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RESEARCH ARTICLE

When can model-based estimates replace surveys of wildlife populations that span many discrete management units?

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Abstract

1. Monitoring widely distributed species on a budget presents challenges for the spatio-temporal allocation of survey effort. When there are multiple discrete units to monitor, survey alternatives such as model-based estimates can be useful to fill information gaps but may not reliably reflect biological complexity and change. The spatio-temporal allocation of survey effort that minimizes uncertainty for the greatest number of units within a budget can help to ensure monitoring is optimized.
2. We used aerial survey-based population estimates of moose (*Alces alces*) across 30 Wildlife Management Units (WMUs) in Ontario, Canada to parameterize simulated populations and test the performance of different monitoring scenarios in capturing WMU-specific annual variation and trends. Firstly, we tested scenarios that prioritized conducting a survey for a unit based on one of three management criteria: population state, population uncertainty or number of years between surveys. Also incorporated in the decision framework were WMU-specific costs and annual budget constraints. Secondly, we tested how using model-based estimates to fill information gaps improved population and trend estimates. Lastly, we assessed how the utility (based on minimizing population uncertainty) of using a model-based estimate rather than conducting a survey was impacted by population density, severity of environmental stressors and years since the last survey.
3. Interval-based monitoring that minimized the number of years between surveys captured accurate trends for the highest number of WMUs, but annual variation was poorly captured regardless of management criteria prioritized. Using model-based estimates to fill information gaps improved trend estimation. Further, the utility of conducting a survey increased with time since the last survey and was greater for populations with low densities when the severity of environmental stressors was high, while being greater for populations with high densities when environmental severity was low.

4. Overall, the utility of aerial survey monitoring was strongly associated with WMU-specific monitoring precision and the predictive power of model-based estimates. If long-term trends are evident, then there is greater value in using alternatives such as model-based predictions to replace surveys, but model-based estimates may be a poor substitute when there is strong annual variation and when using a simple model.

KEYWORDS

aerial survey, model-based estimate, moose, population trends, survey effort, uncertainty, wildlife monitoring

1 | INTRODUCTION

Monitoring of wildlife is essential to inform management actions and assess their effectiveness (Pollock et al., 2002; Yoccoz et al., 2001). Limited resources, including budget, can often constrain the frequency at which populations are monitored, which can lead to uncertainty in population state (Hauser et al., 2006). Widely distributed species are especially at risk of being managed with high uncertainty due to spatial and temporal gaps in monitoring, in addition to uncertainty introduced through variation in the accuracy or precision of survey estimates (Andersen & Steidl, 2020; Ficetola et al., 2018; Nuno et al., 2013). However, the need for monitoring can depend in part on the nature of population change. Consistent long-term population trends can require less frequent monitoring to detect the direction and/or rate of change than stable or temporally variable populations (Ficetola et al., 2018; Reynolds et al., 2011; Row & Fedy, 2017; Wauchope et al., 2019). A decision-making framework that considers the value of new information relative to the cost of obtaining it can therefore help to determine the optimal time and/or conditions under which to conduct a survey (Canessa et al., 2015; Hauser et al., 2006).

Jurisdictions containing multiple management units with discrete populations that are managed independently face the additional challenge of ensuring that each unit is adequately monitored while balancing monitoring needs and costs among units (Ficetola et al., 2018). Typically, populations with low densities, non-uniform distributions and/or poor detectability will require more spatial and temporal replication of monitoring effort to obtain accurate and precise population estimates (Barata et al., 2017; Ficetola et al., 2018; Nuno et al., 2013). Multi-unit monitoring schemes can therefore benefit from designs that balance the utility of monitoring a unit with cost while accounting for utility and costs of all other units. Utility in wildlife monitoring can vary but will typically be based on balancing the benefit that the new information provides with the cost (Canessa et al., 2015; Hauser et al., 2006). Furthermore, there can be multiple management needs (i.e. criteria) to consider that can impact the prioritization of units to monitor each year. Criteria prioritized in monitoring can include tracking population state for vulnerable or managed populations, resolving population uncertainty and/or ensuring that all units are monitored frequently enough to track population state or trend across a larger area (Hauser et al., 2006; Joseph et al., 2009; Morant et al., 2020; Reynolds et al., 2011).

To alleviate uncertainty in population state and/or trends caused by gaps in monitoring information, alternatives to survey-based monitoring can be used. Model-based estimates are a useful alternative to conducting a survey and incorporating them in monitoring information can aid in the optimization of monitoring designs and management decision-making (Hauser et al., 2006; Nishimoto et al., 2021; Westcott et al., 2018). However, model-based estimates require prior knowledge of the conditions that affect population dynamics, which can include complex biological interactions (Ahrestani et al., 2016; Marolla et al., 2021). Developing models that are accurate in predicting population change can be particularly challenging for widely distributed species that occupy variable environments and experience spatially and temporally variable limiting factors (Ahrestani et al., 2016; Marolla et al., 2021; Westcott et al., 2018). Therefore, model-based estimates can be limited in their predictive power and should not always be relied on to replace surveys.

Moose (*Alces alces*) are widely distributed across northern portions of North America. In Canada, populations are experiencing variable trends, including declines in many regions (Timmermann & Rodgers, 2017). Harvest of moose occurs in many jurisdictions, which typically requires regular monitoring of populations to guide licensed harvest allocations and to prevent overharvest (Bottan et al., 2002; Boyce et al., 2012). Aerial surveys are the most common method of monitoring moose across most jurisdictions; however, due to high costs and budget constraints, aerial surveys are usually conducted every few years per management unit (Boyce et al., 2012). Irregular unit-based monitoring can result in gaps in information for unit-specific time series, which can lead to high uncertainty in population state and/or trend (Boyce et al., 2012). Selection of units to monitor can be based on risk-based criteria (e.g. anticipated decline in population size); however, there is often a lack of quantitative approaches to parameterize costs and benefits of monitoring, which can result in inefficient monitoring decisions. Therefore, moose monitoring can benefit from an optimized design that guides survey efforts by addressing when extensive monitoring (such as aerial surveys) is needed to resolve uncertainty for a unit or when alternative methods (such as model-based estimates) will suffice to inform decision-making.

Here, we developed a year-to-year optimization framework to test alternative criteria for selecting management units to survey moose and identify when a model-based population estimate can replace a survey. We used empirical aerial survey data for moose across 30 management units and a time span of 25 years in Ontario, Canada to parameterize simulations of moose population abundance. Our optimization framework also accounted for total monitoring budget and unit-specific costs to survey. Our first two objectives focused on comparing different monitoring scenarios with the goal of capturing annual population variation and trends for the greatest number of units. Firstly, we evaluated how prioritizing one of three risk-based criteria—(a) population uncertainty, (b) population state or (c) number of years since the last survey—when selecting units to monitor affected population abundance and trend estimates. Secondly, we evaluated how using either the previous year's population estimates or a model-based estimate for years without surveys affected population state and trend estimates within our optimization framework. Our third objective was to assess how population density, environmental variability and years since the last survey influenced the utility of model-based estimates to replace aerial surveys with the goal of minimizing uncertainty in annual population estimates.

2 | MATERIALS AND METHODS

2.1 | Study area

The study area spanned 255,879 km^2 in the province of Ontario, Canada. The southern portion of the study area was predominantly deciduous boreal forest (Rowe, 1972), with common species including sugar maple (*Acer* spp.), white spruce (*Picea* spp.) and balsam fir (*Abies* spp.; Goldblum & Rigg, 2005). The northern portion of the study area was composed of mixed deciduous and coniferous boreal forest (Rowe, 1972), consisting of deciduous tree species including trembling aspen (*Populus* spp.) and paper birch (*Betula* spp.) and coniferous species including jack pine (*Pinus* spp.), white spruce (*Picea* spp.), black spruce (*Picea* spp.) and balsam fir (*Abies* spp.; James et al., 2017). Forest harvesting and wildfires were the main contributing factors maintaining early seral stage forests with reduced canopy cover across the study area. Spruce-budworm (*Choristoneura fumiferana*) outbreaks also contributed to substantial reductions in canopy-cover, particularly in the north-western portion of the province (James et al., 2017).

2.2 | Moose aerial survey data

We used moose aerial survey inventory data collected by the Ministry of Natural Resources and Forestry (MNRF) in Ontario over a 25-year period (1991–2015) to generate time series of expected moose population size and trends. Monitoring and harvest management are generally applied independently for each Wildlife Management Unit (WMU) and WMUs were selected to be surveyed approximately every 3–5 years. Only WMUs with a minimum of 5 years of surveys conducted between 1991 and 2015 were used in our analysis, resulting in 30 WMUs.

Moose aerial surveys took place in the winter (January to March) when canopy cover from deciduous trees was low and snow-cover facilitated detection of moose and their tracks. Moose aerial surveys were conducted for WMUs using stratified random sampling of 25-km^2 plots (McLaren, 2006). Each plot was assigned to one of three strata representing variation in moose density. Stratification was based on observations made during previous surveys, as well as habitat suitability (McLaren, 2006). The total number of plots flown varied among surveys and was adjusted mid-survey to improve precision of the population estimate by sampling more plots in strata of greater observed variance, which usually required a minimum of 20 plots in total. Survey precision was measured using the variance in counts across plots in a stratum (McLaren, 2006). Standardized survey protocols were used to reduce detectability bias and improve survey accuracy by setting conditions for flights with respect to weather, snow ground cover, aircraft speed, altitude and the number of observers (McLaren, 2006), but additional sources for detectability bias in aerial monitoring can still be introduced by variable forest canopy cover (Quayle et al., 2001). To understand sources of detectability bias and/or survey precision in our study system, we conducted a supplementary analysis to evaluate the effects of forest canopy cover type and moose population density on aerial survey precision (Appendix SA). The analysis was also used to ascertain both spatial and temporal variability in survey precision at the WMU and year level.

2.3 | Data generation and model development

The following three sections describe how WMU-specific population time series of moose abundance, aerial survey counts, and model-based estimates were generated to derive the population estimates used in our optimization framework. To test the performance of different monitoring scenarios in capturing WMU-specific annual variation and trends, we first generated time series of 'known' moose population size from empirical moose aerial survey data. We then simulated aerial survey-derived population counts based on 'known' population size while accounting for WMU-specific variability in counts of moose during surveys. Lastly, model-based population estimates were generated based on simulated aerial survey estimates within our optimization framework.

2.4 | Generated WMU-specific population time series

Time series of 'known' population size and trend over 25 years (1991–2015) were generated for 30 WMUs using coefficients from a linear mixed-effects model of empirical aerial survey-derived estimates of moose density. Our mixed-effects model used empirical moose density (moose/km^2) to account for differences in WMU size, and included a Gamma log-link distribution with a random intercept for WMU and a random slope for year that were used to derive WMU-specific population trends (Figure SB1[A]). It has been previously identified that the moose population in Ontario has been experiencing a province-wide population decline following a population increase and peak in the early 2000s (Priadka et al., 2022). Because we were interested in simulating a linear trend, we extracted random year slopes from the model fit to the last 15 years of the study period (2001–2015). To address the effect of environmental variability on moose population trends, our model also included a winter severity index (representing snow depth and temperature from January to March) with a 2-year time lag that was previously identified to negatively influence long-term moose population trends in Ontario (Priadka et al., 2022). Methods describing how the winter severity index was generated can be found in Priadka et al. (2022). The coefficient for winter severity was extracted as a fixed effect for all WMUs for the full 25-year time frame and represented an 8% decline in moose density (Figure SB1[A]). Both year and winter severity values were log-transformed. The mixed-effects model was constructed in R (R Core Team, 2013) using package *lme4* (Bates et al., 2015).

Coefficients extracted from the empirically derived mixed model (above; see Table SB1 for a list of WMU-specific mixed model coefficients) were included in 30 independent linear models of 'known' population density (n) that spanned 25 years (i) for each WMU (Figure SB1[B]). Each linear model included β_0 that represented the WMU-specific model intercept, β_1 that represented the WMU-specific year effect and β_2 that represented the WMU-average effect of winter severity with a 2-year time lag ($\text{wint2}_{[i-2]}$):

$$n_{[i]} = \beta_0 + \beta_1 \times year_{[i]} + \beta_2 \times \text{wint2}_{[i-2]}. \tag{1}$$

Winter severity was simulated based on empirical values obtained for the years that survey data were available and was randomly drawn from a normal distribution as a standardized variable with x_i as the mean and σ_i as the standard deviation in winter severity values (Figure SB1[B]):

$$\text{wint2}_{[i-2]} \sim \text{Normal}\,(x_i, \sigma_i)\,. \tag{2}$$

Moose population time series were generated as log-transformed densities to reflect extracted coefficient values from the empirical data model and were transformed back to the exponential scale. Moose densities were converted to population abundance based on WMU area.

2.5 | Simulated aerial survey population estimates

We simulated aerial survey-based population counts across 25 years and for 30 WMUs based on WMU-specific time series generated using linear models (above; Figure SB1[B]). Average counts of moose per stratum were derived from empirical data and were used to calculate a proportion of the total population counted per stratified plot (m_u). Variability in number of plots flown per year was introduced by randomly drawing from a normal distribution with average (x_u) and standard deviation (σ_u) of total number of plots flown y per stratum u for each WMU (with the assumption that these values represented the average number of plots needed to achieve the precision target with temporal variability):

$$y_u = \text{Normal}\,(x_u, \sigma_u)\,. \tag{3}$$

Moose counts at the plot level (n_u) were derived using a Poisson distribution that drew counts for each of the randomly derived number of plots flown per stratum (y_u) based on the average number of moose counted per plot (m_u):

$$n_{u,y} = \text{Poisson}\,(y_u, m_u)\,. \tag{4}$$

To obtain an extrapolated moose population estimate for the WMU (C_W), the sum across strata 1, 2 and 3 was derived for the average of $n_{u,y}$ multiplied by the total number of plots in each stratum (Y_u):

$$C_W = \sum \left(\text{average } n_{1y} \times Y_1\right) + \left(\text{average } n_{2y} \times Y_2\right) + \left(\text{average } n_{3y} \times Y_3\right). \tag{5}$$

In addition to a population estimate, we estimated the average coefficient of variation (CV) in counts that was derived from the standard deviation in counts summed for each stratum (SD_{total}) divided by the population estimate C_W:

$$CV = SD_{total}/C_W. \tag{6}$$

We used CV to represent survey precision (i.e. uncertainty) for comparison with uncertainty derived from model-based estimates. CV represented the variance in counts across plots in each stratum, and therefore the uncertainty in the extrapolated population estimate. Assessment of simulated aerial survey estimates confirmed that they corresponded with empirical aerial surveys estimates and the generated 'known' population time series in reflecting greater spatial (63% CV average) than temporal (14% CV average) variation across WMUs (Table SB2). The R code for the function used to simulate WMU-specific aerial survey counts and population estimates is available in Appendix SC.

2.6 | Model-based population estimates to fill information gaps

To derive model-based population estimates, we used at least 15 years of prior knowledge of the moose population generated as survey estimates in Section 2.5. We used the simulated aerial survey population estimates to derive model-based estimates, as monitoring data would be the primary information source typically available for generating such population models. The inclusion of prior information ensured that our model had the predictive power to estimate annual population

TABLE 1 Scoring system that was applied annually to each Wildlife Management Unit based on three risk-based criteria that prioritized (a) population uncertainty based on the coefficient of variation for stratified and randomly sampled survey precision, (b) population state based on a population objective of 20 moose/100 km^2 and (c) number of years since the last survey

	Risk-based criteria a	Risk-based criteria b	Risk-based criteria c
(a) Population uncertainty (coefficient of variation)			
>3rd quartile of all WMUs province-wide	20	10	10
2nd to 3rd quartile of all WMUs province-wide	15	7.5	7.5
1st to 2nd quartile of all WMUs province-wide	10	5	5
<1st quartile of all WMUs province-wide	5	2.5	2.5
(b) Population state (population density)			
<10/100 km^2	10	20	10
10 > 16/100 km^2	7.5	15	7.5
16 > 18/100 km^2	5	10	5
20 < 18/100 km^2	2.5	5	2.5
>20/100 km^2	0	0	0
(c) Number of years since last survey	10 points/year	10 points/year	20 points/year

change and could inform our analysis on when model-based estimates provided greater utility than aerial surveys to infer population size.

We used a state-space model to derive model-based estimates that incorporated process variance associated with moose population change and observation error in population estimates. State-space models can separately model process and observation-based variance captured in monitoring data (De Valpine & Hastings, 2002) and have been useful for identifying drivers of population dynamics and for predicting population response to exogenous factors in previous wildlife studies (e.g. Ahrestani et al., 2016; Marolla et al., 2021; Westcott et al., 2018). Our process model structure included a year-effect and assumed that we did not know population response to environmental variability (i.e. winter severity). Therefore, our model only predicted change in the population based on the prior 15-year trend. We applied our state-space model using the Markov Chain Monte Carlo (MCMC) Bayesian approach and incorporated second tiers to our model to address process and observation noise.

Our process model for log-transformed population abundance (n) across time (t) included the model intercept (β_0) and the year effect (β_1) applied to year (Y):

$$n_t = \beta_0 + \beta_1 Y_t + \varepsilon_t. \tag{7}$$

Process noise (ε) was normally distributed with mean zero and standard deviation (σ^2) derived from variation across population abundance in the time series:

$$\sigma_n[\varepsilon_t \sim \text{Normal}\left(0, \sigma^2{}_n\right)]. \tag{8}$$

To estimate population abundance n, our observation model incorporated log-transformed population estimates in the time series (C_{t-1}) and assumed that estimates were normally distributed based on population abundance n_{t-1} and uncertainty (standard deviation) in the aerial survey- or model-derived estimates (SD_{t-1}):

$$C_{t-1} \sim \text{Normal}\left(n_{t-1}, SD_{t-1}\right). \tag{9}$$

We provided vague prior probabilities of parent parameters (β_0, β_1, σ_n; see Appendix SD for R code of the model function and prior distributions). Successful convergence of the posterior distribution of population abundance C_t was derived by Bayes theorem using three independent MCMC chains for 2,000,000 iterations and after a burn-in of 100,000 iterations by application of the Gibbs sampler using JAGS 3.3.0 via the R package *rjags* (Plummer, 2011). We sampled one of every 100 iterations from the joint posterior. Convergence of Markov chains was confirmed based on the diagnostic $\hat{R} < 1.1$ for all parameters and by visually inspecting parameter trace plots. Posterior distributions of population abundance were summarized by their mean (C_t) and standard deviation (SD_t) that was used to calculate the coefficient of variation for the model-based estimate (CV_t):

$$CV_t = SD_t / C_t. \tag{10}$$

2.7 | Scenario development

To address our first and second objectives, we developed scenarios to compare the effects of alternative risk-based criteria on the priority ranking of WMUs for monitoring and introduced three options for addressing years without a survey (i.e. missing information). We focused on three risk-based criteria that reflected general monitoring and management concerns: years since the last survey, precision of the last survey (or model-based estimate) and population status (Table 1). Our weighing among the three criteria was intended, in part, to ensure realistic selection of WMUs that did not consistently exclude units with large and/or stable populations. Scores for years since the last survey were cumulative until a survey was conducted, while scores

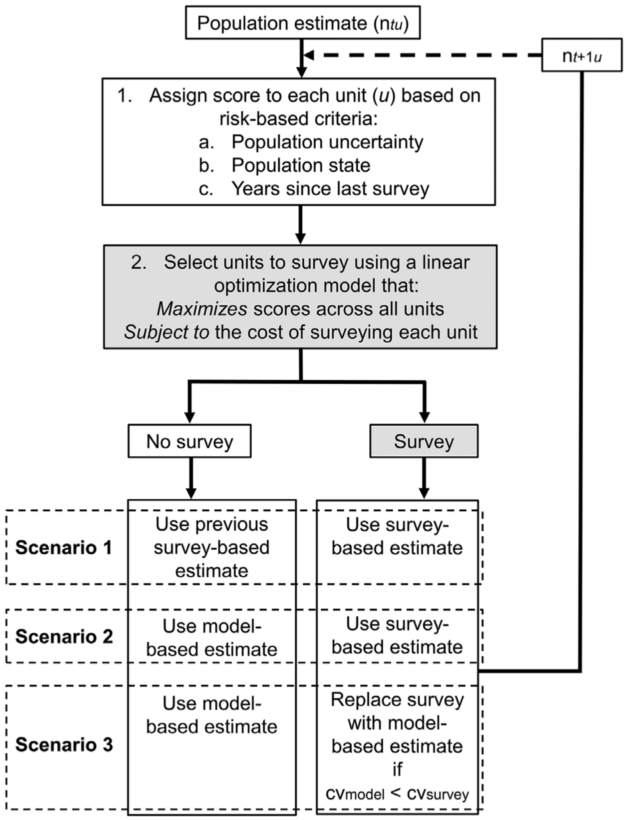

FIGURE 1 Optimization scheme outlining steps taken to select Wildlife Management Units (*u*) to monitor in each year (*t*) based on the unit-specific population estimate (*n*) and its associated uncertainty. In step 1, a score was assigned to each *u* based on three risk-based criteria (described in step 1 a–c). The optimization occurred at step 2 by maximizing scores across all *u* subject to their cost to ensure that the greatest number of *u* are selected, and that monitoring does not exceed the annual budget. If *u* was selected, an aerial survey was conducted to obtain a survey-based estimate (Scenarios 1 and 2) or the coefficient of variation (cv) in precision was compared with uncertainty in a model-based estimate to determine whether a survey-based estimate was used (Scenario 3). If *u* was not selected, either the previous survey estimate was used (Scenario 1) or a model-based estimate was used (Scenarios 2 and 3).

for uncertainty (based on quartiles across all WMUs) and population state (based on a 0.2 moose/km^2 threshold) were assigned based on the annual population estimate (Table 1). In addition to the three risk-based criteria, missing information in time series was treated either by using the previous survey's information (Scenario 1), using a model-based estimate (Scenario 2) or using a model-based estimate when its utility (based on minimizing population estimate uncertainty) outweighed survey-based utility (Scenario 3). The combination of three priority ranking criteria and three survey response options resulted in a total of nine scenarios (Figure 1; Table 2).

We measured utility in Scenario 3 as the difference in the level of uncertainty (CV) derived from each estimate (model- or survey-based; Figure 1). Therefore, utility represented the value of new information (i.e. a survey) and assumed we had prior knowledge of CV for both a survey- and model-based estimate in each year to make the best decision. We acknowledge that in most situations we do not have the advantage of prior knowledge of precision (and therefore uncertainty) for a survey before it is conducted, but our analysis allows us to evaluate when utility for a survey may degrade and how choosing to rely on model-based estimates to replace surveys will impact the accuracy of resulting time series. The decision of replacing surveys with model-based estimates was made following the optimization (step 2 in Figure 1) to ensure that the WMUs being selected were obtained from the same pool of samples as in the other two scenarios, and to prevent WMUs with consistent low scores from not being considered for a survey each year.

Following 10 years of optimization (see Section 2.8), each scenario resulted in a 10-year time-series data set for each WMU in the framework (n = 30). Henceforth, we refer to each of these data sets as an optimized time series. See Figure SB2 for a visual example of how optimized time series were constructed based on the three options for addressing years without a survey.

2.8 | Optimization model framework

Survey selection was optimized on an annual basis to ensure WMUs with the highest risk-based scores were surveyed each year based on WMU-specific cost and an annual budget (Figure 1). In our 25-year time series, the optimization started in year 16 to derive a 10-year optimized data set for each of 30 WMUs. The optimization scheme included two steps: (1) in each year t and for each WMU u, a score (s) was assigned to the population estimate n, and (2) the optimization model selected WMUs in year t by maximizing s_u subject to the cost (c_u) of conducting an aerial survey in each WMU (Figure 1). The optimization problem was conducted using a Linear Integer Programming (LIP) approach, where n was the total number of WMUs to monitor ($n = 30$):

$$\text{Maximize}: \quad \sum_{u=1}^{n} s_u x_u, \tag{11}$$

$$\text{Subject to}: \quad \sum_{u=1}^{n} c_u x_u \leq B, \tag{12}$$

$$\text{wherexisbinary}: \quad x_u \in \{0, 1\}, \text{ for } u = 1, \ldots, n.$$

A budget limit (B) of \$300,000 per year for all surveys was used. The cost of conducting a survey in each WMU was calculated by considering the cost (\$) of a helicopter per hour, the time needed per plot and the average total number of plots flown per WMU. Average cost of conducting a survey per WMU varied from CAD \$18,287 to CAD \$42,032, with an average of 36 total plots flown in a WMU per year (Table SB3). The optimization model and constraints were constructed using R package *lpsolve* (Berkelaar, 2015).

2.9 | Data analysis

2.9.1 | Comparison among monitoring scenarios

To compare the performance of each scenario, we compared each 10-year optimized time series in relation to generated population size

TABLE 2 The three risk-based criteria that were prioritized for selecting units to monitor (rows) and three options for how missing information in each time series was treated (columns) that were used to develop nine scenarios to use in our optimization framework

			How missing information was treated		
			Scenario 1	Scenario 2	Scenario 3
			Use previous survey information	Use model-based estimate	Use model-based estimate if model cv < survey cv
Criteria prioritized to monitor	Risk-based criteria a	Population uncertainty	S1a	S2a	S3a
	Risk-based criteria b	Population state	S1b	S2b	S3b
	Risk-based criteria c	Years since last survey	S1c	S2c	S3c

using two measures. First, we tested the correlation (Pearson's *r*) between time series of optimized estimates and population size and evaluated the proportion of WMUs with Pearson's $r > 0.5$ (indicating a positive linear relationship) for each scenario. Second, we calculated whether each optimized time-series slope/trend significantly varied from the trend in population size. Slope significance was assessed based on *p*-value ≤ 0.05 using a generalized linear model (GLM) with a quasipoisson distribution constructed using R package *lmerTest* (Kuznetsova et al., 2017). The model response was population size and the survey- or model-based population estimate and we tested for an interacting effect of year between time series. We additionally compared trends captured in each scenario by assessing the correlation (Pearson's *r*) and similarity among trends (within 0.01 units) between optimized time series.

2.9.2 | Assessment of factors affecting survey utility

We assessed how population density, environmental variability (winter severity with a 2-year time lag), and years since the last survey influenced the utility of conducting a survey (Scenario 3). We used a generalized linear mixed-effects model (GLMM) with a binomial distribution that treated the binary (0, 1) decision to survey as the response and included a random effect for scenario (S3a, S3b, S3c). We tested a full model that included each explanatory variable and included an interacting effect of density and winter severity to account for the relationship of winter severity driving population density in our study area (Priadka et al., 2022). All variables were tested using Pearson's *r* test to ensure there was no collinearity among variables. Binomial models were constructed using R package *lme4* (Bates et al., 2015). All figures were created using R package *ggplot2* (Wickham, 2011).

3 | RESULTS

3.1 | Comparison among monitoring scenarios

At least 67% (and maximum 97%) of optimized time series (n = 30) accurately reflected population trends in each scenario (Figure 2). However, annual variability was poorly captured in each scenario, with

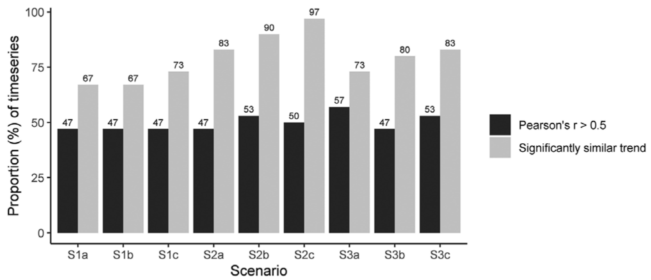

FIGURE 2 The proportion of optimized time series ($n = 30$ WMU; % value indicated above each bar) in each scenario that had a linear relationship (Pearson's $r > 0.5$) and a significantly similar trend (based on linear model results, *p*-value < 0.05) with population size.

no greater than 57% (and minimum 47%) of optimized time series (n = 30) reflecting annual population variation based on Pearson's $r > 0.5$ (Figure 2). Among risk-based criteria, prioritizing years since the last survey performed best at capturing accurate trends for the greatest number of WMUs (S1c, S2c, S3c; Figure 2). Meanwhile, using a model-based estimate to fill information gaps for years when a survey was not selected (S2a–c) resulted in more accurate trends among optimized time series than using the previous survey's estimate (S1a–c) or by replacing surveys with model-based estimates based on utility (S3a–c; Figure 2).

Although Scenario 3 (replacing surveys with model-based estimates based on utility; S3a–c) did not result in the greatest number of accurate trend estimates, comparative analysis revealed that optimized time series in this scenario were highly correlated with time series in Scenario 2 (S2a–c; Pearson's $r = 0.97$) regardless of risk-based criteria prioritized (Figure 3). Additionally, either 87% or 90% of time-series trends in Scenarios 2 and 3 were within 0.01 units of each other, which represented a maximum 10% divergence in population change captured by optimized time series in the two scenarios (Figure 3).

The number of surveys replaced with model-based estimates (Scenario 3) and the result in cost savings over time did not differ greatly based on risk-based criteria prioritized (Figure 4). In all scenarios, cost-savings with model-based replacement decreased over time, reflecting an increase in uncertainty in model-based estimates, and therefore greater utility of conducting a survey, over time (Figure 4).

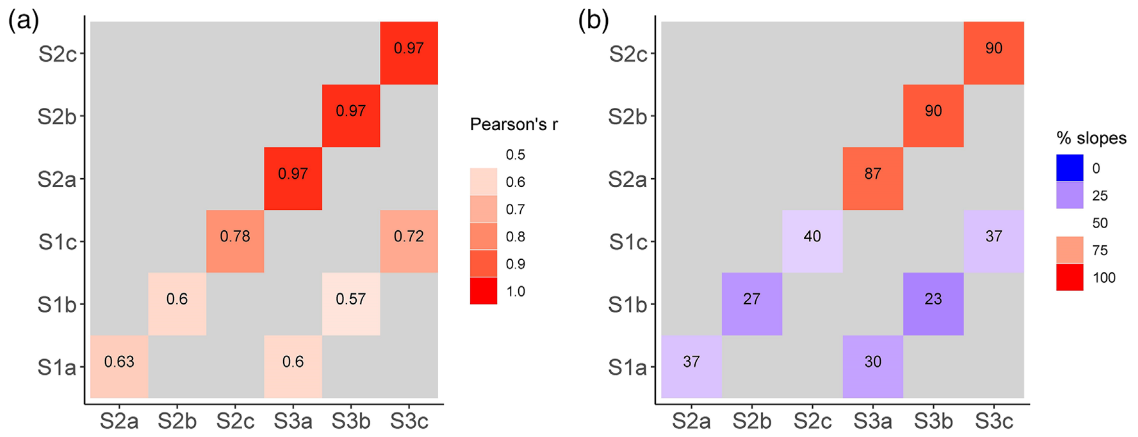

FIGURE 3 Comparative analyses for each scenario based on (a) the linear relationships (Pearson's *r*) amongst unit-level slopes/trends captured in each scenario and (b) the proportion (%) of slopes ($n = 30$) that were within 0.01 degrees of each other. Pearson's *r* and proportional values (%) are indicated in each grid.

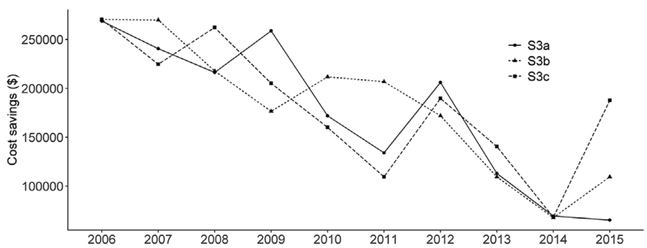

FIGURE 4 Annual cost savings for Scenarios 3a, 3b, and 3c that replaced surveys with model-based estimates based on uncertainty in annual population estimates.

TABLE 3 Model coefficients, standard error and *p*-values for variables that explain when it is the best decision to monitor a unit (binary response) based on utility (level of uncertainty) in aerial survey-derived population estimates compared to utility of model-based estimates. Explanatory variables included moose density (den), winter severity with a 2-year time lag (wint2), year and the interacting effect between moose density and winter severity (den:Wint2)

Variable	Coefficient	Standard error	*p*-value
Intercept	−0.41	0.14	0.004
Den	1.00	0.16	0.000
wint2	−0.15	0.16	0.339
Year	0.35	0.14	0.013
den:wint2	−0.40	0.18	0.023

3.2 | Factors affecting survey utility

When the utility of conducting a survey was evaluated and compared to utility of a model-based estimate, the probability of correctly choosing to survey a WMU in a given year increased with population density and years since the last survey (Table 3; Figure 5). The effect of population density on the probability of correctly choosing to survey declined with more severe winters (which contributed to population decline; Table 3; Figure 5). Visual inspection of model results revealed that the density threshold at which winter severity increased the utility of a survey was at approximately ≤ 0.2 moose/km^2 (Figure 5). Further, visual inspection of model results revealed that after approximately 8 years without a survey, the probability of correctly choosing to survey a WMU increased to approximately $\geq 50\%$; however, the probability did not reach 75% even after 10 years without a survey (Figure 5).

4 | DISCUSSION

4.1 | Comparison among monitoring scenarios

We developed a framework to optimize monitoring based on risk-based criteria and monitoring costs for moose populations spanning multiple management units and experiencing variation in population density, trends and severity of environmental stressors. Our framework allowed us to test different monitoring scenarios while accounting for monitoring budget and ascertain when model-based population estimates could replace conducting an aerial survey for a unit. While our analysis was conducted on moose, our approach can be applied to other species where trend information and precision of survey estimates are important and that face the challenge of optimal spatio-temporal allocation of survey effort across multiple discrete management units.

In our study, we found that minimizing the number of years between surveys performed best at capturing trends for the greatest number of WMUs, revealing that interval-based monitoring can be the optimal choice within monitoring frameworks with many discrete and variable management units. Notably, trends were detected for 97% of WMUs when model-based estimates were incorporated in the decision framework, despite only 2–5 years with a survey across a 10-year period. Previous studies have similarly identified that interval-based

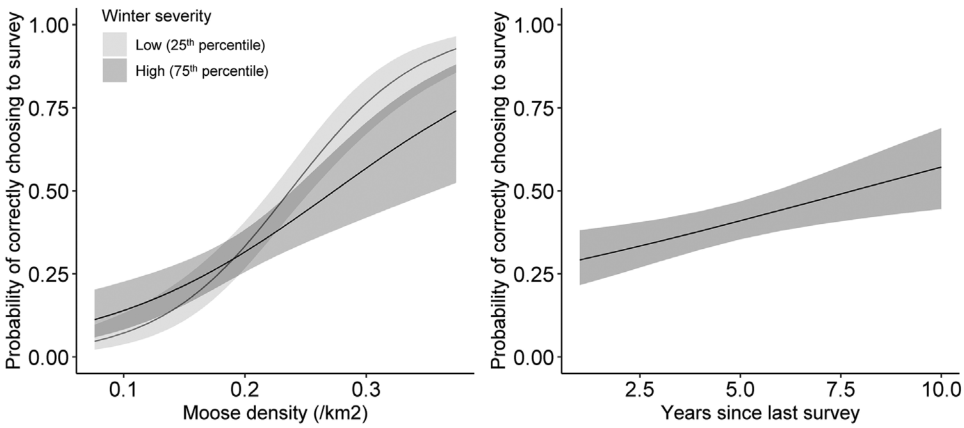

FIGURE 5 Explanatory variables influencing the probability of correctly choosing to survey a given unit each year (binary response), including the interacting effect of moose density and winter severity, and years since the last survey was conducted.

monitoring performs well for trend detection (Andersen & Steidl, 2020; Wauchope et al., 2019) and can be a cost-saving method for multi-unit systems if delays in detecting population changes are acceptable (Reynolds et al., 2011). In line with an interval-based approach, if units are not spatially correlated and vary in population dynamics, it is typically better to sample more units less frequently (Rhodes & Jonzén, 2011). Time series length is also an important contributor to trend detection, and longer periods of monitoring will improve accuracy in detecting rates of population change through time (Ahrestani et al., 2013; Piacenza et al., 2019; Reynolds et al., 2011; Vallecillo et al., 2021). Additionally, larger population changes in a consistent direction (e.g. 30% change in the population) are expected to be easier to detect than more subtle changes (e.g. 15% change in the population; Barata et al., 2017; Wauchope et al., 2019). While we introduced temporal variation in trends in our generated time series, most populations declined on average by 17% across the study time frame. Although our populations did not experience dramatic declines, we were still successful in detecting most trends in each scenario, suggesting that our optimization scheme was adequate.

Our study revealed that incorporating simple (i.e. year-only) model-based estimates can improve detection of long-term population trends. Therefore, if estimation of trends is the primary objective of monitoring, there is value in using simple model-based estimates to replace monitoring in some years. The non-significant differences in optimized time series that used model-based estimates to fill information gaps and those that further replaced surveys with model-based estimates based on utility (Scenarios 2 and 3, respectively) justify using at least a simple trends-based model to improve population trend estimation. The utility of model-based estimates to predict population change is likely to improve by incorporating additional information about population dynamics. However, environmental complexity can make it challenging for wildlife managers to develop and collect data for population models that include both endogenous (i.e. density dependence) and exogenous (i.e. climate) factors. Therefore, our model was simplified (i.e. excluded environmental variability) to reflect the realistic challenge of fully understanding drivers of wildlife population dynamics and variability over time and our results provide a generalized assessment of model-based utility.

Our findings also corresponded with previous studies that found the potential for strong bias and inaccuracy in monitoring data or model-based estimates in capturing annual population change (Wauchope et al., 2019). A main contributing factor to higher uncertainty in population estimates derived from surveys is poor detectability of animals. Detectability can be influenced by population density, distribution characteristics (i.e. open or closed population; Crum et al., 2021; Dambly et al., 2021; Westcott et al., 2012), landscape heterogeneity (Barata et al., 2017; Nuno et al., 2013; Rhodes & Jonzén, 2011), observer experience (Barata et al., 2017; Vallecillo et al., 2021) and weather conditions during monitoring (Morant et al., 2020). While we did not directly assess detectability bias and its effects on accuracy of counts in our study system, our analysis (Appendix SA) revealed that WMU-level variability in population density and dense coniferous forest cover contributed to greater among-plot variability and thus more imprecise population estimates. When monitoring efforts produce consistently imprecise population estimates with high uncertainty, managers should focus monitoring efforts on resolving population uncertainty potentially through increased survey effort (e.g. surveying more plots) or the implementation and/or integration of alternative techniques that may improve accuracy. For example, infrared technology can improve the detection of animals from the air under conditions of open forest canopy (Potvin & Breton, 2005), and sightability correction factors can be applied to improve count-based population estimates (Anderson & Lindzey, 1996). If uncertainty cannot be easily resolved, managers may be limited to relying on trends or the comparison of current state (the population estimate) to the population target to manage populations. While it was beyond the scope of our study, future studies should investigate how improving detectability and accuracy in aerial survey-derived population counts may impact the utility of model-based predictions and the spatio-temporal allocation of survey effort.

In our study, we focused on model-based estimates to fill monitoring gaps, but other sources of information, such as population indices, can be used. For example, harvest indices are commonly used to track population change for harvested species and supplement extensive monitoring (Boyce et al., 2012). However, the reliability of indices is heavily dependent on drivers of observation variance, such as hunter effort (Priadka et al., 2020), and will require validation to ensure natural processes are captured. Although detecting trends is less challenging and effort intensive than monitoring annual population change, it still requires strong reliance on precision over time to prevent misinformed decision-making (Seavy & Reynolds, 2007). Therefore, it is critical to validate any method of monitoring and understand sources of uncertainty that may confound the quality of information it provides. Additionally, it may be important to perform calibration of information for a system using more extensive monitoring to ensure important changes are detected (DeCesare et al., 2016).

4.2 | Factors affecting survey utility

We identified the effects of three important factors on survey utility that improved our understanding of when conducting a survey for a unit will resolve more uncertainty than relying on a model-based estimate. Firstly, we identified that the value of conducting a survey increased with population density. Other studies have similarly found that higher population densities resulted in reduced observation error, improved precision and more accurate trend estimates (Reynolds et al., 2011; Southwell et al., 2019; Steenweg et al., 2019; Tracey et al., 2008). Secondly, our findings revealed that environmental variability can influence the value of conducting a survey with the objective of minimizing population estimate uncertainty. In our study, we only introduced one source of environmental variability impacting moose population dynamics, but we acknowledge that other sources of variability will exist in natural systems. For example, moose populations typically undergo harvest pressure that will impact population dynamics (Brown, 2011) and population response to climate may vary based on habitat type (Priadka et al., 2022). In our simplified analysis, we found that if an environmental driver impacting population density is severe in a given year, then it was best to survey populations with lower densities and units with typically higher monitoring certainty that can provide the best value for the cost of monitoring. Hauser et al. (2006) also found that monitoring value increased with population uncertainty following environmental variability that reduced predictability power of model-based estimates. Population estimates derived from both surveys and models should therefore be used with caution for low population densities or small population sizes that are more unpredictable and sensitive to environmental stochasticity (Field et al., 2004; Hauser et al., 2006). Future studies should evaluate other interactions between environmental factors and/or population density for moose and how this may impact the utility of model-based estimates versus surveys to resolve population uncertainty.

Lastly, our findings revealed that uncertainty in model-based estimates increased with the number of years between surveys, resulting in reduced utility of model-based estimates to replace surveys, and consequently, a reduction in cost savings over time. Given the complexity of natural systems, model-based estimates will always accumulate uncertainty without monitoring (Hauser et al., 2006). Therefore, calibration of model-based estimates is needed for long-term monitoring. Our study identified that reliance on model-based predictions for moose within our study region should not exceed approximately 8 years without a survey (to maintain a 50% probability of correctly choosing to survey), especially if the population is not experiencing a consistent trend that can be predicted using a model-based estimate. These results may differ if using a more informed population model or for species with different life history characteristics (e.g. life span, reproductive rates) and levels of detectability during surveys. Future analyses should therefore focus on how utility can vary based on model type, which can help to justify the need to determine population-specific drivers of population dynamics and develop more informative population models to replace surveys.

In our study, we focused on three common risk-based criteria that can be easily applied to other taxa, but future analysis might also consider monitoring scenarios with other criteria typically prioritized during monitoring based on management needs. For example, more frequent monitoring of units where population management actions, such as harvesting or species recovery, are taking place may be needed to track population response (Pease et al., 2021; Priadka et al., 2020). Applying different criteria and priority scores will also likely impact the success of different monitoring scenarios in obtaining precise population estimates and accurate population trends for the greatest number of units. Optimization frameworks for multi-unit monitoring therefore need to be adaptive and address spatial and temporal variability among units to ensure that monitoring effort is efficiently allocated based on management needs.

5 | CONCLUSION

Here, we developed a year-to-year optimization framework to test alternative criteria for selecting management units to survey moose and identify when a model-based population estimate can replace a survey. We identified the value of interval-based monitoring, which minimizes the number of years between surveys across units, to monitor species spanning multiple discrete management units and with variable population densities, trends and severity of environmental stressors. We recommend that managers consider simple model-based estimates to fill information gaps, as we found evidence that they can improve population trend estimation and reduce the need to survey units more frequently. We found that utility of conducting a survey increased with time since the last survey and was greater for populations with low densities when the severity of environmental stressors was high, while being greater for populations with high densities when environmental severity was low. Overall, the utility of aerial survey monitoring was strongly associated with WMU-specific monitoring precision and the predictive power of model-based estimates. We note that an important limitation for use of model-based estimates is the adequate incorporation of biological complexity that can affect accurate estimation of population status and trends. If long-term trends are evident, then there is greater value in using alternatives such as model-based estimates to replace surveys, but model-based estimates may be a poor substitute when there is strong annual variation and when relying on a simple model.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

Pauline Priadka and Glen S. Brown conceived and designed the study, and Pauline Priadka conducted the analyses and wrote the manuscript. Pauline Priadka, Glen S. Brown, Bradley C. Fedy and Frank F. Mallory contributed critically to the analyses, interpreting results and manuscript drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Moose density data associated with this article are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.k6djh9w8s (Priadka et al., 2022).

PEER REVIEW

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