A REVIEW OF METHODS TO ESTIMATE AND MONITOR MOOSE DENSITY AND ABUNDANCE

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ABSTRACT: Acquiring accurate and precise population parameters is fundamental to the ecological understanding and management and conservation of moose (*Alces alces*). Moose density is challenging to measure and often estimated using winter aerial surveys; however, numerous alternative approaches exist including harvest analysis, public observation, unpiloted aerial system (UAS) surveys, and camera trapping. Given recent developments in a number of field and analytical techniques, there is value in reviewing and synthesizing the strengths and limitations of monitoring methods to best evaluate their respective tradeoffs in management scenarios. We reviewed 89 studies that included 131 estimates or indices of moose density. As expected, aerial surveys were the most common method of obtaining a moose density estimate (58%) followed by use of public data (e.g., harvest records = 27%); more recent studies employed novel methods including UAS. Most estimates (64%) failed to account for imperfect detection of moose (i.e., "sightability") and this tendency has not improved over time. Density estimates ranged from <0.1 to 10.6 moose/km^2 (average = 0.7) and population precision, as measured by the 90% confidence interval, ranged from 6.5 to 120.0% of the density estimate (average = 37.4%). Correlations among estimates obtained for the same populations varied widely, with R^2 values ranging from 0.02 to 0.99 (average = 0.58). Our review indicates that: 1) methods to estimate moose density have been dominated by aerial surveys but are diversifying, 2) precision of density estimates has been highly variable and on average lower than broadly accepted target benchmarks, and 3) many methods did not account for sightability and presumably underestimated moose density. We reflect on these trends and discuss how emerging methods, including camera trapping, UAS surveys, and integrated population modeling (IPM) can complement and improve traditional approaches. We suggest that no single "best" method exists, but rather the best method is one that accounts for sightability bias and yields target precision at reasonable cost, which vary by jurisdiction and goal.

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INTRODUCTION

Obtaining accurate and precise estimates of population parameters is fundamental to the ecological understanding, effective management, and conservation of wildlife (Skalski et al. 2005, Sinclair et al. 2006, Silvy 2012). Such parameters are particularly important for moose (*Alces alces*) because this species is often managed for harvest (Jensen et al. 2020), has both negative and positive economic impact (e.g., vehicle collisions and ecotourism, respectively; Storaas et al. 2001, Silverberg et al. 2003, Sample et al. 2020), and is hypothesized to be susceptible to global climate change (Murray et al. 2006, Jensen et al. 2020). The population parameters required to manage and conserve moose vary by location and context, but typically include density, survival, recruitment, and composition (Gasaway et al. 1986, Krausman 2002, Van Ballenberghe and Ballard 2007). Estimates of density (hereafter, the term *density* includes the related term *abundance*) and proxies thereof are arguably the most fundamental because management is frequently focused on maintaining moose populations at specific densities over time (Leopold 1933, Franzmann and Schwartz 2007).

The estimated global moose population is ~2.2 million, with roughly half in Eurasia and half in North America (Timmermann and Rodgers 2017, Jensen et al. 2020). Recent reviews have highlighted variation in population dynamics across management jurisdictions, with some populations declining and others increasing or stable (Timmermann and Rodgers 2017, Jensen et al. 2020). Population dynamics are complex and geographically varied, but broadly reflect habitat composition, forest management, abiotic environmental conditions, hunter harvest, predation pressure, and parasites (Boutin 1992, Messier 1994, Rempel et al. 1997, Solberg et al. 1999, Musante et al. 2010, Jones et al. 2017, Pekins 2020). Climate change has an underlying influence on these factors as well as moose behavior and susceptibility to parasites and disease (Joly et al. 2012, Tape et al. 2016, Montgomery et al. 2019, Pekins 2020), underscoring the need for techniques that accurately monitor moose populations over time (van Ballenberghe and Ballard 2007, Jensen et al. 2020).

Moose density is challenging to estimate and monitor for logistical, financial, and ecological reasons. Moose are highly mobile and inhabit large ranges that make monitoring difficult by enlarging the scale required for adequate sampling (Krebs 2006, Singh and Milner-Gulland 2011, Harris et al. 2015) and rendering survey efforts expensive (Bontaites et al. 2000, Peters et al. 2014, Boyce and Corrigan 2017). Behavior frequently reduces detection or "sightability" because moose use dense forest cover, avoid human disturbance (including activities associated with surveying populations), and are mostly crepuscular or nocturnal when active (Frid and Dill 2002, Harris et al. 2015). Further, there are practical difficulties associated with surveying populations in remote regions with high topographic relief (van Ballenberghe and Ballard 2007, Kellie et al. 2019). Thus, monitoring moose populations is an "evolving art" (Krebs 2006, p. 367) that is shaped by the advent and implementation of emerging technologies and methods (Boyce and Corrigan 2017, Oyster et al. 2018, McMahon et al. 2021).

Winter aerial surveys are a common method used to estimate and monitor moose density, and often conducted by helicopter with observers counting moose on snow (Gasaway et al. 1985, 1986, van Ballenberghe and Ballard 2007, Timmermann and Rodgers 2017). Many jurisdictions have employed surveys for decades as the backbone of monitoring efforts (e.g., Alaska, USA, and Alberta, Canada, Alberta Environment and Parks 2016, Kellie et al. 2019). Traditionally conducted with a simple single or double-observer method, surveys have evolved to include a distance sampling approach (Gasaway et al. 1986, Alberta Environment and Parks 2016, Oyster et al. 2018). Challenges associated with moose monitoring include high cost, accounting for sightability bias, and danger to aviators and observers (Sasse 2003, Peters et al. 2014, Oyster et al. 2018).

Alternatively, where sufficient harvest occurs, moose populations have been monitored using harvest data analysis (Solberg et al. 1999, Skalski et al. 2005, DeCesare et al. 2016). Hunter observations have also been used as a cost-efficient index for moose density, although such observations require calibration with other data to achieve reliability (Bontaites et al. 2000, Boyce and

Corrigan 2017). Less common approaches include snow tracking, pellet surveys, camera trapping, and aerial surveys using unpiloted aerial systems (UAS) (Bobek et al. 2005, Krester et al. 2016, Pfeffer et al. 2018, McMahon et al. 2021).

The challenges and importance of obtaining accurate moose density estimates are clear and best management requires continuous assessment and adaptation to evolving methodology. Thus, it is valuable to review and synthesize current methods and evaluate their associated strengths and limitations to identify and navigate their trade-offs. Here, we review methods used to estimate and monitor moose density with an emphasis on studies that directly analyzed a method of monitoring moose to derive a density estimate or index. We summarize the results of our literature survey, the limitations of each method, and discuss future direction in monitoring and estimating moose density.

METHODS

We performed a literature survey to review methods for estimating and monitoring moose density with an emphasis on studies with management application. In May 2022 we used the Web of Science to search all collections using the following Boolean string of terms: **TITLE:** ("*Alces alces*" OR moose) *AND* **TOPIC:** (abundance OR density) *AND* **TOPIC:** (management); the search yielded 453 studies. We eliminated irrelevant studies including those focused on other species, purely mathematical or simulation-based studies, and reviews. We only retained studies that were primary sources and omitted those using density estimates from other sources. We retained studies that used densities to test ecological hypotheses, but only if they met the other criteria and included sufficient details regarding study design and density estimation methods. We included the term "management" in the search to emphasize studies relevant to practitioners and to help eliminate irrelevant studies (e.g., those that used moose density estimates from other sources).

For each relevant study, we recoded information according to the framework described below (Fig. 1). We recorded the study location, the spatial scale at which inference was desired (km^2; typically, the study area), and the method(s) employed to estimate or monitor the target population density. We then classified each method as follows.

We first identified the goal type (n = 3) of the method according to Timmermann and Buss (2007): 1) a census, where an attempt was made to count all animals within an area, 2) a sample, where inference regarding density was achieved through sampling and statistical analysis, or 3) an index, where a relative measure representing density was desired. Next, we classified the primary method as either aerial, ground-based, or based on public observations. Aerial methods included fixed-wing aircraft, helicopters, and unpiloted aerial systems (UAS, or "drones"); ground methods included pellet counts, snow track surveys, and camera trapping; public methods included the use of harvest data and public observations (e.g., hunter or citizen science observations). For all methods, we recorded whether the survey design was systematic, random, stratified random, or non-random (e.g., a survey targeting a specific management area). For aerial methods we also recorded whether the sampling scheme was conducted using block searches (an area-based design where "blocks" might also be called "quadrats", "plots", or "sample units") or strip-transects (a line-based design). For public observations, we recorded whether data reporting was mandatory (typical for harvest data) or voluntary.

We recorded the timing (i.e., seasons) of each method, the duration of data collection

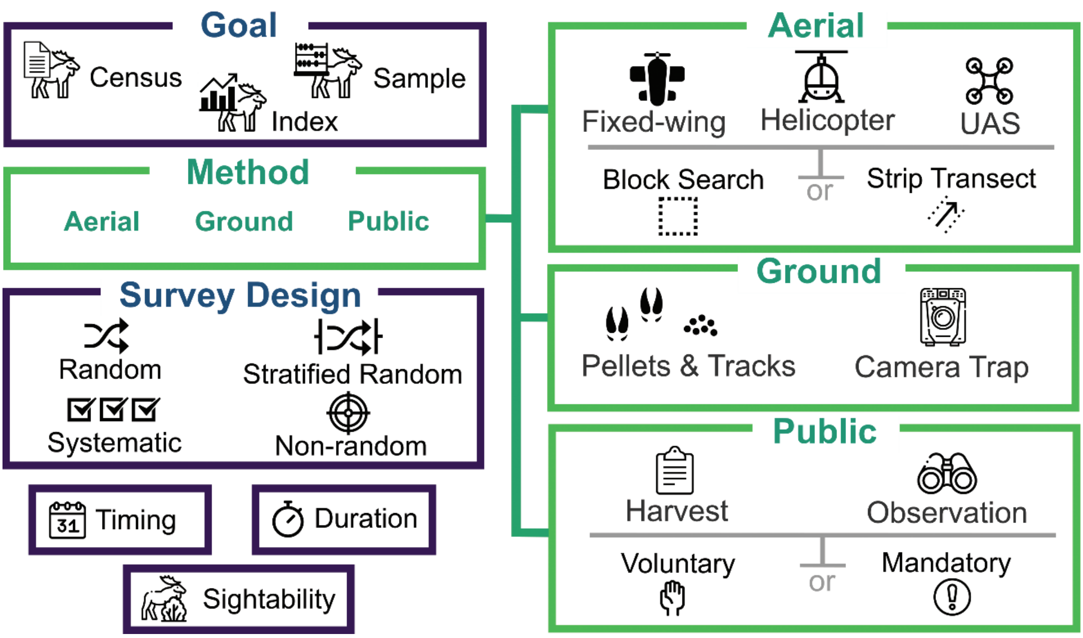

Fig. 1. The framework used to organize and summarize methods used to estimate and monitor moose (*Alces alces*) density and abundance. See text for detailed descriptions of categories. UAS = unpiloted aerial system.

(in years), and whether each method accounted for the imperfect detection of individuals (i.e., an individual is present but not detected; MacKenzie et al. 2002), often referred to as *sightability* (Gasaway et al. 1986). We note that the duration of data collection might not always reflect the duration of monitoring programs, but rather is indicative of the dataset's use for a particular analysis. Thus, this value represents the duration of data collection used to inform the scientific literature rather than the true duration of moose monitoring efforts. Seasons were set as fall (September through November), winter (December through April), and spring-summer (May through August). We also recorded whether the method distinguished the age or sex of individual moose. For aerial and ground surveys, we considered a study to have accounted for sightability if it formally accounted for undetected individuals, including the use of double-observation methods, mark-resight methods, distance sampling methods, or previously calculated sightability correction factors. For public observations, we considered a study to have accounted for sightability if it formally corrected for imperfect reporting (e.g., a moose was observed but not reported) or undocumented harvest. We then used a logistic regression to evaluate whether there was a temporal trend in accounting for sightability, where a binary response of accounting for sightability was modeled as a function of the publication year; $p < 0.05$ was the threshold for inference.

When reported, we recorded the mean population estimate and converted it to moose density (individuals per km^2). We acknowledge the substantial variation in moose densities across their circumpolar range. We report the densities of the studies in our review to quantify this variation broadly and provide to context for the various monitoring methods, which might be informed by local moose densities (e.g., tailoring survey methods for a low-density population; Hinton et al. 2022).

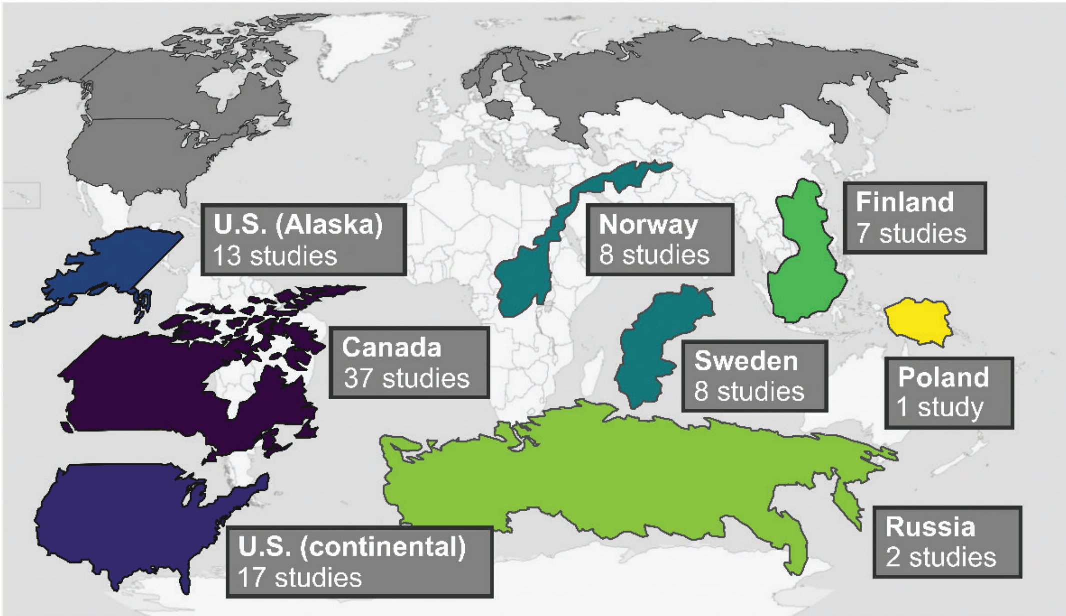

Fig. 2. Geographic distribution of studies included in a literature survey of methods used to estimate and monitor moose (*Alces alces*) density and abundance conducted in May 2022. Note that the sum of studies here exceeds the total number of studies reviewed because several studies were conducted in more than one country.

We recorded the precision of that estimate following Gasaway et al. (1986), according to the equation:

$$\frac{u - \hat{p}}{\hat{p}} \tag{1}$$

where u is the upper value of the 90% confidence interval and $\hat{p}$ is the estimated population value (density or abundance). This precision metric is widely recognized and cited as a target benchmark for management decisions (e.g., Timmermann 1993, Bontaites et al. 2000, Peters et al. 2014). For studies that reported multiple density estimates and precisions (e.g., across management units or years), we recorded the average density and precision across all estimates. In cases where only the standard error was reported for precision, we converted this error into a confidence interval by multiplying it by 1.645 (the Z-value for a 90% confidence interval). Lastly, we recorded whether a study formally compared one population estimate to an estimate produced via another method, and if so, the Pearson's correlation coefficient (r) or R^2 value of each such comparison.

RESULTS

A total of 89 (20%) of 453 studies returned by the literature search met the criteria for review (see Appendix 1), with most (74%) conducted in North America and the remainder in Fennoscandia and Eurasia (Fig. 2). Of these, 65 provided details regarding the spatial scale of desired inference that ranged from as small as 6.0 km^2 to >13.6 million km^2 (see Appendix 1); the average and median values were 278,000 km^2 and 3,456 km^2, respectively, indicating that the distribution of these scales was non-normal and heavily right-skewed.

The 89 studies contained 131 estimates or indices used to monitor moose density. However, the proportional statistics below omit certain studies lacking sufficient detail to adequately characterize the methodology (i.e., NAs in a given category were dropped; see Appendix 1). Across all methods, the most common goal type (n = 79, 61%) was a sample or statistical representative of the broader population density; less common were the index (n = 29, 22%) and census (n = 22, 17%) goal types. A single method employed a cohort analysis that combined multiple data types (see Appendix 1).

Of the three primary methods, aerial surveys were most common (n = 76, 58%), followed by public reporting (n = 35, 27%) and ground surveys (n = 19, 15%) (Fig. 3). Helicopters (n = 35, 46%) and fixed-wing aircraft (n = 26, 34%) were the most common flight modes, in which block (n = 56, 76%) and strip-transect surveys (n = 17, 23%) were used exclusively, other than a single exception, being their combination. Harvest (n = 20, 57%) and public observation (n = 14, 40%) were the most common public reporting methods with mandatory (n = 19, 56%) and voluntary (n = 15, 44%) reporting used in both. Pellet counts (n = 10, 53%) and direct observation (n = 6, 32%) were the most common ground survey methods; snow tracking methods (n = 2, 11%) were used less frequently (Fig. 3).

The most common survey design was non-random (n = 60, 49%), followed by stratified random (n = 37, 30%), systematic (n = 19, 15%), and random (n = 7, 6%). Most (67%) non-random survey designs were associated with public observations, while all stratified random survey designs, except one, were associated with aerial methods (Table 1; Appendix 1). Approximately one-third of all methods formally accounted for sightability (n = 45, 36%). The application of a sightability correction for density estimates in studies did not change linearly over time ($\beta = 0.004$, df = 122, $p = 0.77$; Fig. 4).

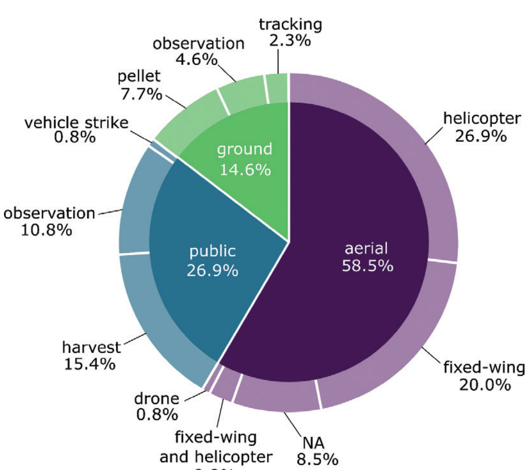

Fig. 3. Primary and secondary methods used to estimate and monitor moose (*Alces alces*) density and abundance according to a literature survey conducted in May 2022. Primary methods are represented in the central circle; associated secondary methods are represented in the outer circle. One method employed a cohort analysis that combined multiple methods, and thus was not included in this figure.

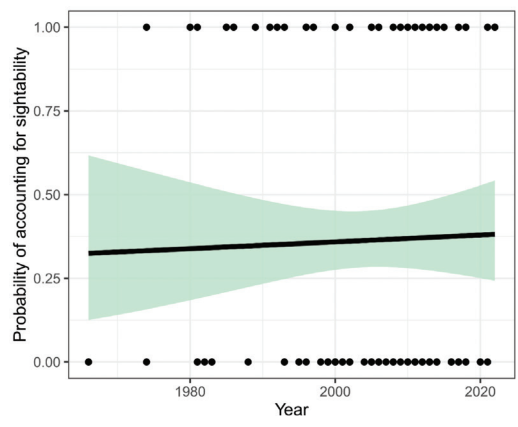

Fig. 4. Model predictions of the probability that a study estimating or monitoring moose (*Alces alces*) densities accounted for sightability, or the imperfect detection of individual moose, as a function of the year the study was published. The slope of the model is not significantly different from zero ($p = 0.83$). Model was fit to data collected from studies returned from a literature survey of methods used to estimate and monitor moose (*Alces alces*) density and abundance conducted in May 2022.

Table 1. A summary of the number of methods used to estimate and monitor moose (*Alces alces*) density and abundance according to a literature survey conducted in May 2022.

		Aerial			Ground		Public	
		Fixed-wing	Helicopter	UAS	Pellets	Tracks	Harvest	Obs.
Goal	Census	8	9	0	0	1	0	2
	Index	2	0	0	3	0	8	14
	Sample	16	26	1	7	0	12	4
Survey design	Non-random	6	7	0	4	1	18	18
	Random	3	1	0	1	0	1	0
	Strat. Rand.	12	16	0	0	0	1	0
	Systematic	3	9	1	4	0	0	1
Timing	Fall	2	0	0	0	0	15	12
	Spr-Su	1	0	1	6	0	0	0
	Winter	17	32	0	2	1	1	1
	Other	5	1	0	1	0	0	6
Sight-ability	Yes	13	20	1	2	0	2	1
	No	12	14	0	8	1	16	19

UAS = unpiloted aerial system, Obs. = observation, Stat. Rand. = stratified random.

Helicopter surveys were the only method that accounted for sightability most (59%) of the time (Table 1). Fifty-four studies reported 68 mean population densities ranging from <0.1 to 10.6 moose/km^2 (average = 0.7; Fig. 5A). The precision of 30 estimates reported or determinable in 24 different studies ranged from 0.07 to 1.20 moose/km^2 (average = 0.37; Fig. 5B); half of these estimates were larger than the 0.25 target benchmark suggested by Gasaway et al. (1986).

Of the 131 estimates, 87% (n = 114) were conducted during a specific season, most in winter (n = 63, 55%) and fall (n = 31, 27%); spring-summer estimates were uncommon (n = 8), as were year-round estimates (n = 5). Aerial estimates more frequently occurred in winter (80% of the time), while public estimates typically occurred in fall (77% of the time; Table 1). Eighty-one estimates (62%) distinguished age (calf vs. adult) and/or sex of moose; however, those studies distinguishing sex did not necessarily distinguish age or vice versa (see Appendix 1).

Study duration ranged from 1 to 73 years. Twenty-four methods (18%) employed a single year of study, typically a single season; 38 methods (29%) were employed for two to five years, 17 (13%) for 6–10 years, 15 (11%) for 11–20 years, and 15 for >20 years. Twenty-two studies did not report duration or varied so greatly in duration and/or spatial coverage (due to funding limitations or other barriers) that they were omitted from the summary (see Appendix 1).

Seventeen studies provided Pearson's correlation coefficient (r) or R^2 values to compare methods. The most frequent comparisons included moose observations by hunters, hunter success rate, density estimates from aerial surveys, and harvest data analysis (see Appendix 2). The R^2 values from these comparisons ranged from 0.02 to 0.99 (average = 0.58). Sample size for these values ranged from 6 to 111 (average = 22).

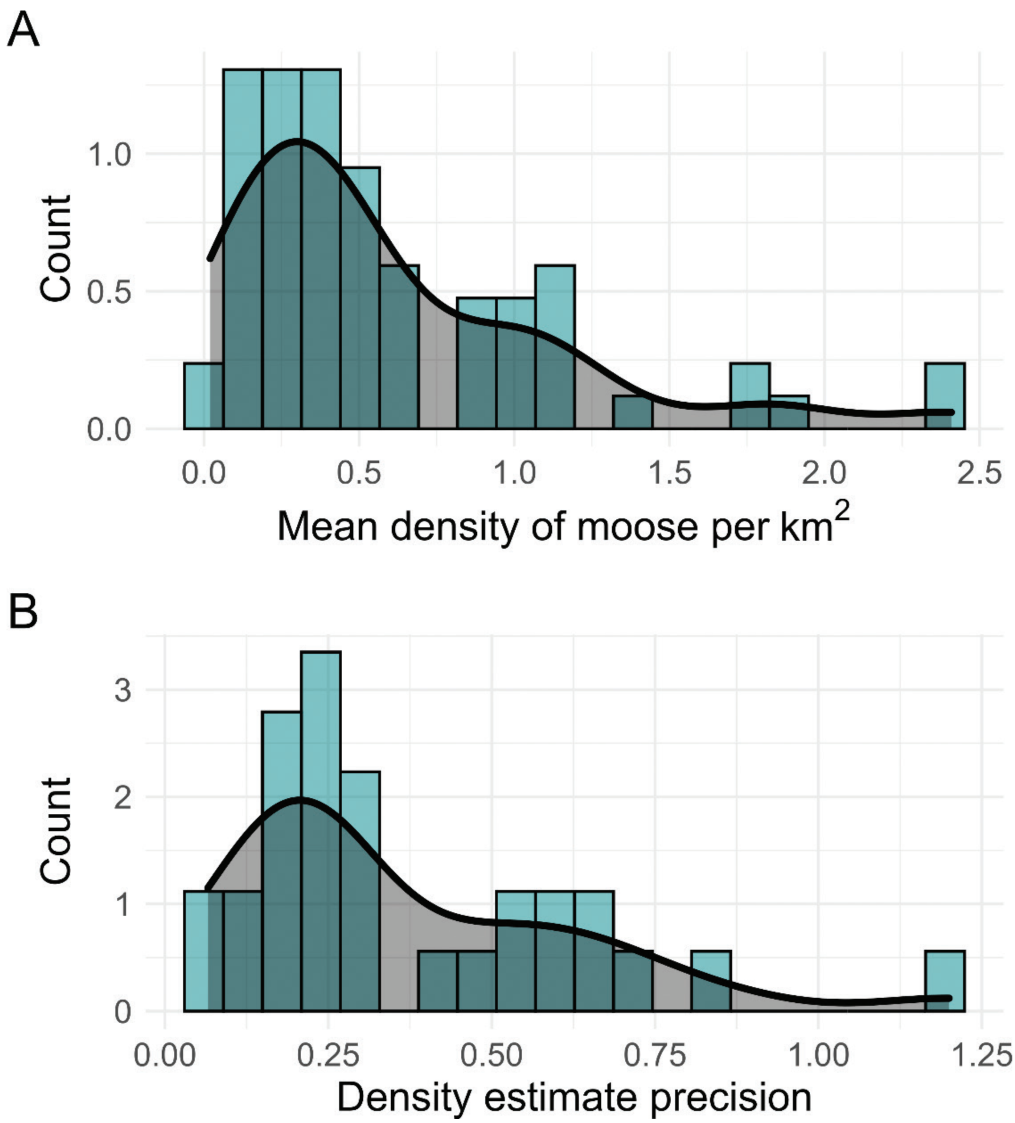

Fig. 5. The mean density of moose/km^2 (Panel A) and the density estimate precision (Panel B) according to a literature survey of methods used to estimate and monitor moose (*Alces alces*) density and abundance conducted in May 2022. For clarity, one outlier density estimate of 10.6 moose/km^2 from a local-scale study was omitted in Panel A (see Appendix 1).

The lowest R^2 values were associated with comparisons between hunter harvest per unit effort and minimum population counts from aerial surveys, and between change-in-ratio abundance estimates and rates of moose-train collisions (Appendix 2). A comparison between hunter harvest per unit effort and an aerial density estimate yielded the highest correlation using a non-linear model fit with small sample size (n = 6; Appendix 2). The complete references for reviewed studies are provided in Appendix 1 available on the *ALCES* website https://alcesjournal.org/index.php/alces.

DISCUSSION

As expected, this literature survey revealed a historical reliance on aerial methods to estimate moose density. Many authors noted limitations to conducting an ideal aerial survey, especially financial and logistical costs and weather (e.g., Peek 1974, Nygrén and Pesonen 1993, Bowyer et al. 1999, Harris et al. 2015, Kellie et al. 2019). Although sightability bias was acknowledged frequently as an issue, almost two-thirds of density estimates across studies did not account for it (Fig. 4). We also found high variation in the precision of density estimates, with only half achieving the benchmark management target of Gasaway et al. (1986). Landscape, habitat, and social factors all appeared to play a role in method choice. For example, aerial surveys were particularly common in Alaska, USA, where habitat is more open and individuals tend to cluster across the landscape, whereas harvest and hunter-based approaches were common in Scandinavia where harvest is high and reporting is strong (Appendix 1). Finally, several recent studies highlighted new technologies and modern analytical developments that hold promise for moose population monitoring, although key questions and challenges remain regarding their reliability and overall efficacy (Table 2).

Surprisingly, the critical issue of sightability bias was usually unaccounted for, with no evidence of improvement over time (Fig. 4), despite its influence on the accuracy and precision of moose population estimates (Evans et al. 1966, Caughley 1974, Gasaway et al. 1986, Peters et al. 2014, Harris et al. 2015). Multiple studies using aerial methods have documented declines in moose sightability with increasing canopy cover, especially in conifer patches. For example, using thermal drone surveys, McMahon et al. (2021) found that sightability declined from near 100% in open habitat to < 25% in 75% canopy cover, and Peters et al. (2014) estimated sightability along transects to be as low as 46% during helicopter flights over non-ideal snow conditions. Regarding public data, sightability can influence physical observation rates or manifest as imperfect reporting or undocumented harvest (e.g., illegal harvest). In these cases, the number of moose present within or removed from the population would be underestimated, and could be a common scenario. Such underestimation is likely pervasive for moose and other species where imperfect detection of individuals is the norm (Caughley 1974, MacKenzie et al. 2002, Stephens et al. 2006). Therefore, a key area of improvement for moose monitoring methods is to explicitly and rigorously account for sightability bias.

Studies accounting for sightability bias varied in approach, ranging from extensive field efforts and sophisticated statistical modeling (e.g., Oyster et al. 2018) to correction factors based upon previous work in the same study area using similar methods (e.g., Bontaites et al. 2000). To increase sightability, aerial surveys are typically conducted in snow conditions that accentuate the contrast between moose and their background environment (Gasaway et al. 1986); however, this reliance on snow cover is problematic from a scheduling perspective. The expectation is that this problem will worsen presuming that climate change reduces the length and timing of snow cover, especially along the southern range of moose (Bormann et al. 2018, Kellie et al. 2019, Jensen et al. 2020). Another approach to quantify sightability in aerial methods is to search for a subset of VHF- or GPS-collared individuals and quantify their detection probabilities as a function of habitat or environmental conditions (e.g., Peters et al. 2014). This approach is effective but usually part of a separate ecological study given the substantial costs of capture, collars, and tracking individual moose. An approach generally absent in our literature survey, but common for other taxa, is using

Table 2. A comparative summary of the predominant methods used to estimate and monitor moose (*Alces alces*) density and abundance.

Method	Advantages	Limitations	Outlook
Fixed-wing and helicopter surveys	Easily understood and trusted by many stakeholders; sometimes considered the "gold standard"	Logistical and financial costs; danger to aviators; often dependent on weather and snow, and sensitive to terrain variation	Useful method in jurisdictions where resources enable consistent surveys; overall prevalence likely to decline as other methods develop
Camera trapping	Relatively low field effort and expense; non-invasive	Must process voluminous image data efficiently; analytical methods are rapidly changing	Increase in prevalence as analytical methods continue to develop
Harvest data analysis	Inexpensive; produces reliable estimates of population when appropriate statistical methods are applied	Limited to areas where harvest is substantial; bias in non-random hunter behavior must be accounted for	A foundational method when harvest is substantial
Pellet and track surveys	Relatively inexpensive; non-invasive	Requires calibration with other density estimates to achieve reliability; low precision; field intensive in terms of person-power; tracking requires snow	Pellet surveys could become more powerful when combined with genetic analyses; tracking a useful low-tech index at local scales
Public or hunter observations	Inexpensive; engages multiple stakeholders	Study design must be carefully considered to avoid reporting bias; indices do not always track with population dynamics	Viable management tool when calibration using other methods occurs regularly
UASs	Less expensive and safer than traditional aerial surveys	Spatial extent and locations of surveys often limited by regulations; unproven as broadscale monitoring method; non-trivial initial purchase costs	Current applications are most effective for local scale studies; regulatory changes could precipitate rapid increase in capacity

UAS = Unpiloted Aerial System. Italicized methods indicate those appearing in recent literature.

repeated surveys in space or time to quantify detection probabilities (e.g., as in occupancy modeling; MacKenzie et al. 2002, Tyre et al. 2003). For moose, this method could be applied by using repeated sampling over time with camera traps, with multiple observers in ground-based surveys or among the public, or by flying transects more than once in rapid succession such that population closure assumptions are reasonably met (Adams et al. 1997, Rota et al. 2009). Depending on context, such strategies are a cost-effective alternative to using radio-marked animals. However, we note that sightability is method-specific and the correction from one method might not apply to another. Whatever the method, it is crucial to consider sightability bias because a failure to do so likely results in density underestimation and leads to bias in other types of inference (e.g., wildlife-habitat relationships; see Kéry et al. 2010). For example, the early successional habitat that moose prefer is associated with decreased sightability. Therefore, a survey that does not separate the observational effects of habitat on moose detection (i.e., a negative effect) from the ecological effects (i.e., a positive effect) risks conflating observation error with ecological inference.

Indices, especially those based on hunter observation and success rate, were a relatively common approach in tracking moose population trends (Appendix 2). Indices are often employed because they are cheaper – sometimes much cheaper – than more field intensive and potentially hazardous methods such as helicopter surveys (Sasse 2003, Krebs 2006). However, indices must be carefully calibrated and regularly reviewed to ensure reliability (Caughley 1974, Bontaites et al. 2000, Hatter 2001, Ueno et al. 2014). Although several papers reported high correlations between an index and population density, sample sizes were often small (e.g., n < 10) and a number of comparisons had only moderate correlation (see Appendix 2). For example, moose observations made by hunters in Maine, USA exhibited only a modest correlation with densities obtained from aerial helicopter surveys (R^2 = 0.32; n = 13; Kantar and Cumberland 2013). Recent work in Ontario, Canada showed that the relationship between harvest and abundance varies by age and sex class, thereby highlighting the need to calibrate indices by demographic categories (Priadka et al. 2020). This study also found non-linear relationships between harvest effort, harvest, and abundance, suggesting that harvest might underestimate abundance when harvest effort is high. These observations emphasize that such indices must account for non-randomness and change in hunter activity relative to spatial coverage, effort, participation rate, weather, and technique, as well as potential non-linear relationships with hunter effort, harvest success, and moose abundance (Fryxell et al. 1988, Kantar and Cumberland 2013, Larson et al. 2014, Priadka et al. 2020).

More broadly, our literature survey suggests there could be untapped utility to use indices (e.g., hunter observations) in more comprehensive integrated population models (IPMs). Such models combine multiple data sources to improve the precision of population parameter estimates, thereby improving management efficiency (Schaub and Abadi 2011, Arnold et al. 2018). For example, Månsson et al. (2011) used simulations to demonstrate how the combination of hunter observations and pellet counts could more accurately inform management than more expensive aerial surveys. Similarly, Marrotte et al. (2021) integrated aerial survey data with hunter-reported data into a single model to estimate moose population trends in relation to harvest and predation. Each of these data sources had unique limitations; the aerial surveys were infrequent but had higher accuracy while the hunter reports were more frequent but less standardized. The IPM developed by Marrotte et al. (2021) partially overcame these challenges, resulting in increased confidence in overall moose population trends.

The target precision for moose density estimates was only achieved half of the time in the studies we analyzed (Fig. 5B; Appendix 1). In their seminal paper, Gasaway et al. (1986) suggested a target precision with a confidence interval width of ±25% of the population estimate; however, the rationale for this target was not provided and they noted that higher precision was desirable, but often prohibitively expensive (p. 5). These authors also endorsed a stratified random sampling design as a means to achieve target precision, which was an approach used in 50% of the aerial surveys we reviewed. Nonetheless, certain studies found that stratification did not increase precision, especially in low-density populations (e.g., Crete et al. 1986). The expanding suite of remote-sensing products (e.g., land cover and digital elevation maps) is making strict stratification less important than a random design that captures the full range of spatial conditions in a study area (Fletcher and Fortin 2018). Spatial modeling using remotely-sensed covariates can improve accuracy and precision, while enabling prediction of moose density beyond sample units (Ver Hoef 2008, Michaud et al. 2014).

The degree to which target precision (Gasaway et al. 1986) is acceptable for management objectives is an open and context-dependent question. Ideally, initial target precision would be informed by power analyses and simulation, then updated with field data in an adaptive management framework (Steidl et al. 1997, Lyons et al. 2008). The utility of this approach was demonstrated by Boyce et al. (2012), where tradeoffs between infrequent but accurate aerial surveys and frequent but less accurate kill-per-unit-effort harvest data were mathematically explored using population projection analysis. Simulation can also inform study design by enabling researchers and managers to estimate required sample sizes for particular precisions (Hinton et al. 2022). For example, Gasaway et al. (1986) recommended an initial aerial survey to stratify landscapes by coarse-scale moose population densities. However, these flights can be expensive, thus simulation using known, assumed, or preliminary data (e.g., habitat suitability) represent an attractive alternative to traditional Gasaway-type stratification. Precision can also be improved through the use of IPMs (Marrotte et al. 2021; discussed further below).

It is often difficult to monitor wildlife population trends over sufficient periods because of the many sources of variation in ecological systems and the short-term funding cycles that support monitoring efforts (Field et al. 2007). Indeed, population monitoring efforts with other taxa are often biased in site selection or not conducted long enough to reliably detect population trends (Fournier et al. 2019, White 2019). Likewise, many studies uncovered by our literature survey lasted just one year, or when they occurred across multiple years were often limited by cost that influenced the survey area in any given year (Appendix 1). Such constraints emphasize the need to creatively and effectively design monitoring programs that inform stated management objectives in a given landscape context. In locations with substantial harvest, cohort analysis and statistical population reconstruction represent powerful methods that can offer high accuracy and precision across broad spatiotemporal scales (Solberg et al. 1999, Skalski et al. 2005). In addition, the impacts of sightability bias related to unknown sources of harvest should be considered (Skalski et al. 2005, Timmermann and Rodgers 2017). For low-density populations or those with little to no harvest, multiple methods that complement each other and account for sightability bias are paramount and will likely co-evolve with technological and analytical developments. In particular, the advantages of advanced statistical modeling coupled with robust geospatial data should be used to "get the most" out of sparse data that are expensive to collect for low-density populations. Hinton et al. (2022) provide an example of this approach by combining non-linear generalized additive models, adaptive sampling, and informative geospatial covariates to monitor a low density population over a large (~25,000 km^2) landscape in New York, USA.

We conclude that several methods deserve additional consideration, and pending evaluation, could be implemented increasingly in moose density estimation and monitoring, foremost camera traps, UAS, and IPM. Technological advancements have increased wildlife detection capability of camera traps and improved their field reliability (Burton et al. 2015, Steenweg et al. 2017). Statistical models that estimate population density with camera trap data have also advanced (Kéry and Royle 2015, Gilbert et al. 2021b), with several capable of estimating habitat relationships used to predict population density in non-sampled areas (Moeller et al. 2018, Nakashima et al. 2020), thereby enabling broader monitoring across spatiotemporal scales. Camera traps can also potentially collect information on sex ratio and age structure of moose. Although no study in the literature survey used camera traps, studies are being implemented in the northeastern United States (R. J. Moll and H. Jones, pers. comm.) and appear in recent literature (see Pfeffer et al. 2018).

Likewise, UAS surveys of wildlife populations are becoming more common due to technological advances related to field reliability and sensor capability (Linchant et al. 2015, Witczuk et al. 2018). Recent UAS surveys for moose in Minnesota yielded high accuracy at a cost lower than traditional aerial surveys; albeit, scale (time and area) and flight regulations remain as issues (McMahon et al. 2021). Nonetheless, UAS can provide aerial surveys at lower cost and without the potential danger of traditional flights (Sasse 2003), and will be especially useful for local scale surveys (McMahon et al. 2021).

IPMs represent an underused approach to improve moose monitoring by enhancing analytical power, reducing bias, and increasing the precision of population estimates (Schaub and Abadi 2011). For example, IPMs can be used to combine known-fate data from collared individuals, counts from aerial surveys, and occupancy data collected by hunter observations to estimate population density and demographic parameters such as survival (Zipkin and Saunders 2018). The ultimate goals of IPMs are usually to estimate abundance over time (i.e., population trends) and obtain demographic parameters that are traditionally difficult to estimate from a single data source (e.g., immigration). Many moose monitoring programs seek these parameters, particularly population change over time, to inform management. To take advantage of the power of IPMs, researchers and managers might first build a process-based model of the target population using standard stage- or age-structured population matrices (Boyce et al. 2012). Then, multiple, independent datasets could be jointly analyzed to estimate parameters of that model, which would in turn be used to predict and project population trends under management scenarios. IPMs require that some parameters be shared among projects with different datasets. Examples of such shared parameters in moose monitoring efforts might include survival (e.g., from capture-recapture or telemetry data) and recruitment rates (e.g., from aerial counts or harvest data; Zipkin and Saunders 2018). While use of IPMs has increased dramatically in other applications and taxa (Schaub and Abadi 2011, Arnold et al. 2018, Zipkin and Saunders 2018, Gilbert et al. 2021a), they are rarely used for moose (although see recent implementation by Marrotte et al. 2021). We direct readers interested in using IPMs for moose monitoring to the comprehensive reviews and texts published in recent years for additional details regarding data requirements and analytical implementation methods (Schaub and Abadi 2011, Zipkin and Saunders 2018, Schaub and Kéry 2021).

Moose and moose managers face a myriad of environmental and conservation challenges in the 21st century, and using accurate and reliable population information will be paramount in management decisions. The broad variation in range, habitat, environmental conditions, and population density precludes a single survey method that can address each jurisdictional goal or need. While aerial surveys are often described as the best method for population estimation and monitoring (e.g., Peters et al. 2014, Boyce and Corrigan 2017), we suggest that the "best" method is case-specific and meets an acceptable target precision while accounting for sightability at a reasonable cost. Fortunately, the technological and analytical toolboxes available to researchers and managers have never been fuller, and developments continue. We emphasize the judicious adaptation and evaluation of new methods and approaches to address context-specific needs and objectives, and likewise encourage coordinated efforts across jurisdictions and spatial scales.

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