ESTIMATING MOOSE ABUNDANCE BY USING STATISTICAL POPULATION RECONSTRUCTION TO FILL TEMPORAL GAPS IN AERIAL SURVEY DATA

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ABSTRACT: Changes in moose populations are often evaluated using aerial surveys, which are expensive and dependent upon weather conditions and logistical constraints that sometimes preclude their completion each year. Statistical population reconstruction (SPR) provides a versatile framework for combining existing information from aerial surveys with auxiliary data such as telemetry-derived survival estimates to fill the temporal gaps in these surveys. We examined the performance of SPR in estimating moose abundance and other demographic characteristics in Minnesota during a year when the survey was not flown (2021; due to the COVID-19 pandemic) by combining data from 5 separate telemetry studies with aerial survey results from 2005–2020 and 2022–2024. We estimated an overall abundance of 3,212 moose (95% CI = 2,130–3,883) in 2021, with a corresponding bull-to-cow ratio of 0.84 (95% CI = 0.46–1.33) and a calf-to-cow ratio of 0.38 (95% CI = 0.22–0.70), which are consistent with previous survey results and independent population models. We used Leave-One-Out Cross-Validation (LOOCV) to confirm the accuracy and precision of these estimates, and to explore how additional years of missing aerial survey data would have impacted reconstructed estimates of demographic parameters. This validation analysis demonstrated that missing a single year of aerial survey data did not substantially impact model performance, and that additional years of missing data would have resulted in small but steady decreases in both the accuracy and precision of model-derived estimates. Our research also highlights the need for telemetry studies of yearling moose survival to improve the performance of SPR and provide a clearer picture of moose demography in Minnesota.

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Moose (*Alces alces*; mooz [singular] and moozoog [plural] in Anishinaabemowin, the Ojibwe language) are a crucial source of sustenance and are spiritually significant for many Indigenous peoples in the northern hemisphere (Tobias and Richmond 2014, Popp et al. 2019, Priadka et al. 2022, Moore et al. 2024). In Minnesota, USA, moose are a key terrestrial subsistence food for the northern Ojibwe Tribes, particularly the Grand Portage and the Fond du Lac Bands of Lake Superior Chippewa and the Bois Forte Band of Chippewa. Moose also play an essential role in hunting traditions and wildlife viewing, contributing to the cultural heritage and tourism of the state. As such, it is important that moose abundance and demographic rates are accurately estimated and monitored to make informed management decisions (Moll et al. 2022). Because of logistical difficulties in estimating moose abundance over the larger spatial scales at which many management decisions are made, moose are generally surveyed from fixed- or rotary-wing aircraft during the late autumn and winter months when plentiful snow provides a white backdrop that improves visual detection from above (Timmermann 1993, Michaud et al. 2014, Harris et al. 2015, Brinkman et al. 2024).

Winter aerial surveys of moose throughout North America present numerous challenges including high costs, adverse weather conditions, insufficient snow cover, personnel availability, and other external factors (Oyster et al. 2018, Kellie et al. 2019, Brinkman et al. 2024). In Alaska, wildlife biologists failed to complete approximately 42% of scheduled aerial surveys from 2007 to 2017, with lack of adequate snow cover and poor flying weather being the most cited reasons (Kellie et al. 2019). Weather and logistics also impeded continuous helicopter surveys of moose in Isle Royale National Park in 2022 (Sovie et al. 2023), and surveys of moose in Washington in 2015 were limited by unsafe fog conditions and one of the warmest and driest winters on record (Oyster et al. 2018). In Minnesota, helicopter crews that have been employed since 2005 cannot conduct flights without at least 20.3 cm (8 in) of snow on the ground (Giudice 2024), as well as a cloud ceiling of at least 305 m (1,000 ft) with 4.8 km (3 mile) visibility (M. Swingen, 1854 Treaty Authority, personal communication). Adverse weather such as high winds or precipitation have also caused flight delays and cancellations throughout the state; more recently, the COVID-19 pandemic precluded a survey from occurring in winter 2021 (DelGiudice and Giudice 2022).

Statistical population reconstruction (SPR) using integrated population models (IPMs), which offers a flexible framework for synthesizing and combining disparate datasets from multiple studies, may provide a reliable and cost-effective means of estimating moose abundance over large spatial scales. In particular, this technique can facilitate estimation of demographic parameters in years when aerial surveys are not conducted. By incorporating relevant information from aerial surveys, radio-telemetry studies, and other sources of data, this method simultaneously estimates multiple demographic parameters (e.g., abundance, recruitment, and survival) and their uncertainties throughout time, and can be used to provide separate estimates for different sexes and age classes (Gove et al. 2002, Skalski et al. 2007, Broms et al. 2010, Clawson et al. 2013). SPR has become a valuable tool for monitoring population trends of grizzly bears (*Ursus arctos*), river otters (*Lontra canadensis*), rock ptarmigans (*Lagopus muta*), and other wildlife throughout the world (Hatter et al. 2018, Sturludottir et al. 2018, Berg and Palmer 2021), but has only recently been applied to moose (Severud et al. 2022).

Most SPR models use age-at-harvest and harvest effort data as the primary source of information to estimate population abundance (e.g., Skalski et al. 2011, 2012;

Berg and Palmer 2021, Berg 2023), while using radio telemetry (e.g., Broms et al. 2010, Berg et al. 2017) or other data (e.g., Skalski et al. 2007, Fieberg et al. 2010) as auxiliary components when available. The accuracy and precision of these models, however, is strongly dependent on the quantity of and variability in these primary data (i.e., a higher number of animals harvested each year and higher variation in the number of hunters leads to greater accuracy in model estimates; Skalski et al. 2007, Clawson et al. 2013, Berg and Palmer 2021, Berg et al. 2024). In Minnesota, moose harvest is very limited, and the number of hunting permits are similar across most years. Given these constraints but conversely a high amount of available aerial survey data, Severud et al. (2022) instead used aerial surveys as the primary source of information to estimate population abundance, with radio-telemetry data again serving as auxiliary. Although this approach yielded robust and biologically realistic estimates of overall moose abundance in Minnesota (Severud et al. 2022), many state and Tribal management agencies that may consider using SPR to monitor moose abundance in their region have substantially less aerial survey data available. As such, a more quantitative understanding of how missing years of aerial survey data influence the accuracy and precision of these SPR models is needed.

In this paper, we use aerial survey and telemetry data to parameterize an updated SPR model to estimate moose abundance in northeastern Minnesota from 2005 to 2024, including filling a missing gap in estimated demographic trends caused by the cancellation of the aerial survey in 2021. Although most of these data were already used in the earlier SPR model of moose in Minnesota (Severud et al. 2022), we incorporated 4 additional years of both aerial survey and telemetry data, as well as data from a previously unused telemetry study. Further, this updated model employs a maximum likelihood estimation formulation (as opposed to minimum χ^2 estimation), which can provide more robust parameter estimates (Berg and Palmer 2021) and allows us to explicitly incorporate the uncertainties in the aerial survey data that were omitted from the earlier model. We also include separate survival parameters for calves, cows, and bulls (as opposed to pooling them together into a single parameter), which allows us to estimate two additional demographic rates that could not be accurately estimated by the original model: calf-to-cow and bull-to-cow ratios. We then conduct a novel cross-validation analysis to evaluate the accuracy and precision of this new model in estimating moose abundance and demographic ratios across a range of scenarios varying in the number of years when aerial survey data are not available.

STUDY AREA

Our research took place in northeastern Minnesota, near the southern edge of the moose's natural range (Lenarz et al. 2010, Timmermann and Rodgers 2017). The study area included parts of the Superior National Forest, various Tribal, state, county, and private lands, as well as federal lands within Voyageurs National Park (VNP). The study area is part of the Northern Superior Upland within the Laurentian mixed forest province (Minnesota Department of Natural Resources [MNDNR] 2015). The landscape features a mosaic of wetlands, northern white cedar (*Thuja occidentalis*), black spruce (*Picea mariana*), tamarack (*Larix laricina*), and upland stands of balsam fir (*Abies balsamea*), jack pine (*Pinus banksiana*), eastern white pine (*P. strobus*), and red pine (*P. resinosa*), intermixed with quaking aspen (*Populus tremuloides*) and paper birch (*Betula papyrifera*).

Moose have historically been and continue to be an essential subsistence food for the Anishinaabeg of the region, including the federally recognized Tribes in northeastern Minnesota (Grand Portage Band of Lake Superior Chippewa [GP], Fond du Lac Band of Lake Superior Chippewa [FDL], and Bois Forte Band of Chippewa [BF]). These Bands exercise their rights to food sovereignty through subsistence hunting and fishing, both on and off Reservations within the lands ceded under the Treaty of 1854, which includes all present-day northeastern Minnesota. The statewide moose hunting season was closed from 1922 to 1971 due to low population numbers (MNDNR 2012). When it reopened, limited permits were issued in the northwestern and northeastern parts of the state. Hunting ceased in the northwest in 1997 but continued in the northeast. By 2007, regulations restricted state hunting to antlered adult males only (DelGiudice 2012). Moose hunting was suspended across Minnesota from 2013 until 2016, when only Tribal subsistence hunting resumed (Edwards 2018, Schrage 2018). Notably, there is no moose hunting within VNP.

METHODS

Available Demographic Data

From 2005 to 2024, the MNDNR conducted aerial surveys of the northeastern moose population in collaboration with FDL and the 1854 Treaty Authority (Giudice 2024). Surveys were typically conducted during the first 2 weeks of January; however, insufficient snow depth postponed the 2012 survey until late January into early February, and the COVID-19 pandemic prevented a survey in 2021 (Severud et al. 2022). The entire survey area of approximately 15,000 km^2 was divided into 436 rectangular plots of approximately 36 km^2 each, 36 to 52 of which were then sampled each year using helicopters. Sampled plots were selected using a stratified random sampling protocol based on moose density (low, medium, high), which was established collaboratively by the MNDNR, FDL, and 1854 Treaty Authority and reevaluated every 5 years. Each sighted moose was classified as either a calf (first winter, ~9 months old, females and males pooled), cow (female, 1 year 9 months or older), or bull (male, 1 year 9 months or older) based on body size and presence of vulva patch or antlers. The total number of calves, cows, and bulls identified throughout all sampled plots were then used to calculate proportionate calf-to-cow and bull-to-cow ratios for that year. A sightability model (Fieberg 2012) was then used to estimate overall abundance and corresponding 90% confidence intervals (Giudice et al. 2012). We used these reported values to extract separate estimates and standard errors for the number of calves, cows, and bulls in each year (Table 1).

Additionally, we used cow and bull survival data collected via 5 separate radio-telemetry studies that spatially and temporally overlapped the available aerial survey data (Table 2). We right-censored animals with collar failures in the year of collar failure as well as animals that likely died as a result of capture (Gove et al. 2002, Berg et al. 2017, Severud et al. 2022). Only animals that were successfully monitored throughout the entire model year (February 1 to January 31) or that died during that year were included in these data, for a final sample size of 454 unique animals and a total of 1,198 animal-years. Notably, there were no available data for the survival of moose from 9 months of age to 1 year and 9 months of age from these telemetry studies.

Table 1. Estimated number (means and standard errors) of calf, cow, and bull moose from aerial winter surveys in northeastern Minnesota from 2005 to 2024. These values, which comprise the aerial survey matrix used in statistical population reconstruction, were estimated from the overall abundance and calf-to-cow and bull-to-cow ratios that were originally reported by Giudice 2024.

Year	Calves	Cows	Bulls
2005	1,658 (329)	3,188 (632)	3,315 (657)
2006	1,237 (218)	3,638 (640)	3,965 (698)
2007	913 (155)	3,147 (534)	2,801 (475)
2008	1,334 (232)	3,704 (645)	2,852 (497)
2009	1,110 (162)	3,469 (507)	3,261 (477)
2010	756 (113)	2,701 (405)	2,242 (336)
2011	626 (97)	2,606 (406)	1,668 (260)
2012	624 (110)	1,734 (306)	1,872 (331)
2013	356 (58)	1,078 (177)	1,326 (218)
2014	714 (149)	1,623 (339)	2,013 (421)
2015	439 (84)	1,513 (288)	1,498 (285)
2016	689 (102)	1,641 (242)	1,690 (249)
2017	588 (82)	1,634 (228)	1,487 (207)
2018	428 (78)	1,157 (211)	1,446 (264)
2019	523 (89)	1,633 (277)	2,025 (343)
2020	502 (93)	1,394 (258)	1,254 (232)
2021	-	-	-
2022	885 (191)	1,967 (425)	1,849 (399)
2023	474 (91)	1,246 (240)	1,570 (302)
2024	623 (129)	1,222 (254)	1,625 (337)

SPR of Moose in Minnesota

SPR typically begins by specifying a deterministic population projection matrix to describe changes in population size, recruitment, and survival over time (Gast 2012, Berg 2016). Consider a hypothetical population of moose divided into $A = 3$ classes (calves, cows, and bulls) monitored over $Y = 20$ consecutive years, where N_{ij} is the winter abundance of moose in year i ($i = 1,\ldots,Y$) of class j ($j = 1,\ldots,A$). Under this framework, all individuals born during the same year constitute a single cohort that is subsequently subjected to annual mortality from various sources such as harvest, predation, and disease.

The number of moose present during a specific year that belong to a specific class (i.e., N_{ij}) can then be written as a function of the initial abundance of the corresponding cohort, as defined by the number of calves, cows, and bulls alive during the first year (i.e., N_{1j}) or the number of calves alive during each subsequent year (i.e., N_{i1}), and the annual rate of survival per class (S_{ij}). The number of cows alive during the winter of the second year (i.e., N_{22}), for example, is a function of the number of calves and cows alive during the first year (i.e., N_{11} and N_{12}, respectively) that survive to the next year, which can be written as

Table 2. Radio-telemetry data on the number of mortalities and associated at-risk counts (in parentheses) for collared cow (left) and bull (right) moose in northeastern Minnesota from 2005 to 2023 from 5 different studies, including 2 from Voyageurs National Park (VNP) and Grand Portage Band of Lake Superior Chippewa (GP), that were used in statistical population reconstruction.

Year	Schrage, unpubl.	VNP, unpubl.	GP, unpubl	Moen, unpubl.	Carstensen et al. (2018)
2005	8 (43) | 9 (33)				
2006	11 (34) | 10 (23)				
2007	4 (23) | 4 (13)				
2008	10 (51) | 2 (9)				
2009	4 (41) | 1 (7)				
2010	7 (37) | 3 (6)	0 (7) | 0 (2)	2 (6) | 0 (2)		
2011	5 (28) | 1 (3)	3 (11) | 0 (6)	3 (11) | 2 (2)	1 (13) | 2 (6)	
2012	4 (22) | 0 (1)	1 (8) | 1 (5)	0 (6) |	1 (6) | 0 (2)	
2013	0 (1) |	0 (7) | 0 (4)	5 (16) | 2 (3)		17 (76) | 4 (23)
2014		0 (5) | 1 (3)	4 (25) | 0 (1)		10 (64) | 2 (29)
2015		1 (3) | 1 (1)	7 (32) | 0 (2)		8 (55) | 6 (29)
2016		1 (2) |	3 (26) | 0 (5)		3 (27) | 3 (16)
2017		1 (1) |	3 (20) | 1 (4)		3 (7) | 2 (8)
2018			2 (14) | 2 (4)		| 0 (1)
2019			1 (20) | 1 (9)		| 1 (1)
2020			5 (34) | 4 (9)		
2021			2 (24) | 0 (4)		
2022			11 (41) | 5 (19)		
2023			3 (34) | 4 (22)		

$$N_{22} = (N_{11} \times S_{11} \times 0.5) + (N_{12} \times S_{12}),$$

where 0.5 represents the assumption of a 50:50 sex-ratio of calves at birth and no sex difference in first-year survival rates (Severud et al. 2022). We included random effects by parameterizing survival as

$$S_{ij} = \frac{e^{\beta_j + \varepsilon_{ij}}}{1 + e^{\beta_j + \varepsilon_{ij}}}$$

where β_j is the mean survival coefficient for class j and ε_{ij} are the normally distributed random effects in year i for class j that allow survival coefficients to vary annually about the mean separately for each class (Gast et al. 2013*a*). These values of initial cohort abundance (i.e., N_{1j} and N_{i1}), mean survival coefficients (i.e., β_j), and random effects about the mean survival coefficients (i.e., ε_{ij}) constitute the set of parameters that are directly estimated by SPR.

Estimating model parameters (i.e., N_{1j}, N_{i1}, β_j, and ε_{ij}) begins by considering the aerial survey matrix a, which summarizes the number of animals of each class j that were estimated to be alive in year i via aerial survey (e.g., Table 1). By assuming that these estimates are asymptotically normally distributed, we can use a probability mass function (PMF) to find the best estimate of model parameters given observed aerial survey data, which can be written as

$$\mathrm{PMF}_{\mathrm{Aerial}} = \prod_{i=1}^{Y} \prod_{j=1}^{A} \frac{1}{\sqrt{2\pi\sigma_{ij}}} e^{-\frac{1}{2}\left(\frac{N_{ij}-a_{ij}}{\sigma_{ij}}\right)^2}$$

where σ_{ij} represents the standard errors for the estimated a_{ij} (Clawson et al. 2013, Berg et al. 2024).

In addition to aerial survey data, we also used survival information from collared cow and bull moose with known fates each year (telemetry information on the survival of calves from their first winter to their second winter was unavailable). These data were used to model the number of observed mortalities each year as a binomial process of the form

$$\mathrm{PMF}_{\mathrm{Telemetry}} = \prod_{i=1}^{Y} \prod_{j=2}^{A} \binom{n_{ij}}{v_{ij}} (1 - S_{ij})^{v_{ij}} \times (S_{ij})^{n_{ij}-v_{ij}}$$

where v_{ij} is the number of collared moose that died during year i of class j and n_{ij} is the corresponding number of collared moose at risk at the start of the year (Gove et al. 2002, Broms et al. 2010, Berg et al. 2017).

In lieu of data on the survival of calves from their first winter to their second winter (i.e., calf survival), we used information on calf-to-cow ratios from the aerial survey data to help estimate the number of calves each year. By assuming that calf-to-cow ratios are asymptotically normally distributed, we calculated the mean and standard deviation of these ratios from years when aerial surveys were conducted, and modeled deviations from this mean as a normal process of the form

$$\mathrm{PMF}_{\mathrm{Ratio}} = \prod_{i=1}^{Y} \frac{1}{\sqrt{2\pi s}} e^{-\frac{1}{2}\left(\frac{R_i - r}{s}\right)^2}$$

where R_i is the model-derived ratio of calves to cows (i.e., N_{i1}/N_{i2}), r is the mean calf-to-cow ratio from aerial survey data (i.e., $\Sigma \frac{a_{i1}/a_{i2}}{Y}$), and s is the standard deviation of this mean. This PMF requires no additional data, which is similar to the catch-effort likelihood used in other SPR models (Gast 2012, Gast et al. 2013*a*). Our preliminary investigations suggest that its inclusion leads to greater stability in the optimization process and improves model accuracy and precision.

The full joint PMF can then be written as the combination of the three PMFs defined earlier as

$$\mathrm{PMF} = \mathrm{PMF}_{\mathrm{Aerial}} \times \mathrm{PMF}_{\mathrm{Telemetry}} \times \mathrm{PMF}_{\mathrm{Ratio}}$$

The model parameters (i.e., initial cohort abundance, survival coefficients, and random effects) are then estimated by maximizing this joint objective function using a combination of several different numerical optimization techniques (i.e., particle swarm optimization, spectral projected gradient, and Broyden-Fletcher-Goldfarb-Shanno) given the observed values of a_{ij}, σ_{ij}, n_{ij}, and v_{ij}. We calculated standard errors for each parameter estimate using a numerical estimate of the inverse Hessian (Fieberg et al. 2010, Skalski et al. 2012, Berg et al. 2017) and derived 95% confidence intervals using Monte Carlo simulations.

We used these estimated model parameters to derive estimates of overall abundance and calf-to-cow and bull-to-cow ratios during 2021 when an aerial survey of moose could not be conducted. To maximize predictive power, we used a heavily parameterized model with separate mean survival rates for calves, cows, and bulls, and included random effects that allowed these rates to vary annually about the mean separately for cows and for bulls. Because we lacked telemetry data for calves, we were unable to incorporate separate random effects on calf survival (i.e., survival of calves from their first winter to their second winter) and instead treated calf survival as constant. Setting interannual fluctuations about calf survival to be proportional to those of a different class (Gast et al. 2013*a*, *b*, Clawson et al. 2022) — either cows or bulls — did not substantially alter our model results.

Model Validation and Missing Data Simulation

We began model validation by using Leave-One-Out Cross-Validation (LOOCV) to determine how accurate and precise estimates are likely to be when a single year of data is missing (Prochazka et al. 2024). This technique was chosen because it mimics the instance of a single year of missing data observed in the original aerial survey data in Minnesota. To that end, we used data from 2005 to 2020, during which aerial surveys were conducted each year, to estimate moose abundance and demographic ratios using SPR (hereafter "full-model estimates"). We then sequentially omitted each year of aerial survey data (i.e., a_{ij} and σ_{ij}) and used SPR to estimate overall abundance and demographic ratios for that year (hereafter "leave-one-out estimates"). The first and last years of aerial survey data (i.e., 2005 and 2020) were always retained and used to bracket the remaining years of available data.

We assessed the accuracy of these leave-one-out estimates of overall abundance and demographic ratios for each missing year by correlating them to the full-model estimates. We also assessed precision by calculating the mean and standard deviation (SD) of the relative absolute deviation (RAD) of the leave-one-out estimates from the full-model estimates, defined for overall abundance as

$$\mathrm{RAD} = \frac{\left|\widehat{N_i} - N_i\right|}{N_i} \times 100\%$$

where N_i is the full-model estimate of overall abundance in year i and $\widehat{N}_i$ is the corresponding leave-one-out estimate (Clawson et al. 2013, Berg 2023, Berg et al. 2024). Similar calculations were performed for the calf-to-cow and bull-to-cow ratios.

Although this LOOCV is well suited for our specific data set, other management agencies may have substantially more years of missing aerial survey data. As such, we also evaluated how the accuracy and precision of the estimated overall abundance and demographic ratios changes if more than a single year is missing from the aerial survey data. To that end, we performed a similar cross-validation analysis for every possible combination of between 2 and 10 years of missing data, again while always retaining the first and last years of aerial survey data (i.e., 2005 and 2020).

RESULTS

Using SPR with all available aerial survey and telemetry data, we estimated that winter moose abundance in 2021 was 3,212 animals (95% CI = 2,130 – 3,883), with a bull-to-cow ratio of 0.84 (95% CI = 0.46 – 1.33) and a calf-to-cow ratio of 0.38 (95% CI = 0.22 – 0.70; Figure 1). We also estimated mean survival coefficients of 1.28 (SE = 0.53), 1.54 (SE = 0.10), and 1.51 (SE = 0.15) for calves, cows, and bulls, respectively, which corresponded to annual baseline survival rates of 0.78 (SE = 0.09), 0.82 (SE = 0.01), and 0.82 (SE = 0.02), respectively. The inclusion of normally distributed random effects allowed for interannual fluctuations around these mean survival coefficients that resulted in annual survival rates ranging from 0.69 to 0.93 for cows and 0.63 to 0.97 for bulls.

In the absence of a single year of aerial survey data, our cross-validation analysis revealed that leave-one-out estimates of overall abundance were highly correlated with the full-model estimates (Pearson correlation coefficient, *r* = 0.98) and had a mean RAD of 8.9% (SD = 5.8%). Leave-one-out estimates of bull-to-cow ratios were moderately correlated with the full-model estimates (*r* = 0.69) but had smaller and more consistent RAD (mean = 5.3%, SD = 4.9%). Leave-one-out estimates of calf-to-cow ratios, on the other hand, were only weakly correlated with the full-model estimates (*r* = 0.36) and had much larger and less consistent RAD (mean = 21.5%, SD = 14.5%; Figure 2).

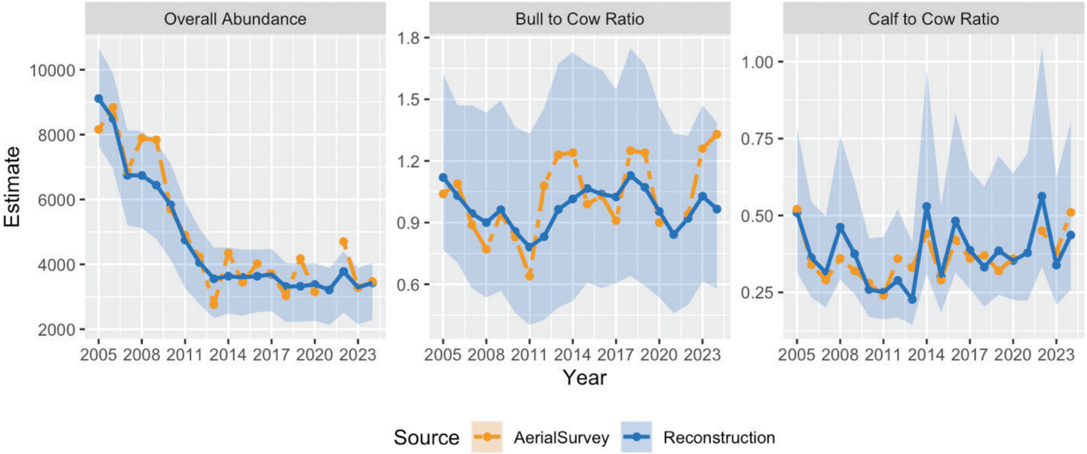

Fig. 1. Estimated trends in overall winter abundance and bull-to-cow and calf-to-cow ratios of moose in northeastern Minnesota from 2005 to 2024 based on the best available reconstruction model, along with associated 95% confidence intervals (shaded areas), as compared to the results of aerial surveys conducted by the Minnesota Department of Natural Resources in collaboration with the Fond du Lac Band of Lake Superior Chippewa and the 1854 Treaty Authority.

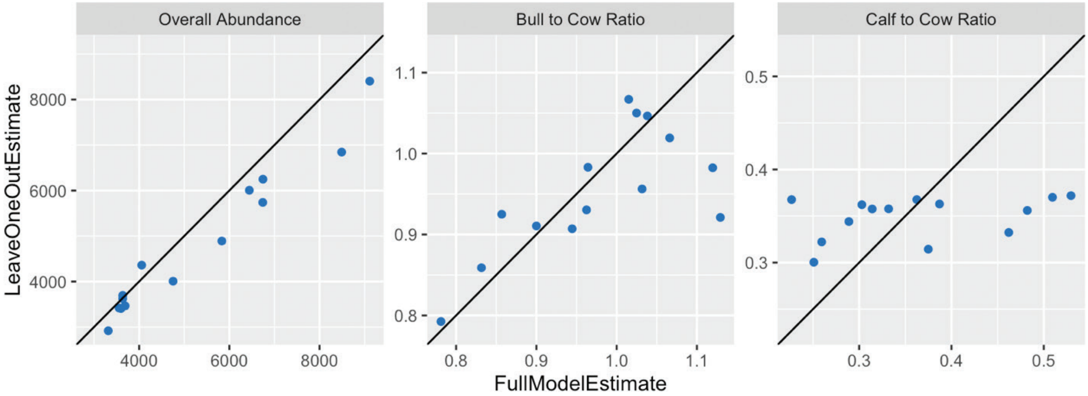

Fig. 2. Comparison of leave-one-out estimates to full-model estimates, along with a solid line to indicate a perfect match, of overall abundance and bull-to-cow and calf-to-cow ratios for a Leave-One-Out Cross-Validation (LOOCV) of using statistical population reconstruction for moose in northeastern Minnesota with one year of missing aerial survey data. Cross-validation was conducted using data from 2005 to 2020 during which aerial surveys were conducted each year.

As the number of years without aerial survey data increased, the accuracy and precision of estimates derived from SPR for each of those missing years declined steadily. When 2, 6, and 10 years of data were omitted, the correlations for overall abundance decreased to 0.97, 0.95, and 0.90, respectively. Correlations for reconstructed demographic ratios followed a similar pattern, decreasing to 0.67, 0.56, and 0.49 for bull-to-cow ratios and to 0.35, 0.32, and 0.23 for calf-to-cow ratios, respectively. The corresponding RAD also increased steadily as the number of missing years increased, reaching 14.3% (SD = 8.7%), 9.0% (SD = 6.4%), and 23.9% (SD = 16.3%) for overall abundance, bull-to-cow ratios, and calf-to-cow ratios, respectively, when ten years of data were omitted (Table 3).

DISCUSSION

We used a statistical method to reconstruct the abundance and other demographic characteristics of moose in northeastern Minnesota during a year when aerial surveys could not be conducted by integrating data from ongoing radio-telemetry studies alongside available aerial survey data from other years. Our best estimate of 3,212 moose (95% CI = 2,130 – 3,883) in 2021 compared favorably with the results of an independent state-space population model developed by MNDNR (~3,600 moose, Figure A1 in Giudice 2024), and was consistent with the aerial survey estimates of abundance in 2020 and 2022. This provided some external confirmation of our reconstruction results and suggested that the model accurately estimated moose abundance throughout the state. These point estimates would have indicated that the moose population was relatively stable during those years; however, the width of the corresponding confidence intervals made it challenging to determine if the population was actually stable (as indicated by the point estimates) or was instead increasing or decreasing (both of which are possible given the width of the confidence intervals). Our best estimate for the bull-to-cow and calf-to-cow ratios of 0.84 (95% CI = 0.46 – 1.33) and 0.38

Table 3. Pearson correlation coefficients (*r*) and relative absolute deviations (RAD) of leave-k-out estimates to full-model estimates of overall abundance and bull-to-cow and calf-to-cow ratios from a cross-validation of using statistical population reconstruction for moose in northeastern Minnesota as the number of years of missing aerial survey data increases. Cross-validation was conducted using data from 2005 to 2020 during which aerial surveys were conducted each year.

Years Removed	Overall Abundance		Bull-to-Cow Ratio		Calf-to-Cow Ratio	
	r	RAD	*r*	RAD	*r*	RAD
1	0.98	8.9 (5.8)	0.69	5.3 (4.9)	0.36	21.5 (14.5)
2	0.97	9.4 (5.7)	0.67	5.6 (4.9)	0.35	21.6 (14.1)
3	0.97	9.8 (5.8)	0.64	5.9 (5.1)	0.35	21.7 (14.2)
4	0.97	10.3 (6.1)	0.62	6.3 (5.3)	0.34	21.8 (14.2)
5	0.96	10.8 (6.4)	0.59	6.7 (5.4)	0.33	22.0 (14.4)
6	0.95	11.4 (6.8)	0.56	7.1 (5.6)	0.32	22.2 (14.6)
7	0.94	12.0 (7.2)	0.53	7.5 (5.8)	0.31	22.4 (14.8)
8	0.93	12.7 (7.6)	0.51	8.0 (6.0)	0.29	22.8 (15.2)
9	0.91	13.5 (8.1)	0.50	8.4 (6.2)	0.26	23.2 (15.6)
10	0.90	14.3 (8.7)	0.49	9.0 (6.4)	0.23	23.9 (16.3)

(95% CI = 0.22 – 0.70), respectively, albeit with large confidence intervals, were also consistent with survey estimates from that time. These reconstructed estimates also eliminated the biologically unrealistic fluctuations sometimes observed in the original aerial survey estimates, such as overall abundance increasing by 58% from 2013 to 2014 or bull-to-cow ratios increasing by 69% from 2011 to 2012. This further reinforced the utility of using SPR models to combine multiple datasets to produce more accurate and robust estimates of population abundance and other demographic parameters than could be derived from any one dataset on its own.

Our cross-validation analysis for this specific scenario of missing one year of aerial survey data largely supported our conclusions regarding the accuracy with which SPR can be used to estimate overall abundance during that year. The high correlation and low RAD between the leave-one-out and full-model estimates were comparable to the best simulated performance of other SPR models (e.g., Clawson et al. 2013, Berg et al. 2024) and indicated that missing a single year of aerial survey data did not substantially impact model performance. Our validation analysis also demonstrated that decreases in both the accuracy and precision of model-derived estimates were relatively small when faced with multiple missing years of aerial survey data. Even when over 60% of the aerial survey data were omitted, SPR-derived estimates of overall abundance were still highly correlated with the full-model estimates and had only moderately higher and more variable RAD. This suggested that SPR was not only sufficient to fill the gap in abundance estimates caused by the missing year of aerial survey data in 2021, but that it could continue to provide reliable estimates even if additional years of data were missing (e.g., if resources became more limiting, necessitating longer intervals between surveys). For example, the estimates derived from the aerial survey conducted in 2013, which indicated a very sharp decline from the previous year, may not have been accurate because snow conditions were less than ideal for aerial surveys (DelGiudice 2014). Our results indicated that SPR could potentially be used to provide a more accurate estimate of overall abundance for that year if the corresponding aerial survey data were omitted. Further, this finding is also important for wildlife managers who might be hesitant about pursuing population reconstruction because of less consistent aerial survey data, but who have sufficient radio-telemetry data to fill these gaps.

Our cross-validation analysis also indicated that model-derived estimates of bull-to-cow and calf-to-cow ratios were markedly less accurate and precise than those of overall abundance, regardless of whether only one or multiple years of aerial survey data were missing. Although reconstructed estimates of bull-to-cow ratios had a mean RAD that was even lower than that of overall abundance, they were only moderately correlated with the full-model estimates. This was likely because estimates of bull-to-cow ratios were fairly stable over time, whereas estimates of overall abundance were much more varied because of the sharp population decline before 2013. Reconstructed estimates of calf-to-cow ratios, on the other hand, had a mean RAD that was roughly double that of either of the other two demographic parameters and much higher than the optimal performance simulated by Clawson et al. (2013) and Berg et al. (2024). These leave-out estimates were also only weakly correlated with the full-model estimates, which suggested that our best estimate of the calf-to-cow ratio in 2021 (when the aerial survey could not be conducted) should be treated with caution.

One limitation of our modeling approach is that the lack of data on survival of calves from 9 months to 1 year 9 months of age (i.e., surviving from their first winter to their second winter, or their calf winter to their yearling winter) prevented us from incorporating random effects on calf survival that would have allowed this parameter to vary independently from year to year. This likely explains the lack of accuracy and precision with which our model could estimate calf-to-cow ratios when compared to other demographic characteristics. Although we set this survival parameter to be constant over time, the survival of calves from their first winter to their second winter likely fluctuated from year to year because of a variety of factors including weather, predation, harvest, and disease. Most moose research in Minnesota, however, has focused on collaring older and reproductively active animals (Lenarz et al. 2010, Carstensen et al. 2018, Severud et al. 2022). Further research on yearling survival, as well as causes of mortality, pregnancy rates, and twinning rates, could greatly improve the performance of SPR models and provide a clearer and more complete picture of moose demography in Minnesota (Eberhardt 2002, Lenarz et al. 2010).

Cost-benefit analyses of various data inputs, costs of implementation, and resulting performance of SPR models would be a useful future direction for this application. For example, helicopter costs to conduct moose aerial surveys (fuel, maintenance, insurance, hangar space, etc.) were ~$82,000 USD in 2022 (MNDNR, personal communication), which does not even include staff time or travel costs for the 2 pilots and 4 to 6 observers. Telemetry-based monitoring of survival also comes with additional costs such as wildlife capture, collars, and monitoring. Our approach provides a means to estimate overall moose abundance and other demographic parameters during years when aerial surveys are not conducted by instead relying on radio-telemetry data from that year; however, it includes costs associated with alternative data sources, as well as loss of precision. Optimal balancing of these various data collection methods and resulting targets for precision could be addressed with future cost-benefit analyses.

Finally, these findings illustrate the value of Indigenous co-stewardship in the management and conservation of moose populations, particularly within the Grand Portage Indian Reservation, the 1854 Ceded Territory, and northeastern Minnesota. Moose hold profound cultural, spiritual, and subsistence significance for the Ojibwe people, and their population health is intricately linked to both Indigenous practices and co-management principles (Popp et al. 2019, Priadka et al. 2022, Moore et al. 2024). This collaborative and integrated approach to monitoring trends in population abundance and other demographic parameters can foster more sustainable moose populations, supporting both the ecological health of the region and the cultural heritage of the Indigenous communities that rely on these animals.

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