modelled calf-at-heel occupancy (ψ) estimates that accommodates summer calf mortality. Detection probabilities were most efficiently modelled with seasonal variation, with the lowest probability of detecting calves-at-heel occurring during parturition (i.e. May) and later autumn periods (after August). Our most efficiently modelled detection probability estimate for summer was 0.80 (SE=0.05). During the four years of this study, ψ estimates ranged from 0.54–0.84 (SE=0.08–0.11). Accounting for 91.7% monthly calf survival corrected ψ estimates downward ($\psi=0.42$ –0.65). Our results suggest that repeated ground-based observations of individual cow moose, during summer months, can be a cost-effective strategy for estimating a productivity parameter for moose. Ground survey results can be further improved by accounting for calf mortality.

Keywords: *Alces alces*, Colorado, detection probability, ground-surveys, moose, occupancy models

Management of wildlife populations is typically a dynamic process. As an example, harvest management of many large ungulate species often requires biologists to inform decision-makers about how many hunting licenses a herd can support. Under these scenarios, population monitoring data are pivotal. For many large ungulates, these data are collected via aerial and ground surveys. Yet survey data have associated bias (Williams et al. 2001, White 2005). As an example, even when available for observation, a proportion of animals remain undetected. This form of nonresponse error, also referred to as a detection probability, introduces a consistent negative influence on observation data (Thompson et al. 1998, White 2005). While nonresponse error is most often associated with human subjects who choose not to return a survey, animals that go undetected during a survey have functionally made the same ‘choice’ and are treated in the same manner. Detection probability estimates capture the bias associated with the failure to observe some animals. When properly estimated, detection probabilities can be

used to inflate raw count data, reducing negative bias associated with nonresponse error.

Investigations of detection error have occurred for multiple species and for multiple survey techniques. For example, mark–resight methods quantify and extrapolate resighting probabilities of marked animals to correct for unobserved animals within a population (Williams et al. 2001, White 2005). These techniques have been applied to aerial surveys for mule deer *Odocoileus hemionus* (Bergman et al. 2014), moose *Alces alces* (Bowden and Kufeld 1995), brown bears *Ursus arctos* and black bears *Ursus americanus* (Miller et al. 1997), but also to ground surveys for bighorn sheep *Ovis canadensis* (McClintock et al. 2006, Johnson et al. 2010). Distance sampling approaches model and correct for the decay in detection probability as distances between observers and animals increase (Buckland et al. 2008). While less common, distance sampling has also been used for moose (Oyster et al. 2018) and white-tailed deer *Odocoileus virginianus* (Anderson et al. 2013). More commonly, aerial sightability models quantify the underestimation of raw count data due to habitat type, animal behavior, seasonal conditions and observer platform, and provide a numerical inflation to correct for bias. Examples of sightability models can be found for elk (Samuel et al. 1987, Cogan and Diefenbach 1998, Walsh et al. 2011),

This work is licensed under the terms of a Creative Commons Attribution 4.0 International License (CC-BY) <<http://creativecommons.org/licenses/by/4.0/>>. The license permits use, distribution and reproduction in any medium, provided the original work is properly cited.

moose (Anderson and Lindzey 1996, Giudice et al. 2011), mule deer (Bartmann et al. 1986, Zabransky et al. 2016), mountain goats *Oreamnos americanus* (Poole 2007, Rice et al. 2009) and bighorn sheep (Bodie et al. 1995, Udevitz et al. 2006). Of note, the majority of past research on this topic for large ungulates has focused on aerial surveys. While ground surveys are less common, often due to high labor costs and landscape accessibility constraints, they provide a cost effective approach to collecting data. In several jurisdictions, ground-based observations of moose by hunters have been highlighted as a useful management tool (Ericsson and Wallin 1999, Solberg and Sæther 1999, Boyce and Corrigan 2017).

Prior to the 1970s, moose presence in Colorado was sporadic. However, during the late 1970s and early 1980s Colorado Parks and Wildlife (CPW) permanently established moose through translocations from neighboring states (Nowlin et al. 1979). Since then, the total moose population has grown to nearly 3000 animals (Colorado Parks and Wildlife, unpubl.). However, relative to other large ungulate species such as elk, deer and pronghorn *Antilocapra americana*, moose are scarce in Colorado, and thus, resources for aerial moose population monitoring are limited. Likewise, most of Colorado's moose herds are located in areas with dense, closed-canopy forests, mountainous terrain and at high elevations, also limiting the feasibility and utility of aerial surveys. In spite of these limitations but directly related to the moose population growth during the past three decades, CPW's biologists are confronted with the need for reliable population data to facilitate herd management. Under these circumstances, data from ground-based surveys and opportunistic observations have the potential to be cost-effective and useful.

A moose population parameter of interest to CPW's biologists is the young (calf)/adult female (cow) ratio. Young/adult female ratios change throughout the year as a birth pulse pushes the ratio to its maximum and then declines as calves die. These ratios, when estimated as a parameter, can be used in population modelling (White and Lubow 2002), but also as indicators of trends within recruitment (Bergman et al. 2011). Yet it is important to consider what point in time the ratio represents to properly incorporate it in a population model. Moreover, uncorrected observations to estimate young/adult female ratios are biased. Thus, our objective was to provide an estimation of the ground-based detection probability of moose calves-at-heel, with the goal of providing biologists with a numerical correction that will minimize bias and improve the utility of field surveys and observations.

Material and methods

Study area

Our research occurred in three study areas, two of which were located in the northern and central mountains of Colorado, whereas the third was located in the San Juan Mountains of southwest Colorado (Fig. 1). The first of the northern study areas, North Park, was located in Jackson County, near the town of Walden. North Park was the site of moose translocation efforts during the late 1970s, and it encompasses the most longstanding moose herd in Colorado. The North Park study area was a wide (14–46 km), high elevation valley (2400–2750 m) that was comprised of rolling sagebrush *Artemisia* spp. hills mixed with irrigated agricultural

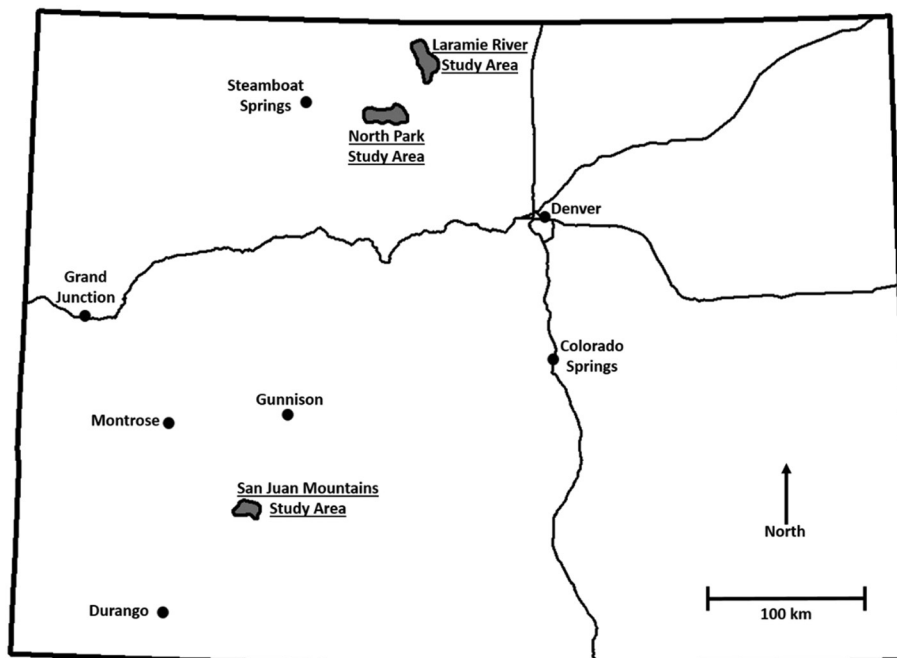


Figure 1. Map of Colorado, USA depicting three moose research study areas (gray filled polygons, with underlined names) in relation to nearby and major communities. Research study areas depict areas where moose cows and calves were observed in order to estimate calf-at-heel detection probabilities between 2015 and 2018. Black continuous lines throughout the map depict Interstate roadways to provide spatial reference.

fields. North Park had many small rivers and streams which were closely surrounded by willow *Salix* spp. communities, as well as a diversity of native grasses and sedges. Moving up in elevation (2750–3660 m), away from the North Park valley floor, sagebrush and agricultural communities transitioned to spruce–fir, *Picea engelmannii* and *Abies lasiocarpa*, and aspen *Populus tremuloides* forests. The highest portions of the North Park study area occurred above tree line and fell within the alpine tundra vegetation zone.

The second study area, also located in northern Colorado, was along the Laramie River. The Laramie River study area was approximately 40 km to the northeast of the North Park study area, but separated by the Rawah Mountains (3200–3840 m). Moose were translocated to Laramie River during the early 1980s and consistently occupied the study area since then. The Laramie River study area was comprised of a narrow valley floor (3.0–8.5 km wide) that ranged from 2470 to 2800 m in elevation. Lower elevations were vegetated with small willow stands along the river and stream corridors, but also spruce–fir forests. Sagebrush and aspen also occurred in the Laramie River study area, but at much lower frequencies and densities than North Park. Higher elevation (2800–3660 m) portions of the Laramie River area were comprised of spruce–fir, but also alpine tundra above tree line.

The third study area was located in the northern San Juan Mountains. Moose were translocated to the San Juan Mountains study area during the early 1990s and consistently occupied that area since then. The San Juan Mountains study area mirrored the Laramie River with narrow valley bottoms (0.5–1.5 km wide), although elevations ranged from 2750 to 3130 m. Moose used spruce–fir forests, willow and alpine tundra habitats in the San Juan Mountains, but at higher elevations (3350–4020 m) than what was available in the other two study areas.

Moose were actively managed via limited bull and cow hunting opportunities in all study areas. Likewise, predator assemblages were consistent among study areas. Black bears, mountain lions *Puma concolor*, and coyotes *Canis latrans* were present in all three study areas, whereas wolves *Canis lupus* and grizzly bears *Ursus arctos* were absent. It was believed that black bears and mountain lions preyed upon moose, although this predation was likely opportunistic as moose densities were much lower than the densities for elk and mule deer, which were the preferred prey for both predators. Relative to other jurisdictions, particularly in the Rocky Mountains, Alaska, western Canada and northern Europe, the predation pressure on moose in Colorado was minimal.

Field methods

Between 20 December and 27 January of each winter (2015–2018), we captured adult (≥ 2 years old) female moose via helicopter darting. Moose were sedated 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). After handling, capture drugs were antagonized with naltrexone (100 mg, antagonist for carfentanil and thiafentanil), tolaz-

line (500 mg, antagonist for azaperone and xylazine) and atipamezole (100–150 mg, antagonist for medetomidine and xylazine). Once sedated, moose were blindfolded to minimize stress. Moose also received oxygen, via nasal cannula, to minimize risks of adult and fetal hypoxia. Moose were subsequently fitted with satellite and GPS equipped VHF radio-collars (Vectronics Aerospace GmbH, Berlin, Germany model: Vertex Plus, and Advanced Telemetry Systems, Isanti, MN, USA model: G5-2D), as well as uniquely numbered ear tags. At the time of capture, blood samples were collected to allow for subsequent determination of pregnancy status via pregnancy specific protein B (PSPB, Wood et al. 1986).

Following the first year of capture, some previously captured moose were recaptured, but only on a random basis. Our efforts to maintain a random sample of moose each year led to scenarios in which the pregnancy status of some radio-collared moose was unknown. As an example, an individual moose only captured during year 1 of the study had known pregnancy status for that year, but unknown pregnancy status for subsequent years. These moose, with unknown pregnancy status, continued to wear satellite collars and remained available for summer field observation. Beginning in mid-May of each year, we initiated ground observations of all collared moose. Typically, one observer completed ground observations by radio-tracking to collared moose to document presence or absence of newborn calves. Last known GPS locations and VHF signals expedited ground observation. When a single observer failed to gain an observation of a moose after >3 repeated efforts, we utilized a two-observer approach. During these scenarios, the second observer was positioned along the exit route that a cow moose was expected to take, and the first observer radio-tracked to the cow moose in the same manner as a single observer approach. A cow moose and the presence or absence of a calf was recorded when the cow's entire body and the surrounding 1–2 m area were observed.

Repeated observations were made of study animals beginning in mid-May and continued through the end of August. Moose were initially prioritized for observation based on whether or not they had been captured the previous winter (i.e. moose with known pregnancy status were a higher priority for observation). However, once annual summer observations began and moose had been observed at least once, priority was then given to animals based on timing of most recent observation (i.e. individual moose observed most recently were lowest priority for upcoming observations, and animals who had not been recently observed were a higher priority). In addition to observations that occurred as part of the formal study process, CPW biologists and hunters made opportunistic observations during autumn months. Observations made by hunters occurred when study animals were harvested during hunting seasons. Opportunistic observations were only included in our analyses when individual identification of moose (possible due to unique ear tags) was provided.

Analytical methods

Moose calf detection probability was estimated using an occupancy-modelling framework. Whereas occupancy models commonly treat geographic areas as sites, we treated

individual cow moose during a given year as a site. We modelled the presence or absence of a calf with each cow as occupancy (i.e. cow moose observed with at least one calf were occupied, cow moose observed without calves were unoccupied). Some individual cow moose were observed during multiple years of this study, in which case each animal by year combination was treated as a unique site. Observation data were condensed by month (May, June, July, August, Autumn) for each animal by year combination. For these ‘month’ models, estimation of p for each month was independent of observations made during any other month. We also included an ‘effort’ covariate, which was the numerical count of observations for individual moose during a given month, which allowed us to evaluate the effect of field effort on detection probabilities. Likewise, observations were condensed such that for each month, study animals were occupied (≥ 1 calf observed), unoccupied (no calves observed) or unknown. While a potential source of bias, observational data for the Shiras subspecies of moose in Colorado (Colorado Parks and Wildlife, this study), Utah (K. Hersey, Utah Division of Wildlife Resources, unpubl.) and Montana (N. DeCesare, Montana Fish, Wildlife and Parks, unpubl.) suggest that twinning rates are consistently low and often range between 5% and 10%.

We conducted occupancy analyses, using a maximum likelihood framework, in Program MARK (White and Burnham 1999). Occupancy models were structured to estimate detection probability (p) as well as occupancy (ψ). In this scenario, estimates of ψ were summer calf-at-heel ratio estimates. Models were compared using Akaike’s information criterion (AIC_c) that was corrected for small sample size (Burnham and Anderson 2002). Our global model allowed p to vary by study area and month (May, June, July, August and Autumn). Additionally, for moose that were captured the previous winter, our global model treated pregnancy status as an individual covariate. Observer effort was also included in our global model. Models that included temporal, spatial variation and pregnancy status were additive in structure. We did not evaluate models with multiplicative interactions (i.e. which would have allowed p to vary by study area and year). Simpler models that condensed or removed temporal and geographical effects for p were also included in the model set. These simpler models included a seasonal model that generated three estimates for p (parturition, summer and fall), as well as a constant model that estimated a single value for p . For all models, year was treated as a group, which allowed for four calf-at-heel ratio ψ estimates.

Births and deaths of animals violated our model assumption of population closure. The detection probability estimated in occupancy models is the intersection of birth, survival and detection, and subsequently, ψ represented the proportion of adult females that gave birth. To obtain an estimate of ψ later in the summer, ψ can be multiplied by survival for the time from the beginning of the survey until the time of interest. For example, a young/adult female ratio three months after the start of the survey would be

$$\Psi_{3\text{month}} = \Psi S^3$$

where S is monthly survival.

Results

We captured and observed 98 unique individual moose as part of this study. When spread among the four years of this study, these 98 individuals allowed for 156 unique animal by year combinations, and a total of 247 ground observations. The mean number of ground observations per cow moose during the study was 1.6 ($SD=0.7$), and the maximum number of observations of a single individual was 4. The majority of observations occurred during June, whereas the number of observations that occurred during May, July and August were more similar (Table 1). The fewest number of observations occurred during autumn (Table 1). Observations made of moose while they were moving tended to be short in duration, but effective for observing calves. In these situations, calves were typically directly behind cows (1–2 m) and easily observed. Observations of docile (bedded or feeding) cow moose ranged from 2 to 20 min in duration and were also effective at observing calves. Observations of docile cows ended when moose either foraged or stood and walked out of view.

We compared 15 models (Table 2). The single best model, based on AIC_c , allowed p to vary by season, but did not include study area or pregnancy status. Models that allowed p to vary by month were not as well supported as seasonal models, but they consistently outperformed models with a constant p (Table 2). This pattern strongly suggests that p does indeed vary through time. More specifically, estimates of p during the month of May, the primary parturition month, were consistently lower (Fig. 2, 3). Estimates of p ranged from 0.37 to 0.41 ($SE=0.09-0.14$). However, detection probability estimates of moose calves during summer months were consistently high. Monthly estimates of p ranged from 0.77 to 0.88 (SE range 0.07–0.14) between June and August. Our AIC_c best model estimated a single summer p of 0.80 ($SE=0.05$). Similar to the parturition period, detection probability of moose calves during the fall was lower than during summer months ($p=0.71$, $SE=0.13$).

Regardless of how temporal variation was structured (seasonal versus monthly), incorporating spatial variation within p (i.e. study area differences) consistently reduced model support. Similarly, there was little support for pregnancy status in our models (i.e. knowing the pregnancy status of a cow moose did not intrinsically improve the detection probability of a calf-at-heel). Including observer effort (i.e. the number of observations per month) as a covariate for estimating p also did not increase support for models. In nearly all cases, the 95% confidence intervals for beta estimates included 0. While the beta estimate for observer effort

Table 1. Numerical summary of visual observations made of colored adult female moose from Colorado. Categorized by month and year, these data were used to estimate detection probabilities (p) and calf-at-heel estimates (ψ) using occupancy models.

	May	June	July	August	Fall	Total
2015	11	38	13	7	1	70
2016	13	18	16	8	13	68
2017	8	16	8	10	1	43
2018	16	15	12	16	7	66
Total	48	87	49	41	22	247

Table 2. Comparison of different models used to estimate detection probabilities of moose calves-at-heel of adult female moose from 2015 to 2018. Models are ranked according to increasing values of Akaike's information criterion (ΔAIC_c) which was corrected for small sample size. Only models within $<3 \Delta AIC_c$ are presented in model results. Model output also includes relative model weights (w_i) and the number of parameters estimated for each model (k).

Model ¹	ΔAIC_c	w_i	Log(L)	k
p (season) ²	0 ³	0.31	-150.95	7
p (season + effort + pregnancy status)	0.58	0.24	-144.34	13
p (season + effort)	2.34	0.10	-146.41	12
p (season + study unit + pregnancy status)	2.65	0.08	-148.89	10
p (season + effort + study unit + pregnancy status)	2.93	0.07	-143.08	15
p (season + study unit)	3.39	0.06	-150.41	9
p (month)	3.69	0.05	-150.56	9
p (month + effort + study unit + pregnancy status)	4.42	0.03	-142.59	16
p (month + effort)	6.39	0.01	-146.04	14
p (season + effort + study unit)	6.64	0.01	-146.16	14
p (month + study unit + pregnancy status)	6.83	0.01	-148.65	12
p (month + study unit)	7.59	0.01	-150.21	11
p (constant)	11.64	0.00	-158.95	5
p (study unit)	14.62	0.00	-158.26	7
p (study unit + pregnancy status)	15.47	0.00	-157.58	8

¹ Variation in model structure was restricted to detection probability (p). All models also estimated annual occupancy (ψ), which was the probability of a cow moose having at least one calf-at-heel. Occupancy estimates accounted for four estimated parameters (k) in each model. The effort covariate accounted for five additional parameters. The season covariate accounted for three parameters, whereas month accounted for five parameters. Study unit accounted for three parameters and pregnancy status accounted for one parameter.

² The top performing model was a post hoc exploratory model, evaluated due to its management implications.

³ AIC_c for the best model was 316.66.

during July was positive ($\beta=0.32$), suggesting that more observations increased detection probability, the variance surrounding this estimate limited the inference that could be drawn from that result (95% confidence interval range: -0.53 to 1.17).

Calf-at-heel ratios decline throughout the summer as calves die at a higher rate than adult females. The result is a decay curve as a function of ψ at the start of the survey, and time. For a monthly survival probability of 0.90 and $\psi = 0.80$, the calf-at-heel ratio after three months would be 0.63 (Fig. 4). Our models generated four estimates for ψ , which aligned with the four years of this study (2015–2018).

Given this, we computed model averaged estimates for ψ , weighted by model weights. Estimation of ψ on an annual basis did capture some of the biological variability inherent within that parameter. During 2015 and 2016, calf-at-heel ratios were 0.81 (SE=0.10) and 0.84 (SE=0.08), respectively, before dropping to 0.54 (SE=0.11) during 2017 (Fig. 5). This ratio increased to 0.68 (SE=0.09) during the final year of the study (Fig. 5). Application of the monthly survival correction using a literature-based summer monthly survival estimate of 0.917 (Musante et al. 2010) shifted our range of estimates for ψ from 0.54–0.84 down to 0.42–0.65.

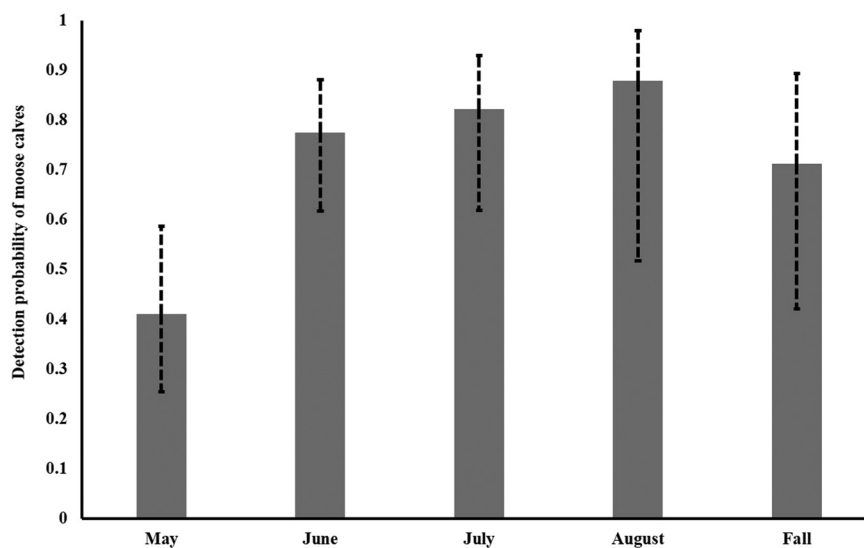


Figure 2. Monthly estimates of moose calf-at-heel detection probabilities (p) from Colorado. Maximum likelihood detection probabilities and 95% confidence intervals, reflected by solid gray bars and dashed black lines, respectively, were estimated using an occupancy modelling framework.

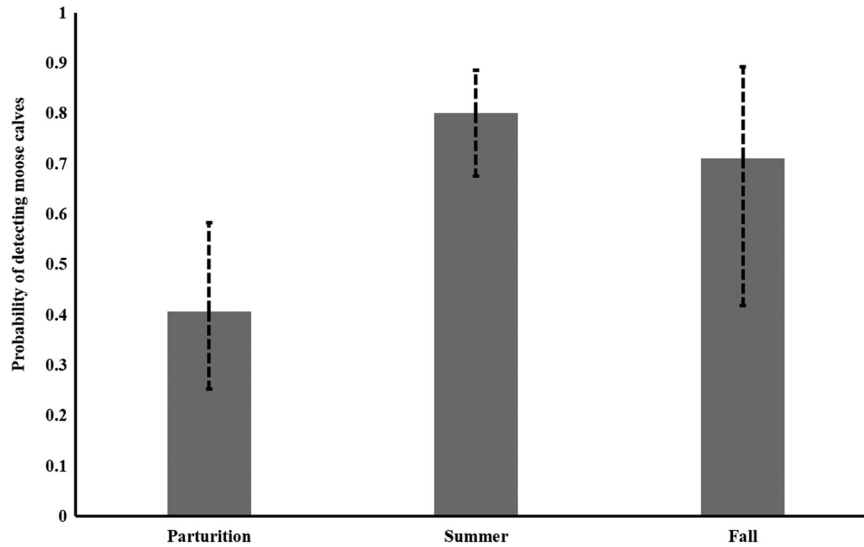


Figure 3. Seasonal estimates of moose calf-at-heel detection probabilities (p) from Colorado. Maximum likelihood detection probabilities and 95% confidence intervals, reflected by solid gray bars and dashed black lines, respectively, were estimated using an occupancy modelling framework. A single, summer (June, July and August) detection probability embodies the most parsimonious approach to estimating summer calf-at-heel ratio estimates for moose population monitoring and management purposes.

Discussion

As expected, nonresponse error occurred during the collection of our moose calf-at-heel data. However, the bias associated with that error was quantifiable and easily incorporated into calf-at-heel ratio estimates. As noted, we documented strong temporal variation in p . The low p estimates during May were not surprising. During the parturition period, pregnant moose who were yet to give birth were intrinsically observed without a calf-at-heel. Without the use of vaginal implant transmitters that would have alerted observers to the exact timing of birth, it would be difficult to quantitatively disentangle the visual similarity between a cow

carrying a fetus versus a cow that had given birth but the neonate was well hidden. Lower p estimates also occurred after August (autumn observations). Detection probabilities of moose calves during this period were expected to be lower for two reasons. First, we suspect moose calves became behaviorally more independent from their dams during September, as weaning occurred (Franzmann and Schwartz 2007, Severud et al. 2019). Thus, during autumn, the spatial separation between cows and calves was higher, which reduced the detection probability of calves. Secondly, and further reducing detection probabilities of calves during autumn was the reality that calf mortality occurred between May and August of each year. Cows who lost calves dur-

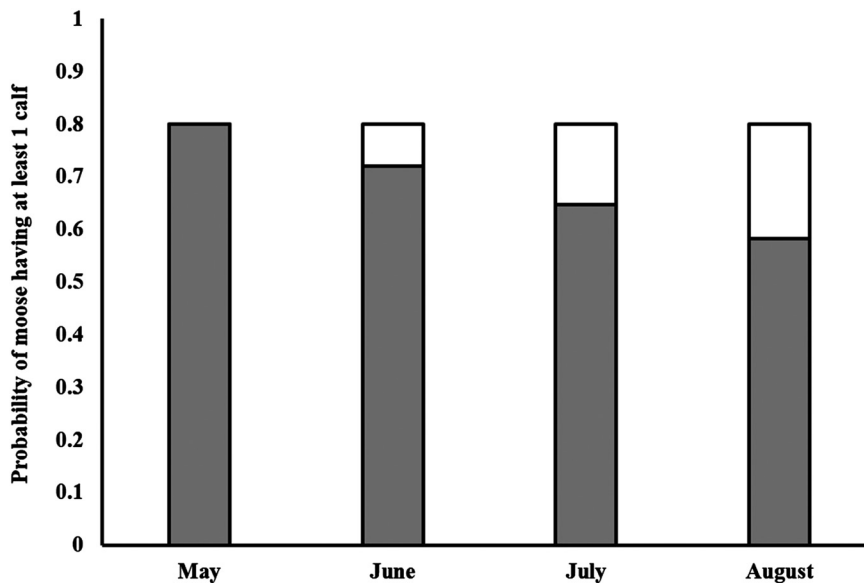


Figure 4. Predicted trends in summer moose calf-at-heel ratio estimates (ψ), as predicted by occupancy models. White bars reflect modelled ψ estimates, a maximum value, yet calf-at-heel ratios decline throughout summer as moose calves die at a higher rate than adult females. Gray bars reflect the decay in ψ that would be expected from 90% monthly survival in moose calves.

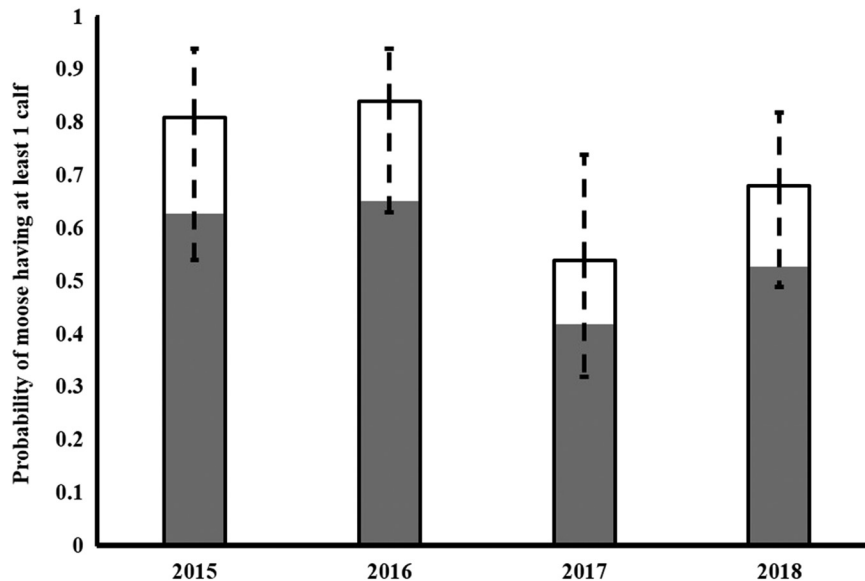


Figure 5. Late summer (August) moose calf-at-heel ratio estimates (ψ) from Colorado, as predicted by occupancy models from 2015 to 2018. White bars reflect modelled maximum likelihood probabilities and dashed black lines reflect 95% confidence intervals. Gray bars reflect a reduction in ψ estimates necessary to correct for three months of moose calf mortality. In the absence of Colorado specific monthly moose calf survival estimates, a summer monthly calf survival rate of 0.917 was extracted from research in comparable systems and used for the first three months of life.

ing the summer were observed without a calf-at-heel during autumn. Similar to the case with pregnant cows during May, our models for p could not distinguish between calves that were undetected due to hiding versus those that were not observed because they were no longer living.

The lack of support for spatial variation in p was likely due to the large degree of habitat similarity among study areas. While the broad-scale variation among our study areas was evident, the fine-scale habitat similarities resulted in no discernible difference in p as observers attained visuals of cows and calves. Similarly, there was no apparent effect on observer's ability to detect calves if they knew a cow had been pregnant the preceding winter. Likewise, accounting for the number of observer visits each month (i.e. effort) did not measurably improve detection probability. While surprising, these results were likely driven by the fact that p was quite high for moose in general.

Prior to our research, parturition and summer calf-at-heel data had not been collected in Colorado. Our approach provided a useful tool for biologists, and it provided estimates of a reproductive parameter. We considered ψ , the occupancy estimate, to be synonymous with parturition, and early summer recruitment. From a harvest management standpoint, estimating recruitment, even during summer, can be useful. The survival adjustment presented provides a method for estimating recruitment at the 6 or 9 month periods, which would be even more useful. Our modelled ψ estimates, which ranged from 0.54 to 0.84 demonstrated how population parameters can vary (Fig. 5). Long-term research results from Alaska exemplify the utility of reproductive parameter data (Boertje et al. 2019). Timing of parturition, age of first reproduction and recruitment of young have been linked to nutrition (Keech et al. 2000, Ruprecht et al. 2016, Boertje et al. 2019), yet data collected to estimate those parameters need to be corrected for potential bias. Our

results provide a preliminary correction to one method for collecting those data. As an example, earlier research used methods similar to ours, but provided no correction for detection probability (Ruprecht et al. 2016).

In the future, to be fully useful for biologists during population and harvest management processes, estimation of ψ should occur not only on an annual basis, but also at the herd level. In particular, development of explanatory covariates for variation in ψ are occurring as part of this ongoing research, but a thorough evaluation of ψ will require more data than what were available for our analyses. Likewise, as moose research and management opportunities continue in Colorado, we expect that estimation of the components of variation (i.e. process versus sampling variation) will become feasible. In the meantime, estimation of calf-at-heel ratios will continue to provide an index of Colorado's moose population health.

Our estimation of detection probabilities and calf-at-heel ratios was possible because we had radio-collared female moose that were reliably observed on multiple occasions. In Colorado, radio-collared moose are not a long-term asset. For management purposes, the lack of individually identifiable animals would introduce the potential for unintended repeated observations of individual animals. This dilemma could bias calf-at-heel ratio estimation in either direction, but it would inherently result in an overestimation of the precision of any ratio estimate. However, many cow moose exhibit unique visual attributes, such as misshapen ears or bald spots. These attributes can serve as individually identifiable characteristics and minimize the risk of bias or artificial deflation of precision. Similarly, high-intensity and short-duration sampling strategies can also be used to minimize bias and improve precision. Such strategies would deploy many observers to simultaneously observe unmarked moose within unique spatial areas, reducing the potential of double

counting. While fraught with more complex sampling issues, estimation of autumn moose calf detection probabilities from hunter observations is also a reasonable extension of our results. Regardless, our results suggest that in Colorado, implementation of rapid ground surveys post parturition will minimize misclassifications of calf-at-heel stemming from unknown parturition status, while also reducing the potential for bias stemming from calf mortality.

Despite the utility of our results, we recognize several key limitations and assumptions to our work, and we suggest future research address several issues. First, our analyses did not accommodate cows with multiple calves. In the course of our research, 4.5% of cow moose were observed with twin calves. Thus, our estimates are a reflection of cows with at least one calf-at-heel but they remain biased slightly low. In Colorado, for wildlife management purposes, the magnitude of that bias is considered to be negligible. In other jurisdictions, particularly those that manage subspecies of moose with higher twinning rates, the magnitude of this bias should be of greater concern. In such a scenario, multi-state occupancy models would provide a useful tool for accommodating observations that include high frequency counts of multiple outcomes (i.e. 0, 1 or 2 calves observed). Second, our modelling approach required the assumption that moose calf mortality was negligible during summer months. However, we could only correct for this assumption after-the-fact by applying the calf mortality decay function to ψ estimates. We used a literature-based monthly survival estimate of 0.917 (Musante et al. 2010). From a management standpoint, utilization of this post hoc correction by CPW's biologists is likely because two key predators of moose calves, wolves *Canis lupus* and brown bears, are largely absent from the landscape. Ideally, managers can apply locally collected calf survival estimates. This was not an option in our study.

The effects of a changing environment on large ungulate population dynamics has been and continues to be a topic of research (Solberg et al. 2001, Dittmer et al. 2018, Weiskopf et al. 2019). Similarly, in some jurisdictions, harvest management plans allow for female harvest based on reproductive status (or reproductive output) of adult females (Boertje et al. 2009, Rughetti et al. 2017). These studies often link changes in the environment, an independent variable, to productivity parameters. In these cases, productivity parameters are treated as a dependent variable, thus continued efforts to remove bias expands the scope of inference that can be drawn from those studies. Ultimately, estimation of moose calf detection probabilities and calf-at-heel ratios through ground observation provided CPW with productivity parameter estimates that were previously unavailable. These results and future survey methods will be a useful tool for future use in evaluating both the effects of ecological change and harvest management decisions on moose in Colorado. As long as unintended double counting of individual moose is mitigated through sampling design, and through appropriate timing of surveys, application of a p estimate of 0.80 to early summer observations of Colorado's moose would provide a reasonable correction to raw count data. Late summer estimates would require application of the mortality driven decay function.

Acknowledgements – We are indebted to A. Howell, S. Peterson and B. Smith for help with data collection. We are also indebted to M. Alldredge, K. Logan and S. Côté for critical comments that improved this paper.

Funding – Financial and logistical support for this research was provided by Colorado Parks and Wildlife.

Permits – Moose capture, handling and field observation protocols were approved by the Institutional Animal Care and Use Committees (IACUC) at CPW (IACUC approval number 08-2013) and the University of Montana (IACUC approval number AUP 032-17).

References

- Anderson Jr., C. R. and Lindzey, F. G. 1996. Moose sightability model developed from helicopter surveys. – *Wildl. Soc. Bull.* 24: 247–259.
- Anderson, C. W. et al. 2013. Comparison of indirect and direct methods of distance sampling for estimating density of white-tailed deer. – *Wildl. Soc. Bull.* 37: 146–154.
- Bartmann, R. M. et al. 1986. Accuracy of helicopter counts of mule deer in pinyon–juniper woodland. – *Wildl. Soc. Bull.* 14: 356–363.
- Bergman, E. J. et al. 2011. Biological and socio-economic effects of statewide limitation of deer licenses in Colorado. – *J. Wildl. Manage.* 75: 1443–1452.
- Bergman, E. J. et al. 2014. Habitat and herbivore density: response of mule deer to habitat management. – *J. Wildl. Manage.* 79: 60–68.
- Bodie, W. L. et al. 1995. A sightability model for bighorn sheep in canyon habitats. – *J. Wildl. Manage.* 59: 832–840.
- Boertje, R. D. et al. 2009. Managing for elevated yield of moose in interior Alaska. – *J. Wildl. Manage.* 73: 314–327.
- Boertje, R. D. et al. 2019. Lifetime, known-age moose reproduction in a nutritionally stressed population. – *J. Wildl. Manage.* 83: 610–626.
- Bowden, D. C. and Kufeld, R. C. 1995. Generalized mark–resight population size estimation applied to Colorado moose. – *J. Wildl. Manage.* 59: 840–851.
- Boyce, M. S. and Corrigan, R. 2017. Moose survey app for population monitoring. – *Wildl. Soc. Bull.* 41: 125–128.
- Buckland, S. T. et al. 2008. Advanced distance sampling: estimating abundance of biological populations. – Oxford Univ. Press.
- Burnham, K. P. and Anderson, D. R. 2002. Model selection and multimodel inference: a practical information–theoretic approach, 2nd edn. – Springer.
- Cogan, R. D. and Diefenbach, D. R. 1998. Effect of undercounting and model selection on a sightability–adjustment estimator for elk. – *J. Wildl. Manage.* 62: 269–279.
- Dittmer, M. A. et al. 2018. Moose at their bioclimatic edge alter their behavior based on weather, landscape and predators. – *Curr. Zool.* 64: 419–432.
- Ericsson, G. and Wallin, K. 1999. Hunter observations as an index of moose *Alces alces* population parameters. – *Wildl. Biol.* 5: 177–185.
- Franzmann, A. W. and Schwartz, C. C. 2007. Ecology and management of the North American moose, 2nd edn. – Univ. of Colorado Press, Boulder, CO, USA.
- Giudice, J. H. et al. 2011. Spending degrees of freedom in a poor economy: a case study of building a sightability model for moose in northeastern Minnesota. – *J. Wildl. Manage.* 76: 75–87.
- Johnson, H. E. et al. 2010. Combining ground count, telemetry and mark–resight data to infer population dynamics in an endangered species. – *J. Appl. Ecol.* 47: 1083–1093.
- Keech, M. A. et al. 2000. Life-history consequences of maternal condition in Alaskan moose. – *J. Wildl. Manage.* 64: 450–462.

- McClintock, B. T. et al. 2006. A robust design mark-resight abundance estimator allowing heterogeneity in resighting probabilities. – *J. Agric. Biol. Environ. Stat.* 11: 231.
- Musante, A. R. et al. 2010. Characteristics and dynamics of a regional moose *Alces alces* population in the northeastern United States. – *Wildl. Biol.* 16: 185–204.
- Miller, S. D. et al. 1997. Brown and black bear density estimation in Alaska using radiotelemetry and replicated mark-resight techniques. – *Wildl. Monogr.* 133: 1–55.
- Nowlin, R. A. et al. 1979. Initial progress of the Colorado moose reintroduction. – *Alces* 15: 187–212.
- Oyster, J. H. et al. 2018. Hierarchical mark-recapture distance sampling to estimate moose abundance. – *J. Wildl. Manage.* 82: 1668–1679.
- Poole, K. G. 2007. Does survey effort influence sightability of mountain goats *Oreamnos americanus* during aerial surveys? – *Wildl. Biol.* 13: 113–119.
- Rughetti, M. et al. 2017. Ecological and evolutionary effects of selective harvest of non-lactating female ungulates. – *J. Appl. Ecol.* 54: 1571–1580.
- Ruprecht, J. S. et al. 2016. Reproduction in moose at their southern range limit. – *J. Mammal.* 97: 1355–1365.
- Rice, C. G. et al. 2009. A sightability model for mountain goats. – *J. Wildl. Manage.* 73: 468–478.
- Samuel, M. D. et al. 1987. Visibility bias during aerial surveys of elk in northcentral Idaho. – *J. Wildl. Manage.* 51: 622–630.
- Severud, W. J. et al. 2019. Survival and cause-specific mortality of moose calves in northeastern Minnesota. – *J. Wildl. Manage.* 83: 1131–1142.
- Solberg, E. J. and Sæther, B.-E. 1999. Hunter observations of moose *Alces alces* as a management tool. – *Wildl. Biol.* 5: 107–117.
- Solberg, E. J. et al. 2001. Effects of density-dependence and climate on the dynamics of a Svalbard reindeer population. – *Ecography* 24: 441–451.
- Thompson, W. L. et al. 1998. Monitoring vertebrate populations. – Academic Press.
- Udevitz, M. S. et al. 2006. Evaluation of aerial survey methods for Dall's sheep. – *Wildl. Soc. Bull.* 34: 732–740.
- Walsh, D. P. et al. 2011. Measurement error and survey design in sightability model development. – *J. Wildl. Manage.* 75: 1228–1235.
- Weiskopf, S. R. et al. 2019. Climate change effects on deer and moose in the Midwest. – *J. Wildl. Manage.* 83: 769–781.
- White, G. C. 2005. Correcting wildlife counts using detection probabilities. – *Wildl. Res.* 32: 211–216.
- White, G. C. and Burnham, K. P. 1999. Program MARK: survival estimation from populations of marked animals. – *Bird Study* 46: S120–S139.
- White, G. C. and Lubow, B. C. 2002. Fitting population models to multiple sources of observed data. – *J. Wildl. Manage.* 66: 300–309.
- Williams, B. K. et al. 2001. Analysis and management of animal populations. – Academic Press.
- Wood, A. K. et al. 1986. Serum assays for detecting pregnancy in mule and white-tailed deer. – *J. Wildl. Manage.* 50: 684–687.
- Zabransky, C. J. et al. 2016. A detection probability model for aerial surveys of mule deer. – *J. Wildl. Manage.* 80: 1379–1389.