

Optimizing monitoring of harvested moose (*Alces alces*) in Ontario, Canada

by

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Abstract

Monitoring of widely distributed wildlife species across multiple discrete management units presents challenges for the optimal allocation of monitoring effort. By balancing value in new information gained through monitoring with costs, monitoring effort can be optimally allocated to maximize benefit to wildlife management. The main research objective of this thesis was to identify factors affecting the optimal allocation of monitoring effort for moose (*Alces alces*) across multiple Wildlife Management Units (WMUs) in Ontario, Canada that have variable moose population densities and dynamics. Moose are a harvested species across their range in North America and require monitoring to ensure sustainable harvest and that population management objectives are met. The main approaches used to monitor moose in the study area included aerial surveys and hunter harvest information, and I used both sources of data collected by the Ontario Ministry of Natural Resources and Forestry. In this thesis, I determined (1) the utility of harvest data as a proxy of moose population abundance under a selective harvest system; (2) the role of synergistic climate-habitat relationships in shaping spatio-temporal variation in moose population dynamics; and (3) the monitoring design that optimized the use of aerial surveys to estimate population abundance, while balancing the needs and monitoring costs of multiple discrete WMUs. My findings revealed that restricted harvest of adult moose reflected spatial variability in moose abundance better than less restricted calf harvest; but this effect was impacted by high levels of both hunter effort and landscape disturbance that can influence the detectability of moose to hunters. Further, my work revealed that moose population response to climate was variable at local (i.e. WMU) scales and was mediated or exacerbated by habitat conditions that can alter ecological links, including parasite transmission and predation. I incorporated my findings of drivers of moose population variability into population models to evaluate how prioritizing alternative

management criteria, in addition to using model-based estimates to replace information-gaps, impacted WMU-specific population and trend estimates. Also incorporated in the decision framework were WMU-specific costs and annual budget constraints. I further evaluated how the utility (based on minimizing population estimate 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. My results showed that interval-based monitoring and incorporating model-based estimates that accounted for previous survey uncertainty captured population trends for the highest number of units across a 10-year period. The utility of conducting a survey increased with time since the last survey and was greater for low population densities when the severity of environmental stressors (i.e. winter severity) was high, while being greater for high population densities when winter severity was low. My thesis findings can be applied to other widely distributed and harvested species that are managed and monitored using multi-unit frameworks spanning environmental gradients that contribute to variability in population uncertainty.

Keywords

Bayesian state-space model; climate-habitat interactions; linear integer programming; mixed-effects models; multi-unit monitoring; optimized monitoring; population uncertainty; population index; selective harvesting; wildlife management.

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Co-authorship and Publication Statement

While this thesis was written with me as the primary author, co-authors were involved in varying aspects of this work. Individual contributions to research chapters are outlined below, though any oversights or errors throughout the thesis are my own.

Chapter Two: Sex and age-specific differences in the performance of harvest indices as proxies of population abundance under selective harvesting

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Chapter One: General Introduction

Background

Uncertainty in monitoring

Monitoring of wildlife provides critical information to understand and identify changes in populations and to help guide management decision-making (Yoccoz et al. 2001; Yokomizo et al. 2004). Obtaining reliable estimates of population state that are both accurate and precise can be challenging and sometimes cost-prohibitive for species that are widely distributed at low densities, particularly in remote settings (Rönnegård et al. 2008; Kindberg et al. 2009). Assessing uncertainty in monitoring information is therefore important to know how to best interpret new information (Milner-Gulland and Shea 2017) and determine when additional information and further monitoring is required (Hauser et al. 2006; Canessa et al. 2015).

Uncertainty in monitoring information can be categorized into two types. It is common for high proportions of variance in wildlife monitoring data to be attributed to variability in the system introduced through demographic and environmental stochasticity, commonly referred to as process variance (Westcott et al. 2018; Ahrestani et al. 2013, 2016). Additionally, variance in monitoring information can be introduced through imperfect detection of animals, which results in observation error (Ahrestani et al. 2013; Nuno et al. 2013). Both process and observation variance can affect the reliability of monitoring information to track changes in system state, and therefore, effective and timely management response. The two variance types can also interact to result in increased levels of uncertainty. For example, climate change can affect species distributions and movement patterns, while also impacting the detectability of animals, resulting

in increased uncertainty in derived population estimates (Conroy et al. 2011; Nichols et al. 2011). Additional sources of observation error during monitoring can be attributed to factors impacting the visibility and/or detectability of animals to observers, including landscape/habitat type and temporal factors such as weather, time of year and/or day (Guillera-Arroita 2017). Survey type, levels of survey effort and/or experience/skills of observers may also impact the reliability of information gained and should be carefully considered when interpreting monitoring information (Nuno et al. 2015; Guillera-Arroita 2017). Commonly, indices of population size that are collected by a citizen science approach are easier to obtain than conducting census-based surveys but face greater levels of error due to inconsistent observational effort and/or skills among observers (Kindberg et al. 2009; Clare et al. 2019). Understanding associated level of uncertainty in monitoring information and its sources can help to ensure proper inferences are made and prevent the use of unreliable information in management decision-making.

As monitoring is often limited by budget, time and staff constraints, careful allocation of monitoring effort is often needed to maximize information gained in relation to uncertainty being resolved (Canessa et al. 2015; Maxwell et al. 2015). It can therefore be useful to consider the cost versus benefit of monitoring to decide whether new information contributes to improved understanding of the system or if monitoring effort and cost could be allocated elsewhere (Hauser et al. 2006; Maxwell et al. 2015). The cost and time limitations of monitoring can be particularly challenging for endangered or harvested species that require more frequent assessment of population state to ensure that conservation and management objectives have been met. A decision-making framework that considers the value of new information relative to the costs of obtaining it can further help determine the optimal time and/or conditions under which to conduct a survey for a system (Hauser et al. 2006). The benefit of knowing when to survey can be especially

helpful for multi-unit monitoring programs where units (e.g. wildlife management units) share budget and resource constraints, and unit-specific monitoring frequency depends on an annual decision of which unit(s) to monitor.

Study System

Moose (*Alces alces*) is a widely distributed species that is difficult and expensive to monitor, resulting in information gaps and uncertainty in monitoring information. However, monitoring moose is often of high conservation importance. The species has high economic and societal value across North America as a harvested species (Boyce et al. 2012), and holds cultural and social importance to many First Nation communities that rely on it for subsistence and to maintain ways-of-life (Popp et al. 2019, 2020). In recent decades, moose populations in North America have had variable trends (Timmermann and Rodgers 2017), which have been associated with both direct and indirect effects of habitat and climate change (Murray et al. 2006; Brown 2011; Rempel 2011; Laforge et al. 2017). As a harvested species, uncertainties in moose population state can have detrimental consequences to management decisions, particularly for setting harvest allocations and quotas that can influence population dynamics and stability over time (Fryxell et al. 2010). Moose monitoring efforts therefore attempt to minimize uncertainty in population state. However, budget constraints limit the spatial allocation of monitoring effort each year, which results in many units being managed without up-to-date monitoring information.

In Ontario, moose are monitored and managed within distinct Wildlife Management Units (WMUs). As the term population has variable definitions in the broad discipline of ecology, a population of moose in this thesis is defined as all individuals within the boundaries of a WMU. Monitoring of each moose population in the province is conducted in the winter using aerial surveys every 3-5 years in each WMU. Aerial surveys consist of a stratified random sample of

plots within WMUs, and observers record the number of moose seen by sex and age class (calf or adult), and the number of track aggregates when moose cannot be found (McLaren 2006). In Ontario, aerial-survey derived moose population estimates are not corrected for observation error, but previous studies have identified that variance in correctly observing animals during aerial surveys can be attributed to spatial factors, particularly forest canopy type and density (Quayle et al. 2001). Moose are also managed at the WMU-level by a selective harvesting system and hunter harvest information is submitted annually through mailed questionnaires from hunters. Information on moose harvest is used to supplement aerial-survey monitoring and provide indices of population trends for moose bulls, cows, and calves. During the study period, hunter questionnaires were submitted voluntarily by hunters.

Being logistically difficult and expensive, moose monitoring can benefit from an optimized design that addresses when extensive monitoring (such as aerial surveys) is needed to resolve uncertainty for a unit or when alternative methods (such as harvest data or model-based estimates) can be relied on. Identifying the optimal allocation of monitoring effort can be especially useful for multi-unit monitoring frameworks - such as the WMU monitoring framework in Ontario where units share budget and resource constraints. Further, validating the reliability of harvest information as an index of population change is key to ensuring monitoring information reflects natural processes, particularly as harvest is heavily dependent on hunter effort (Willebrand et al. 2011; Kahlert et al. 2015). As a priority species for monitoring that is anticipated to experience greater uncertainty in population state due to increasing climate and habitat change (Murray et al. 2006; Laforge et al. 2017), moose are an optimal focal species for developing an optimized monitoring strategy that can help managers decide when to monitor.

Thesis Objectives

The main goal of this thesis was to explore factors that contribute to uncertainty in both moose harvest and aerial-survey derived-population estimates and to identify a monitoring design that optimizes the allocation of monitoring effort across multiple discrete management units. In this thesis, I address (1) the reliability of harvest data as a proxy of moose population abundance under a selective harvest system; (2) the role of synergistic climate-habitat relationships in shaping spatio-temporal variation in moose population dynamics; and (3) the monitoring design that optimizes the selection of units to monitor each year based on ranked priorities and by maximizing population uncertainty resolved, while also accounting for the constraints of an annual budget and unit-specific costs of conducting a survey.

Thesis Structure

I begin my thesis (Chapter 1) with a general introduction on uncertainty in population monitoring and my study system of moose in Ontario, Canada. To achieve my thesis goal and first objective, I first (Chapter 2) evaluate the reliability of sex- and age-specific moose harvest as an index of population abundance. Specifically, I assess the relationship between harvest and aerial-derived moose abundance for moose bulls, cows and calves across 58 Wildlife Management Units (WMUs) and 16 years in Ontario, Canada. I further assess how harvest-abundance relationships are affected by hunter effort, weather (including temperature and precipitation during the hunting season), and landscape features (including forest type, forest disturbance and road access). I use the findings of this study to determine the feasibility of use of harvest information to fill population (i.e. WMU) level information gaps in aerial survey monitoring.

In Chapter 3, I assess how spatio-temporal variation in moose abundance is influenced by climate and habitat to identify different processes driving moose population dynamics across Ontario. Specifically, I investigate the impacts of seven climatic stressors on moose demographics (i.e. moose density and mid-winter recruitment) to identify the capacity of habitat quality to mediate climate effects across 50 WMUs and 36 years. This chapter provides important information for understanding drivers of moose population dynamics and their localized (i.e. WMU) effects. I use the findings of this study in Chapter 4 to generate 30 WMU-specific population models and test rank-based alternatives for prioritizing units to monitor by aerial-survey within a multi-unit monitoring framework. Rank-based alternatives included prioritizing units to monitor based on: population state relative to management objectives, population uncertainty, and years since the last survey. In addition to incorporating variance in environmental drivers of moose population dynamics across WMUs (i.e. process uncertainty), I also account for WMU-specific precision in aerial-survey derived population estimates (i.e. observation uncertainty) in my simulations. I use this framework to further assess how years since the last survey, population density, and environmental severity contribute to the utility of conducting an aerial survey for a unit (based on minimizing population estimate uncertainty), rather than using a model-based prediction. Lastly, in Chapter 5 I synthesize the findings of Chapter 2 to 4 and provide general conclusions and management recommendations.

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Chapter Two: Sex and age-specific differences in the performance of harvest indices as proxies of population abundance under selective harvesting

Abstract

Harvest indices are commonly used as proxies to direct population monitoring but sources of variability, including hunter effort and factors influencing detectability of animals to hunters, are rarely considered. Harvest indices may further be influenced by selective harvesting with regulatory differences in hunter effort across sex and age classes. To evaluate how sex and age-specific harvests perform as proxies of abundance under selective harvesting, we assessed harvest–abundance relationships (H–A) for moose *Alces alces* bulls, cows and calves across 58 wildlife management units (WMUs) in Ontario, Canada. Selective harvesting in our study area resulted in more regulated harvest of bulls and cows than calves. We therefore predicted more proportional H–A for calves than bulls and cows, with variability in H–A influenced by hunter effort, in addition to weather and landscape features that may influence moose detectability to hunters. In contrast to our expectation, we found that H–A was more proportional for adult moose than calves. Additionally, we found harvest was proportionally highest for bulls, despite greater hunter effort for calves. A positive effect of hunter effort on harvest as moose abundance increased helped to explain proportional H–A for adult moose. However, the effect of hunter effort on harvest was curvilinear at high effort levels, indicating that harvest will underestimate abundance when effort by hunters is high. Additionally, we found evidence of lower harvest in relation to abundance in WMUs with higher levels of recent disturbance from wildfire burns and clear-cuts. We demonstrate that the relationship between harvest and abundance can vary across selectively

harvested sex and age-classes, while variability in H–A can be attributed to spatial variability in hunter effort and the landscape. We caution that sources of variability in H–A, both across and among sex and age classes, should not be ignored when using harvest indices, especially for selectively harvested species.

Introduction

Indices of population abundance are commonly relied on in wildlife management to replace or supplement direct population monitoring (Rönnegård et al. 2008; Månsson et al. 2011, Stephens et al. 2015). Indices are typically derived from information that is cheaper and less laborious to collect compared to field-based methods that directly count animals on the landscape (e.g. aerial surveys), particularly to monitor species that are widely distributed at low densities and in remote settings (Morellet et al. 2007; Kindberg et al. 2009). There has been a wide range of applications of indices in wildlife management, including to understand population structure (sex or age ratios), spatial distribution, and habitat occupancy and to track changes in population abundance (Morellet et al. 2007; Stephens et al. 2015). Despite their convenience, the suitability of indices to inform management decisions is often questioned (Anderson 2001; Stephens et al. 2015). Of particular concern is the level of uncertainty and bias that may accumulate through indirect sampling of the population (Anderson 2001; Morellet et al. 2007; Stephens et al. 2015). Sources of uncertainty and bias typically include variable sampling effort and detectability in different environments, which introduces non-biological variability and may impact accurate tracking of the biological parameter of interest (Anderson 2001; Morellet et al. 2007). Although not always a trivial task, accounting for sources of non-biological variability, along with appropriate interpretation, can result in

successful characterization of indices across space and time for use in population monitoring (Morellet et al. 2007; Stephens et al. 2015).

For harvested species, a common and indirect method of monitoring is the collection of harvest data. Assessment of harvest is an attractive approach to population monitoring for wildlife managers, as harvest data are relatively cost-effective and easy to obtain in comparison to direct monitoring approaches such as aerial surveys (Månsson et al. 2011; Boyce et al. 2012). The number of individuals of a species harvested is assumed to reflect population abundance and may be used to assess population structure (i.e. sex and age-ratios), and track spatial distribution and/or change through time (Cattadori et al. 2003; Boyce et al. 2012). A common method used to validate indices is their proportionality with abundance (Kindberg et al. 2009; Kahlert et al. 2015). While a proportional relationship between population abundance (or density) and harvest has been reported for several species including game birds (Cattadori et al. 2003) and Cervids (Ueno et al. 2014), other studies have found poor linear correspondence for a range of species (Choate et al. 2006; Pettorelli et al. 2007; Imperio et al. 2010; Willebrand et al. 2011; DeCesare et al. 2016). Non-linear relationships between harvest and abundance may arise because of variability in factors associated with harvest success (e.g. hunter effort), as well as factors such as levels of detectability on the landscape (Schmidt et al. 2005; Willebrand et al. 2011; Ueno et al. 2014). Such discrepancies suggest that a better understanding of harvest–abundance relationships is required to determine whether harvest indices can be used as reliable proxies of population abundance.

A main driver and source of variability in harvest is hunter effort by hunters (Willebrand et al. 2011; Kahlert et al. 2015). Hunter effort can reflect the number of tags allocated by managers (i.e. quotas) or directly reflect the number of hunters and time spent hunting, depending on the harvest system in place (Fryxell et al. 2010; Kahlert et al. 2015). When hunter effort is regulated

by managers using tags, harvest may reflect management objectives and tradeoffs that do not exclusively rely on population abundance (Robinson et al. 2016). Tag-regulated hunter effort may therefore introduce variability in how well harvest reflects abundance. The effects of hunter effort on harvest may also differ between sex and age-classes within a species due to selective harvesting. For example, males are often targeted for many deer species and hunters are more likely to continue hunting until they are successful in obtaining a male (Fryxell et al. 1988; Solberg et al. 2000; Bhandari et al. 2006), while harvest of females and young may experience less hunter effort and total harvest. To prevent overharvest of certain sex and/or age-classes, managers will often restrict harvest by limiting hunting tags (i.e. quotas) for classes that may experience higher hunter effort. Accounting for sex and age-specific differences in how harvest is managed is rarely considered in the assessment of harvest as a proxy of abundance but may be critical in understanding harvest–abundance relationships. Variable hunter effort across sex and age-classes may be of particular concern if harvest is used to compare trends across classes or infer sex and/or age-specific parameters that assume an equal proportion of the population has been sampled, such as recruitment and/or sex ratios.

In addition to hunter effort, variables influencing detectability of animals to hunters, and therefore, number of animals harvested, may help explain the relationship between harvest and abundance. For example, weather (e.g. average temperature and precipitation), as well as landscape features (e.g. proportion of suitable habitat), may affect both animal and hunter activity directly, influencing the likelihood of hunters successfully harvesting an animal (Schmidt et al. 2005; Lebel et al. 2012; Kahlert et al. 2015). Higher density of road access to huntable areas may also improve encounter rates of animals to hunters, and therefore, the number of animals that are harvested (Rempel et al. 1997; Schmidt et al. 2005). Sex and age-specific differences in preference

to certain habitat types or weather conditions within a species are also possible and can consequently influence harvest sex and age-ratios (Solberg et al. 2000; Bunnefeld et al. 2009). Harvest indices are often employed uniformly across management areas, yet these variables may vary from year to year and among management areas, further complicating the relationship between harvest indices and population abundance.

In this study, we evaluated the use of sex and age-specific harvest as a proxy of population abundance for moose (*Alces alces*) across 58 wildlife management units (WMUs) in Ontario, Canada. Moose is a large mammal species that is widely distributed across North America and is typically found at low densities (Timmermann and Rodgers 2005). Although moose are directly monitored in Ontario using aerial surveys, their large distribution permits that only a small fraction of WMUs inhabited by moose are sampled each year, leaving gaps in monitoring information. Moose harvest by resident hunters is used to fill information gaps between years and to detect changes in population abundance among WMUs. Harvest indices used to supplement moose monitoring are not corrected for potential sources of non-biological variability (e.g. hunter effort) to ensure proportionality between harvest and abundance. Harvest is additionally used in the province to inform management decisions regarding moose harvest regulations (i.e. tags and season length). Since 1980, the province has adopted a selective harvesting system with restrictions on the number of tags available for adult moose (particularly for cows) while permitting higher harvest of calves. Sex- and age-specific difference in harvest–abundance relationships should therefore be expected but are not considered when relying on harvest indices as proxies of abundance. In our study, we assessed sex- and age-specific differences in harvest–abundance relationships (hereafter referred to as H–A) for moose bulls, cows and calves. Specifically, we expected less restricted calf harvest to result in abundance explaining a greater proportion of

variation in harvest (higher r^2) for calves than for bulls or cows. We further expected that less restricted calf harvest would result in proportionally higher rate of change in calf harvest in relation to abundance (higher slope of regression line), compared to bull and cow harvest. We further assessed whether hunter effort, as well as the confounding effects of weather, including temperature and precipitation during the hunting season, and landscape features, including forest type, forest disturbance and road access, could account for additional unexplained variation in sex and age-specific H–A.

Methods

Study area

The study area extended across continuous moose range in Ontario, Canada and was located predominately in the Boreal Shield ecozone, extending into the Hudson Bay Lowlands ecozone in the north-east of the province (Fig. 2-1). The Boreal Shield is dominated by the Boreal forest region in the north and Great Lakes St-Lawrence forest region in the south, while the Hudson Bay Lowlands are made up of a mixture of boreal forest and extensive wetlands (Rowe 1972). Temperatures across Ontario can vary based on the season and region and ranged monthly on average from -13°C in winter to 13°C in summer (Girardin and Mudelsee 2008). Forestry practices have been increasing across the Boreal Shield since the 1950s, with clear-cuts being the most common silviculture system (Perera and Baldwin 2000). Wildfire burns are also common across the Boreal Shield but are variable in frequency and severity due to active fire suppression and/or forestry practices (Girardin and Mudelsee 2008).

Moose range in Ontario overlaps with three other ungulate species, including: white-tailed deer *Odocoileus virginianus*, boreal woodland caribou *Rangifer tarandus caribou* and elk *Cervus canadensis*. Primary predators are shared by all ungulate species in the province and include wolves *Canis lupus*, coyotes *Canis latrans* and black bears *Ursus americanus*.

Ontario is divided into wildlife management units (WMUs) that facilitate the monitoring and management of wildlife, primarily of harvested species. Our study included 58 WMUs that overlap moose range in the province, spanning an area of 564 989 km² (Fig. 2-1). WMUs ranged in size from 842 to 40 657 km² and were selected based on the availability of both harvest records and moose aerial inventory data for the same year.

Moose population abundance

Year-specific estimates of moose population abundance were derived from aerial surveys conducted by the Ontario Ministry of Natural Resources and Forestry (MNR) between the years 2000 and 2015. Aerial surveys were conducted every 3–5 years in each WMU during the winter following the annual moose hunting season and used plot-based stratified random sampling or, in some northern WMUs with low moose density, systematic transects. With respect to plot-based surveys, each WMU was divided into a grid of 25 km² plots and a stratified random sample of plots was flown with a helicopter to record all moose observations by sex and age-class (bull, cow or calf). Moose numbers were projected for the entire WMU by the MNR based on observed counts within each stratified plot (McLaren 2006). Observation error that may result from variation in moose detectability (e.g. vegetative cover and observer experience) was not accounted for in projected counts, therefore, measures of moose population abundance are likely under-represented for each WMU (Crête et al. 1986; McLaren 2006). Effort to maintain consistency in the proportion of the population surveyed was achieved by flying surveys under a set of guidelines (e.g. under

conditions that will improve moose visibility to observers) and during the same time each year (McLaren 2006).

Harvest indices

The hunting season for moose in Ontario takes place from September to December, with dates and season length varying slightly among WMUs and by firearm type (gun or archery). Bull and cow harvest are regulated through a lottery-based moose validation tag draw with bull and cow tag numbers varying according to management decisions and moose population objectives specific to each WMU. Calf tags were available for purchase to all licensed hunters, with a limit of one calf tag per hunter, across most WMUs. Four WMUs in our study area had restricted calf harvest since 2004 with tags issued based on a validation tag draw. Mailed-out postcard surveys were used to collect harvest information from a random sample of hunters each year. Harvest reporting was voluntary across the province during our study period except in WMUs where calf harvest was restricted. Harvest information collected from hunters included number of bulls, cows or calves killed and hunter effort (number of hunters and days spent hunting). Our analysis included moose harvest records from 1999 to 2014, starting in the year that information on hunter effort began to be collected by the province. Due to non-mandatory reporting by hunters across most WMUs during the period of our study, raw harvest-records likely under-represented harvest by hunters. To account for variable reporting, we used projected rather than raw harvest in our analysis. Projected harvest for each WMU and year was provided by the MNRF and was calculated as the proportion of hunters with a tag that successfully harvested a moose divided by the return rate of postcard surveys for a given WMU and year.

Predictors of harvest–abundance relationships

To explore variability in harvest not accounted for by abundance, we assessed the effects of hunter effort, as well as the confounding effects of weather and landscape features on H–A. We used number of hunters to represent hunter effort because this metric was correlated ($r > 0.65$) with both days spent hunting and tags allocated (for bulls and cows) or sold (for calves). To assess how the effect of hunter effort may vary based on population abundance, we evaluated the interacting effect between hunter effort and population abundance on sex and age-specific harvest. We expected hunter effort to have a higher effect on harvest when population abundance was high, as higher population abundance should increase the encounter rates of moose by hunters (Schmidt et al. 2005; Willebrand et al. 2011; Ueno et al. 2014). Further, weather and landscape variables were predicted to influence hunter success in encountering and harvesting a moose, and therefore, how well harvest linearly reflected abundance. At the WMU scale in our analysis, we expected similar factors to influence detectability of moose to hunters across sex and age-classes.

Weather variables considered to impact moose harvest included averaged maximum monthly temperature ($^{\circ}\text{C}$) and average precipitation (mm) during the hunting season (Table 2-1). While temperatures are typically mild during the moose hunting season (on average between 15 and -5°C), warmer temperatures in the fall have been found to result in an increased use of densely forested areas for thermal cover and increasing nocturnal activity by moose (Dussault et al. 2004). Higher temperatures during the hunting season may therefore result in lower detectability of moose to hunters and lower harvest rates. Similarly, precipitation or snow depth may limit daily movement of moose (Lowe et al. 2010) as well as hunters, which may result in reduced harvest. Maximum monthly temperatures were averaged over the months overlapping the hunting season (between September and December) for each WMU and year included in the study. Similarly,

monthly precipitation was averaged over the hunting season (between September and December) for each WMU and year. Weather data was extracted for each WMU/year from monthly, spatially continuous grids composed by Natural Resources Canada (McKenney et al. 2006, 2007).

Landscape variables considered to impact moose harvest included: proportion of roads, dense forest cover, sparse forest cover, mixed-deciduous forest cover and disturbances including wildfire burns and clear-cuts (Table 2-1). Moose prefer mixed-deciduous forest cover (Dussault et al. 2006; Brown 2011) and forest disturbances, such as wildfire burns and forestry clear-cuts, where forest regeneration provides forage opportunities (Dussault et al. 2006). Moose, particularly cows, may also avoid recent (< 10 year) forest disturbances such as clear-cuts and wildfire burns, as these areas likely offer poor forage opportunity and low cover from predators (Maier et al. 2005; Dussault et al. 2006). Forested areas that provide adequate cover from predators have similarly been found to be selected by moose, especially cows with calves (Kunkel and Pletscher 2000; Dussault et al. 2005), with avoidance of open areas with sparse cover during the day (Bjørneraas et al. 2011). Likely in consequence, harvest success may also increase in sparser forested areas near forest disturbances where hunters have greater visibility (Brinkman et al. 2009; Lebel et al. 2012). Additionally, roads have also been associated with higher moose density at larger spatial scales (Brown 2011; Beyer et al. 2013) and they provide access to moose habitat for hunters, which may result in increased harvest (Rempel et al. 1997; Schmidt et al. 2005).

We generated landscape variables using the Ontario land cover classification (Anonymous 2004), which was updated with annual forest harvest and wildfire layers available from the MNRF to integrate year-specific landscape changes. We derived landscape variables from raster layers as a percent area covered for each WMU based on year included in the study. We conducted all spatial analysis involving covariate data extraction using ArcMap ver. 10.2.2 (ESRI 2014).

Statistical analysis

We evaluated the linear relationship between annual moose harvest and aerial survey-based moose abundance using linear mixed-effect models (LMER) in R package *lme4* version 1.1-21 (Bates et al. 2015). Due to multiple years of sampling within WMUs, both random effects of WMU (to accounting for spatial variability) and year (to account for temporal variability) were included in each model. To address anticipated differences in H–A across sex and age-classes, we initially evaluated how abundance explained variation in harvest for bulls, cows and calves combined. An interaction term for sex and age-class (bull, cow or calf) was included to assess whether there was a significant difference in how abundance explained variation in harvest among sex and age classes. We then modelled bull, cow and calf H–A separately to further assess sex and age-specific differences in linear model fit. We used the fit of the regression line (r^2) to evaluate how well abundance explained variation in harvest and the slope of the regression line to evaluate proportional rate of change in harvest in relation to abundance.

We further assessed whether variability in harvest that was not attributed to abundance could be explained by hunter effort and weather and landscape variables using generalized additive models (GAMs; R package *mgcv* ver. 1.8-28; Wood 2011). We fit smoothing curves to predictor variables to assess non-linear relationships with harvest using thin plate regression splines and limited degrees of freedom (df) to 3 for each predictor variable to avoid model overfitting. Assessing non-linear relationships permitted us to characterize deviations from linear H–A. Nine candidate models were assessed for each sex and age-class that evaluated the role of population abundance, hunter effort, weather, landscape features and their combinations in affecting harvest. Abundance was retained in each candidate model to assess the additive effects of each variable on harvest. We additionally tested the significance of an interaction term between hunter effort and

abundance for each sex and age-class by fitting a tensor product-based smooth function for interactions to the predictors. A random effect of WMU and year was included in each model set. All predictor variables were standardized with a mean 0 before analysis and evaluated for collinearity to prevent correlated variables ($r > 0.7$; Dormann et al. 2013) from being included in the same model. GAMs were fit with a Gaussian distribution and identity link and heteroscedasticity was addressed by square-root transforming response variables after adding 0.5 to each value to account for 0s in the data (Zuur et al. 2007). Model residuals were further assessed to ensure that they were normally distributed following the transformation of response variables. During model evaluation, smooth functions were removed from predictor variables if df was equal to 1. Candidate models were compared to identify the most parsimonious model using Akaike's weights based on maximum likelihood (w_i) and difference in Akaike's information criterion (ΔAIC) (Burnham and Anderson 2002). The proportion of null model deviance explained (total sum of squares equivalent) was also evaluated for each model (Zuur et al. 2007; Wood 2011). Final model selection for bulls, cows and calves was based on model fit determined by w_i and ΔAIC (Zuur et al. 2009). If $\Delta AIC \leq 2$ for two or more models, the final model was chosen based on w_i and preference was given to the model with a lower number of predictor variables. Model coefficient estimation was conducted using restricted maximum likelihood (REML). The importance of each predictor variable and its effect on sex and age-specific H-A was further assessed by plotting component smooth functions and linear term effects for all significant ($p < 0.05$, based on Wald test) predictors in each final model (Wood 2011). Plotted GAM curves provided a visual representation of individual predictor variable effects and potential thresholds in smoothed terms based on confidence intervals (Zuur et al. 2009). All statistical analyses were conducted using R software ver. 3.5.3 (<www.r-project.org>).

Results

Relationship between harvest indices and abundance

We used 216 WMU-year samples that had both moose harvest and aerial survey data available. Return rates of harvest reports from hunters averaged 60% across WMUs and years. Fill rates of adult tags (total moose killed/total tags issued) were low across WMU-years at 35% on average for bulls and 30% for cows. Harvest success rates (total moose killed/total number of hunters) averaged 40% for bulls, 41% for cows and 3.5% for calves.

Linear regression revealed a significant interaction between moose abundance and sex/age-class (analysis of variance F value = 37.8, $p < 0.0001$), so we subsequently ran separate H–A models for bulls, cows and calves. Regression analysis revealed that a linear model relating abundance to harvest had an explained deviance of $r^2 = 0.79$ for bulls, $r^2 = 0.68$ for cows and $r^2 = 0.51$ for calves when variation among WMUs and years was accounted for. Regression coefficients, indicating the rate at which harvest increased in proportion to abundance, were highest for the bull H–A model (slope = 0.07, SE = 0.01, df = 209.1, $t = 6.5$, $p < 0.0001$), followed by the calf H–A model (slope = 0.06, SE = 0.01, df = 194.2, $t = 4.8$, $p < 0.0001$) and lastly the cow H–A model (slope = 0.02, standard error = 0.003, df = 118.6, $t = 8.2$, $p < 0.0001$) (Fig. 2-2). When the relationship between harvest and abundance was evaluated with splines, a non-linear relationship performed better than linear (df > 1) for cow H–A ($r^2 = 0.80$, $F = 37.8$, smoothed df = 1.56, $p < 0.0001$) and calf H–A ($r^2 = 0.61$, $F = 22.8$, smoothed df = 1.96, $p < 0.0001$), but linear model best described bull H–A ($r^2 = 0.88$, $F = 24.2$, smoothed df = 1, $p < 0.0001$).

Variables influencing harvest–abundance relationships

Hunter effort explained the greatest proportion of null model deviance for bull and cow harvest, while abundance explained the greatest proportion of null model deviance for calf harvest

(Table 2-2). Additive effects of hunter effort and abundance did not greatly improve deviance explained for any sex or age-class model, however, the interaction between hunter effort and abundance did improve model fit in all cases. Final models selected for bulls, cows and calves included the main effects of hunter effort and abundance, their interaction and landscape predictors (Table 2-2, 2-3). Inclusion of weather predictors in final models did not improve model deviance explained, and although ΔAIC was < 1 in the calf model that included weather predictors (Table 2-2), w_i was higher for the model that excluded weather, therefore, the most parsimonious of the two models was chosen. There was no collinearity among variables included in each model set (hunter effort, abundance and landscape) (Table A2-1), permitting the inclusion of predictor variables in final models for each sex and age-class.

In final models, bull and calf abundance had a linear effect on respective harvest, while the effect of cow abundance on harvest was positive and curvilinear at high abundance levels (Table 2-3, Fig. 2-3). Calves showed the widest range of harvest for a given abundance (Fig. 2-3). Hunter effort had an approximately quadratic relationship with harvest for bulls, cows and calves that either plateaued or decreased at high levels of hunter effort (Fig. 2-3). Calves showed the widest range of harvest for a given level of hunter effort, while the relationship was approximately linear for adult moose at lower levels of hunter effort (Fig. 2-3). A significant interaction effect between abundance and effort on harvest revealed that bull and cow harvest increased linearly with abundance as hunter effort increased, but the effect was curvilinear when hunter effort was high (Table 2-3, Fig. A2-1). Alternatively, hunter effort did not increase linearly with abundance for calves, resulting in higher calf harvest at high abundance and low effort levels, followed by approximately mid-abundance and high effort levels (Fig. A2-1). Both bull and cow harvest were also high at

high abundance and low effort levels. Cow harvest was additionally high at approximately mid-levels of hunter effort and low levels of abundance (Fig. A2-1).

Habitat variables showed a range of importance in explaining variation in harvest based on F-values, but only forest disturbance (representing < 10 year old forestry clear-cuts and burns) was significant ($p \leq 0.05$) for each sex and age-class (Table 2-3). Based on GAM response curves, the relationship between forest disturbance and harvest was curvilinear and a negative effect was significant (confident intervals non-overlapping zero) at approximately $\geq 25\%$ WMU area disturbed for bulls, $\geq 20\%$ WMU area disturbed for cows and $\geq 18\%$ WMU area disturbed for calves (Fig. 2-3).

Discussion

Whereas the use of harvest as an index of population abundance can offer a convenient alternative to direct monitoring (Morellet et al. 2007; Stephens et al. 2015), sources of variability, particularly across sex and age-classes, are rarely considered. Our findings indicated that harvest–abundance relationships may reflect differences in harvest regulations across sex and age-classes, warranting caution in the use of harvest indices as proxies of abundance for selectively harvested species. In contrast to our prediction, the use of harvest to inform on spatial and temporal variability in abundance across WMU was more justified for harvest of adult moose (i.e. bulls and cows, for which harvest was more tightly managed) than for calves. Linear H–A model fit was similar for bulls and cows, suggesting that harvest restrictions (i.e. limited number of tags) may have contributed to the proportionality found between harvest and abundance for adult moose. A positive interaction between hunter effort and population abundance, regardless of the harvest

system in place, is possible if encounter rates of moose by hunters increases proportionally with population abundance (Schmidt et al. 2005; Willebrand et al. 2011; Ueno et al. 2014). We found that an approximately positive linear interaction as hunter effort and abundance increased was most evident for bull harvest. Noise in the interaction between hunter effort and abundance for cows can explain the non-linear H–A identified in the final cow model and reveals that cow harvest was proportionally higher at high cow abundance in response to greater hunter effort. In contrast, the weak proportionality found between harvest and abundance for calves may suggest that hunter effort for calves was not directly reflective of calf abundance. Additionally, we found calf hunter effort did not greatly improve model deviance explained in calf H–A compared to calf abundance alone, despite calf harvest varying widely across abundance levels. We suggest that the number of moose hunters (i.e. hunter effort) was more influenced by the availability of tags for adult moose than the perceived abundance of calf moose in the population.

Although hunter effort was not a strong predictor of variability in calf harvest, high hunter effort for calves was evident in H–A model slopes. Calf harvest was found to be proportionally higher in relation to abundance than cow (but not bull) harvest. Selective harvest strategies that permit higher hunter effort on calves assume that the proportion of calves harvested during the harvest season is near or below the proportion susceptible to natural mortality (Boyce et al. 1999). Nonetheless, selective harvesting that restricts hunter effort for adult moose may result in higher calf harvest due to re-directed hunter effort (Sæther et al. 2001). Re-direction in hunter effort from adults to calves in our study system was particularly feasible, as number of calf tags for purchase by resident hunters was unrestricted (except in four WMU). Low proportional cow harvest detected in our study was expected, as cow harvest was maintained at low quotas (except in one WMU) in our study area. Alternatively, the high slope in H–A for bulls may reflect male-biased

harvesting where bull hunters may be more willing to continue hunting until successful compared to hunting for cows or calves (Fryxell et al. 1988; Solberg et al. 2000; Bhandari et al. 2006). Additionally, bulls may be more active than cows and calves during the hunting season that overlaps the rut (breeding season), which may result in greater success of bull harvest (Neumann et al. 2009). The varying effects of hunter effort on bull, cow and calf harvest suggest that harvest indices should not be compared across sex or age classes (i.e. to estimate age or sex ratios), which requires that the population has been equally sampled. Ensuring indices are reliable is particularly important for managing harvested species, as poorly informed management decisions can lead to the potential over or under-harvest of populations (Fryxell et al. 2010).

Our analysis of the interaction effect between hunter effort and abundance revealed that low hunter effort in WMUs with high moose abundance led to a positive effect on bull, cow and calf harvest. This interaction suggests there is high harvest success when moose abundance is high but number of hunters in a WMU is low. Additionally, the curvilinear effect of high hunter effort on H–A for all sex and age-classes suggests that the effect of hunter effort will become saturated (i.e. plateau) at a certain point, making harvest less reliable in WMUs with high hunter effort levels. A saturated effect of hunter effort on harvest was particularly evident for bulls, while the interaction between hunter effort and abundance revealed that harvest was highest just below maximal hunter effort levels. Previous studies have also suggested that hunter effort may not be linearly related to harvest (Schmidt et al. 2005) and will become saturated at high animal densities (Van Deelen and Etter 2003; Kahlert et al. 2015). A potential contributing factor to the saturation of the effect of hunter effort as population abundance increases may be a form of hunter interference, specifically high hunter densities driving animals away from heavily hunted areas (Fryxell et al. 1988). Previous studies have identified that moose will avoid areas where hunter

activity is greater during the hunting season (Rempel et al. 1997; Laurian et al. 2008), a pattern also seen for white-tailed deer (Lebel et al. 2012). Evidence of non-linear relationships between harvest and hunter effort has also led to criticism in the use of effort-corrected harvest indices (e.g. kills per hunter-day) that may result in biased estimates of population change (Schmidt et al. 2005; Willebrand et al. 2011; DeCesare et al. 2016). Our results agree with these findings and further provide evidence of variability in how hunter effort will influence harvest–abundance relationships under selective harvesting.

We also found evidence of landscape features influencing bull, cow and calf H–A across WMUs, suggesting that animal behavior and hunter decisions made during the hunting season can also impact the reliability of harvest as a proxy of abundance. Despite forestry activity typically being associated with increased access into wildlife habitat, as well as increased visibility for hunters (Rempel et al. 1997; Brinkman et al. 2009; Lebel et al. 2012), our findings indicated that moose harvest was lower in WMUs with a greater proportion of recent clear cuts and burns present. This is likely a result of moose avoiding < 10-year-old forest disturbances that provide poor cover from predators and low forage opportunity (Maier et al. 2005; Dussault et al. 2006). Additionally, hunters may avoid heavily disturbed management units or are generally less successful at harvesting moose in these units. Moose avoiding areas of higher hunter activity may also explain why roads had no effect on H–A. Hunters can choose alternative methods of travel, including boat or off-road vehicle, to access moose habitat (Schmidt et al. 2005), however, hunter access will still be constrained by distance from a road or trail (Lebel et al. 2012). Further, we found no effect of weather (i.e. temperature and precipitation) on moose H–A, corresponding with results by Lebel et al. (2012) who similarly found weather variables did not influence harvest success or detectability of animals to hunters. Because moose hunting occurred during only one climatic

season each year, and hunters could choose when during the season to hunt (e.g. during low snow cover), it is likely that variability in weather variables during time spent hunting was minimized or was not detectable within this study.

Evidence of landscape features influencing H–A highlights the importance of accounting for spatial and temporal variability when assessing harvest as an index of abundance, and that accounting for variability in the effect of hunter effort alone may be insufficient. Any source of population monitoring should consider factors that can influence monitoring precision, in addition to accuracy, over time and space to be a reliable index of population change (Anderson 2001; Morellet et al. 2007; Stephens et al. 2015). Mandatory reporting of harvest information may further improve the accuracy of harvest indices and may help future studies reveal additional patterns influencing H–A not detected in this study. It is likely that we did not test all factors that may influence H–A for moose and future studies may expand on this analysis to address other confounding variables, such as the influence of firearm type on harvest success.

Further, while our analyses provided evidence that a general pattern of abundance across space could be detected with harvest, we did not evaluate whether harvest reflected population dynamics (i.e. trends over time). Previous studies have suggested that even when a relationship between harvest and abundance can be identified, harvest may still not be a proper index for assessing population parameters such as WMU specific population trends, recruitment, sex ratios etc. (Ranta et al. 2008; Ueno et al. 2014). Unless proportionality between harvest and abundance over time is validated at the WMU scale, harvest may be best used to supplement monitoring or be integrated as a parameter in models that can provide better estimation of population change (e.g. time-to-event Weibull regression; Schmidt et al. 2005). Also, it is important to note that our results are likely both species and scale dependent, and the influence of different predictors on

harvest may vary according to the species and spatial scale (Pettorelli et al. 2007; Imperio et al. 2010). Nonetheless, this study highlights the importance of assessing how well harvest reflects abundance across sex and age-classes that experience different levels of hunter effort.

Conclusion

Here we demonstrate that the relationship between harvest and abundance can vary by sex and age-class within a species in response to selective harvesting. Restricted harvest of adult moose performed better as an index of abundance than the less regulated calf harvest that was prone to higher hunter effort by hunters. Abundance alone explained 79% of variation in harvest for bulls, 68% for cows and 51% for calves. Although there was greater proportionally found between harvest and abundance for adult moose, we identified that harvest is likely to underestimate abundance in WMUs with highest hunter effort. We additionally identified that the relationship between harvest and abundance was not driven by hunter effort alone and can be affected by spatial variability in landscape features that have the potential to influence the detectability of animals to hunters, and consequently, harvest success. We found that harvest is likely to underestimate abundance in WMUs with a higher proportion of recent (< 10 year old) forest disturbances (including clear-cuts and wildfire burns). Whereas hunter effort can be regulated by management, factors influencing success rates by hunters are less easily managed, adding complexity to the application and reliability of harvest as a proxy of abundance. If harvest is used as a proxy to detect change in population abundance, managers should not ignore variability in hunter effort, both across and among sex and age-classes, as well as temporal and spatial variability in the landscape (Bhandari et al. 2006; Kahlert et al. 2015). We caution that harvest may act better as a

supplementary index to inform on spatial variability in population abundance rather than as a substitute for direct monitoring approaches for species that experience selective harvesting.

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Tables and Figures

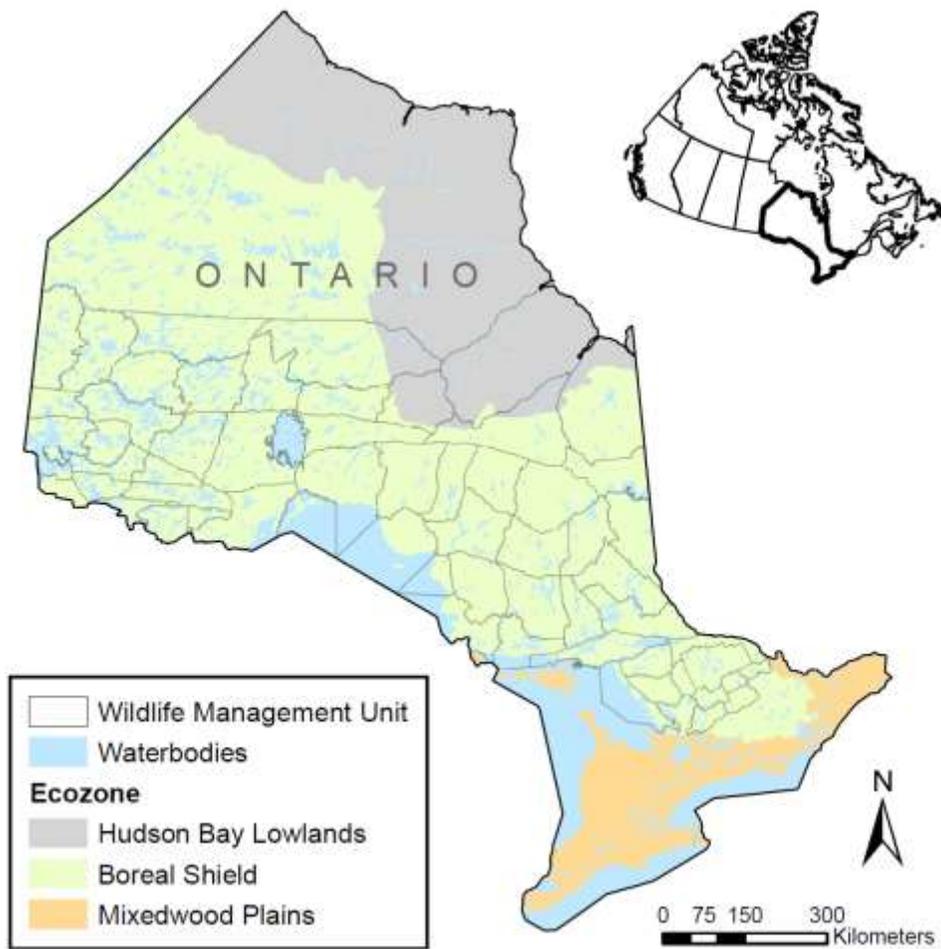


Figure 2-1. Map outlining the wildlife management units in Ontario, Canada included in the study.

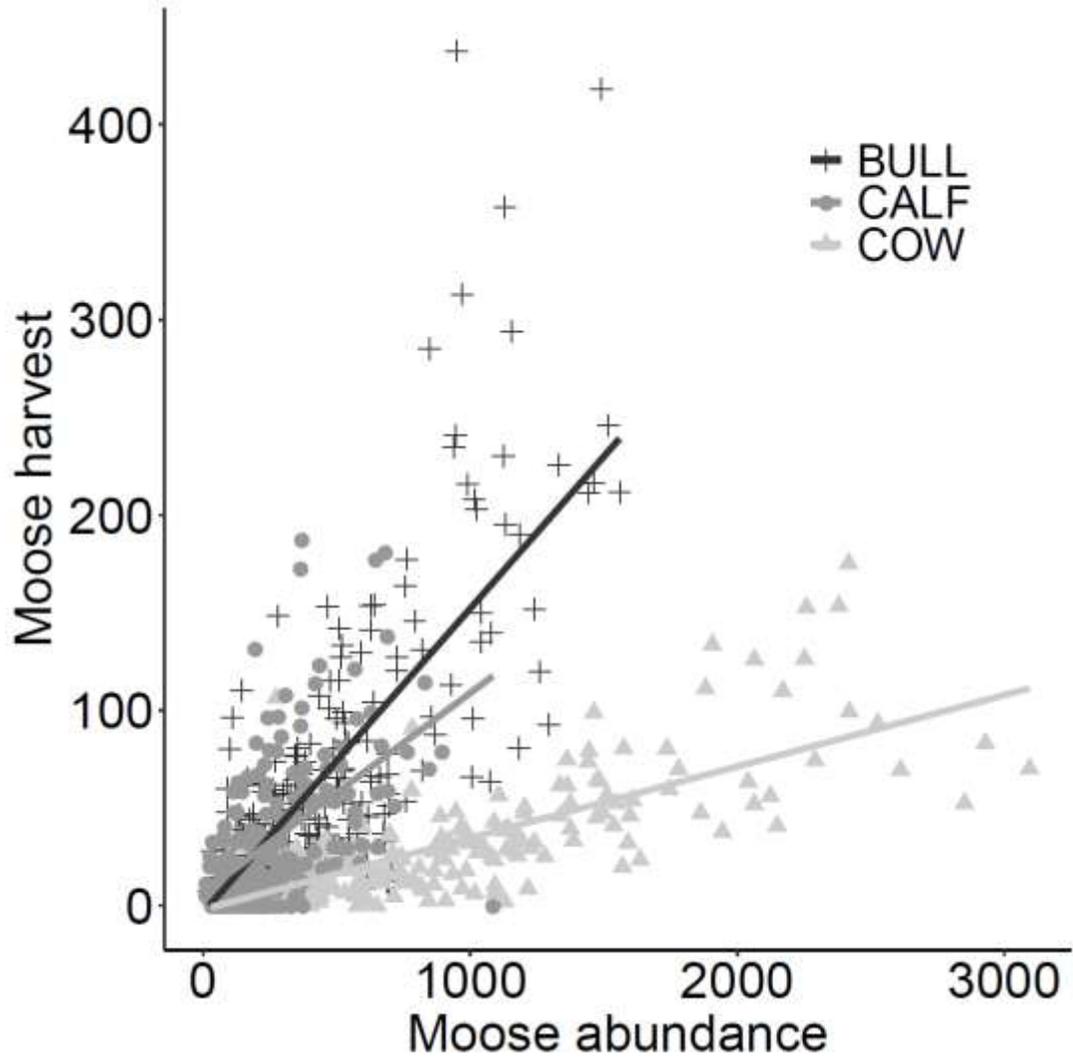


Figure 2-2. Linear relationship between moose harvest and abundance for bulls, cows and calves.

The slope of each regression line was significantly different from zero ($p < 0.0001$).

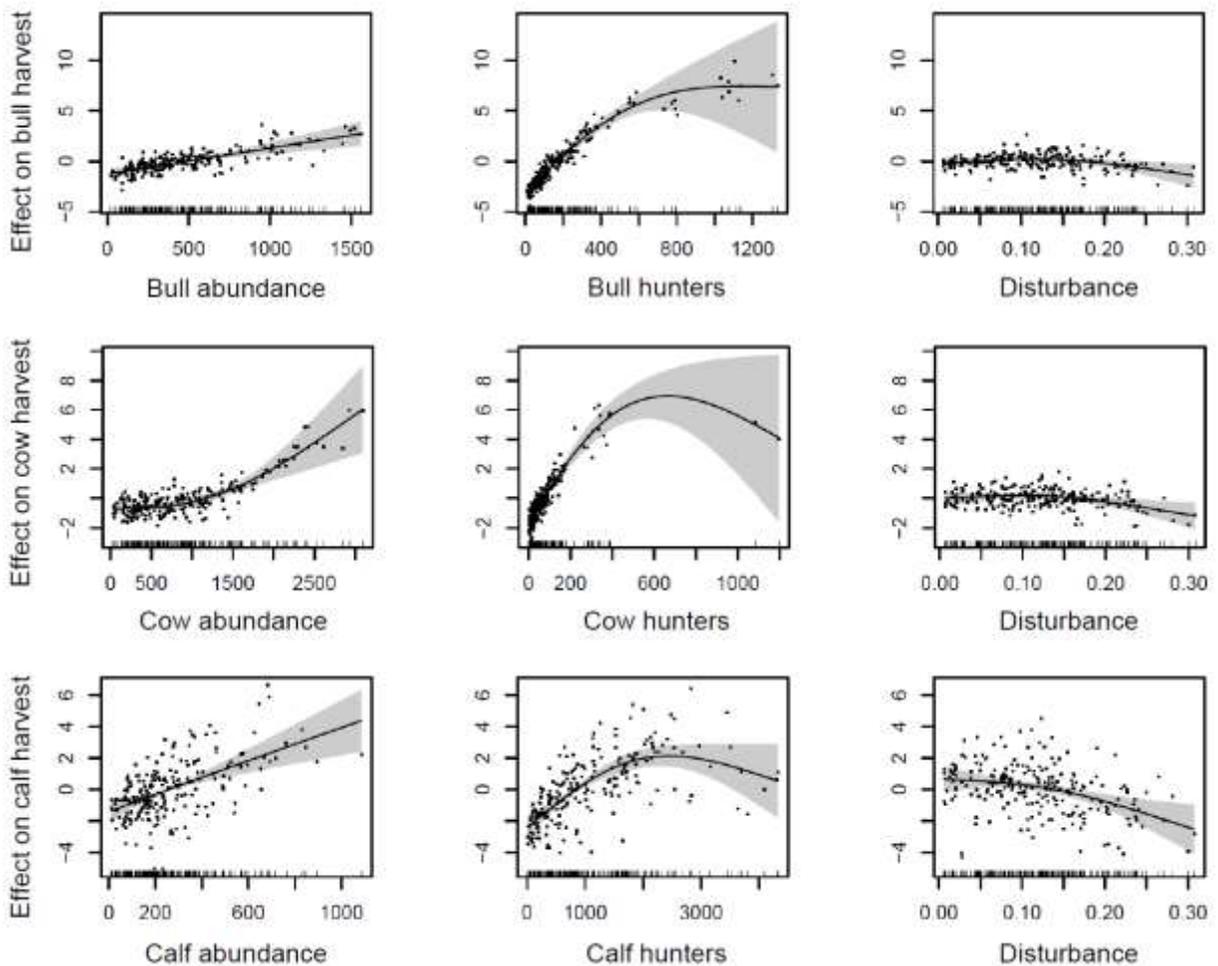


Figure 2-3. Generalized additive model response curves describing the combined additive effects of abundance (first column), hunter effort represented by number of hunters (second column) and forest disturbance of recent clear-cuts and burns (last column) on bull (top row), cow (middle row) and calf (bottom row) harvest. Each row corresponds to a separate model. Mean response of each variable (solid line) and 95% confidence intervals (gray areas) are indicated and integrate random effects of wildlife management unit and year. Dots indicate residuals of each effect on sex and age-specific harvest. Smooth terms were fit using thin plate regression spline with 3 degrees of freedom. Tick marks on the x-axis of each plot correspond to sample observations.

Table 2-1. Model variables predicted to influence the linear relationship between moose harvest and abundance. Means, standard error (\pm SE) and range of values for each variable are based on all Wildlife Management Units (WMUs) and years included in the study (n=216).

Predictor set	Variable	Description	Mean	\pm SE	Range
Abundance	Bull abundance	number of bull moose	487	23	22 – 1560
	Cow abundance	number of cow moose	871	43	30 – 3095
	Calf abundance	number of calf moose	261	13	10 – 1086
Hunter effort	Bull hunters	number of bull hunters	201	17	9 – 1332
	Cow hunters	number of cow hunters	85	9	1 – 1197
	Calf hunters	number of calf hunters	1083	63	8 – 4323
Weather	Temperature	average maximum temperature ($^{\circ}$ C) during the hunting season	10.1	0.157	15 – 2
	Precipitation	average precipitation (mm) during hunting season	88.3	2.8	25 – 224
Landscape	Dense	% continuous forest canopy	0.19	0.005	0.02 – 0.41
	Sparse	% patchy or sparse forest canopy	0.13	0.005	0.03 – 0.31
	Mixed-deciduous	% mixed deciduous forest	0.11	0.004	0.02 – 0.30
	Disturbance	% < 10-year-old forest clear-cuts and burns	0.12	0.004	0.01 – 0.31
	Roads	% major roads and development (including forestry roads)	0.005	0.0003	0 – 0.02

Table 2-2. Model comparison with ΔAIC , Akaike weights (w_i) and % deviance explained for each generalized additive model fit using maximum-likelihood and analyzed with a random effect of wildlife management unit and year.

Model	Bull			Cow			Calf		
	ΔAIC	w_i	Deviance explained (%)	ΔAIC	w_i	Deviance explained (%)	ΔAIC	w_i	Deviance explained (%)
Abundance	196	0	91.3	207	0	84.7	57	0	70
Effort	64	0	94.9	63	0	92.6	49	0	67.7
Weather	185	0	91.9	170	0	88.2	75	0	68.7
Landscape	179	0	92	172	0	87.9	64	0	68.9
Abundance + Effort	54	0	95.1	63	0	92.3	30	0	71
Abundance + Effort + Abundance*Effort	10	0	96.4	6	0	94.5	3	0	75.8
Abundance + Effort + Abundance*Effort + Weather	12	0	96.4	9	0	94.4	4	0	75.8
Abundance + Effort + Abundance*Effort + Landscape	0	1	96.6	0	1	94.6	0	1	75.4

Abundance + Effort									
+ Abundance*Effort	3	0	96.6	3	0	94.6	1	0	75.4
+ Weather + Landscape									

Note: AIC, Akaike's information criterion;
 *interaction term fit using a tensor product-based smooth function

Table 2-3. Generalized additive model (GAM) results for final bull, cow and calf harvest models fit using restricted maximum likelihood. Results include either linear or smooth effect terms for predictor variables in each model. All smoothed predictors were fit using thin plate regression splines and the interaction between hunter effort and abundance was fit using a tensor product-based smooth function.

Variable	Linear terms				Smooth terms		
	Estimate	SE	t-value	P-value	df	F	P-value
Bull							
Intercept	6.34	0.38	16.52	< 0.0001			
Abundance	0.00	0.00	4.19	< 0.0001			
Effort					1.92	82.54	< 0.0001
Dense					1.58	0.49	0.5
Sparse	-0.16	0.17	-0.95	0.3			
Mixed-deciduous					1.77	2.01	0.2
Disturbance					1.83	3.34	0.02
Roads	0.29	0.17	1.67	0.1			
Abundance* Effort					9.44	4.08	< 0.0001
WMU					40.14	4.94	< 0.0001
Year					10.21	3.32	0.01
Cow							
Intercept	5.06	0.17	29.16	< 0.0001			
Abundance					1.89	12.76	< 0.0001
Effort					1.97	66.62	< 0.0001
Dense	-0.08	0.12	-0.67	0.5			
Sparse					1.51	0.34	0.6
Mixed-deciduous	0.08	0.11	0.72	0.5			
Disturbance					1.83	2.74	0.05
Roads					1.70	2.34	0.2
Abundance* Effort					8.94	7.02	< 0.0001
WMU					35.80	2.92	< 0.0001
Year					9.21	2.72	0.002
Calf							
Intercept	3.63	0.36	10.15	< 0.0001			
Abundance	0.01	0.00	4.42	< 0.0001			
Effort					1.94	22.13	< 0.0001

Dense	-0.22	0.20	-1.11	0.3			
Sparse					1.47	0.26	0.6
Mixed- deciduous	-0.30	0.21	-1.40	0.2			
Disturbance					1.78	4.44	0.01
Roads					1.85	3.16	0.08
Abundance* Effort					5.67	6.68	< 0.0001
WMU					25.47	0.97	0.0003
Year					7.18	1.09	0.03

Appendix

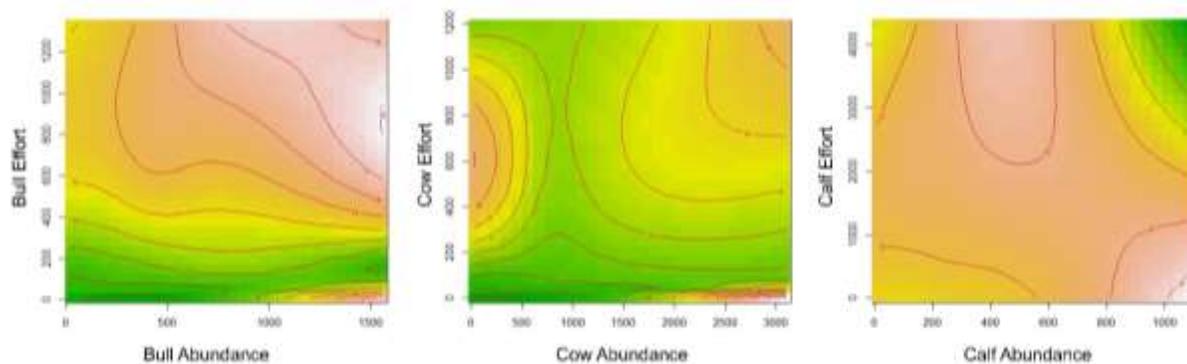


Figure A2-1. The interactive effects of abundance and effort on moose bull, cow, and calf harvest. Contour lines represent strength in interaction (with numbers indicating positive or negative interaction effects) on the response (harvest). Colours aid in visualizing the strength in the effects, with yellow, pink and white reflecting increasingly strong interaction effects and green reflecting relatively weak interaction effects. Axes are based on un-transformed values of each variable.

Table A2-1. Pearson's correlation values for all pairs of predictor variables included in model selection of moose bull, cow and calf harvest. Only abundance and effort variables varied by sex and age-class. All values reflect samples for WMU and years included in the study (n = 216).

Bull									
	Abundance	Effort	Max temp	Precipitation	Dense	Sparse	Mixed-deciduous	Disturbance	Roads
Abundance	1.00	-	-	-	-	-	-	-	-
Effort	0.63	1.00	-	-	-	-	-	-	-
Max	-0.21	-0.16	1.00	-	-	-	-	-	-
Precipitation	-0.14	-0.11	0.01	1.00	-	-	-	-	-
Dense	-0.01	0.08	-0.22	-0.14	1.00	-	-	-	-
Sparse	-0.05	-0.21	0.04	-0.02	-0.35	1.00	-	-	-
Mixed-deciduous	0.05	0.19	0.32	0.09	-0.11	-0.05	1.00	-	-
Disturbance	0.37	0.37	-0.18	-0.09	-0.02	-0.26	0.10	1.00	-
Roads	0.42	0.53	0.19	-0.01	0.04	-0.02	0.35	0.23	1.00
Cow									
	Abundance	Effort	Max temp	Precipitation	Dense	Sparse	Mixed-deciduous	Disturbance	Roads
Abundance	1.00	-	-	-	-	-	-	-	-
Effort	0.53	1.00	-	-	-	-	-	-	-
Max	-0.15	-0.08	1.00	-	-	-	-	-	-
Precipitation	-0.13	-0.05	-	1.00	-	-	-	-	-
Dense	-0.05	-0.04	-	-	1.00	-	-	-	-
Sparse	-0.05	-0.11	-	-	-	1.00	-	-	-
Mixed-deciduous	0.10	0.18	-	-	-	-	1.00	-	-
Disturbance	0.42	0.30	-	-	-	-	-	1.00	-
Roads	0.50	0.32	-	-	-	-	-	-	1.00
Calf									
	Abundance	Effort	Max temp	Precipitation	Dense	Sparse	Mixed-deciduous	Disturbance	Roads
Abundance	1.00	-	-	-	-	-	-	-	-
Effort	0.45	1.00	-	-	-	-	-	-	-
Max	-0.11	0.19	1.00	-	-	-	-	-	-
Precipitation	-0.16	0.06	-	1.00	-	-	-	-	-
Dense	0.04	-0.07	-	-	1.00	-	-	-	-
Sparse	0.03	-0.01	-	-	-	1.00	-	-	-
Mixed-deciduous	0.08	0.58	-	-	-	-	1.00	-	-
Disturbance	0.24	0.18	-	-	-	-	-	1.00	-
Roads	0.43	0.61	-	-	-	-	-	-	1.00

Chapter Three: Habitat quality mediates demographic response to climate in a declining large herbivore

Abstract

Understanding the interacting role of climate and habitat in shaping wildlife population dynamics can help to reveal synergistic pathways that drive population resilience or decline across variable and changing environments. Moose (*Alces alces*) is a pan-boreal herbivore experiencing population declines across large portions of North America; however, the species has shown variable response to climate across its distribution. We investigated moose demographic response to climate and evaluated the interacting role of habitat across 36 years and along a biogeographic gradient in Ontario, Canada that has experienced decadal changes to climate and habitat quality. Moose density exhibited a nonlinear trend that initially increased and then decreased over the study timeframe and was negatively affected by regional and local patterns of winter severity and later frost onset. Recruitment exhibited a monotonic decline and was positively affected by spring heat and deciduous forest cover, while also exhibiting density-dependent effects. The negative response of moose density to winter severity was reduced in Wildlife Management Units (WMUs) with higher proportions of dense canopy cover, supporting expectations that this habitat type improves moose winter mobility and predator avoidance. The negative effect of later frost onset was greater in WMUs with more regenerating forest, and both variables are associated with higher exposure to parasites and predators. Further, density-dependent effects on recruitment were suppressed by warmer springs that support vegetation productivity and in WMUs with higher proportions of dense canopy cover that can provide concealment from predators. Our study illustrates the

important role habitat conditions can have to mitigate, or exacerbate, climate-change effects for a wide-spread herbivore occupying variable environments by potentially altering pathways relevant to energetic balance, predation, and parasite transmission. In this system, moose occupying sparse or regenerating forests are more susceptible to adverse climatic effects and should be managed accordingly.

Introduction

Anticipating and managing the impacts of climate change requires an understanding of the mechanisms driving population-level responses (Hughes 2000). Climate can exert both direct and indirect effects on wildlife populations and may involve multiple mediators acting concurrently. For example, there is growing evidence that species are more susceptible to adverse climatic effects in areas of poor habitat quality in human-altered landscapes (Travis 2003), and where habitat quality has been degraded due to climate change (Northrup et al. 2019). In extreme cases, concurrent changes in climate and habitat can result in ecosystem shifts that shape interspecific interactions, such as predation and competition, with consequences for population density and distribution (Peers et al. 2020; Platts et al. 2019). Isolating interacting from additive climate-habitat effects is therefore integral to revealing the environmental conditions that promote population resilience or decline (Brook et al. 2008; Mantyka-Pringle et al. 2012).

Moose (*Alces alces*) is a large herbivore species that occupies variable environments in temperate and boreal regions. The species is experiencing population declines across some regions in North America, particularly in central Canada and northern USA (Arsenault et al. 2020;

DeCesare et al. 2014; Timmermann and Rodgers 2017), and there is evidence of northward range shifts across southern portions of their continental range (Lenarz et al. 2009). Observed population changes might be attributed to warming seasonal temperatures and associated heat stress, particularly in summer and spring (Lenarz et al. 2009; Monteith et al. 2015; Murray et al. 2006; Rempel 2011); however, population responses to climate have varied with some studies showing moose population persistence and range expansion in previously perceived poor environmental conditions (Darimont et al. 2005; Laforge et al. 2017; Murray et al. 2012). One hypothesis is that moose populations can persist where dense forest canopy is used to mediate heat stress (Melin et al. 2014; van Beest et al. 2012). Additionally, moose, particularly cows with calves, use dense forest cover in the winter to avoid deep snow that can reduce mobility and increase energy expenditure needed to browse and avoid predators (Dussault et al. 2005).

Moose declines have also been attributed to range expansions of white-tailed deer (*Odocoileus virginianus*). Both moose and white-tailed deer are positively associated with deciduous and early seral forest following forestry activity that provides high quality forage (Bowman et al. 2010; Fisher and Wilkinson 2005), despite trade-offs with increased predation risk (Francis et al. 2021). White-tailed deer range overlaps much of the southern distribution of moose in North America (Weiskopf et al. 2019) and their range is expected to expand northward in response to shorter winters with decreased snow depth (Dawe and Boutin 2016; Fisher et al. 2020). The northern expansion of white-tailed deer may suppress moose populations through apparent competition, a process whereby increasing abundance of one prey species indirectly decreases the abundance of another through the numerical response of a shared predator (Holt 1977). Apparent competition is believed to be a proximal cause of boreal woodland caribou (*Rangifer tarandus caribou*) declines throughout much of Canada (Frenette et al. 2020; Latham et al. 2011), and has

been hypothesized as a possible cause of moose declines in eastern North America (Barber-Meyer and Mech 2016). Thus, habitats that support both moose and white-tailed deer and consequently, more predators, may host greater adverse effects of reduced winter severity on moose.

Moreover, white-tailed deer can host two parasites, winter tick (*Dermacentor albipictus*) and meningeal worm (*Parelaphostrongylus tenuis*) that may be leading causes of mortality in moose in eastern North America (Jones et al. 2019; Lankester 2018; Ranta and Lankester 2017). High tick infestations can lead to blood loss, over-grooming, and hair loss (Fig. A3-1) that can influence a moose's ability to thermoregulate during the winter (Jones et al. 2019; Samuel 2007); whereas meningeal worm infestation leads to neuromotor impairment (Lankester 2018). Both winter tick and meningeal worm are transmitted to moose prior to frost onset in late summer/fall, and larval drop-off occurs in early spring with larval survival declining with the presence of snow and freezing temperatures (Lankester 2018; Pickles et al. 2013; Samuel 2007). Milder winters are therefore expected to increase the exposure of moose to parasites due to prolonged transmission (i.e. loading) periods, increased larval survival in the spring, and greater white-tailed deer densities, particularly in habitats optimal to both herbivores (Ditmer et al. 2020; Lankester 2018; Pickles et al. 2013). However, the role of climate-habitat interactions on parasite-mediated population response in moose is not well understood and requires further study.

In this study, we investigate the impacts of climatic stressors on moose demographics and identify the capacity of habitat quality to mediate climate effects. We focused on two population responses, moose density and mid-winter recruitment of calves, across 36 years and 50 wildlife management units (WMUs) in Ontario, Canada that captured large-scale spatio-temporal variability in both demographic parameters (Fig. 3-1). Moose populations were monitored annually along a north-south productivity gradient, facilitating an analysis of naturally occurring

variation of both habitat (Fig. A3-2) and climate (Fig. A3-3) that has undergone changes due to development and climate warming throughout the study period. Climatic stressors in our study area occur seasonally and are likely to impact moose through similar processes at each life stage (Fig. 3-2). We additionally tested the impact of the North Atlantic Oscillation (NAO) index as a regional measure of winter severity on moose population demographics. Our analysis focused on three habitat types, including dense canopy cover, deciduous forest cover and regenerating forest, which are associated with higher moose adult and calf density and are expected to mediate direct and indirect climatic effects on the population. We hypothesized that: (1) dense canopy cover mitigates adverse climatic effects on the population in response to direct thermoregulatory benefits, increased mobility, and improved predator avoidance; and (2) occupying deciduous forest and regenerating forest following forestry activity exacerbates adverse climatic effects on the population in response to increased risk of predation and parasite transmission. Additionally, we expected recruitment to be density-dependent in our study area (Brown 2011) and hypothesized that (3) climate and habitat variables that increase moose survival would suppress density-dependent effects on recruitment.

Materials and Methods

Study area

Our study area in central Canada encompassed approximately 395,000 km² and spanned 7° latitude from southern to northern Ontario. The climatic gradient varies from mild in the southern temperate region to cold in the northern boreal region. In the south, daily winter (i.e. January and

February) temperatures averaged -6 °C to -12 °C, while summer temperatures (i.e. June and July) averaged 20 °C to 23 °C, and growing season length was approximately 188 to 198 Julian days. In the north, daily winter temperatures were on average -14 °C to -20 °C with average summer temperatures of 18 °C to 20 °C and average growing season length of 167 to 182 Julian days. Winter precipitation also varied largely, with average accumulated snowfall depths of 119 to 164 mm in the south and 344 to 468 mm in the north; winter snow depth tends to be deeper around large lakes where local conditions result in lake-effect snow.

Forest structure in our study area transition from predominantly deciduous Great Lakes-St. Lawrence forest in the south, to mixed deciduous and coniferous boreal forest in the north (Fig. A2-2). Large portions of the study area were composed of continuous forest, exposed bedrock, lakes, and rivers typical of boreal ecosystems. The landscape was maintained, in part, through natural forest disturbance such as wildfire, which was more prevalent in the northwest portion of the study area. Much of the study area was managed for commercial forestry, resulting in a mosaic of forest ages arising from both natural and anthropogenic disturbance. The resulting forest mosaic supported moose, white-tailed deer, woodland caribou, elk (*Cervus canadensis*), and their shared predators: grey wolves (*Canis lupus*) and black bear (*Ursus americanus*). Moose and deer were the most abundant large herbivores throughout most of the study area. Moose ranged in density from 0.015 to 0.98 moose/km² (this study). White-tailed deer were uncommon in the northern portion of the study area but, where they occurred, were often more numerous than moose (0.01 to 9.2 deer/ km²; Whitlaw and Lankester 1994). Caribou primarily occurred in low densities in the northern portion of the study area, whereas elk were located in a small number of discrete herds. Wolves and black bears occurred across the study area and were generally more numerous in productive portions of the landscape (Howe et al. 2013; Patterson et al. 2004).

Population data

Moose density and recruitment (calf to cow ratio) data were obtained from the Ontario Ministry of Natural Resources and Forestry (MNR). We focused our study on plot-based aerial surveys conducted between 1980 and 2015 (McLaren 2006). The moose population in Ontario was managed with a sex- and age-selective harvest system initiated across the province in the early 1980's (Priadka et al. 2020). Aerial surveys were conducted in the winter following the fall hunting season (September to December) and took place at the WMU scale approximately every 3 to 5 years. All moose data included in our analysis was collected by helicopter using a stratified random sampling approach of 25 km² plots. Survey conditions were standardized to reduce observer bias in relation to inclement weather, snow conditions, time of a day, and other factors that may affect moose behavior and detectability (McLaren 2006). To further reduce error in population estimates, we removed surveys that had less than 20 plots flown for a given WMU. Moose density was calculated for each survey by summing the products of the average number of moose in each stratum by the corresponding number of plots in that stratum. Our final dataset included a total of 471 samples of moose density and recruitment collected over 50 WMU and 36 years.

Climate data

The North Atlantic Oscillation (NAO) index reflects interannual air pressure oscillations that drive regional variation in climatic variables such as winter wind, precipitation, and temperature from subtropical to subpolar regions across the North Atlantic (Hurrell 1995). In central North America, NAO has been positively related to warmer winters, reduced winter precipitation, increased plant productivity, and improved herbivore nutrition (DeWitt et al. 2017; Ottersen et al. 2001; Vucetich and Peterson 2004). We obtained yearly winter (December – March average) NAO

index values from <https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-station-based>.

We characterized local variation in climate by calculating WMU-specific climate indices predicted to influence moose density and recruitment over time. Based on our study system (Fig. 3-2), we created indices as continuous variables of winter severity (WINT), onset of spring thaw (THAW), spring-snow (DROP), spring severity (SPR), summer heat stress (SMR), and the onset of fall frost (FROST) (Table 3-1). Three climate indices: WINT, DROP and SPR, were created using North American Regional Reanalysis climate data provided by NOAA's Physical Sciences Laboratory (Boulder, Colorado, USA) obtained from <https://psl.noaa.gov/>. NARR climate data were high-resolution Network Common Data Form files for years 1979 to 2014. The three climate indices: SMR, THAW, and FROST, were derived from spatial grids provided by Natural Resources Canada (McKenney et al. 2007). Descriptions of each index is included in Table 3-1. As density and recruitment data were collected in the winter (December – March) each year, we calculated climate indices for the year preceding moose data collection, and at one- and two-year time lags. If climate data were not available for the full time-lag interval, we averaged values across available years. All climate indices were summarized by WMU and year using ArcMap version 10.5 (Environmental System Research Institute Inc., Redlands, CA, USA) and R software version 4.0.2 (R Core Team 2020).

Habitat data

Habitat was characterized as continuous variables for each WMU and year using two data sources. We obtained a land cover classification (28 classes) derived from multispectral Landsat Thematic Mapper data collected from 1986 to 1997 (MNR 2000). Additionally, we obtained annual forestry activity layers (including clear-cuts, partial cuts, and associated logging roads)

from the MNRF. We then used the combined data sources to summarize habitat quality across both time and space, including up to a three-year time lag between forestry activity. For each WMU and year, we calculated the proportion of continuous deciduous and coniferous forest canopy cover (COVER), proportion of continuous deciduous forest cover (DECID), and proportion of regenerating forest following recent (≤ 10 -year-old) forestry activity (REGEN) (Table 3-1). Because we were primarily interested in terrestrial habitats, we excluded lakes and rivers when calculating land-cover proportions.

Mixed-effect regression modelling

We modelled moose density and recruitment as a gamma process, $Y_{it} \sim \text{Gamma}(\mu, \sigma)$, where the Y_{it} is the population response at WMU i during year j . We estimated μ and σ using a log link to account for the fact that population density and recruitment are continuous non-zero values for a given WMU. We included year as a predictor variable to account for and predict trends in density and recruitment over time and included a random intercept for each WMU to account for correlated error structure arising from repeated sampling of the same unit. Statistical models were estimated using generalized linear mixed-effect models (GLMMs) in R package *lme4* (Bates et al. 2015).

We used a multi-step process to test the importance of our six local climate indices (Fig. 3-2), NAO, and three habitat variables in explaining moose density and recruitment (Table 3-1). First, we compared the model fit of linear versus two-term polynomial year effects for density and recruitment and identified the most parsimonious model using Akaike's information criterion corrected for small sample sizes (AICc; Hurvich and Tsai 1989). Second, we ranked models of individual climate indices and selected those that outperformed the best fitting year-only models. We then estimated a series of climate models that combined year with selected climate indices and selected the most parsimonious model using AICc and normalized AIC weights (AIC_w) (Burnham

and Anderson 2002). All predictor variables were standardized (mean = 0, sd = 1) prior to model construction to facilitate comparisons among variables. We additionally screened variables based on their biological appropriateness and multicollinearity ($-0.5 < \text{Pearson's } r < 0.5$) with other variables (Table A3-1). Third, once we selected the most parsimonious climate models for density and recruitment, we tested two additional model sets for each response; one set with habitat variables included as additive terms and a second set with habitat variables included as two-way interactions with each climate index. Habitat variable interactions were only assessed for local climatic indices (excluding NAO) based on hypothesized relationships (Table 3-1). We also tested the effect of density-dependence on recruitment by introducing moose density (DEN) as a predictor in recruitment models and assessed interacting effects between DEN and climate indices selected in the second step, and DEN and habitat variables. Finally, we conducted model averaging in each model set for models with $\Delta\text{AICc} \leq 2$ (Anderson 2007) and identified informative parameters based on whether 95% confidence intervals overlapped with zero (Arnold 2010). Marginal effects of climate-habitat models were visualized using R package *ggeffects* (Lüdtke 2018).

Results

Marginal trends in moose density and recruitment

Our analysis of year effects indicated that regional change in moose population density was non-linear with abundance increasing in the 1980's, peaking in approximately 2000, then declining until the end of our study period in 2015 ($R^2 = 0.54$; Table 3-2; Fig. 3-1; Fig. 3-3). Regional

recruitment (number of calves per cows) declined linearly at a rate of 2.6% per year over the same period ($R^2 = 0.46$; Table 3-2; Fig. 3-1; Fig. 3-3). The fit of null models indicated that there was substantial spatial variation in these trends across WMUs (density null model $R^2 = 0.45$; recruitment null model $R^2 = 0.20$; Fig. 3-1).

Climate and habitat effects on demographic response

Model selection revealed that moose density was best explained by a polynomial year effect, a positive association with NAO with a one-year time lag, and by negative associations with winter severity with a two-year time lag and frost onset (Fig. 3-4; Table 3-3; Table A3-2). Habitat variables improved the fit of climate-only models of moose density (Table A3-3); however, they were not informative (Table 3-3). Model selection revealed that recruitment was best explained by a negative association with year and moose density and a positive association with spring severity (Fig. 3-4; Table 3-3; Table A3-2). Again, habitat variables improved the fit of climate-only models (Table A3-3). Deciduous forest cover had a positive effect on recruitment (Fig. 3-4), whereas dense forest cover and regenerating forest were non-informative (Table 3-3).

The best fitting interacting climate-habitat models for both moose density and recruitment outperformed the best fitting models with additive climate and habitat terms (density $\Delta AICc = 3.3$; recruitment $\Delta AICc = 11.1$; Table A3-3, Table A3-4) and for climate alone (density $\Delta AICc = 7.9$; recruitment $\Delta AICc = 13.8$; Table A3-2, Table A3-4). Our analyses showed that winter severity (with a two-year time lag) had a reduced negative effect on moose density in WMUs with higher proportions of dense canopy cover ($\beta_{WINT(t-2) \times COVER} = 0.05$, $SE = 0.02$; Table 3-3; Fig. 3-5), consistent with our hypothesis that dense canopy cover reduces adverse climatic effects. Meanwhile, frost onset had a greater negative effect in WMUs with higher proportions of regenerating forest ($\beta_{FROST \times REGEN} = -0.04$, $SE = 0.02$; Table 3-3; Fig. 3-5), supporting our

hypothesis that regenerating forest associated with forestry activity exacerbates adverse climatic effects. Our analyses further showed that population density had a reduced negative (i.e., density-dependent) effect on calf recruitment during warmer springs ($\beta_{\text{DEN} \times \text{SPR}} = 0.04$, SE = 0.02; Table 3-3; Fig. 3-5) and in areas with higher proportions of dense-canopy cover ($\beta_{\text{DEN} \times \text{COVER}} = 0.06$, SE = 0.02; Table 3-3; Fig. 3-5). Contrary to our hypothesis, the interaction between spring severity and dense canopy cover was not informative (Table 3-3).

Discussion

Understanding the roles of additive and interacting climate-habitat effects can inform on the environmental conditions that support population resilience or decline (Brook et al. 2008; Mantyka-Pringle et al. 2012). Our results show that population response to climate in a large herbivore differed by habitat type. These findings provide supporting evidence for synergistic pathways associated with energetic and mobility limitations, and interspecific interactions that influence rates of predation and parasite transmission.

At a regional scale, the trend in moose density across the study area was nonlinear, consistent with studies from central (Arsenault et al. 2020) and western (Kuzyk et al. 2018) Canada. Our study provides additional support that long-term population dynamics in moose density are partially driven by previous years' NAO (Vucetich and Peterson 2004), and shows that climate can have an important role in driving large-scale dynamics in harvested moose populations. Climatic oscillations such as the NAO and Northern Pacific Oscillation (NPO) influence large portions of North America and could have widespread effects on moose population dynamics

across the species' continental distribution. While synchrony in population trends is less studied for moose, previous studies have attributed region-wide climate reflected in large-scale indices such as NAO with synchrony in large herbivore population trends across geographically large distributions (Grøtan et al. 2005; Post and Forchhammer 2002). By further evaluating local climate variables and their interaction with habitat, we were able to isolate local demographic drivers from distribution-wide demographic responses to better explain spatio-temporal demographic variability.

We found that local winter severity had a negative effect on moose population density, and this effect was reduced in areas with dense canopy cover. This finding supports our hypothesis that dense canopy can be effective at off-setting negative winter effects on moose. Our finding of a two-year lag in the effect of winter severity on moose population response is supported by previous studies that have identified delayed effects of both large- (Forchhammer et al. 2002; Laforge et al. 2017; Vucetich and Peterson 2004) and fine-scale (Grøtan et al. 2009; Patterson and Power 2002) winter processes on large herbivores. The effects of winter severity on large herbivore populations have been previously identified to act cumulatively over years (Lenarz et al. 2009; Patterson and Power 2002) and may interact with other seasonal climatic effects to mitigate or exacerbate population response (Rempel 2011). In our study area, winter severity (WINT) was positively correlated with spring snow presence and colder temperatures (DROP). Therefore, the direct negative effects of severe winters on moose populations may have been balanced by reduced parasite survival and transmission to moose the following fall. Further, moose populations in areas with sparse forest cover may have been more susceptible to adverse winter effects due to increased fitness requirements needed to move through deep snow (Dussault et al. 2005) and due to higher exposure to parasite transmission in open areas (Healy et al. 2018). Moose experiencing high

parasite loads are also more susceptible to reduced health (Jones et al. 2019) and mobility to forage and avoid predation, which is likely aggravated during colder winters with more precipitation. Additionally, we evaluated population-level responses that may take longer to be detected when evaluated at large spatial scales, particularly if effects are related to energy expenditure that can result in long-term effects on survival and reproductive ability (Lenarz et al. 2009; Patterson and Power 2002). Notwithstanding, our study identified a direct contrast in demographic response to winter severity based on habitat type and suggests moose are more vulnerable to direct and/or indirect climate effects in areas with sparse forest cover.

We also found that late frost onset had a negative effect on moose, but this effect was suppressed in areas where regenerating forest following forestry activity was low. This relationship is consistent with apparent competition, whereby white-tailed deer decrease moose density through increased exposure to parasites or predators. Winter ticks and the gastropod hosts of meningeal worm prefer mild temperatures and sparsely forested areas, particularly following disturbance (Ditmer et al. 2020; Healy et al. 2018). Late frosts can extend periods of winter tick and meningeal worm loading on moose, as parasite survival declines with the presence of snow and freezing temperatures (Bergeron and Pekins 2014; Pickles et al. 2013). Additionally, mild fall temperatures can result in prolonged persistence of white-tailed deer in areas that would otherwise be unoccupied during that time of year (Fisher et al. 2020), possibly increasing exposure of moose to predators and parasites (Ditmer et al. 2018; Lankester 2018). As a result of these relationships, populations occupying areas with higher proportions of regenerating forests may have limited population growth as seasonal temperatures increase. Host-parasite dynamics can vary across species' ranges, and our study reveals a possible mechanism between fall temperatures, habitat and parasites. However, additional research will be required to isolate the specific conditions that

promote parasite survival and transmission to moose and its limiting effects on moose population dynamics.

While previous studies have found that warmer winter temperatures in northern latitudes can increase calf survival (Grøtan et al. 2009; Sivertsen et al. 2012), we did not find this effect but rather found a positive response of recruitment to warmer spring temperatures. Our finding suggests that warmer springs in our study area may be associated with more nutrient-rich and/or longer periods of vegetation green-up that improve maternal condition immediately before, and during, parturition (Renecker and Hudson 1988). Alternatively, Monteith et al. (2015) found that warmer temperatures and rapid rates of spring vegetative growth decreased recruitment for moose in their southern distribution in the USA; however, the authors suggest this effect may be a result of reduced duration of high-quality forage and the addition of thermoregulatory stress where temperatures are more likely to surpass thermoregulatory thresholds (Lenarz et al. 2009; Murray et al. 2006). Given the mechanistic link between maternal nutrition and recruitment, understanding how climate can impact the nutritional landscape is critical to predicting when warmer springs may prove beneficial (our study) or detrimental (Monteith et al. 2015) across spatio-temporal scales.

Notably, spring temperatures influenced the strength of density-dependent effects on recruitment. Our analysis showed that calf recruitment was density-dependent during cold springs and density independent during warm springs. This suggests delayed vegetative growth associated with cold temperatures may limit calf survival where moose density is already high. Previous studies have identified that carrying capacity of moose habitat is higher in more productive landscapes, including those consisting of mixed-deciduous forests where spring green-up occurs (Brown 2011; Street et al. 2017). Additionally, our additive models revealed that moose

recruitment was highest in deciduous forests that support vegetative growth and nutritional requirements of moose. However, deciduous forests also support higher densities of white-tailed deer and consequently increase risks of predation and parasite transmission to moose (Barber-Meyer and Mech 2016; Ditmer et al. 2020). Calves have been previously found to be more susceptible to higher tick loads than adults (Bergeron and Pekins 2014), with heavy tick infestations halving calf survival in some areas (Ellingwood et al. 2020; Jones et al. 2019). Winter ticks can also indirectly reduce recruitment by impacting cow body mass prior to parturition (Pekins 2020). Consequently, indirect effects of interspecific interactions on recruitment may be cumulatively contributing to observed declines in calves observed across the study area, despite nutritional support offered by selected deciduous forests.

Additionally, while deciduous forest type was found to support higher calf densities, density-dependent effects on moose recruitment were only observed in areas with low dense forest cover. As calves are more vulnerable to predation, cows may use dominantly coniferous cover during parturition and then move with calves to areas of both coniferous and deciduous forest type to balance nutritional needs with concealment from predators (Severud et al. 2019). Heavy use of dense forest cover by cows with calves may contribute to the exceeding of carrying capacity, particularly where lower quantities of this optimal habitat type are found, and result in density-dependent effects on recruitment. Further, forestry activity in the study area is an important source limiting the availability of dense forest cover needed to support high calf survival and ultimately may be contributing to observed density-dependent effects. Our study was not designed to identify ultimate mechanisms driving long-term declines in calf recruitment; however, our results provide evidence that density, forest management, and climate are all proximate mechanisms of recruitment.

While our results supported our predictions that habitat quality mediates population responses to climate, we did not have continuous long-term data on white-tailed deer, predators, or parasites. Thus, while our study highlights important interactions between habitat, climate, and density, additional research is required to elucidate the mechanistic pathways by which climate-habitat interactions lead to moose population declines. Additional disturbances that promote forest regeneration, including the effects of forest fires and spruce budworm outbreaks (*Choristoneura fumiferana*; Ranta and Lankester 2017), as well as moose harvest (Brown 2011; Priadka et al. 2020), may also provide valuable insights into synergistic pathways that can inform moose management. Revealing both direct and indirect effects of climate change in relation to habitat quality can help ecologists anticipate future population-level responses, particularly across variable and changing environments.

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Tables and Figures

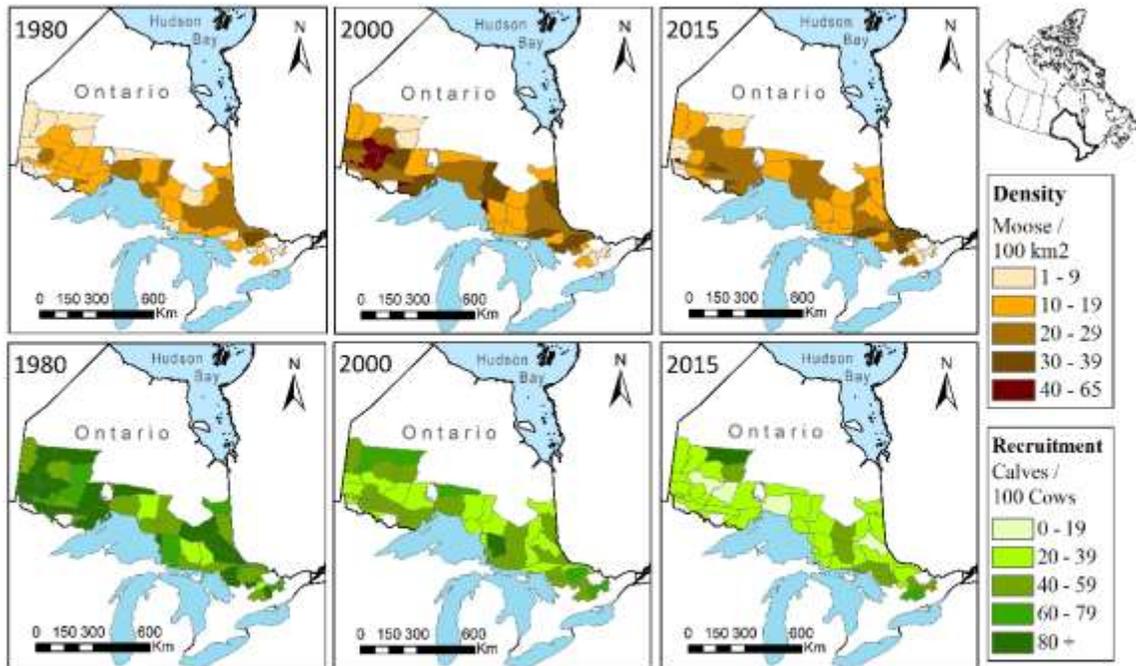


Fig. 3-1. Local variability in moose density and recruitment in the study area in Ontario, Canada estimated by aerial survey for years 1980, 2000, and 2015 (associated years are indicated on the top left corner of each plot). Polygons outlined in grey reflect Wildlife Management Unit boundaries. Blue polygons indicate major waterbodies.

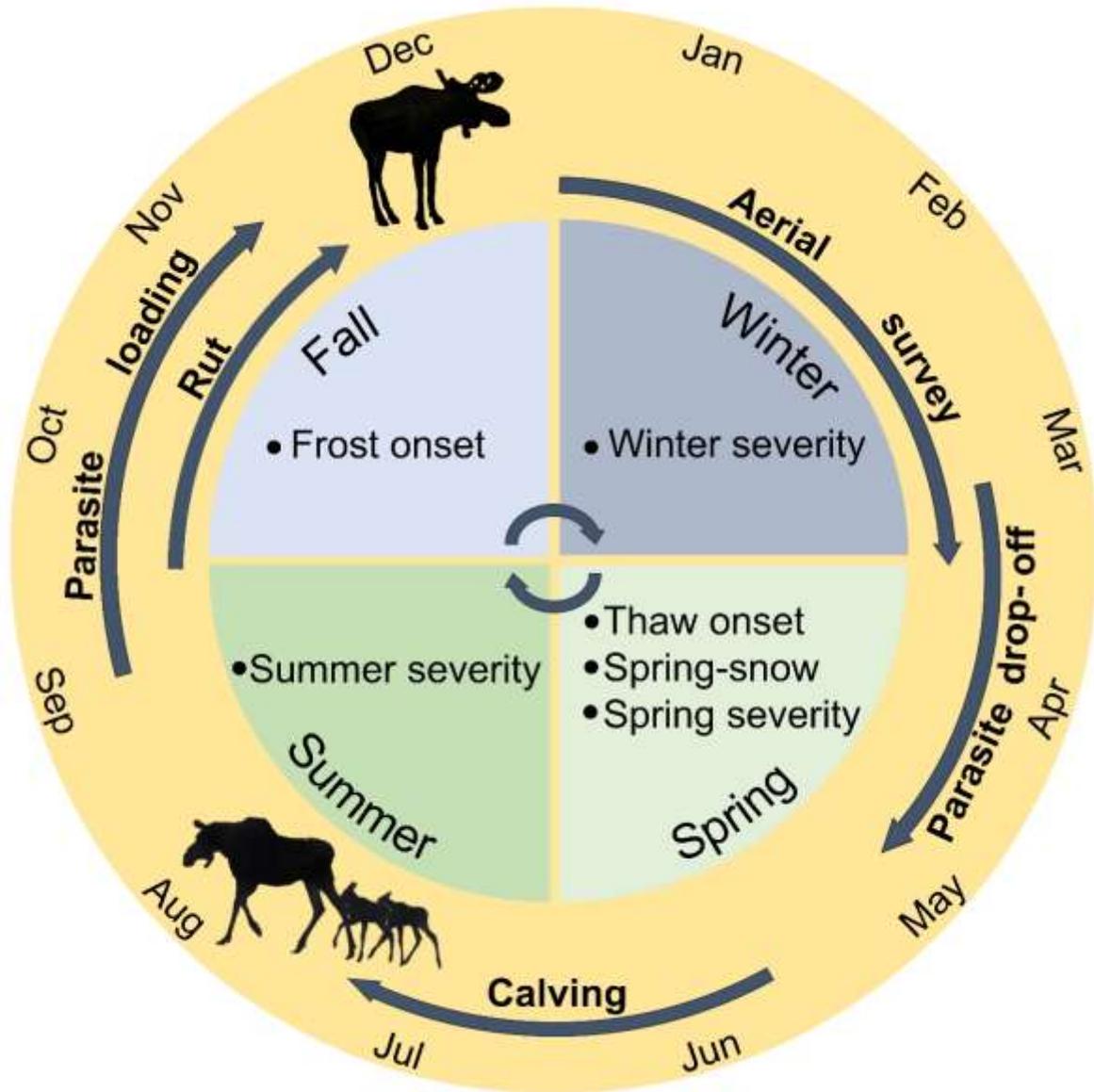


Fig. 3-2. Seasonal climate stressors and life history events of moose expected to influence moose density and recruitment. Climate stressors are shown in the center, whereas life-history events and data collection timing are shown in the periphery.

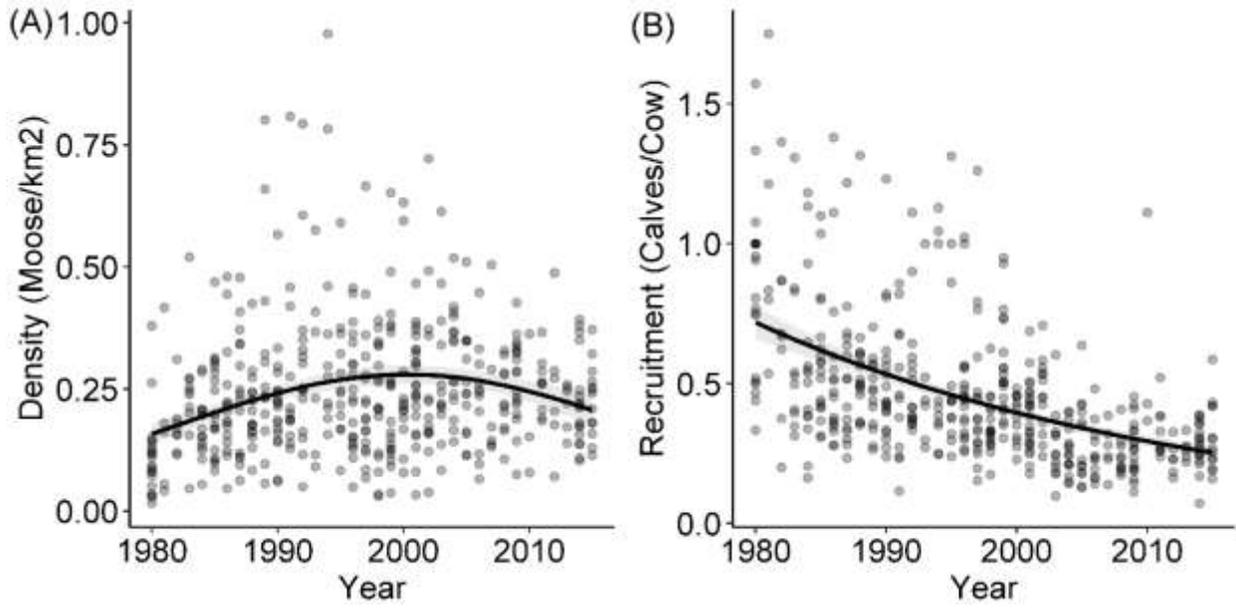


Fig. 3-3. Estimated temporal trend for moose (A) density, and (B) recruitment. Dots represent samples and lines represent the estimated mean with 95% confidence intervals.

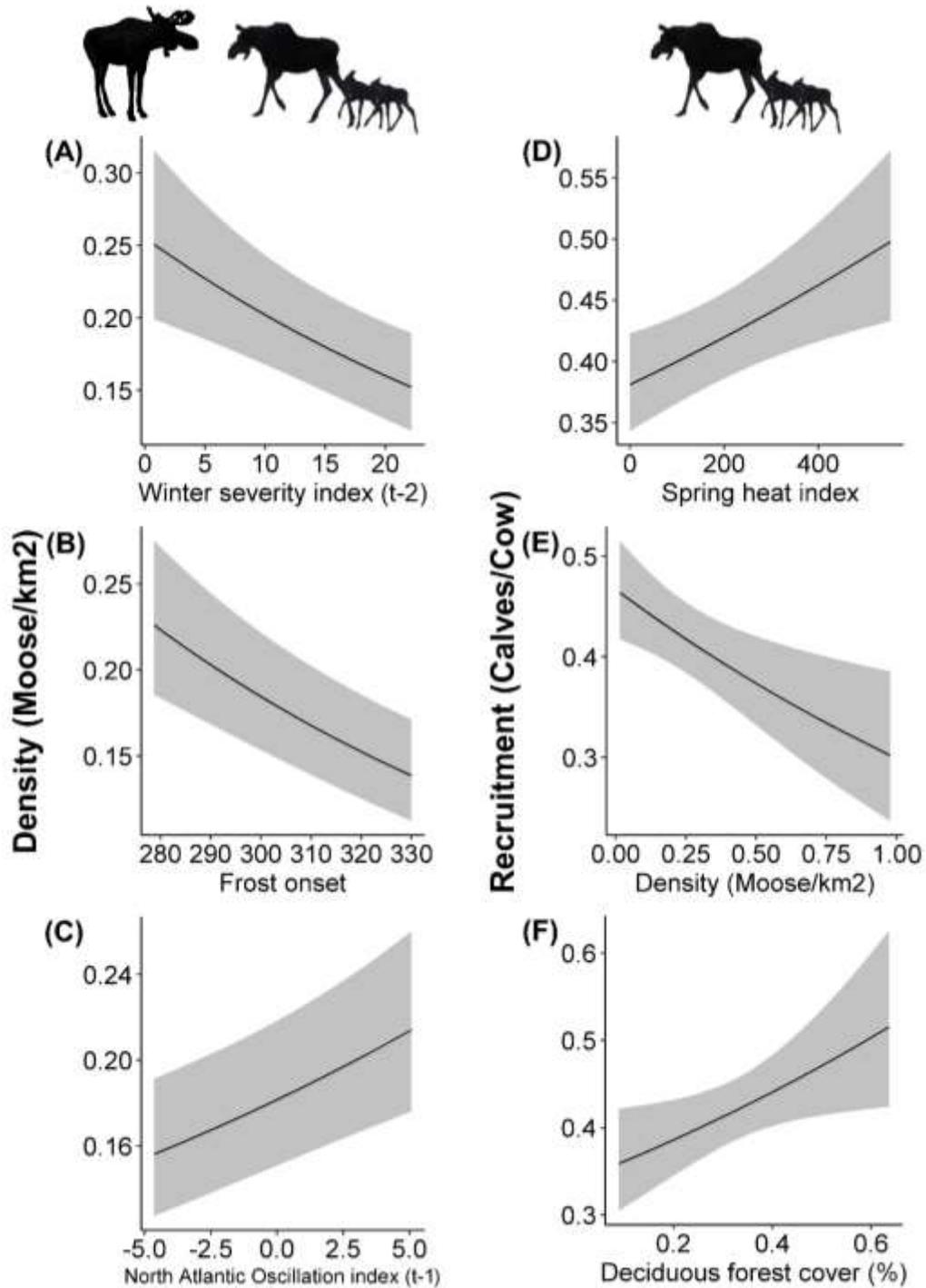


Fig. 3-4. Marginal effects of explanatory variables with 95% confidence intervals that did not overlap with zero for cumulative climate and habitat models of moose (A – C) density and (D – F) recruitment. All other variables in each model are held constant at their median values. Models

were fit with a gamma distribution and log-link function and included a random effect of Wildlife Management Unit. Numbers in parentheses indicate time-lag of year (t). Grey areas reflect 95% confidence intervals of predicted effects.

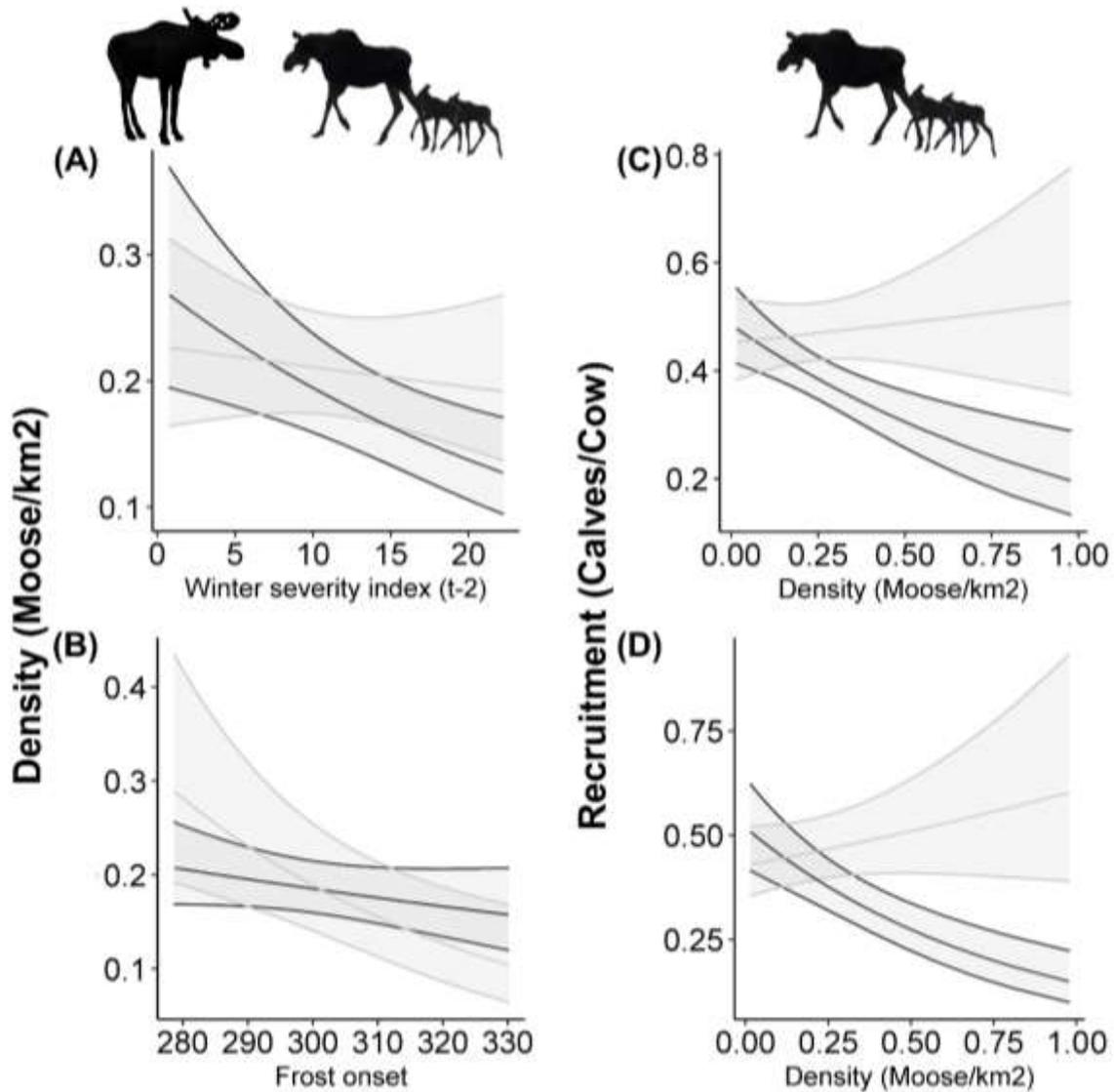


Fig. 3-5. Marginal effects of interacting climate and habitat variable terms for models of moose (A and B) density and (C and D) recruitment. All other model variables were held constant at median values. Models were fit with a gamma distribution and log-link function and included a random effect of Wildlife Management Unit. Numbers in parentheses indicate time-lag of year (t). Grey lines reflect high (97.5% quantile) and black lines reflect low (2.5% quantile) levels of (A and D) dense canopy cover, (B) regenerating forest and (C) spring severity. Lines reflect mean predicted values with upper and lower 95% confidence intervals.

Table 3-1. Climate indices expected to positively (+) or negatively (-) affect moose density and recruitment and three habitat variables expected to support greater moose density and recruitment and mitigate (+) or exacerbate (-) climatic effects through associations with thermoregulation and mobility, and/or interspecific interactions (i.e. predation and parasite transmission). Habitat variables are calculated as proportions of each Wildlife Management Unit (WMU).

Variable (name)	Description	Hypothesis		
		Thermoregulation & mobility	Predation	Parasites
North Atlantic Oscillation index (NAO)	December, January, February and March index average (Hurrell 1995)	+	-	
Winter severity (WINT)	January and February average snow depth (m) - (January and February average temperature (°C))	-	+	+
Thaw onset (THAW)	Julian day of growing period start			+
Spring-snow (DROP)	March average snow depth (m) + # March days with average temperatures below -2°C			+
Spring severity (SPR)	Cumulative degrees above 14°C in April and May	-		
Summer severity (SMR)	Warmest annual quarter average temperature (°C)	-		
Frost onset (FROST)	Julian day of growing period end			-
Dense canopy cover (COVER)	Dense deciduous and coniferous canopy cover (% of WMU)	+	+	
Deciduous canopy cover type (DECID)	Deciduous canopy cover (% of WMU)		-	-
Regenerating forest (REGEN)	Regenerating forest following forestry activity (% of WMU)		-	-

Table 3-2. Standardized regression coefficients (β), standard errors (SE), Akaike's information criterion corrected (AICc) and difference in AICc (Δ AICc) for density and recruitment models fit with year (YEAR) as a second-degree polynomial or linear term. Models were fit with a gamma distribution and log-link function and included a random effect of Wildlife Management Unit.

Model	Variable	Density				Recruitment			
		β	SE	AICc	Δ AICc	β	SE	AICc	Δ AICc
Polynomial	Poly(YEAR, 2)1	2.23	0.35	-1027.3	0	-5.58	0.37	-410.1	0
	Poly(YEAR, 2)2	-2.76	0.35			0.71	0.35		
Linear	YEAR	0.10	0.02	-973.8	53.5	-0.26	0.02	-408.1	2

Table 3-3. Standardized regression coefficients (β), standard errors (SE), and lower (LCI) and upper (UCI) 95% confidence intervals for the model-averaged fixed terms of generalized linear mixed-effect models for moose (A, C) density and (B, D) recruitment, and (A, B) without and (C, D) with interaction terms. Models were fit with a gamma distribution and log-link function and included a random effect of Wildlife Management Unit. Numbers in parentheses indicate time-lag of year (t).

Variable	β	SE	LCI	UCI
(A) Density climate and habitat model				
Intercept	-1.68	0.09	-1.85	-1.52
Poly(YEAR, 2)1	1.55	0.47	0.63	2.47
Poly(YEAR, 2)2	-2.88	0.39	-3.64	-2.13
WINT(t-2)	-0.09	0.03	-0.14	-0.04
FROST	-0.09	0.02	-0.13	-0.04
NAO(t-1)	0.07	0.02	0.03	0.10
COVER	0.03	0.08	-0.12	0.18
DECID	0.07	0.10	-0.12	0.26
REGEN	0.00	0.05	-0.22	0.20
(B) Recruitment climate and habitat model				
Intercept	-0.86	0.04	-0.95	-0.78
YEAR	-0.25	0.02	-0.28	-0.21
SPR	0.06	0.02	0.02	0.09
DEN	-0.06	0.02	-0.10	-0.02
COVER	0.00	0.02	-0.07	0.10
DECID	0.09	0.04	0.01	0.17
REGEN	-0.01	0.03	-0.13	0.05
(C) Density climate x habitat model				
Intercept	-1.66	0.09	-1.84	-1.48
Poly(YEAR, 2)1	1.64	0.47	0.71	2.56
Poly(YEAR, 2)2	-3.01	0.39	-3.77	-2.25
WINT(t-2)	-0.07	0.02	-0.12	-0.02
FROST	-0.07	0.02	-0.12	-0.03
NAO(t-1)	0.05	0.02	0.01	0.08
COVER	-0.20	0.08	-0.36	-0.04
REGEN	0.10	0.10	-0.09	0.29
WINT(t-2):COVER	0.05	0.02	0.004	0.09
FROST:REGEN	-0.04	0.02	-0.08	-0.002
(D) Recruitment climate x habitat model				
Intercept	-0.86	0.04	-0.94	-0.77
YEAR	-0.24	0.02	-0.28	-0.20
SPR	0.05	0.02	0.02	0.09
DEN	-0.06	0.02	-0.10	-0.02
COVER	0.05	0.04	-0.03	0.13
SPR:COVER	-0.03	0.02	-0.07	0.004

DEN:SPR	0.04	0.02	0.01	0.07
DEN:COVER	0.06	0.02	0.03	0.09

Note: Coefficients were estimated by model-averaging best models (Δ Akaike Information Criterion corrected ≤ 2) in each model set. WINT = winter severity, FROST = frost onset, NAO = North Atlantic Oscillation index, SPR = spring severity, DEN = moose density, COVER = dense canopy cover, DECID = deciduous canopy cover, and REGEN = regenerating forest.

Appendix



Figure A3-1. A bull (male) moose in the spring (May) with hair loss showing evidence of being subjected to a heavy winter tick infestation the previous winter.

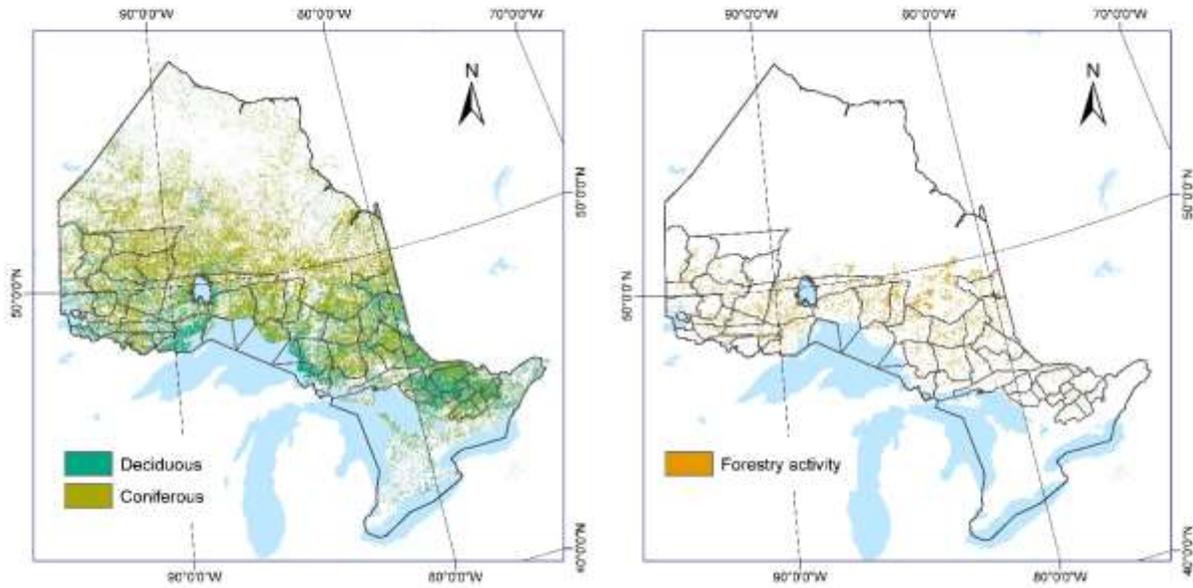


Figure A3-2. Spatial representation of continuous forest canopy cover by deciduous and coniferous forest type and regenerating forest following recent (< 10-year-old) forestry activity for the year 1999. Polygons reflect Wildlife Management Units included in the study.

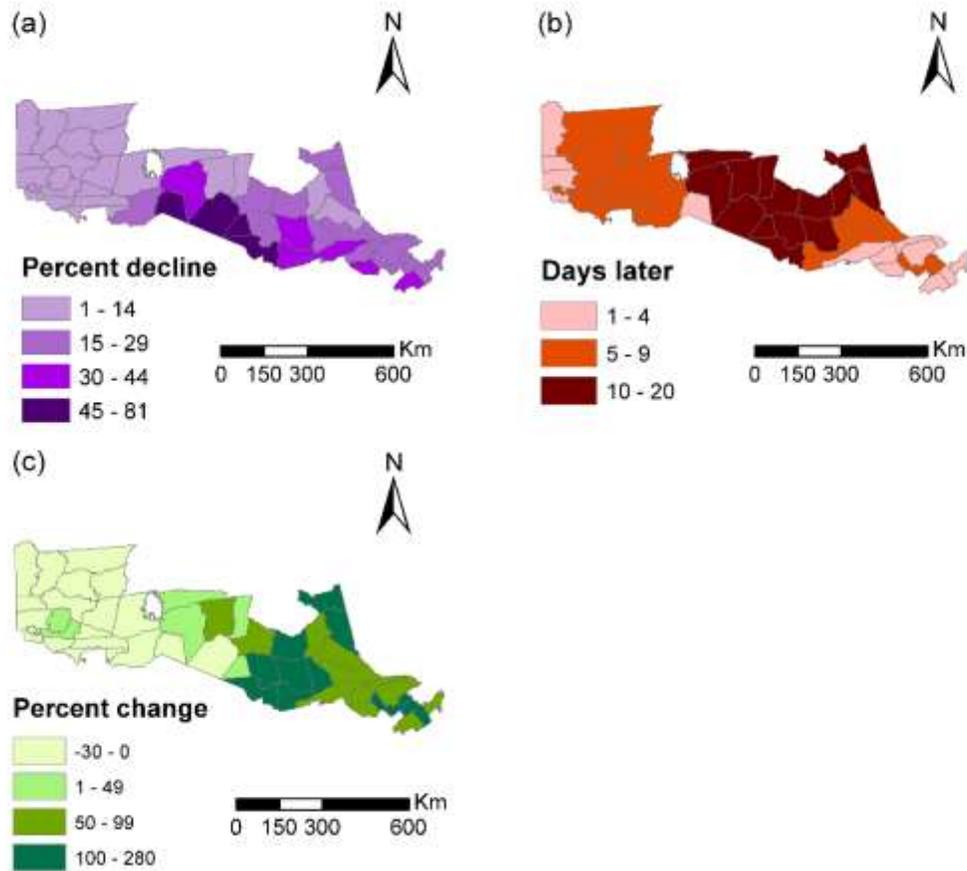


Figure A3-3. Spatial variability in temporal changes of important climatic stressors found to influence moose demographic response in the study area between the years 1979 – 2014. Values of climatic stressors include: (a) percent decline in winter severity, (b) number of Julian days later for frost onset, and (c) percent change in spring heat severity. Values were averaged per Wildlife Management Unit (polygons).

Table A3-1. Correlation matrix for climate variables used in the study. Values greater than 0.5 and lower than -0.5 are bolded. Numbers following variable names reflect time lags in years.

	NAO	NAO1	NAO2	WINT	WINT1	WINT2	THAW	THAW1	THAW2	DROP	DROP1	DROP2	SPR	SPR1	SPR2	SMR	SMR1	SMR2	FROST	FROST1	FROST2	YEAR	COVER	DECID	REGEN
NAO	1.000	0.088	0.026	-0.049	0.141	-0.226	0.072	-0.044	-0.219	-0.111	0.342	-0.237	-0.052	0.257	0.324	0.017	0.013	0.080	-0.043	-0.028	-0.326	-0.104	0.102	0.012	-0.042
NAO1	0.088	1.000	0.112	0.024	-0.097	0.130	-0.052	0.066	-0.051	-0.019	-0.256	0.326	-0.069	-0.029	0.243	-0.025	0.056	-0.030	0.010	0.007	-0.029	-0.151	-0.057	0.040	0.015
NAO2	0.026	0.112	1.000	0.183	0.062	-0.076	0.125	-0.018	0.161	0.210	-0.004	-0.186	-0.160	-0.034	-0.060	-0.046	-0.046	0.043	-0.138	0.069	-0.053	-0.083	0.047	-0.076	-0.098
WINT	-0.049	0.024	0.183	1.000	0.614	0.568	0.347	0.193	0.067	0.520	0.277	0.293	0.014	0.103	0.178	-0.370	-0.213	-0.253	-0.409	-0.595	-0.497	-0.223	-0.058	-0.433	-0.017
WINT1	0.141	-0.097	0.062	0.614	1.000	0.555	0.308	0.288	0.152	0.295	0.537	0.217	-0.027	0.060	0.034	-0.211	-0.416	-0.253	-0.391	-0.363	-0.612	-0.292	-0.004	-0.388	0.023
WINT2	-0.226	0.130	-0.076	0.568	0.555	1.000	0.078	0.317	0.300	0.389	0.272	0.512	0.087	-0.087	-0.032	-0.099	-0.223	-0.395	-0.451	-0.411	-0.351	-0.333	-0.077	-0.352	0.010
THAW	0.072	-0.052	0.125	0.347	0.308	0.078	1.000	0.358	0.239	0.219	0.073	-0.148	-0.565	-0.113	-0.086	-0.260	-0.110	-0.094	-0.305	-0.278	-0.376	0.065	-0.097	-0.296	-0.040
THAW1	-0.044	0.066	-0.018	0.193	0.288	0.317	0.358	1.000	0.340	0.153	0.194	0.116	-0.169	-0.511	-0.102	-0.146	-0.239	-0.179	-0.137	-0.311	-0.320	0.072	-0.052	-0.211	-0.007
THAW2	-0.219	-0.051	0.161	0.067	0.152	0.300	0.239	0.340	1.000	0.128	0.118	0.216	-0.160	-0.311	-0.545	-0.174	-0.125	-0.230	-0.157	-0.133	-0.279	-0.003	-0.097	-0.266	-0.059
DROP	-0.111	-0.019	0.210	0.520	0.295	0.389	0.219	0.153	0.128	1.000	0.035	0.142	-0.084	0.021	-0.034	-0.185	-0.092	-0.177	-0.238	-0.238	-0.238	-0.149	0.059	-0.191	0.028
DROP1	0.342	-0.256	-0.004	0.277	0.537	0.272	0.073	0.194	0.118	0.035	1.000	0.074	0.085	-0.136	-0.019	-0.155	-0.271	-0.146	-0.296	-0.289	-0.327	-0.311	0.102	-0.155	0.035
DROP2	-0.237	0.326	-0.186	0.293	0.217	0.512	-0.148	0.116	0.216	0.142	0.074	1.000	0.233	0.025	-0.078	-0.160	-0.164	-0.264	-0.050	-0.316	-0.196	-0.223	-0.011	-0.085	0.093
SPR	-0.052	-0.069	-0.160	0.014	-0.027	0.087	-0.565	-0.169	-0.160	-0.084	0.085	0.233	1.000	0.311	0.221	0.094	-0.001	0.042	-0.008	-0.196	0.044	0.104	0.054	0.008	0.174
SPR1	0.257	-0.029	-0.034	0.103	0.060	-0.087	-0.113	-0.511	-0.311	0.021	-0.136	0.025	0.311	1.000	0.466	0.023	0.112	0.076	-0.179	-0.055	-0.107	0.168	0.062	-0.051	0.126
SPR2	0.324	0.243	-0.060	0.178	0.034	-0.032	-0.086	-0.102	-0.545	-0.034	-0.019	-0.078	0.221	0.466	1.000	0.064	0.088	0.083	-0.091	-0.164	-0.022	0.180	0.084	-0.035	0.104
SMR	0.017	-0.025	-0.046	-0.370	-0.211	-0.099	-0.260	-0.146	-0.174	-0.185	-0.155	-0.160	0.094	0.023	0.064	1.000	0.641	0.576	0.179	0.295	0.232	0.120	-0.141	0.012	-0.089
SMR1	0.013	0.056	-0.046	-0.213	-0.416	-0.223	-0.110	-0.239	-0.125	-0.092	-0.271	-0.164	-0.001	0.112	0.088	0.641	1.000	0.650	0.234	0.244	0.338	0.206	-0.147	0.022	-0.084
SMR2	0.080	-0.030	0.043	-0.253	-0.253	-0.395	-0.094	-0.179	-0.230	-0.177	-0.146	-0.264	0.042	0.076	0.083	0.576	0.650	1.000	0.206	0.320	0.261	0.252	-0.139	-0.018	-0.089
FROST	-0.043	0.010	-0.138	-0.409	-0.391	-0.451	-0.303	-0.137	-0.157	-0.238	-0.296	-0.050	-0.008	-0.179	-0.091	0.179	0.234	0.206	1.000	0.498	0.420	0.195	0.089	0.401	0.054
FROST1	-0.028	0.007	0.069	-0.595	-0.363	-0.411	-0.278	-0.311	-0.133	-0.238	-0.289	-0.316	-0.196	-0.055	-0.164	0.295	0.244	0.320	0.498	1.000	0.502	0.176	0.024	0.328	-0.016
FROST2	-0.326	-0.029	-0.053	-0.497	-0.612	-0.351	-0.376	-0.320	-0.279	-0.238	-0.327	-0.196	0.044	-0.107	-0.022	0.232	0.338	0.261	0.420	0.502	1.000	0.224	0.084	0.359	-0.017
YEAR	-0.104	-0.151	-0.083	-0.223	-0.292	-0.333	0.065	0.072	-0.003	-0.149	-0.311	-0.223	0.104	0.168	0.180	0.120	0.206	0.252	0.195	0.176	0.224	1.000	-0.127	-0.090	0.037
COVER	0.102	-0.057	0.047	-0.058	-0.004	-0.077	-0.097	-0.052	-0.097	0.059	-0.102	-0.011	0.054	0.062	0.084	-0.141	-0.147	-0.139	0.089	0.024	0.084	-0.127	1.000	0.347	0.077
DECID	0.012	0.040	-0.076	-0.433	-0.388	-0.352	-0.296	-0.211	-0.266	-0.191	-0.155	-0.085	0.008	-0.051	-0.035	0.012	0.022	-0.018	0.401	0.328	0.359	-0.090	0.347	1.000	0.179
REGEN	-0.042	0.015	-0.098	-0.017	0.023	0.010	-0.040	-0.007	-0.059	0.028	0.035	0.093	0.174	0.126	0.104	-0.089	-0.084	-0.089	0.054	-0.016	-0.017	0.037	0.077	0.179	1.000

Note: NAO = North Atlantic Oscillation index, WINT = winter severity, THAW = thaw onset, DROP = spring-snow, SPR = spring severity, SMR = summer severity, FROST = frost onset, COVER = dense canopy cover, DECID = deciduous canopy cover, REGEN = regenerating forest.

Table A3-2. Akaike's information criterion corrected (AICc), difference in AICc ($\Delta AICc$), and AIC weights (AIC_w) for top-ranking climatic density and recruitment models. Model terms were standardized and included a log-link. Numbers in parentheses indicate time lags from year t .

Model	Density			Recruitment		
	AICc	$\Delta AICc$	AIC_w	AICc	$\Delta AICc$	AIC_w
Poly(YEAR, 2) + WINT(t-2) + FROST + NAO(t-1)	-1046.8	0.0	0.54	-	-	-
Poly(YEAR, 2) + WINT(t-2) + SPR(t-2) + FROST + NAO(t-1)	-1045.7	1.1	0.32	-	-	-
Poly(YEAR, 2) + WINT(t-2) + SPR(t-2) + FROST	-1042.9	3.9	0.08	-	-	-
Poly(YEAR, 2) + WINT(t-2) + FROST	-1041.1	5.7	0.03	-	-	-
Poly(YEAR, 2) + SPR(t-2) + FROST + NAO(t-1)	-1040	6.8	0.02	-	-	-
Poly(YEAR, 2) + SPR(t-2) + FROST	-1039.4	7.4	0.01	-	-	-
Poly(YEAR, 2) + WINT(t-2) + SPR(t-2) + NAO(t-1)	-1037.2	9.6	0.01	-	-	-
Poly(YEAR, 2) + WINT(t-2) + SPR(t-2)	-1036	10.8	0	-	-	-
NULL	-948.9	97.9	0	-	-	-
YEAR + SPR + DEN	-	-	-	-418	0.0	0.39
YEAR + THAW + SPR + DEN	-	-	-	-417.6	0.4	0.31
YEAR + THAW + DEN	-	-	-	-417.3	0.7	0.27
YEAR + THAW + SPR	-	-	-	-412.8	5.2	0.03
NULL	-	-	-	-225.9	192.1	0

Note: WINT = winter severity, FROST = frost onset, NAO = North Atlantic Oscillation index, SPR = spring severity, THAW = thaw onset, and DEN = moose density.

Table A3-3. Akaike's information criterion corrected (AICc), difference in AICc ($\Delta AICc$) and AIC weights (AIC_w) for density and recruitment models with additive top-ranking climate variables and one of three habitat variables (COVER, DECID, and REGEN). Model terms were standardized and included a log-link. Numbers in parentheses indicate time-lags of year (t).

	Density			Recruitment		
	AICc	$\Delta AICc$	AIC _w	AICc	$\Delta AICc$	AIC _w
Poly(YEAR, 2) + WINT(t-2) + FROST + NAO(t-1) + COVER	-1051.4	1.4	0.45	-	-	-
Poly(YEAR, 2) + WINT(t-2) + FROST + NAO(t-1) + COVER + REGEN	-1050	1.6	0.24	-	-	-
Poly(YEAR, 2) + WINT(t-2) + FROST + NAO(t-1) + COVER + DECID	-1049.8	3.3	0.19	-	-	-
Poly(YEAR, 2) + WINT(t-2) + FROST + NAO(t-1) + COVER + DECID + REGEN	-1048.1	6.0	0.08	-	-	-
Poly(YEAR, 2) + WINT(t-2) + FROST + NAO(t-1) + DECID	-1045.4	6.7	0.02	-	-	-
Poly(YEAR, 2) + WINT(t-2) + FROST + NAO(t-1) + REGEN	-1044.7	8.0	0.02	-	-	-
Poly(YEAR, 2) + WINT(t-2) + FROST + NAO(t-1) + DECID + REGEN	-1043.4	1.4	0.01	-	-	-
YEAR + SPR + DEN + DECID	-	-	-	-420.7	0	0.4
YEAR + SPR + DEN + DECID + REGEN	-	-	-	-419.4	1.3	0.21
YEAR + SPR + DEN + COVER + DECID	-	-	-	-418.7	2.0	0.15
YEAR + SPR + DEN + COVER	-	-	-	-417.5	3.2	0.08
YEAR + SPR + DEN + COVER + DECID + REGEN	-	-	-	-417.5	3.2	0.08

YEAR + SPR + DEN + REGEN	-	-	-	-416	4.7	0.04
YEAR + SPR + DEN + COVER + REGEN	-	-	-	-415.7	5.0	0.03

Note: WINT = winter severity, FROST = frost onset, NAO = North Atlantic Oscillation index, SPR = spring severity, DEN = moose density, COVER = dense forest canopy cover, DECID = deciduous forest canopy cover, and REGEN = regenerating forest.

Table A3-4. Akaike's information criterion corrected (AICc), difference in AICc ($\Delta AICc$) and AIC weights (AIC_w) for density and recruitment models with interacting top-ranking climate variables and one of three habitat variables (COVER, DECID, REGEN). Model terms were standardized and included a log-link. Numbers in parentheses indicate time-lags of year (t).

	Density			Recruitment		
	AICc	$\Delta AICc$	AIC _w	AICc	$\Delta AICc$	AIC _w
Poly(YEAR, 2) + WINT(t-2) x COVER + FROST x REGEN + NAO(t-1)	-1054.7	0	0.9	-	-	-
Poly(YEAR, 2) + WINT(t-2) x COVER + FROST x DECID + NAO(t-1)	-1050.8	3.9	0.1	-	-	-
Poly(YEAR, 2) + WINT(t-2) x DECID + FROST x REGEN + NAO(t-1)	-1045.1	9.6	0	-	-	-
Poly(YEAR, 2) + WINT(t-2) x REGEN + FROST x REGEN + NAO(t-1)	-1045	9.7	0	-	-	-
Poly(YEAR, 2) + WINT(t-2) x DECID + FROST x DECID + NAO(t-1)	-1043.3	11.4	0	-	-	-
Poly(YEAR, 2) + WINT(t-2) x REGEN + FROST x DECID + NAO(t-1)	-1039.9	14.8	0	-	-	-
YEAR + SPR x COVER + DEN x SPR + DEN x COVER	-	-	-	-431.8	0	0.9
YEAR + SPR x COVER + DEN x COVER	-	-	-	-427.1	4.7	0.1
YEAR + SPR x COVER + DEN x SPR + DEN x REGEN	-	-	-	-422.2	9.6	0
YEAR + DEN x SPR	-	-	-	-419.4	12.4	0
YEAR + SPR x COVER + DEN x SPR + DEN x DECID	-	-	-	-419.2	12.6	0
YEAR + SPR x COVER + DEN x REGEN	-	-	-	-419.1	12.7	0
YEAR + SPR x COVER + DEN x DECID	-	-	-	-416.9	14.9	0

Note: WINT = winter severity, FROST = frost onset, NAO = North Atlantic Oscillation index, SPR = spring severity, DEN = moose density, COVER = dense forest canopy cover, DECID = deciduous forest canopy cover, and REGEN = regenerating forest.

Chapter Four: Optimization of monitoring for managed wildlife populations spanning many discrete management units: When can model-based predictions replace surveys?

Abstract

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 for filling gaps in monitoring; however, survey alternatives are typically limited and may not accurately reflect biological complexity and change. Understanding the spatio-temporal allocation of survey effort that maximizes uncertainty resolved and captures accurate and precise information for the greatest number of units within a budget can help to ensure monitoring efforts are optimized. We used field-parameterized simulations of moose (*Alces alces*) abundance and aerial survey-based population estimates for 30 Wildlife Management Units (WMUs) to test how prioritizing one of three management criteria: population state, population uncertainty, or years between surveys, in addition to using model-based estimates to fill information-gaps, impacted WMU-specific population and trend estimates. Also incorporated in the decision framework was WMU-specific costs and annual budget constraints. We further identified how the utility (based on minimizing population estimate 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. Interval-based monitoring that prioritized 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 and the utility of conducting a survey rather than using a model-based estimate increased with time since the last survey. Further, the utility of conducting a survey 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 that was related to population density and the predictive power of model-based estimates. If long-term trends are expected, there is value in using alternatives such as model-based predictions to replace surveys, especially in WMUs with consistently high survey-based uncertainty (typically low-density populations) and when there is low annual variability in environmental stressors.

Introduction

Monitoring of wildlife is essential to inform management actions and assess their effectiveness (Yoccoz et al. 2001; Pollock et al. 2002). Limited resources, including budget, can often constrain the frequency at which populations can be 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 (Nuno et al. 2013; Ficetola et al. 2017; Andersen and Steidl 2019). However, the need for monitoring can depend in part on the nature of population change. For example, 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 (Reynolds et al. 2011; Row and Fedy 2017; Ficetola et al. 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 for a system (Hauser et al. 2006; Canessa et al. 2015).

Jurisdictions containing multiple management units with discrete populations that are managed independently but share monitoring resources and budget face the additional challenge of ensuring each unit is adequately monitored while balancing the needs and monitoring costs of other units (Ficetola et al. 2017). 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 (Nuno et al. 2013; Ficetola et al. 2017; Barata et al. 2017). Therefore, multi-unit monitoring schemes can benefit from designs that balance the utility of deciding to monitor 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 the benefit that new information provides, and whether it is worth the cost or can be replaced by alternatives (Hauser et al. 2006; Canessa et al. 2015). 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 (i.e. increasing or decreasing), resolving population uncertainty, and/or ensuring that all units are monitored frequently enough to track patterns across the larger area (Hauser et al. 2006; Joseph et al. 2009; Reynolds et al. 2011; Morant et al. 2020).

Alternatives to survey-based monitoring, such as model-based estimates, can be used to alleviate uncertainty in population state caused by gaps or imprecision in monitoring information. Models can therefore be a useful tool to aid in the optimization of monitoring designs and management decisions-making (Hauser et al. 2006; Westcott et al. 2018; Nishimoto et al. 2021).

However, model-based estimates require prior knowledge of the conditions that affect population dynamics, which can involve complex biological interactions (Ahrestani et al. 2016; Marolla et al. 2020). Developing models with high predictive power of population demographics can be particularly challenging for widely distributed species that occupy variable environments and experience spatially and temporally variable limiting factors (Ahrestani et al. 2016; Westcott et al. 2018; Marolla et al. 2020).

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 and 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 (Boyce et al. 2012). Selection of units to monitor can be based on risk-based criteria (e.g. anticipated declining 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 to inform decision-making for a unit or when alternative methods (such as model-based estimates) will suffice.

Here, we developed a framework to test alternative monitoring criteria and identify when a model-based population estimate can replace conducting a survey. We used empirical aerial-

survey data on moose across 30 management units and a timespan of 10 years in Ontario, Canada to parameterize models of moose population abundance and simulate aerial-survey derived population estimates. Our first objective was to evaluate how prioritizing different risk-based monitoring criteria within a year-to-year optimization framework influenced the accuracy of unit-specific trends and precision in annual population estimates. Specifically, we evaluated how prioritizing (a) population uncertainty, (b) population state, or (c) years since the last survey to select units to monitor while accounting for monitoring budget and unit-specific costs to survey affected population and trend estimates with the goal of capturing precise population estimates and accurate population trends for the greatest number of units. Our second objective was to determine whether using a model-based estimate that accounted for uncertainty in population estimates from previous years to fill timeseries gaps improved population and trend estimates. Lastly, our third objective was to determine how population density, environmental variability, and years since the last survey influenced the utility of model-based estimates to replace aerial surveys with the objective of minimizing uncertainty of annual population estimates.

Methods

Study area

The study area spanned 255,879 km² 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 and 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 northwestern portion of the province (James et al. 2017).

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 timeseries 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 five years of surveys conducted between 1991 – 2015 were used in our analysis, resulting in 30 WMUs.

Moose aerial surveys took place in the winter (January – 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 25km² 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

(McLaren 2006). Standardized survey protocols were used to reduce detectability bias 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). We conducted supplementary analysis to evaluate how forest canopy cover type and moose population density impacted aerial survey precision (Table A4-1, A4-2, and Figure A4-1). The supplementary analysis informed on sources of variability in survey precision across WMUs and how much could be attributed to observation error. While observation error was not directly modelled into simulated aerial-survey derived population estimates, this source of variance was captured in the simulations in this study by incorporating proportions of moose seen/counted each year per plot flown for each WMU.

Population timeseries

To evaluate the accuracy of aerial-survey derived population trends and precision in annual estimates, we generated timeseries of “known” moose population size and simulate aerial survey-derived population estimates based on the “known” population size per WMU and year. Timeseries of population size and trend over 25 years were generated for 30 WMUs using coefficients from a linear mixed-effect model of empirical aerial-survey derived estimates of moose density. Our mixed-effects model used moose density (/km²) 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 was used to derive WMU-specific trends. 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 2000’s (Chapter Three). 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 – March) with a two-year time lag that was identified in a previous study (Chapter Three) to negatively influence long-term moose population trends in Ontario. Methods describing how the winter severity index was generated can be found in this thesis, Chapter Three. The coefficient for winter severity was extracted as a fixed effect for all WMUs for the full 25-year timeframe and represented an 8% decline in moose density across all years. Both year and winter severity values were log-transformed. The mixed-effects model was constructed in R (R Core Team) using package *lme4* (Bates et al. 2015).

We generated 30 WMU-specific timeseries of “known” population density (n) that spanned 25 years (i) using a linear model. Coefficients extracted from the empirically derived model were included in the linear model as 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 two-year time lag ($wint2_{[i-2]}$):

$$n_{[i]} = \beta_0 + \beta_1 * year_{[i]} + \beta_2 * wint2_{[i-2]}$$

Winter severity was simulated based on empirical values obtained for the years that survey data was 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:

$$wint2_{[i-2]} \sim Normal(x_i, \sigma_i)$$

Moose population timeseries 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.

See Appendix, Figure A4-2 and Table A4-3 for more information on model parameters and coefficients that were used to inform the generation of WMU-specific timeseries.

Simulated aerial survey estimates

We simulated aerial-survey based population estimates at the WMU-level. 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). Further, 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):

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

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):

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

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):

$$C_w = \sum (\text{average } n_{1y} * Y_1) + (\text{average } n_{2y} * Y_2) + (\text{average } n_{3y} * Y_3)$$

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 :

$$CV = SD_{total}/C_W$$

We used CV to estimate survey precision (i.e. uncertainty) for comparison of uncertainty derived from model-based estimates. CV represented the precision in counts per plot 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 timeseries in reflecting greater spatial (63% CV average) than temporal (14% CV average) variation across WMUs (Table A4-4). The R code for the function used to simulate WMU-specific aerial-survey counts and population estimates is available in Appendix A4-1.

Model-based population estimates

To derive model-based estimates, we used 15 years of prior knowledge of the moose population to inform model-based predictions. Prior knowledge for the initial 15 years was populated as simulated aerial-survey based counts. This prior information ensured that our model had the predictive power to estimate annual population change and could inform our analysis of 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 (Valpine and 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; Westcott et al. 2018; Marolla et al. 2020). 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; Gelman et al. 2013) 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):

$$n_t = \beta_0 + \beta_1 Y_t + \varepsilon_t$$

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

$$\sigma_n[\varepsilon_t \sim \text{Normal}(0, \sigma_n^2)]$$

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}):

$$C_{t-1} \sim \text{Normal}(n_{t-1}, SD_{t-1})$$

We provided vague prior probabilities of parent parameters (β_0 , β_1 , σ_n ; see Appendix A4-2 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 2,000,000 MCMC

simulations and a burn-in of 100,000 simulations by application of the Gibbs sampler. Models were analyzed using JAGS 3.3.0 via the R package *rjags* (Plummer 2003). 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):

$$CV_t = SD_t/C_t$$

Scenario development

We developed scenarios to compare the effects of alternative risk-based criteria on the priority ranking of WMUs for monitoring. 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 4-1). 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 for uncertainty (based on quartiles across all WMUs) and population state (based on a 0.2 moose/km² threshold) were assigned based on the annual population estimate (Table 4-1). In addition to the three risk-based criteria, we introduced three options for addressing years without a survey (i.e. missing information), including: using the previous survey's information (Scenario 1), using a model-based estimate (Scenario 2), or using a model-based estimate when its utility 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 4-1; Table 4-2).

We measured utility in Scenario 3 as the difference in the level of uncertainty (CV) derived from each estimate (model or survey-based; Figure 4-1). 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 and precision in the resulting timeseries. The decision of replacing surveys with model-based estimates was made following the optimization (step 2 in Figure 4-1) 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 *Optimization model* section), each scenario resulted in a 10-year timeseries dataset for each WMU in the framework ($n = 30$). Henceforth, we refer to each of these datasets as an optimized timeseries. See Figure A4-3 for a visual example of how optimized timeseries were constructed based on the three options for addressing years without a survey.

Optimization model

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 4-1). In our 25-year timeseries, the optimization started in year 16 to derive a 10-year optimized dataset 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 4-1). The optimization problem was conducted using a Linear Integer Programming (LIP) approach, where n was the total number of WMUs to monitor ($n = 30$):

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

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

$$\text{where } x \text{ is binary:} \quad x_u \in \{0,1\}, \text{ for } u = 1, \dots, n$$

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 \$18287 – CAD \$42032, with an average of 36 total plots flown in a WMU per year (Table A4-5). The optimization model and constraints were constructed using R package *lpsolve* (Berkelaar 2015).

Data analysis: accuracy measures

We assessed the accuracy and precision of 10-year optimized timeseries for each WMU and scenario in relation to generated population size using two measures. First, we tested the correlation (Pearson's r) between timeseries of optimized estimates and population size and evaluated the proportion of WMUs with $r > 0.5$ (indicating a positive linear relationship) for each scenario. Second, we calculated whether each optimized timeseries slope/trend significantly varied from the trend in population size. Slope significance was assessed based on $P\text{-value} \leq 0.05$ using a generalized linear model (GLM) with a quasipoisson distribution constructed using R package *lmerTest* (Kuznetsova et al. 2020). The model response was population size or survey-based population estimate and we tested for an interacting effect of year between timeseries. Further, to compare results between Scenarios 2 and 3, we assessed the correlation (Pearson's r) and similarity among trends (within 0.01 units) between the optimized timeseries for each WMU.

Data analysis: survey utility

We further assessed how population density, environmental variability (winter severity with a two-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 (see Chapter Three). 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).

Results

Accuracy among scenarios

Annual variability was poorly captured by optimized timeseries in each scenario, with no scenario resulting in greater than 57% (and minimum 47%) of optimized timeseries ($n = 30$) reflecting annual population variation based on Pearson's $r > 0.5$ (Figure 4-2). Further, at least 67% (and maximum 97%) of optimized timeseries in a scenario ($n = 30$) reflected accurate population trends (Figure 4-2). 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 4-2). 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 timeseries than using the previous survey's estimate (S1a – c) or by replacing surveys with model-based estimates based on utility (S3a – c; Figure 4-2).

Although replacing surveys with model-based estimates based on utility in Scenario 3 (S3a – c) did not result in the greatest number of accurate trend estimates, comparative analysis revealed that optimized timeseries in this scenario were highly correlated with timeseries in Scenario 2 (S2a – c; Pearson's $r = 0.97$) regardless of risk-based criteria prioritized (Figure 4-3). Additionally, either 87% to 90% of timeseries trends in Scenarios 2 and 3 were within 0.01 units of each other, representing a maximum 10% divergence in population change captured per year (Figure 4-3).

The number of surveys replaced with model-based estimates (Scenario 3) and the result in cost saving over time did not differ greatly based on risk-based criteria prioritized (Figure 4-4). 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 4-4).

Monitoring utility

When the utility of conducting a survey was evaluated and compared to uncertainty in 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 4-3, Figure 4-5). Further, the effect of population density on the probability of correctly choosing to survey declined with more severe winters (which contributed to population decline; Table 4-3, Figure 4-5). 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/km² (Figure 4-5). Additionally, 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 at 10 years without a survey (Figure 4-5).

Discussion

We developed a framework to optimize monitoring based on risk-based criteria and cost across multiple management units experiencing variation in population density, trends, and severity of environmental stressors. In our study, we found that prioritizing years since the last survey 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 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 monitoring performs well for trend detection (Andersen and Steidl 2019; 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 and Jonzén 2011). Time series length is also an important contributor to trend detection, and longer periods of monitoring will be more accurate at detecting rates of population change through time (Ahrestani et al. 2013; Reynolds et al. 2011; Piacenza et al. 2019; Vallecillo et al. 2020). 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). We introduced temporal variation in trends in our generated timeseries; however, 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, suggesting that our optimization was adequate.

Our findings also correspond 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 low precision in annual population estimates based on monitoring is the poor detectability of animals. Detectability can be influenced by population density, distribution characteristics (i.e. open or closed population; Westcott et al. 2012; Crum et al. 2021; Dambly et al. 2021), landscape heterogeneity (Rhodes and Jonzén 2011; Nuno et al. 2013; Barata et al. 2017), observer experience (Barata et al. 2017; Vallecillo et al. 2021), and weather conditions during monitoring (Morant et al. 2020). Our supplemental analysis (Appendix A) revealed that variance in empirical aerial-survey derived population estimates included in our study varied more across WMUs than over time, suggesting that uncertainty in population estimates were generally comparable across years when a survey was conducted for a given WMU. Further, uncertainty in population estimates was likely to be lower in WMUs with greater moose population density but higher in WMUs with higher proportions of dense coniferous cover. Monitoring efforts that produce consistently inaccurate population estimates do not represent useful or efficient expenditure of budget and resources. In these situations, monitoring efforts should focus on lowering uncertainty potentially through increased efforts or the implementation and integration of alternative types of monitoring. As we identified, obtaining consistently poor or uncertain population estimates from aerial-surveys may be due to WMU-specific factors influencing detectability and does not indicate that the method does not work well in other units.

Further, our study revealed that using model-based estimates can improve detection of long-term population trends but not annual changes in population size. Therefore, if estimation of trends is the objective of monitoring, there is value in using model-based estimates to replace monitoring in some years. We focused in our study 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 and 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).

In our optimization framework, the use of a model-based estimates improved the ability for optimized timeseries to capture population trends (Scenario 2); however, this improvement declined in Scenario 3 that represented a reduced number of surveys to save costs. Our model was simplified (excluded environmental variability) to reflect the realistic challenge of fully understanding drivers of wildlife population dynamics and variability over time. Limiting the inclusion of likely sources of variability influencing population dynamics can explain the reduced power in model-based estimates to predict annual population change. However, the non-significant differences in optimized timeseries between Scenarios 2 and 3 justify replacing certain surveys

with even a simple (i.e. year-only) model-based estimate, particularly if long-term trends are expected and detection of such trends are the primary objective of monitoring.

When model-based estimates were incorporated in the optimization framework, 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 (Tracey et al. 2008; Reynolds et al. 2011; Southwell et al. 2019; Steenweg et al. 2019). Additionally, detecting a stable population trend with high certainty can be challenging (Wauchope et al. 2019), and as identified in this study, attempting to predict stable population size with a trend-based model can result in high uncertainty or misinformed estimates. Further, spatial variation in population densities or dynamics within a sampling unit can introduce bias in trend estimates (Weiser et al. 2019). Under stratified sampling, a balance between stratum types is therefore needed to prevent over or under sampling certain population densities. For example, sampling more high-density plots that contain high quality habitat may result in over-precise estimates and missed changes in the population (Rhodes et al. 2006; Crum et al. 2021).

Our findings further revealed that environmental variability can influence the value of conducting a survey with the objective of minimizing population estimate uncertainty. 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 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). As identified in our study, populations with lower densities that have experienced higher environmental severity, here identified as winter snow depth and cold temperatures, are less predictable by model-based estimates and should be surveyed more often under these conditions.

Additionally, our findings revealed that uncertainty in model-based estimates increased with years between surveys, resulting in reduced utility to replace surveys and consequently, reduced 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 eight 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). Moreover, our study focused on three risk-based criteria that are commonly considered in wildlife monitoring; however, we acknowledge that other management needs exist and will influence the annual selection of units to monitor. For example, more frequent monitoring of units where active management, such as recovery actions, are taking place may be needed to track population response (Pease et al. 2021). Optimization frameworks for multi-unit monitoring therefore need to be adaptive and address spatial and temporally variability among units to ensure that monitoring effort is efficiently allocated based on management needs.

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Tables and Figures

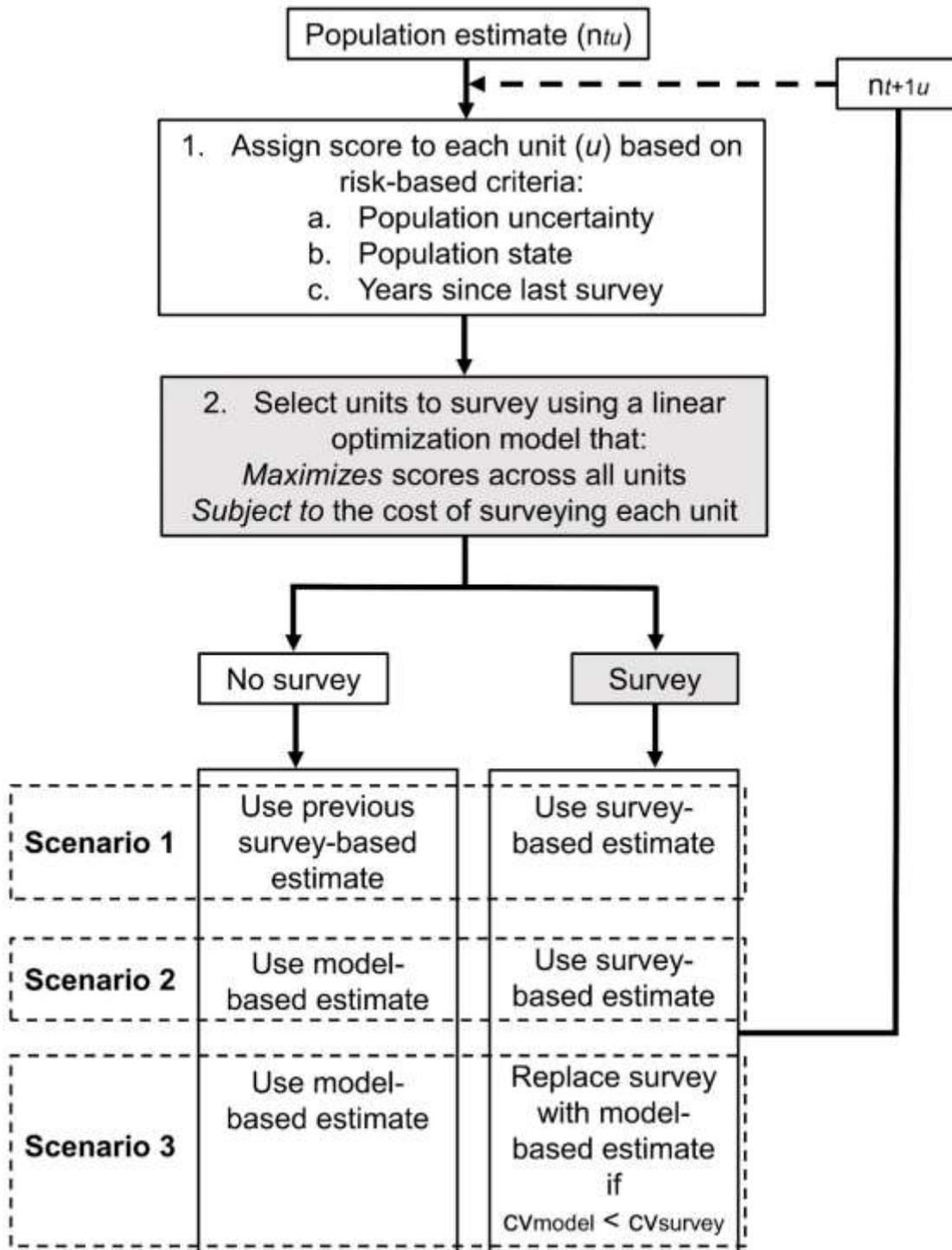


Figure 4-1. Optimization scheme outlining steps taken to select Wildlife Management Units (u) to monitor in each year (t) based on the unit-specific population estimate (n) and its associated uncertainty. In step 1, a score was assigned to each u based on three risk-based criteria (described in step 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 is selected, an aerial-survey is conducted to obtain a survey-based estimate (Scenario 1 and 2) or the coefficient of variation (cv) in precision is compared with uncertainty in a model-based estimate to determine whether a survey-based estimate is used (Scenario 3). If u is not selected, either the previous survey estimate is used (Scenario 1) or a model-based estimate is used (Scenario 2 and 3).

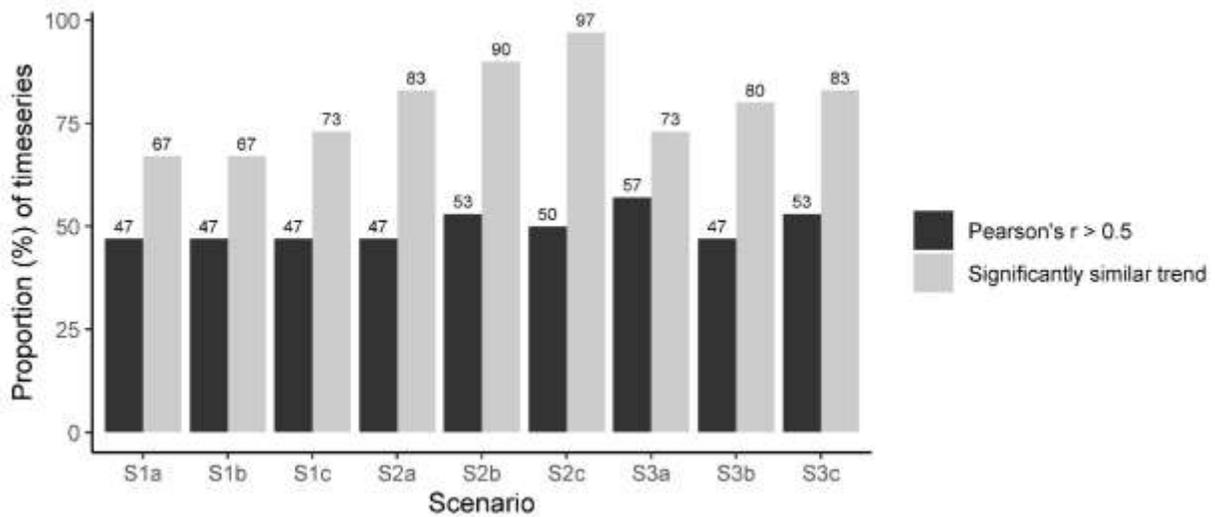


Figure 4-2. The proportion of optimized timeseries ($n = 30$ WMU; % value indicated above each bar) in each scenario that had a linear relationship (Pearson's $r > 0.5$) and a significantly similar trend (based on linear model results, P -value < 0.05) with population size.

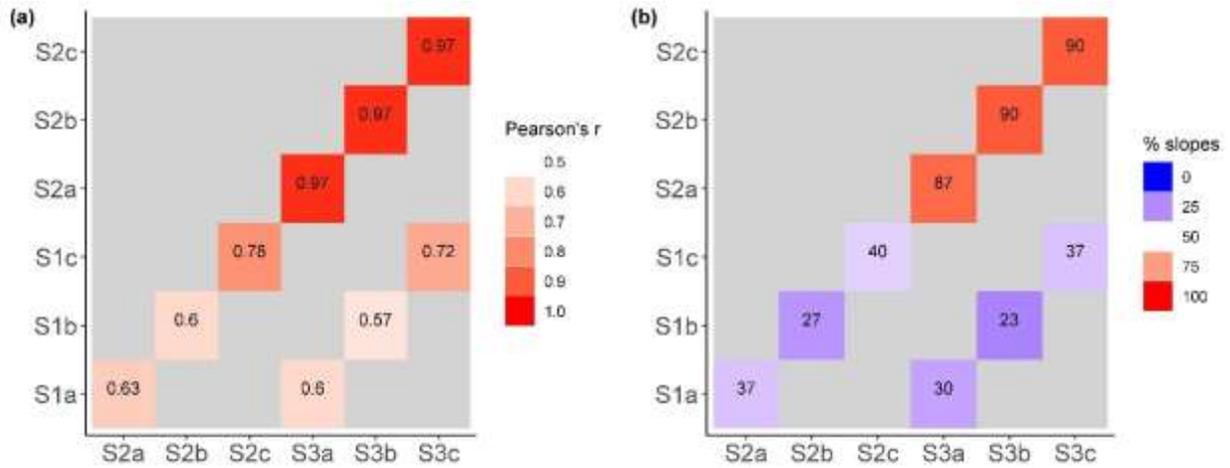


Figure 4-3. Comparative analyses for each scenario based on (a) the linear relationships (Pearson's r) amongst unit-level slopes/trends captured in each scenario and (b) the proportion (%) of slopes (n = 30) that were within 0.01 degrees of each other. Pearson's r and proportional values (%) are indicated in each grid.

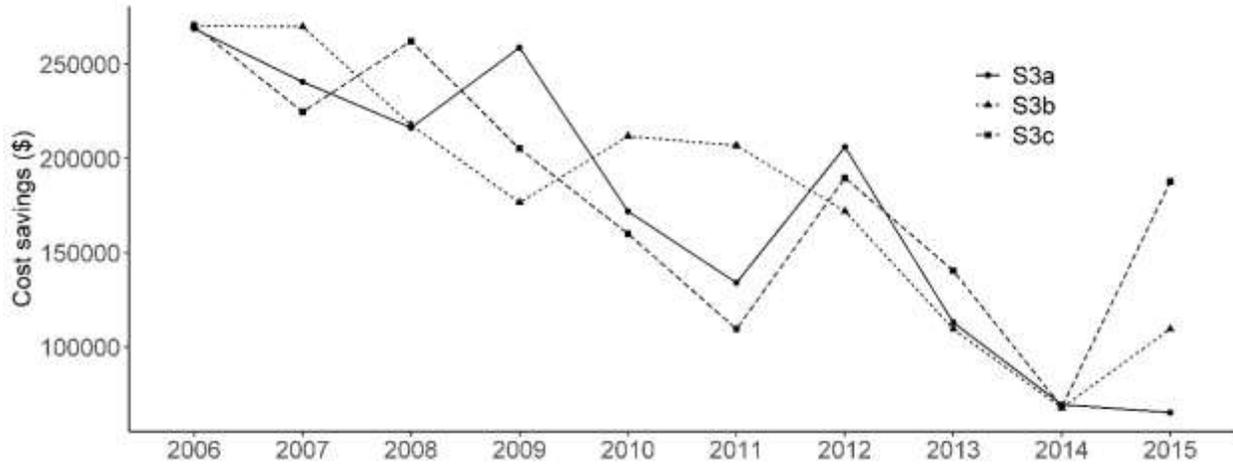


Figure 4-4. Annual cost-savings for Scenario's 3a, 3b, and 3c where surveys were replaced with model-based estimates based on uncertainty in annual population estimates.

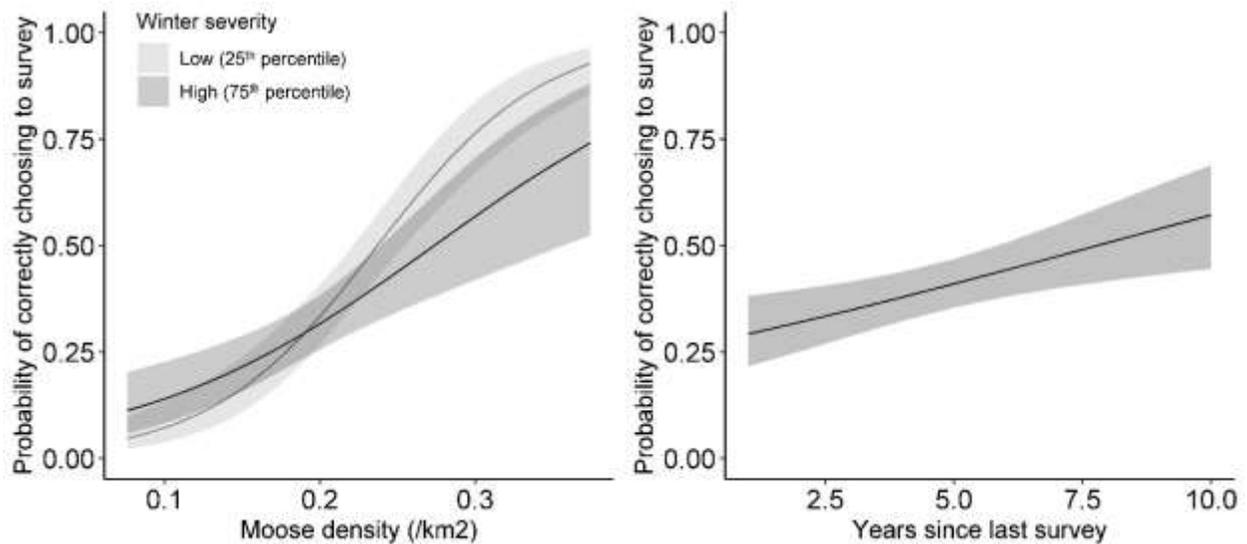


Figure 4-5. Explanatory variables influencing the probability of correctly choosing to survey a given unit each year (binary response), including the interacting effect of moose density and winter severity, and years since the last survey was conducted.

Table 4-1. 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 km², 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 > 16/100km ²	7.5	15	7.5
16 > 18/100km ²	5	10	5
20 < 18/100km ²	2.5	5	2.5
> 20/100km ²	0	0	0
(c) Number of years since last survey	10 points/year	10 points/year	20 points/year

Table 4-2. The three risk-based criteria that were prioritized for selecting units to monitor (rows) and three options for how missing information in each timeseries 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	
Criteria prioritized to monitor		Use previous survey information	Use model-based estimate	Use model-based estimate if model cv < survey cv	
	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

Table 4-3. 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 two-year time lag (wint2), year, and the interacting effect between moose density and winter severity (den:wint2).

Variable	Coefficient	Standard error	P-value
Intercept	-0.414	0.144	0.004
den	1.000	0.163	0.000
wint2	-0.151	0.158	0.339
year	0.352	0.141	0.013
den:wint2	-0.400	0.176	0.023

Appendix

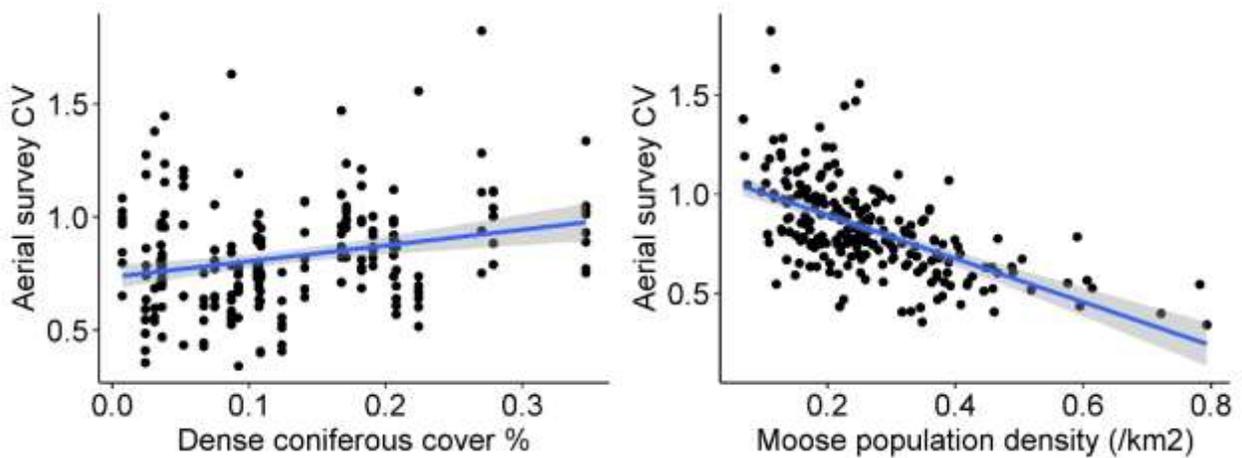


Figure A4-1. Explanatory variables influencing empirical aerial survey-based moose population estimate uncertainty represented as the coefficient of variation (CV). Explanatory variables were at the scale of Wildlife Management Unit and per year.

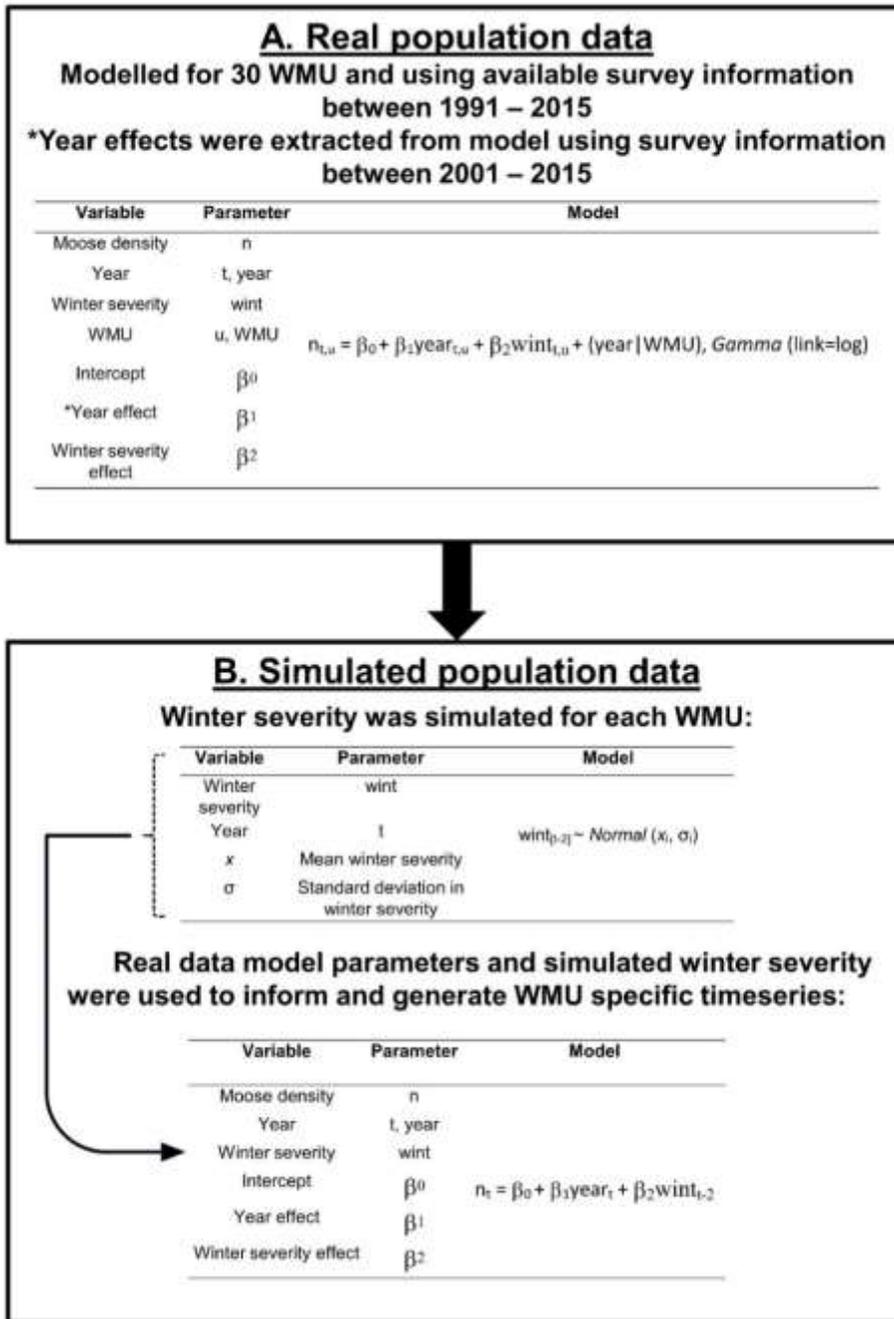


Figure A4-2. A flowchart describing (A) the linear model used to extract parameter coefficients based on aerial-survey derived moose abundance for 30 Wildlife Management Units (WMUs) and between years 1991 – 2015 that were used to (B) generate 30 WMU-specific timeseries of “known” population size. Values of winter severity over time were simulated for each WMU in (B) based on the mean and standard deviation of WMU-specific empirical values.

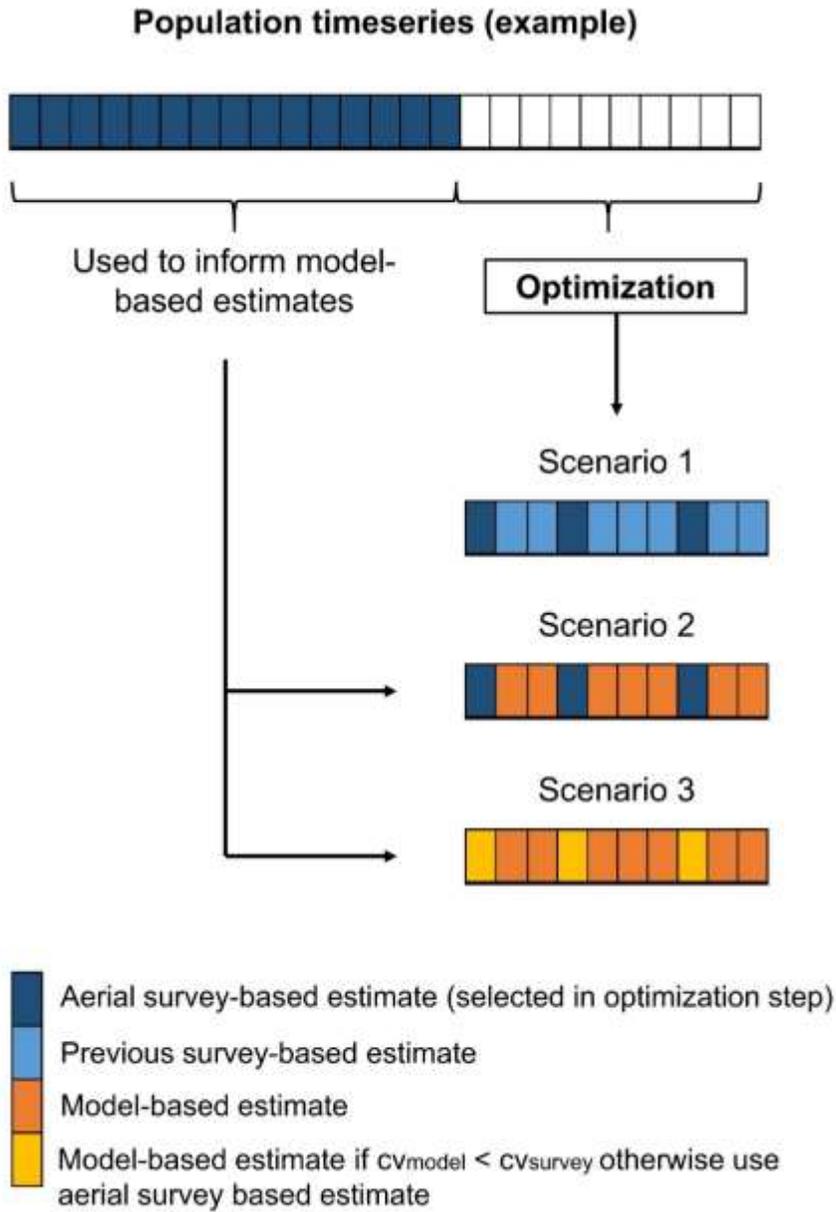


Figure A4-3. An example of a 25-year population timeseries used in our optimization framework and how missing information was treated when an aerial survey was not conducted (this decision was based on units selected during optimization and varied by timeseries). In the figure, each rectangle represents a year. The optimization was performed annually for the last 10 years of each timeseries, and information for the initial 15 years was filled using aerial-survey based estimates to improve the predictive power of model-based estimates.

Table A4-1. Linear mixed-effect model results (Akaike Information Criteria corrected (AICc) and coefficient of determination (R^2)) explaining variation in uncertainty in empirical aerial-survey derived moose population estimates (survey coefficient of variation as response) spanning 25 years (1991 – 2015) and 30 Wildlife Management Units (WMUs). A random effect for WMU and year were included in each model. Model predictors included proportions of WMU composed of: dense coniferous forest cover (dc), dense deciduous forest cover (dd) and coniferous forest cover (conif), as well as the WMU-average density of moose (den).

Model	AICc	R^2
dc + den	-103.14	0.40
dd + den	-92.01	0.38
conif + den	-94.33	0.38
den	-99.74	0.38

Table A4-2. Linear mixed-effect model results for the best performing model explaining variation in uncertainty (coefficient of variation) in empirical aerial survey-based moose population estimates. The model included a random effect of Wildlife Management Unit (WMU) and year. Explanatory variables included dense coniferous forest cover (dc) and WMU-average moose density (den).

Variable	Fixed-effect					Random-effect	
	Coefficient	Standard error	df	t-value	P-value	Variance	Standard deviation
Intercept	0.82	0.02	25.88	41.25	0.00		
dc	0.05	0.02	23.51	2.88	0.01		
den	-0.13	0.01	160.07	-9.22	0.00		
WMU						0.00497	0.07053
year						0.00224	0.04735

Table A4-3. Coefficients extracted from an empirically derived linear model of moose aerial-survey estimates including random intercepts representing moose density and year effects representing rate of change in moose density per year for each Wildlife Management Unit (WMU) included in the study.

WMU	Population density (random intercept) on exponential scale representing moose/km ²	Year effect/trend (random slope) representing % change in moose density per year
3	0.18	5.31
4	0.20	1.96
5	0.38	-19.07
6	0.19	-40.86
07B	0.15	-10.86
8	0.32	-37.18
09A	0.33	-29.83
09B	0.24	-20.60
11A	0.19	-10.66
11B	0.34	-6.92
12A	0.27	1.84
12B	0.32	-17.56
13	0.30	-15.86
14	0.30	-1.18
15A	0.29	-9.63
15B	0.24	2.43
19	0.18	-13.10
21A	0.25	-5.58
21B	0.24	0.90
22	0.25	-3.28
28	0.27	-22.94
29	0.25	-6.52
31	0.17	-2.66
35	0.20	-24.02
36	0.16	-2.60
37	0.22	-17.93

38	0.16	-8.52
48	0.25	17.62
51	0.35	3.44
54	0.26	12.49

Table A4-4. The maximum and minimum values for moose population estimates and average spatial and temporal coefficient of variation (CV) for empirical data, generated population size, and simulated aerial-survey population estimates derived for 30 Wildlife management Units (WMUs) and 25 years.

	Max value	Min value	Average CV spatial (across WMU)	Average CV temporal (across years)
Empirical data (moose population estimates from aerial surveys for each WMU)	6363	103	57%	27%
Generated timeseries of “known” population size for each WMU	5601	300	59%	10%
Simulated aerial survey-based population estimates based on “known” population size for each WMU	5498	232	63%	14%

Table A4-5. Calculation of the average annual costs to survey each Wildlife Management Unit (WMU) included in the study using plot-based aerial surveys flown by helicopter.

WMU	Avg # Plots	Avg Time per plot (minutes)	Avg Time per plot (/60)	Avg cost (\$) per year [(cost per hr * avg time per plot / 60) * avg number plots]
3	43	43.8	0.73	40491
4	41	34.3	0.57	30098
5	33	45.7	0.76	33072
6	32	43.0	0.72	30046
07B	41	43.7	0.73	38505
8	38	41.5	0.69	33809
09A	33	40.9	0.68	29022
09B	35	41.9	0.70	31320
11A	33	36.3	0.61	25955
11B	20	42.2	0.70	18287
12A	35	40.3	0.67	30212
12B	36	43.9	0.73	33766
13	39	44.3	0.74	37625
14	28	45.3	0.76	27155
15A	40	38.9	0.65	33545
15B	41	47.9	0.80	42032
19	44	35.7	0.60	34034
21A	38	41.5	0.69	34528
21B	43	41.4	0.69	38392
22	36	46.3	0.77	35913
28	38	48.9	0.82	40261
29	38	41.1	0.69	34062
31	40	37.5	0.63	32500
35	37	45.8	0.76	36964
36	35	42.0	0.70	32214
37	39	43.6	0.73	37157
38	41	39.9	0.67	35228
48	33	48.4	0.81	34868
51	34	47.2	0.79	35180
54	22	58.8	0.98	28028

Appendix A4-1. R code for simulation of aerial survey-based population estimates.

```
#####  
#Function to simulate WMU specific  
#moose aerial observations/counts with 3 strata  
#and a random sampling approach  
#####  
#Returns "list" of projected moose abundance (C),  
#90% CI, Lower 90% CI, Upper 90% CI and  
#coefficient of variation (CV).  
#Based on counts across strata from 1991 to 2015  
#All values are WMU specific  
#####  
#R code adapted from:  
# MRNF Science and Research Branch  
# Biodiversity and Monitoring  
# Philip DeWitt  
# 2016 Nov 04  
#####  
  
data.fn2 <- function(N, #WMU specific population abundance (not density) for a given year  
count1, #average number of counts in strata1  
count2, #average number of counts in strata2  
count3, #average number of counts in strata3  
nplot1, #average number of plots flown in strata1  
nplot2, #average number of plots flown in strata2  
nplot3, #average number of plots flown in strata3  
strata1, #total plots in strata1  
strata2, #total plots in strata2  
strata3) #total plots in strata3  
{  
  
#WMU specific distribution of N  
countt <- sum(count1, count2, count3)  
count1p <- count1/countt  
count2p <- count2/countt  
count3p <- count3/countt  
  
#Average N per strata  
N1 = N*count1p  
N2 = N*count2p  
N3 = N*count3p  
  
#Average N per plot: subtracted 1 from strata1 and strata2 from the plot-level mean  
#to account for missed moose  
N1 = ((N1/strata1)-1)
```

```

N2 = ((N2/strata2)-1)
N3 = N3/strata3

#Round N to whole number
N1 = round(N1, digits = 0)
N2 = round(N2, digits = 0)
N3 = round(N3, digits = 0)

#plots flown per year
plot1 <- rnorm(1, nplot1, (nplot1*0.3))
plot2 <- rnorm(1, nplot2, (nplot2*0.2))
plot3 <- rnorm(1, nplot3, (nplot3*0.2))

#Round number of plots to whole number
plot1 = round(plot1, digits = 0)
plot2 = round(plot2, digits = 0)
plot3 = round(plot3, digits = 0)

plot <- sum (plot1, plot2, plot3)

#Observations/counts in each strata using a Poisson distribution
C1 = rpois(plot1, N1)
C2 = rpois(plot2, N2)
C3 = rpois(plot3, N3)

#strata sample mean
xbar1 <- mean(C1)
xbar2 <- mean(C2)
xbar3 <- mean(C3)

#estimated moose abundance per strata
moose1 <- strata1*xbar1
moose2 <- strata2*xbar2
moose3 <- strata3*xbar3

#sample sum of squares
ssm1 <- sum((C1-xbar1)^2)
ssm2 <- sum((C2-xbar2)^2)
ssm3 <- sum((C3-xbar3)^2)

#sample variance
s2_1 <- ssm1/(plot1-1)
s2_2 <- ssm2/(plot2-1)
s2_3 <- ssm3/(plot3-1)

s1_sd <- sqrt(s2_1)

```

```

s2_sd <- sqrt(s2_2)
s3_sd <- sqrt(s2_3)

#variance of the mean
s2x_1 <- s2_1/plot1
s2x_2 <- s2_2/plot2
s2x_3 <- s2_3/plot3

#finite population correction factor
fpc1 <- (strata1-plot1)/strata1
fpc2 <- (strata2-plot2)/strata2
fpc3 <- (strata3-plot3)/strata3

#variance of the mean for a finite population
s2x_f1 = s2x_1*fpc1
s2x_f2 = s2x_2*fpc2
s2x_f3 = s2x_3*fpc3

#variance of moose in each stratum
mvar1 <- (strata1^2)*s2x_f1
mvar2 <- (strata2^2)*s2x_f2
mvar3 <- (strata3^2)*s2x_f3

#total extrapolated moose abundance
C <- sum(moose1, moose2, moose3)

#standard error of total moose estimated
se_strata <- sqrt(sum(mvar1, mvar2, mvar3))

sd_strata <- se_strata * (sqrt(plot))

#coefficient of variation for total moose estimated
cv_strata <- sd_strata/C

Upper90strat = C + 1.645 * se_strata
Lower90strat = C - 1.645 * se_strata
CI = (1.645 * se_strata) / C
CI90 = CI*100

my_list <- list(C, CI90, Upper90strat, Lower90strat, cv_strata)
return(my_list)

} # end of function

```

Appendix A4-2. R code to derive state-space model-based population estimates.

```
#####  
##Model-based estimate of Population size ###  
#####  
  
###upload WMU-specific timeseries data and include empty cell for year t+1  
###Use this model to predict Nt+1  
  
#Use log-transformed values of population timeseries estimates (C) and their year-specific  
uncertainty (sd)  
#Use scaled values of year  
  
str(win.data1 <- list(Y = C, sd.obs = sd, yr = year))  
  
# Specify model in BUGS language  
sink("model_1.txt")  
cat("  
  model {  
  
    # Priors  
    b0 ~ dnorm(0, 1.0E-6)           # Prior for intercept  
    b1 ~ dnorm(0, 1.0E-6)           # Prior for year effect  
    sigma.proc ~ dunif(0, 1)        # Prior for sd for state process (variability in C)  
    tau.proc <- 1/pow(sigma.proc, 2)  
    sigma2.proc <- pow(sigma.proc, 2) # Process error  
  
    #Likelihood  
    #Process  
    for (t in 1:(length(Y))) {  
      log.pop.mu[t] <- b0 + b1*yr[t]  
      log.pop[t] ~ dnorm(log.pop.mu[t], tau.proc)  
    }  
  
    #Observation model  
    for (t in 1:length(Y-1)) {  
      Y[t] ~ dnorm(log.pop[t], sd.obs[t])  
    }  
  
    # Population size on real scale  
    for (t in 1:length(Y)) {  
      real.pop[t] <- exp(log.pop[t])  
    }  
  }  
  
",fill = TRUE)
```

```
sink()
params <- c("b0", "b1", "sigma2.proc", "real.pop")

inits <- function()list(b0 = 0.99, b1 = 0.99, sigma.proc = 0.99)

# MCMC settings
ni <- 2000000 ; nt <- 100 ; nb <- 100000 ; nc <- 3

# Call JAGS from R
# Summarize posteriors:

out1 <- jags(win.data1, inits, params, "model_1.txt", n.chains = nc,
            n.thin = nt, n.iter = ni, n.burnin = nb)

print(out1, dig = 3)
```

Chapter Five: General Conclusions

Finding efficiencies in the allocation of monitoring effort for wildlife is important to reduce cost, time, and resources spent monitoring while ensuring managers have reliable information to make decisions (Hauser et al. 2006; Canessa et al. 2015). My research explored factors contributing to uncertainty in harvest indices and aerial-survey derived moose population estimates, and identified a monitoring design that optimized the allocation of monitoring effort across multiple discrete management units with the goal of maximizing resolved uncertainty in population state within a budget.

Firstly, my work contributes to the understanding of sources of bias in a typically applied index of population abundance - harvest data, under a selective harvest system. Harvest indices are relatively cost-effective and easy to obtain in comparison to direct monitoring approaches such as aerial surveys (Månsson et al. 2011; Boyce et al. 2012). However, the relationship between harvest and abundance may be non-linear due to factors associated with hunter effort and the detectability of animals (Schmidt et al. 2005; Willebrand et al. 2011; Ueno et al. 2014). My results revealed that restricted harvest of moose adults reflected abundance more linearly than less restricted calf harvest, but that caution should be taken when interpreting harvest numbers for Wildlife Management Units (WMUs) that have both high levels of hunter effort and greater levels of landscape disturbance that can influence the detectability of moose to hunters. While harvest data captured spatial variability in population abundance, it did not capture temporal variability at the WMU-level. Therefore, harvest data was not used to replace surveys in my fourth chapter, and I caution against its use to inform on year-specific changes in population abundance and trends at the WMU-level.

Further, my work revealed that moose population response to climate can be variable at local (i.e. WMU)-levels and can be attributed to synergistic relationships with habitat that can influence non-direct ecological links. I found that the negative effect of winter severity on moose, which is associated with energetic balance and predator avoidance (Dussault et al. 2005), was lower in areas with more dense forest canopy cover. Further, the negative effect of frost onset on moose, which is associated with white-tailed deer survival and parasite transmission (Lankester 2018; Pickles et al. 2013; Samuel 2007), was greater in areas with more regenerating forest cover. These findings suggest that moose in areas with more sparse and regenerating forests may be more susceptible to adverse climatic effects that contribute to increased risk of predation and parasite transmission for moose. As climate change continues and results in less severe winters and later frost onsets that are linked to northward shifts in white-tailed deer distribution (Dawe and Boutin 2016; Fisher et al. 2020), climate-related factors negatively impacting moose will become exacerbated with potential consequences to the conservation status of the species. Additionally, an increase in environmental variability is likely to increase uncertainty in population state and make population trends less predictable, which can influence monitoring needs and efficiency (Hauser et al. 2006; Wauchope et al. 2019).

I addressed the challenge of optimal allocation of monitoring effort across a multi-unit framework with variable moose population dynamics, and found that interval-based monitoring performed best. Although I focused on three risk-based criteria that are commonly considered in wildlife monitoring: population state, population uncertainty, and years between surveys, other management needs may exist that can influence the annual selection of units to monitor. Generally, my findings revealed that when monitoring efforts and resources are limited and shared for multiple units, interval-based monitoring can be a cost-efficient method that provides accurate

estimation of trends for the greatest number of units. Further, environmental variability can contribute to population uncertainty and increase the need to monitor (Hauser et al. 2006). My findings provide evidence that populations with low densities and that have experienced high environmental severity – here identified as winter snow depth and cold temperatures, are less predictable by model-based estimates and should be surveyed more often under these conditions. Given their vulnerability to stochastic environmental stressors, populations with lower densities should remain priorities in monitoring, particularly if environmental stressors are extreme in certain years.

Overall, the contributions of this thesis can inform decision-making regarding the use of alternative monitoring sources and how to best allocate monitoring effort to reduce uncertainty in population estimates while accounting for monitoring cost. My findings can be applied to other widely distributed and harvested species that are managed and monitored using multi-unit frameworks spanning environmental gradients that contribute to variability in population estimate uncertainty.

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