Statistical Population Reconstruction of Moose (*Alces alces*) in Northeastern Minnesota using Integrated Population Models

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Abstract

Given recent and abrupt declines in the abundance of moose (*Alces alces*) throughout parts of Minnesota, accurately estimating statewide population trends and demographic parameters is a high priority for their continued management and conservation. Statistical population reconstruction using integrated population models provides a flexible framework for combining information from multiple studies across the state to produce robust estimates of population abundance, recruitment, and survival. We used this framework to combine aerial survey data and survival data from telemetry studies to recreate trends and demographics of moose in northeastern Minnesota, USA, from 2005 to 2020. Statistical population reconstruction confirmed the sharp decline in abundance from an estimated 7,841 (90% CI = 6,702–8,933) in 2009 to 3,386 (90% CI = 2,681–4,243) animals in 2013, but also indicated that abundance has remained relatively stable since then, except for a slight decline to 3,163 (90% CI = 2,403–3,718) in 2020. Subsequent stochastic projection of the population from 2021 to 2030 suggests that this modest decline will continue for the next ten years. Both annual adult survival and per-capita recruitment (number of calves that survived to 1 year per adult female alive during the previous year) decreased substantially in years 2005 and 2019, from 0.902 (SE = 0.043) to 0.689 (SE = 0.061) and from 0.386 (SE = 0.030) to 0.303 (SE = 0.051), respectively. Sensitivity analysis revealed that moose abundance was more sensitive to fluctuations in adult survival than recruitment, leading us to conclude that the steep decline in 2013 was driven primarily by decreasing adult survival. Our analysis demonstrates the potential utility of using statistical population reconstruction to monitor moose population trends and to identify population declines more quickly. Future studies should focus on providing better estimates of per-capita

recruitment, using pregnancy rates and calf survival, which can then be incorporated into reconstruction models to help improve estimates of population change through time.

Key Words: *Alces alces*, integrated population model, Minnesota, moose, population reconstruction, survival, telemetry

Federally recognized Indian tribes in northeastern Minnesota, USA, including the Grand Portage Band of Lake Superior Chippewa, Bois Forte Band of Chippewa, and Fond du Lac Band of Lake Superior Chippewa, proudly exercise their rights to food sovereignty through subsistence hunting and fishing. Moose are a primary subsistence food used by the Anishinaabeg (people) historically and presently. Management for and research on maintaining this moose population as a vital subsistence species thus sets the context for this paper examining the population trends of this culturally important resource.

Introduction

Effective management and conservation of wildlife species requires an accurate understanding of population abundance, recruitment, survival, and age- and sex-ratios, and how these parameters change over time and in response to various extrinsic factors, such as hunting and habitat alteration. Unfortunately, accurately estimating parameters such as these is challenging, because direct monitoring of animals is often costly and impractical, particularly in densely forested regions or for animals that occur at low densities. Given these difficulties, most abundance estimates have relied on methods that are limited to small geographical areas or sample sizes, including track surveys [1], analysis of camera traps [2] and telemetry data [3]. Unfortunately, each of these methods by themselves do not provide a cost-effective means of estimating abundance and other demographic parameters across larger spatial scales at which most management occurs.

Statistical population reconstruction using integrated population models (IPMs) has emerged as a flexible framework for combining information from multiple studies, and even from different parts of a state or region, to provide a more robust and cost-effective means of estimating species abundance and demographics across large spatial scales [4,5]. This method simultaneously estimates multiple demographic parameters (e.g., annual abundance, recruitment, and survival) and their uncertainties throughout time, and can be used to provide separate estimates for different sexes and age classes. Such models have already been used to estimate abundance and trends of wildlife species, such as American marten (*Martes americana*), black bears (*Ursus americanus*), and mountain lions (*Puma concolor*) [6–8].

Accurately estimating the abundance and trajectory of the moose (*Alces alces*) population in northeastern Minnesota is of current interest due to a recent and abrupt decline that was detected via aerial surveys between 2010 and 2013 [9]. At its nadir in 2013, this population was 69% lower than when at its peak in 2006 (2,760 versus 8,840), but it appeared to have stabilized during 2012–2020 as estimated by aerial surveys [9,10]. A study of demographics of the northeastern population in 2002–2008, predicted a slow reduction in numbers (long-term stochastic annual growth rate [λ] of 0.85,) with modeled adult and calf survival rates of 0.74–0.85 and 0.24–0.56, respectively [11]. However, the abrupt decline in northeastern Minnesota was not detected by the annual aerial surveys until 2010 [11–13], which illustrated that demographic modeling may reveal population trajectories before they are reflected in total population estimates by aerial survey.

In response to the rapid decline in the northeastern population, the Minnesota Department of Natural Resources (MNDNR), Grand Portage Band of Lake Superior Chippewa, and Voyageurs National Park all independently initiated studies of adult and calf survival and cause-specific mortality (Fig. 1). These studies built upon previous research [11,14], but aimed to better understand causes of mortality [15,16]. The more recent research employed state-of-the-art global positioning system (GPS) collars and other remote monitoring techniques (e.g., internal temperature monitors, movement analyses) to track survival, habitat use, causes of mortality, physiological condition, and disease transmission dynamics [17–27].

Our goal was to integrate these multiple data streams into a unified model that would accurately describe past population dynamics and future projections of the northeastern Minnesota moose population. Specifically, we used statistical population reconstruction to not only provide more robust estimates of population abundance and recruitment than those provided by aerial survey data, but also to estimate survival rates that were previously unknown prior to collaring studies. We also examined the sensitivity of model estimates to fluctuations in adult survival and per-capita recruitment (number of calves that survived to 1 year per adult female alive during the previous year) to determine which may be more important in predicting population growth and used time series analysis to project population estimates 10 years into the future.

Materials and Methods

Study Area

Northeastern Minnesota is along the southern edge of North American moose range (Fig. 1) [11,28]. Moose are a subsistence food used by the Anishinaabeg (people) of the Grand Portage Band of Lake Superior Chippewa historically and presently. The Grand Portage Band is a federally recognized Indian tribe in extreme northeastern Minnesota and proudly exercises its rights to food sovereignty through subsistence hunting and fishing. Voyageurs National Park is just west of primary moose range (Fig. 1). Statewide moose harvest was closed during 1992–

1971 because of low moose numbers, and then reopened in the northwestern and northeastern portions of the state with limited permits issued [29]. Harvest was stopped in the northwest in 1997 but continued in the northeast. In 2007, state-licensed hunters were restricted to harvesting antlered bulls only [29]. Moose harvests were then suspended in Minnesota from 2013 until 2016, when a tribal subsistence harvest was resumed [30–32]. Moose harvests do not occur in VNP.

Our study area is a mosaic of the Superior National Forest and various Tribal, state, county, and private lands (6,068 km^2) between 47°06′N and 47°58′N latitude and 90°04′W and 92°17′W longitude (Fig. 1), as well as the federal lands of VNP. This region is part of the Northern Superior Upland within the Laurentian mixed forest province [33]. The vegetative cover is a mosaic of wetlands, stands of 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*).

Primary moose range in this region overlaps with gray wolves (*Canis lupus*) and American black bears, both of which prey upon adult and calf moose [14,20,25,34,35]. Adult and calf moose hair was present in relatively very few wolf scats from VNP compared to scats from primary moose range in MN [36,37]. The moose population in northeastern MN are afflicted by various parasites and disease, including infestation by winter ticks (*Dermacentor albipictus*) and infection by meningeal worm (*Parelaphostrongylus tenuis*) and giant liver fluke (*Fascioloides magna*) [24,26,38].

Aerial Surveys

As part of the ongoing monitoring and management of moose in northern MN that has taken place since the 1960s, the MNDNR, in cooperation with Fond du Lac Band of Lake Superior Chippewa (FDL) and 1854 Treaty Authority, has conducted an aerial survey of the northeastern moose population each winter using an updated and standardized approach since 2005 [9]; however, a survey was not conducted in 2021 due to the COVID-19 pandemic. The surveys were conducted using helicopters over a total area of approximately 15,500 km^2. This area was divided into 436 rectangular survey plots of approximately 36 km^2 each, 36 to 52 of which were selected each year using a stratified random sampling protocol based on moose density (low, medium, high). Moose density strata were classified collaboratively by MNDNR, FDL, and 1854 Treaty Authority staff and are reevaluated every 5 years based on expert knowledge and previous survey results. Each sighted moose was visually identified as either a calf, cow, or bull; uncorrected estimates (without a sightability correction) adjusted for sampling were then used to calculate bull:cow and calf: cow ratios at the population level [9,39]. A sightability model was then used to estimate overall abundance. Visual obstruction was calculated as the proportion of area within a 10-m radius surrounding the first moose observed in a group that was not visible and used to adjust each estimate and corresponding 90% confidence intervals (CI; Table 1)[9,39]. We used the estimated annual abundance of calves, cows, and bull derived from the aerial surveys in the IPM below. We scaled the variance of the overall point count on the proportion of calves to obtain variance estimates for calf abundance.

Adult Survival Rates

In addition to aerial survey data, we used adult moose survival data collected via telemetry from 2005 to 2019 by four different studies throughout northeastern Minnesota (Fig. 1). We excluded animals with collar failures from the data in the year of collar failure (i.e., rightcensoring), animals that died as a result of capture, and young-of-the-year from any further analysis. Collar failure was assumed to be independent of moose fate. The remaining animals in each study were pooled together to determine annual mortality and associated at-risk counts as a measure of adult survival rates (Table 2).

We extracted annual adult survival rates from published work by MNDNR, FDL, and the 1854 Treaty Authority [11,14,24,40]. The earlier MNDNR-FDL-1854 Treaty Authority study was conducted during 2002–2008 and collared 150 adult moose (95 F/55 M) [11]; however, we only used survival rates that coincided with the aerial survey (2005–2007). Lenarz et al. (2010) did not detect a difference in survival between males and females, so we used pooled adult survival estimates. The more recent MNDNR study was conducted from 2013 to 2016 and contained 173 adults (123 F/50 M) [24]. Differences in survival between males and females were not reported, so we used the pooled adult survival estimates from the cited work. Details of animal capture, handling, collaring, and monitoring can be found in the cited works [11,14,24,40].

We used 2 additional sources of adult moose survival data from study sites that are adjacent to the aerial survey area (Fig. 1). Voyageurs National Park collared 21 moose (14 F/7 M) to study moose survival from 2010 to 2017. Grand Portage Indian Reservation collared 99 adult moose (76 F/23M) between 2010 and 2019. All capture and handling protocols were conducted in accordance with requirements of the University of Minnesota Institutional Animal Care and Use Committee (protocols 1803-35736A and 0192A75532) and the guidelines of the American Society of Mammalogists [41]. We calculated Kaplan-Meier survival estimates using the “survival” package in Program R [42,43]. Because adult moose captures typically occurred in mid-winter (Jan–Mar), we modeled annual survival using the calendar year (i.e., t_0 = 1 Jan)

[44]. Collared moose that survived multiple years contributed an observation for each year they were alive, yielding 98 moose-years for Voyageurs National Park and 302 moose-years for Grand Portage. We used the "survdiff" function in the "survival" R package, which uses a log-rank test, to examine differences in overall survival between sexes [42,43].

Population Reconstruction of Moose in Minnesota

Population reconstruction typically begins by specifying a projection matrix to describe the change in the number of animals in each cohort over time. Consider a hypothetical population of moose divided into four classes (male and female, calves and adults) monitored over Y consecutive years, where N_{ij} is the abundance in winter of animals of class j in year i. Under this framework, all individuals born during the same year constitute a single cohort that is subsequently subjected to annual mortality from various causes. Previous reconstructions have then used an age-at-harvest matrix to represent each cohort; however, with the exception of tribal subsistence harvest averaging about 40 moose per year [31,32], moose are not regularly harvested in Minnesota. In lieu of these data, we used aerial survey data to represent each cohort as a separate diagonal, where the observed counts, a_{ij}, are a function of the initial abundance of the corresponding cohort and the annual survival rate (to be estimated as parameters). Due to the difficulty associated with identifying sex of moose calves during aerial surveys, we pooled male and female calves into a single cohort, for a total of $A = 3$ classes (calves, adult females or cows, and adult males or bulls; Table 1).

An objective function or estimator was then used to determine which set of model parameters best describes the observed data. We used a chi-square objective function to model the difference between the observed and predicted number of animals in each cohort and the joint difference for the entire matrix as

$$\Lambda_{Joint} = \sum_{i=1}^{Y} \sum_{j=1}^{A} \chi_{ij}^2 \,,$$

where χ_{ij}^2 is the cell-specific chi-square calculation [7,45]. The difference for the cell represented by the total number of cows (i.e., adult females) in year 2 (i.e., N_{22}), for example, can be written as follows:

$$\chi_{22}^2 = \frac{(a_{22} - N_{22})^2}{N_{22}} = \frac{(h_{13} - (N_{11} \times 0.5 + N_{12}) \times S_1)^2}{(N_{11} \times 0.5 + N_{12}) \times S_1},$$

where a_{22} is the number of cows in year 1 observed via aerial survey, N_{11} and N_{12} are the initial calf and cow cohort abundance in year 1, S_1 is the annual survival rate in year 1 (which we assumed to be constant for males and females but different between years), and 0.5 represents the sex-at-birth ratio to separate calves into cows and bulls after the first year of life [46].

In addition to aerial survey data, we used information from collared individuals with known fates to help estimate annual survival by comparing the observed number of mortalities each year to that expected under the model parameterization as follows:

$$\Lambda_{Telemetry} = \sum_{i=1}^{Y} \frac{(v_i - n_i(1 - S_i))^2}{n_i(1 - S_i)},$$

where S_i is again the annual survival rate in year i, n_i is the number of collared animals alive at the beginning of year i, and v_i is the number of collared adult moose that died in year i.

We then used a spectral projected gradient method using the "spg" function in the BB package in Program R [47] to numerically solve for the minimum chi-square estimate. This allowed us to directly estimate yearly survival (i.e., S_i), initial cohort abundances in year 1 (i.e., N_{11},N_{12},N_{13}), and recruitment in subsequent years (i.e., N_{21},N_{31},...,N_{Y1}). All other female and male adult abundances were estimated based on the invariance property:

$$N_{i2} = (N_{i-1,1} \times 0.5 + N_{i-1,2}) \times S_i,$$
$$N_{i3} = (N_{i-1,1} \times 0.5 + N_{i-1,3}) \times S_i.$$

We calculated standard errors (SEs) for the minimum chi-square estimates using a numerical estimate of the inverse Hessian [48–50] using the "numDeriv" package in Program R [51]. Because reconstruction models consistently underestimate uncertainty [52], we inflated all standard errors by the goodness-of-fit scale parameter suggested by previous research [53]:

$$\sqrt{\frac{\chi^2_{df}}{df}},$$

where the χ^2_{df} statistic is based on the observed aerial survey data (a_{ij}) and their expected values under the reconstruction (N_{ij}). The degrees of freedom (df) are equal to $A \times Y - K$, where K is the number of parameters estimated by the reconstruction. We then used these inflated standard errors to construct 90% confidence intervals for the model-derived estimates of yearly population abundance and recruitment for moose in Minnesota.

Sensitivity Analysis of Reconstruction Estimates

Given the rapid decline in animals seen during aerial surveys between 2009 and 2013 (64.8% in five years), we investigated the sensitivity of reconstructed population estimates during these years by incrementally increasing either adult survival or recruitment, while holding the other constant, until the population decline was reversed (i.e., population abundance in 2013 was within 10% of that in 2009).

Population Projection using Reconstruction Estimates

We projected our estimates of per-capita recruitment (number of calves that survived to 1 year per adult female alive during the previous year) and adult survival for an additional ten years using the "forecast" package in Program R [54]. We then used the reconstructed estimates of calf, cow, and bull cohort abundance in 2020 as a starting point from which to predict cohort abundance from 2021 to 2030 using a stochastic version of the projection matrix approach described above [55].

Results

Survival Estimates from Collared Moose

We did not detect a difference in overall survival in VNP by sex ($\chi^2_1 = 0.20$, $P = 0.70$). Adult annual survival estimates in years 2011 to 2017 for Voyageurs National Park ranged from 0.741 (95% CI 0.484–1.00) in 2015 to 0.929 (95% CI 0.803–1.00) in 2014, with a mean annual survival of 0.893 (95% CI 0.833–0.958; Table 3). In 2010 and 2013, no collared moose mortalities occurred in VNP, precluding an estimate of variation in survival in those years. We did not detect a difference in overall survival in Grand Portage by sex ($\chi^2_1 = 0.60$, $P = 0.40$). Grand Portage adult annual survival in years 2010 to 2019 ranged from 0.591 (95% CI 0.417–0.837) in 2013 to 0.931 (95% CI 0.843–1.00) in 2019, with a mean annual survival of 0.833 (95% CI 0.794–0.874; Table 3). In 2012, no collared moose mortalities occurred in Grand Portage Indian Reservation, precluding an estimate of variation in survival that year.

Population Reconstruction of Moose in Minnesota

Using statistical population reconstruction with available aerial survey and telemetry data, we estimated fluctuations in adult survival, ranging from a maximum of 0.902 (SE = 0.043) in 2005 to a minimum of 0.690 (SE = 0.061) in 2019. Per-capita recruitment (number of calves that survived to 1 year per adult female alive during the previous year) followed a similar cyclical pattern as survival, decreasing slightly from 0.386 (SE = 0.030) in 2005 to 0.303 (SE = 0.051) in 2019. Winter moose abundance estimates showed a slow decline from an estimated 8,304 (90% CI = 7,797–8,788) animals in 2005 to 7,841 (90% CI = 6,702–8,933) in 2009. This was followed by a sharp decline to 3,386 (90% CI = 2,681–4,243) animals in 2013, but remained steady afterward to an estimated 3,163 (90% CI = 2,403–3,718) in 2020. Annual recruitment followed a similar pattern and varied from a high of 1,683 (90% CI = 1,380–1,943) animals in 2005 to 502 (90% CI = 343–647) in 2020.

Sensitivity Analysis of Reconstruction Estimates

Abundance estimates during the rapid decline from 2009 to 2013 were more sensitive to changes in adult survival than recruitment. A 27.0% change in survival during the four years, while holding recruitment constant, resulted in a 2013 population abundance that was just 10% lower than that in 2009. To achieve a similar result while holding survival constant required an increase of 248.6% in recruitment during the four years.

Population Projection using Reconstruction Estimates

Stochastic projections using forecasted fecundity and survival estimates resulted in a slowly decreasing population from a high of 3,244 (90% CI = 2,936–3,461) in 2021 to a low of 2,680 (90% CI = 1,298–4,550) in 2030, and a corresponding annual growth rate of 0.984 (90% CI = 0.940–1.020).

Discussion

Statistical population reconstruction was consistent with a substantial decline in the northeastern Minnesota moose population between 2009 and 2013, as was indicated by the original aerial surveys conducted throughout the region. Reconstruction estimates indicated that during this time, the number of moose in primary moose range in MN decreased substantially from about 7,800 animals in 2009 to about 3,400 in 2013, corresponding to a >50% decline over just four years. Since 2013, however, the population largely stabilized and displayed an oscillatory pattern with a slight overall decrease of approximately 6.6% over the next seven years to an estimated 3,163 (90% CI = 2,403–3,718) animals in 2020. Stochastic projections using forecasted demographic rates indicated that this trend is likely to continue for the next ten years to an estimated 2,680 (90% CI = 1,298–4,550) animals in 2030. This estimate closely matches simulated populations under a constant harvest of 150 bulls each year, but is less than populations under low harvest (40–80 bulls/yr; ~4,000 moose)[56].

Our results demonstrate the utility of using statistical population reconstruction to monitor moose population trends throughout northeastern Minnesota and other parts of their North American range. When compared to estimates derived from aerial surveys, reconstruction estimates produced substantially narrower confidence intervals around similarly sized abundance estimates. For example, both aerial surveys and population reconstruction estimated similar abundances of 8,161 and 8,304 animals in 2005, respectively. However, the confidence interval around this reconstructed point estimate was approximately 20% of the confidence intervals around the aerial survey point estimate, a five-fold increase in precision. Although the increase in precision gained from reconstruction was substantially lower during many of the other years, reconstruction nonetheless provided a consistent improvement in precision when compared to estimates derived from aerial surveys (Fig. 2). Weather conditions at the time of aerial surveys can contribute added variability affecting sightability and consequently point estimates. Using statistical population reconstruction also eliminated the biologically unrealistic fluctuations in population abundance observed in the original aerial survey estimates. For example, aerial survey estimates indicated that moose abundance rebounded from 2,760 (2,160–3,650) animals in 2013 to 4,350 (3,220–6,210) in 2014, representing an increase of 57.1% in just one year. Given moose reproductive patterns, such a steep increase over such a short period of time is biologically impossible [46,57]. Reconstruction estimates during the same time period, on the other hand, indicate an increase of only 13.4%, from 3,386 (90% CI = 2,681–4,243) to 3,840 (90% CI = 3,146–4,650), which is a reasonable increase given reported moose reproduction estimates [46,57]. Conversely, the minimum modeled adult survival rate of 0.69 in 2019 may warrant caution because such a low estimate is not biologically consistent with observed population trends and calf:cow ratios [56].

An additional benefit of using statistical population reconstruction to monitor moose throughout the northeastern region is that it can retroactively provide abundance estimates during years when aerial surveys are not conducted. The COVID-19 pandemic prevented the statewide aerial survey for moose in 2021. After aerial survey and telemetry data are collected in subsequent years, statistical population reconstruction can be used to impute the missing number of calves, cows, and bulls in 2021. Similarly, estimates of annual survival derived from telemetry studies often include years where no animals were monitored. In the present study, to our knowledge there were no published telemetry data collected in 2008 and 2009, precluding a direct estimate of survival during those years. However, with the use of statistical population reconstruction, we were able to estimate survival during those years.

Annual survival of moose in Minnesota appears to follow a pattern of years of high survival followed by years of low survival (Fig. 3). However, there was a consistent period of low survival between 2009 and 2013, corresponding to the observed and subsequently confirmed population decline of moose during this time [24]. Combined with the results of the sensitivity analysis, which indicated that population growth is more sensitive to fluctuations in adult survival than in per capita recruitment, these results suggest that the observed decline in population abundance was most likely caused by lower adult survival from 2009 to 2013. The two lowest collared moose survival rates measured on the Grand Portage Indian Reservation also occurred during this time period. Additionally, opportunistically collected free-ranging moose that were necropsied showed health and disease issues were common during this same period

[38]. Subsequent research on cause-specific mortality of adult moose in northeastern Minnesota further highlighted the significant effect of disease and parasites, such as winter tick and meningeal worm, on adult moose survival [24,26,38].

One overall caution is that incorporating auxiliary data from telemetry studies is based on the assumption that the parameters they help estimate are the same for both collared and uncollared animals, i.e., that the collared animals are representative of the population of interest [6]. A significant amount of effort has been put into understanding and minimizing the effects of immobilizing, handling, and collaring on animal behavior and survival [58–60]. Moose collared in the MNDNR study did represent the free-ranging moose population in terms of correlated relationships between incidence of severe nutritional restriction and survival rates [61], but there may be bias toward capturing and collaring moose that do not flee from pursuit by a helicopter. Another caution arises from using adult survival estimates from 4 different sources, two that originated from study sites within the aerial survey area and 2 from adjacent study areas. The Grand Portage moose are within primary moose range whereas VNP moose occur just west. Offsetting this, the larger sample sizes of collared moose from within the aerial survey area contribute more observations for estimating adult survival and therefore more weight in the overall model.

We believe our general approach was useful for an initial assessment of moose population dynamics of northeastern Minnesota based on the integration of several different sources of information (i.e., aerial surveys and four separate telemetry studies). Future research should build upon this foundation to explore how the incorporation of other supporting data can improve reconstruction estimates and help to estimate additional model parameters not considered here. Data on annual pregnancy rates, calf survival, and twinning rates, for example, could be used to separate the effects of reproductive success from calf mortality, thereby allowing us to better identify the driving forces behind observed trends in annual recruitment. Additional finer-scale studies, such as those ongoing at Grand Portage (S. A. Moore, unpublished data), that incorporate predator density, experimental manipulations of predator density, and effects of alternate (non-moose) prey of predators will be useful in teasing apart factors driving recruitment and mortality.

Conclusion

Statistical population reconstructions confirmed that moose abundance in northeastern Minnesota declined rapidly from 2009 to 2013, but has remained relatively stable during 2013–2020. Our results suggest that this decline was due primarily to low adult survival during those years. Our approach increased precision of population estimates gained from the state's annual aerial survey, and can further be used to impute missing values when surveys cannot be conducted, such as occurred in 2021 due to the COVID-19 pandemic. Continued monitoring of vital rates of collared moose through the use of telemetry, such as that continuing to be undertaken by Grand Portage Band of Lake Superior Chippewa on Grand Portage Indian Reservation and in ceded territory in Superior National Forest, will aid in refining future estimates of population trends and projections and contribute to more precise knowledge of the population across time. As of publication, a moratorium on state-permitted collaring of moose is still in effect; this order does not restrict tribal activities (Executive Order 15-10, 28 Apr 2015). Without additional data streams to inform the aerial survey estimates, projections are less useful to managers of moose populations, especially when explicit mechanisms driving the trends are unknown.

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TABLES

Table 1. Age-class-specific aerial survey data with corresponding yearly totals and 90% confidence intervals for moose in northeastern Minnesota, USA, 2005-2020 [9]. Total abundance is corrected for sightability, abundance of calves, cows, and bulls is derived from reported calf:cow and bull:cow ratios.

Year	Calf	Cow	Bull	Total
2005	1,658	3,188	3,315	8,160 (6,090–11,410)
2006	1,237	3,638	3,965	8,840 (6,790–11,910)
2007	913	3,147	2,801	6,860 (5,320–9,100)
2008	1,334	3,704	2,852	7,890 (6,080–10,600)
2009	1,110	3,469	3,261	7,840 (6,260–10,040)
2010	756	2,701	2,242	5,700 (4,540–7,350)
2011	626	2,606	1,668	4,900 (3,870–6,380)
2012	624	1,734	1,872	4,230 (3,250–5,710)
2013	356	1,078	1,326	2,760 (2,160–3,650)
2014	714	1,623	2,013	4,350 (3,220–6,210)
2015	439	1,513	1,498	3,450 (2,610–4,770)
2016	689	1,641	1,690	4,020 (3,230–5,180)
2017	588	1,634	1,487	3,710 (3,010–4,710)
2018	428	1,157	1,446	3,030 (2,320–4,140)
2019	539	1,633	2,008	4,180 (3,250–5,580)
2020	502	1,394	1,254	3,150 (2,400–4,320)

Table 2. Telemetry data from four different studies of yearly mortality (v) and associated at-risk counts (n) for yearling and adult moose in northeastern Minnesota, USA, 2005–2019.

	Lenarz et al. 2009		**Carstensen et al. 2018**		**Voyageurs National Park**		**Grand Portage Indian Reservation**	
Year	v	n	v	n	v	n	v	n
2005	13	51						
2006	10	32						
2007	10	57						
2008								
2009								
2010					0	11	2	10
2011					2	19	5	15
2012					3	19	0	12
2013			20	105	0	14	9	22
2014			12	101	1	14	4	28
2015			14	93	2	11	8	38
2016			8	57	1	5	3	36
2017					1	4	4	31
2018							4	28
2019							2	29

Table 3. Estimates of annual survival and sex ratios of collared adult moose in Voyageurs National Park and Grand Portage Indian Reservation, MN, USA, 2010–2021.

	Voyageurs National Park			Grand Portage Indian Reservation		
Year	**Survival**	**95% CI**	**F:M**	**Survival**	**95% CI**	**F:M**
2010	1.000		9:2	0.800	0.587–1.00	7:3
2011	0.895	0.767–1.000	13:6	0.667	0.466–0.953	12:3
2012	0.842	0.693–1.000	12:7	1.000		12:0
2013	1.000		10:4	0.591	0.417–0.837	20:3
2014	0.929	0.803–1.000	10:4	0.851	0.727–0.997	27:1
2015	0.741	0.484–1.000	9:2	0.781	0.658–0.928	35:3
2016	0.800	0.516–1.000	5:0	0.915	0.828–1.00	32:6
2017	0.750	0.426–1.000	4:0	0.866	0.752–0.998	27:8
2018				0.851	0.726–0.998	23:8
2019				0.931	0.843–1.00	20:9
2020				0.778	0.659–0.918	34:10
2021				0.887	0.806–0.977	40:18
Overall	**0.893**	**0.833–0.958**	**72:25**	**0.833**	**0.794–0.874**	**289:72**

FIGURES CAPTIONS

Figure 1. Primary moose range in Minnesota (red outline) that is surveyed annually by cooperators MNDNR, Fond du Lac Band of Lake Superior Chippewa, and 1854 Treaty Authority; and 4 study areas that contained collared moose: Voyageurs National Park (A), Grand Portage Indian Reservation (B), MNDNR study (2012–2016; C), and MNDNR-FDL-1854 Treaty Authority study (2005–2008; D).

Figure 2. Estimated trends in abundance (top) and calf recruitment (bottom) into the winter population of moose in Minnesota (thick solid lines) between 2005 and 2020 based on statistical population reconstruction using integrated population models (IPMs), along with associated 90% confidence intervals (shaded regions).

Figure 3. Estimated trends in annual survival (top) and per-capita recruitment (number of calves that survived to 1 year per adult female alive during the previous year) for moose in Minnesota (thick solid lines) between 2005 and 2019 based on statistical population reconstruction using integrated population models (IPMs), along with associated standard errors (error bars).

Figure 4. Stochastic population projection of moose in Minnesota from 2020 to 2030 using forecasted estimates of annual survival and per-capita recruitment (number of calves that survived to 1 year per adult female alive during the previous year). Shaded regions represent 90% confidence intervals from 1,000 individual simulations.

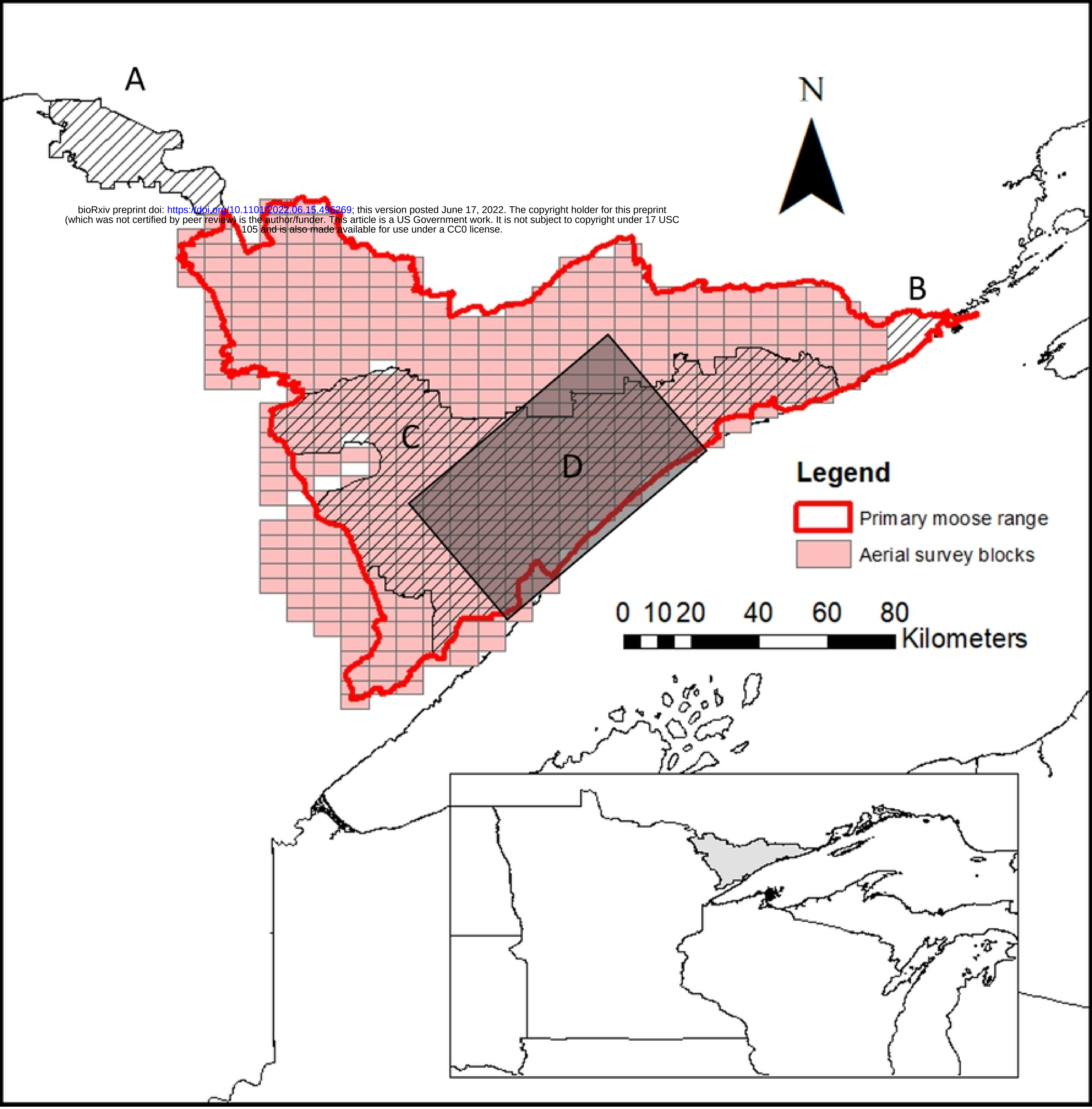
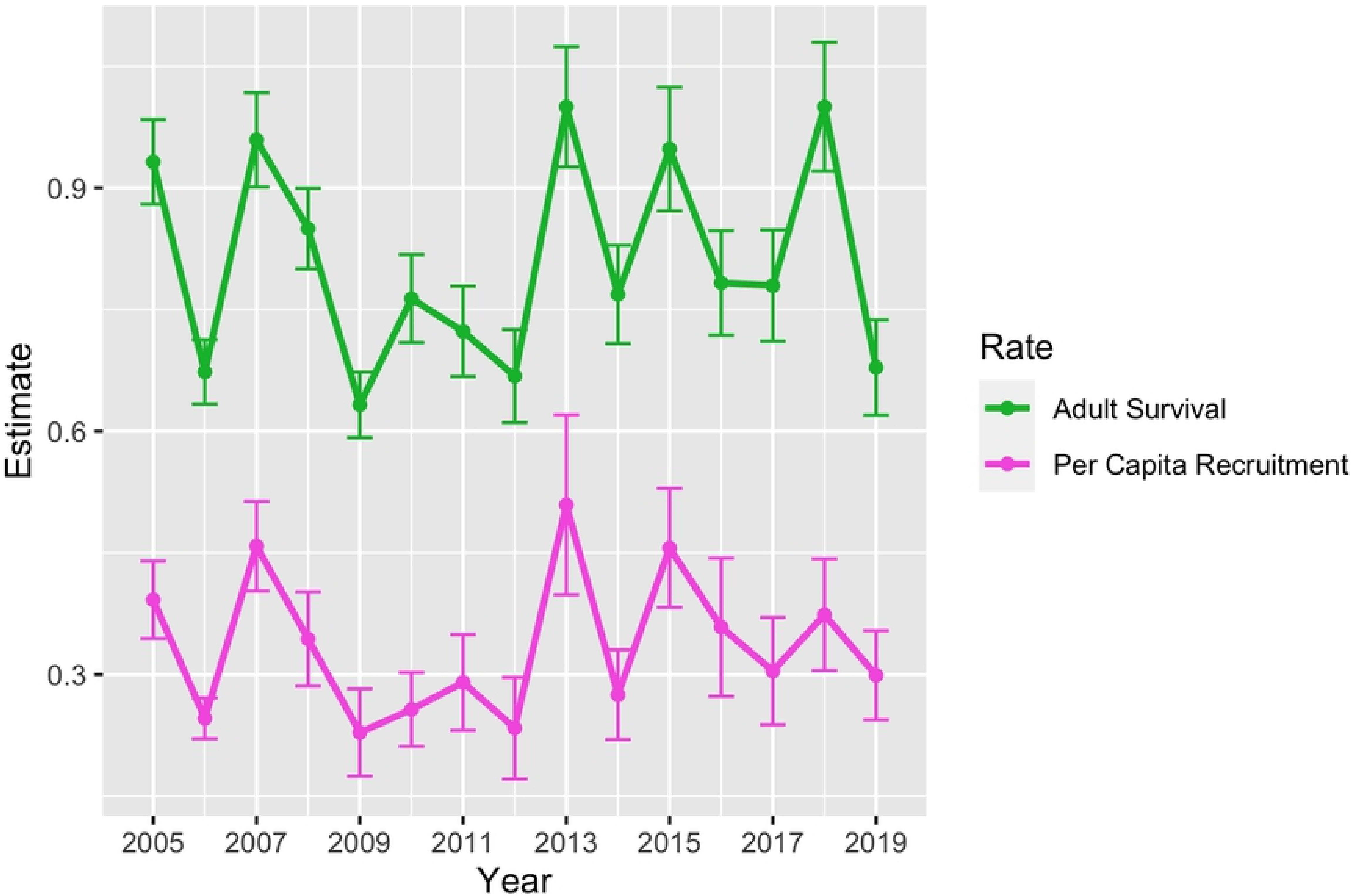

A
N
B
C
D
Legend
Primary moose range
Aerial survey blocks
0 10 20 40 60 80
Kilometers

Figure 1


Abundance
10000
7500
5000
2500
2005
2008
2011
2014
2017
2020
Estimate
Recruitment
2000
1500
1000
500
2005
2008
2011
2014
2017
2020
Year
Method
Aerial Survey
Reconstruction

Figure 2



Estimate
0.9
0.6
0.3
2005
2007
2009
2011
2013
2015
2017
2019
Year
Rate
Adult Survival
Per Capita Recruitment

Figure 3

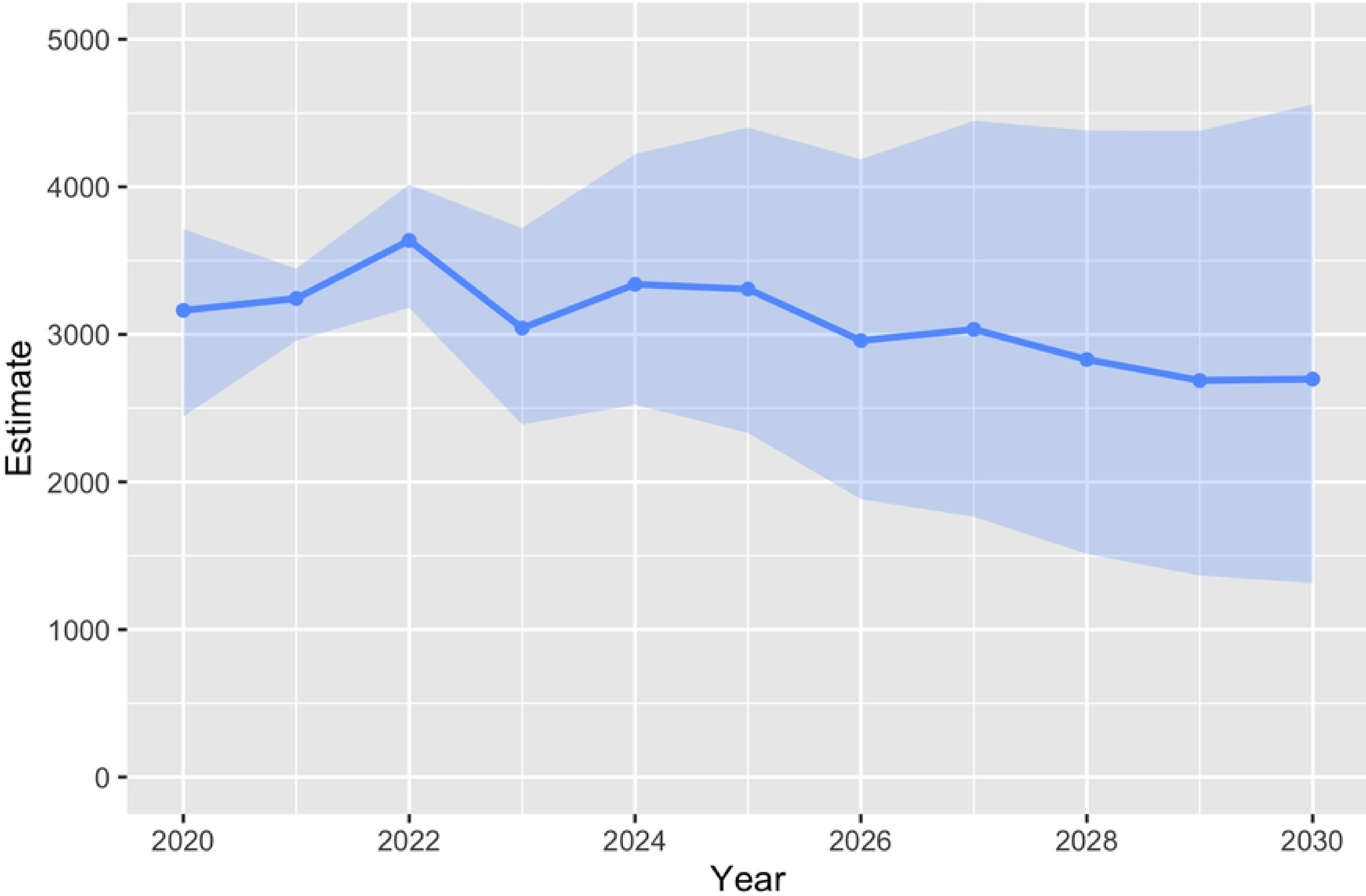

5000
4000
3000
2000
1000
0
Estimate
2020
2022
2024
2026
2028
2030
Year

Figure 4