

Contents lists available at ScienceDirect

Ecological Informatics



journal homepage: www.elsevier.com/locate/ecolinf

Integration of national demographic-disturbance relationships and local data can improve caribou population viability projections and inform monitoring decisions

Josie Hughes^{*}, Sarah Endicott, Anna M. Calvert, Cheryl A. Johnson

Landscape Science and Technology Division, National Wildlife Research Center, Environment and Climate Change Canada, 1125 Colonel By Dr, Ottawa, ON K1S 5B6, Canada

ARTICLE INFO

Keywords: Woodland caribou (Rangifer tarandus caribou) Anthropogenic disturbance scenarios Population viability Value of information Monitoring decisions Species at risk Prior information

ABSTRACT

Across fifty-eight boreal caribou study areas in Canada, survival and recruitment decrease with the percentage of the study area that is disturbed. There is variation in demographic rates among study areas, particularly where anthropogenic disturbance is low, but no populations inhabiting areas with high anthropogenic disturbance are considered viable. Demographic projections derived from local population-specific data are uncertain for populations with limited monitoring. We propose a simple Bayesian population model that integrates prior information from a national analysis of demographic-disturbance relationships with available local demographic data to improve population viability projections, and to reduce the risk that a lack of local data will be used as a reason to delay conservation action. The model also acknowledges additional uncertainty and potential bias due to misidentification of sex or missing calves, through a term derived from a simple model of the recruitment survey observation process. We combine this Bayesian model with simulations of plausible population trajectories in a value of information analysis framework to show how the need for local monitoring varies with landscape condition, and to assess the ability of alternative monitoring scenarios to reduce the risk of errors in population viability projections. Where anthropogenic disturbance is high, reasonably accurate status projections can be made using only national demographic-disturbance relationships. At lower disturbance levels where initial uncertainty is high local data improve accuracy but each additional year of monitoring provides less new information. The estimated probability of viability indicates whether more information is needed to improve accuracy of population viability projections.

1. Introduction

The number of species threatened with extinction is high and getting higher (IPBES, 2019). Reliable information on the status of populations and likely impacts of management are needed to inform conservation action, but effective monitoring is challenging and costly (Dunham et al., 2023; Legg and Nagy, 2006; Lindenmayer and Likens, 2018; Wintle et al., 2010). Resources to support conservation and recovery are limited (Buxton et al., 2022; Gerber, 2016; McCarthy et al., 2012; Wintle et al., 2019), delays in action increase risk (Martin et al., 2012), and some populations have been monitored to extinction (Lindenmayer et al., 2013). A recent analysis of action plans for Canadian species at risk found that half of recovery actions are research and monitoring, and this proportion is highest for species with higher risk of extinction,

highlighting a need to more carefully consider when, where, and why additional information is needed to inform conservation action (Buxton et al., 2022). Analysis of the implications of monitoring outcomes can help to clarify whether additional monitoring is necessary to inform conservation action (Bennett et al., 2018; Dunham et al., 2023; Gregory et al., 2012; Runge et al., 2011).

Boreal caribou are widely and sparsely distributed through the Canadian boreal region across a gradient of anthropogenic disturbance (ECCC, 2011; Johnson et al., 2020) that includes some of the most intact and inaccessible places remaining on earth (Hirsh-Pearson et al., 2022; Ibisch et al., 2016; Venter et al., 2016). Across 58 boreal caribou study areas, both survival and recruitment decrease with the percentage of the area that is disturbed, and no populations inhabiting areas with high anthropogenic disturbance are considered viable, defined as a

https://doi.org/10.1016/j.ecoinf.2025.103095

Received 18 October 2024; Received in revised form 24 February 2025; Accepted 25 February 2025 Available online 2 March 2025

1574-9541/Crown Copyright © 2025 Published by Elsevier B.V. This is an open access article under the CC BY license (http://creativecommons.org/licenses/by/4.0/).

^{*} Corresponding author. E-mail address: josie.hughes@ec.gc.ca (J. Hughes).

population experiencing stable or positive growth (>0.99) in the absence of interventions such as predator control or maternal penning (ECCC, 2011; Johnson et al., 2020). We acknowledge that other considerations such as population size are important, but our focus in this analysis is population growth rate. Identifying populations that are declining is important for clarifying where and when conservation action is needed. Disturbance affects caribou demography both through direct impacts on habitat availability and use, and indirect impacts on predators and alternate prey (ECCC, 2011; NBCKC, 2022a). Decreasing recruitment with increased disturbance has also been observed over time where historic demographic data exist (Hervieux et al., 2013; Rudolph et al., 2017), but many places lack sufficient data to characterize local demographic-disturbance relationships (Johnson et al., 2020). There is also variation in demographic rates among study areas, particularly where anthropogenic disturbance is low (Fortin et al., 2017; Gagné et al., 2016; Johnson et al., 2020; Neufeld, 2021), which leads to uncertainty in projections that rely only on national-scale relationships (Dyson et al., 2022; Stewart et al., 2023).

Analysis methods that can make better use of available monitoring data to inform conservation decisions include Bayesian population modelling (Schaub and Kery, 2021) and value of information analyses (Bennett et al., 2018; Dunham et al., 2023; Gregory et al., 2012; Runge et al., 2011). For sparsely monitored populations, incorporating prior information from elsewhere can help reduce uncertainty (Drummond et al., 2018; Parlato et al., 2021; Tufto et al., 2000). Various efforts have been made to improve caribou population viability projections +++and growth rate estimates using Bayesian methods (Dalgarno et al., 2024; Eacker et al., 2019; Lamb et al., 2024; McNay et al., 2022; Moeller et al., 2021). An advantage of Bayesian demographic models is that they account for multiple sources of uncertainty (Eacker et al., 2017; Schaub and Abadi, 2011; Schaub and Kery, 2021). However, Bayesian caribou population models developed to-date (Dalgarno et al., 2024; Eacker et al., 2019; Lamb et al., 2024; McNay et al., 2022; Moeller et al., 2021) have not included prior information about the observed distribution of demographic rates across the country that could reduce uncertainty about the status of poorly monitored populations.

Here, we offer a simple Bayesian population model for boreal caribou (*Rangifer tarandus caribou*) that integrates prior information about the impacts of landscape change (i.e. demographic-disturbance relationships in Johnson et al., 2020) with available demographic data to reduce uncertainty in population viability projections. We also offer a novel method of acknowledging and accounting for errors in composition surveys. Following a value information analysis framework for conservation status assessments (Dunham et al., 2023), we combine this Bayesian model with simulations of plausible population trajectories (Dyson et al., 2022; Stewart et al., 2023) to (i) show how the value of local monitoring varies with landscape condition, and (ii) assess the ability of alternative monitoring scenarios to reduce the risk of errors in population viability projections.

Our proposed model represents an important improvement over less formally integrated methods for estimating and projecting impacts of disturbance on population viability (ECCC, 2011; Johnson et al., 2020) because it accounts for uncertainties in both local data and demographic-disturbance relationships. We show that integrating the most informative predictor of outcomes for boreal caribou across their range can substantially reduce uncertainty in local demographic projections and improve the accuracy of population viability projections on changing landscapes. This approach can help clarify where available information is - and is not - sufficient for assessing and projecting population viability, and thereby reduce the risk that uncertainty is used as a reason to delay conservation action for imperiled populations (Bissonnette and Teitelbaum, 2020; Boan et al., 2018). Our approach is tailored to boreal caribou, but could be adapted for other species at risk found in multiple populations that are costly to monitor and sensitive to habitat disturbance.

2. Methods

2.1. Overview of methods and notation

To investigate how the accuracy and precision of predictions vary with both landscape condition and monitoring effort, we analyze simulated data using a Bayesian model with informative priors (section 2.4) and a composition survey bias term (section 2.1). Steps in our analysis procedure include defining anthropogenic disturbance and monitoring scenarios (section 2.2), simulating population dynamics and monitoring (section 2.3) to produce example demographic trajectories for each scenario, and analyzing example demographic trajectories with a Bayesian model that enables integration of (simulated) local demographic data with prior knowledge of demographic-disturbance relationships (section 2.4). Outcomes of interest include expected population growth rate, the probability of correctly assessing population status, the posterior probability of population viability, and the expected value of local information (section 2.5). We refer to the model used to simulate example trajectories as the "national" model because parameters are from a national analysis of demographic-disturbance relationships (Johnson et al., 2020). We distinguish this national model from the Bayesian model that is used to analyze simulated example demographic trajectories. Where appropriate the national model and the Bayesian model share the same structure, and we have selected notation to highlight the similarities. Bayesian model estimates are distinguished from observed values, estimated expected values, true values, and true expected values using \sim and - symbols respectively; for example, S_t is the Bayesian estimate of survival in year *t*, \hat{S}_t is observed survival, \tilde{S}_t is the Bayesian estimate of expected survival (without stochastic interannual variation), \dot{S}_t is true survival, and $\overline{S_t}$ is true expected survival (without stochastic interannual variation). For reference, all variables and parameters are defined in supplemental Table A1.

2.2. Caribou population monitoring data and composition survey errors

The most widely available source of boreal caribou demographic information is from cows fitted with telemetry collars (e.g. Courtois et al., 2003; DeCesare et al., 2012; Hervieux et al., 2013; Rettie and Messier, 1998), though genetic methods are playing an increasingly important role in some caribou monitoring programs (e.g. Flasko et al., 2017; Hettinga et al., 2012; Jones et al., 2023; McFarlane et al., 2018, 2021, 2022; Moeller et al., 2021). Caribou cows are typically captured via net-gun from aircraft in late winter, and affixed with collars that send a mortality signal when no longer active (see NBCKC, 2021a), thus allowing estimation of adult survival (e.g. Dalgarno et al., 2024; Eacker et al., 2019; Hervieux et al., 2013; Lamb et al., 2024; McLoughlin et al., 2003). Recruitment is estimated from aerial surveys of the composition of groups of animals that include collared animals (NBCKC, 2022b). Groups typically also contain uncollared animals, and a critical assumption in these surveys is that different demographic groups are equally detectable (Ellington et al., 2020). Errors that can bias composition survey results include misidentifying young bulls as cows or vice versa, and failing to detect calves (DeCesare et al., 2012; Ellington et al., 2020). Survival and recruitment survey data can be combined in a simple recruitment-mortality population model (Hatter, 2020; Hatter and Bergerud, 1991) that serves as the basis for many herd viability assessments (Dalgarno et al., 2024; DeCesare et al., 2012; Eacker et al., 2019; ECCC, 2011; Johnson et al., 2020; Serrouya et al., 2017).

While we believe that using available information to reduce uncertainty is important, we also believe it is important to acknowledge remaining uncertainty. In general, parametric Bayesian population models include a number of simplifying assumptions, and misspecified models can yield biased or overconfident results (Schaub and Kery, 2021). More specifically, models that do not account for observation errors can be misleading (Schaub and Kery, 2021). Although several authors have pointed out that misclassification of adults and missing calves in composition surveys can bias recruitment estimates from those surveys (DeCesare et al., 2012; Ellington et al., 2020), none have thus far integrated these sources of error into Bayesian caribou population models (Dalgarno et al., 2024; Eacker et al., 2019; Lamb et al., 2024; McNay et al., 2022; Moeller et al., 2021). We address this gap with a bias term derived from a simple model of the recruitment survey observation process.

To derive a composition survey bias term we assume each group of animals in a calf:cow composition survey contains one or more collared adult females (T), and may also include: uncollared adult females misidentified as young bulls or unknown sex (U); correctly identified uncollared adult females (V); young bulls correctly identified as male or unknown sex (O); young bulls misidentified as uncollared adult females (P); observed calves (J); and unobserved calves (K). The apparent number of adult females in the group is T + V + P = Tw, where *w* is the observed ratio of the apparent number of adult females to collared animals in the recruitment survey. The ratio of young bulls to uncollared adult females in the group is q = (P + O)/(U + V). Assuming an equal probability *u* of misidentifying young bulls as adult females and vice versa, we get V = (U + V)(1 - u) and P = (O + P)u. Given a probability z of missing calves, we get J = (J + K)(1 - z). Given these assumptions and definitions, the sex and bias-adjusted recruitment rate X can be written as a function of the observed calf:cow ratio *R*, the cow multiplier w, the ratio of young bulls to uncollared adult females q, and the misidentification probabilities u and z (see Supplement B for details). For simplicity, we combine the probabilities into a bias term c that is integrated into the national simulation model (section 2.4) and the Bayesian model (section 2.5):

$$c = \frac{w(1+qu-u)}{(w+qu-u)(1-z)}; X = cR/2.$$
(1)

2.3. Anthropogenic disturbance and monitoring scenarios

In simulated monitoring scenarios, we assume collars are deployed in January, and continue to function for up to 6 years. The target number of collared females *n* varies among scenarios, as does the total duration of the monitoring program *d* and the ratio of observed adult females to collared animals in the recruitment survey *w* (Table 1). Collars lost to mortality may be replaced each year (o = 1), or there may be a 3 year gap between deployments (o = 4).

We focus on exploring a set of scenarios in which anthropogenic disturbance, measured as the percentage of area within 500 m of some type of anthropogenic disturbance (ECCC, 2011; Johnson et al., 2020), increases by 1 % per year (Fig. 1). The duration of monitoring prior to the projection period varies among scenarios from 1 to 24 years. The projection period begins in 2024, and we consider how uncertainty changes as the projection period increases from 5 to 20 years. The amount of anthropogenic disturbance at the beginning of the projection period varies from low (0 %) through medium-low (20 %) and medium-high (40 %) to high (60 %). These simple hypothetical scenarios span a large range to show how the need for local monitoring to reduce uncertainty depends on landscape state, not to represent the reality of landscape change. Scenarios in which anthropogenic disturbance remains the same or decreases over time are included in Supplement D.

Table 1

Monitoring scenario parameters and values used in simulations.

Symbol	Description	Units	Values
d	Monitoring duration.	years	1,2,4,8,16,24
n	Target # of collars.	cows	0,15,30,60
0	Years between collar deployments.	years	1,4
w	Cows per collared animal in composition	ratio	6
	survey.		

2.4. Simulation of population dynamics and monitoring

To investigate the effectiveness of various monitoring strategies, and to show how this varies with landscape condition, we begin by simulating example demographic trajectories and observations of those trajectories using a modified version of Johnson et al.'s (2020) demographic model described by Dyson et al. (2022). For brevity, we refer to this as the "national" model, and for clarity we include a full description in the following paragraphs. Together, a set of example trajectories from the national model represent alternative hypotheses about the true state of a particular caribou population. To assess the accuracy of population status assessments and the expected value of alternative monitoring strategies (Dunham et al., 2023; Runge et al., 2011) we analyze each trajectory of simulated observations using the Bayesian model (section 2.4). We also use the sets of simulated trajectories to confirm that prior predictions from our Bayesian model are consistent with knowledge of the observed distribution of outcomes for caribou across the country (Johnson et al., 2020).

Given a population of post-juvenile females at the beginning of year t, \dot{N}_t , the number that survive to the census, \dot{W}_t , is binomially distributed with true survival probability \dot{S}_t : $\dot{W}_t \sim \text{Binomial}\left(\dot{N}_t, \dot{S}_t\right)$. Realized recruitment rate varies with population density (Lacy et al., 2017), and the number of juveniles recruiting to the post-juvenile class at the census $\left(\dot{J}_t\right)$ is a binomially distributed function of the number of surviving post-juvenile females (\dot{W}_t) and the maximum potential recruitment of female calves per cow (\dot{X}_t):

$$\dot{J}_t \sim \text{Binomial}\left(\dot{W}_t, \dot{X}_t \left[p_0 - (p_0 - p_k)\left(\frac{\dot{W}_t}{k}\right)^b\right] \frac{\dot{W}_t}{\dot{W}_t + a}\right),$$
 (2)

Given the values of parameters p_0, p_k, a , and b used by Johnson et al. (2020) (Table A1), recruitment rate is lowest $(0.5\dot{X}_t)$ when $\dot{N}_t = 1$, approaches a maximum of \dot{X}_t at intermediate population sizes, and declines to $0.6\dot{X}_t$ as the population reaches carrying capacity of k = 10000. The post-juvenile female population in the next year includes both survivors and new recruits: $\dot{N}_{t+1} = min(\dot{W}_t + \dot{J}_t, r_{max}\dot{N}_t)$, where the maximum potential population growth rate is $r_{max} = 1.3$.

The observable calf:cow ratio \dot{R}_t is adjusted for sex ratio and composition survey errors (Supplement B) to get the maximum potential recruitment of female calves per cow \dot{X}_t :

$$\dot{X}_{t} = \dot{c}\dot{R}_{t}/2; \\ \dot{c} = \frac{w(1 + \dot{q}\dot{u} - \dot{u})}{(w + \dot{q}\dot{u} - \dot{u})(1 - \dot{z})},$$
(3)

where *w* is the ratio of observed adult females to collared animals, \dot{q} is the ratio of young bulls to adult females, \dot{u} is the probability of misidentifying young bulls as adult females and vice versa, and \dot{z} is the probability of missing a calf. We examine sensitivity to these unknown parameters by selecting values for each simulated example population from plausible ranges: \dot{u} and \dot{v} vary uniformly between 0 and 0.2, and \dot{q} varies uniformly between 0 and 0.6. The distinction between the true composition bias term \dot{c} and the term c we include in the Bayesian model (eq. (1)) is that the (simulated) truth is known, and the Bayesian model bias is uncertain.

Interannual variation in survival and recruitment is modelled using truncated beta distributions [rtrunc function; Novomestky and Nadarajah, 2016]: $\dot{R}_t \sim$ TruncatedBeta($\bar{R}_t, \nu_R, l_R, h_R$); $\dot{S}_t \sim$ TruncatedBeta ($\bar{S}_t, \nu_S, l_S, h_S$). Coefficients of variation among years (ν_R, ν_S) and maximum/minimum values l_R, h_R, l_S, h_S for recruitment and survival are given in Table A1. Expected recruitment (\bar{R}_t) and survival (\bar{S}_t) vary with disturbance according the beta regression models estimated by Johnson et al. (2020):



Fig. 1. Anthropogenic disturbance and monitoring scenarios. Anthropogenic disturbance increases by 1 % per year, and the amount of disturbance at the beginning of the projection period varies from low (0 %), through low-med (20 %) and med-high (40 %) to high (60 %). These simple hypothetical scenarios are intended to show how the need for local monitoring to reduce uncertainty varies with landscape state, and not intended to reflect real landscape change. In all scenarios, the projection period begins in 2024, and the monitoring period occurs prior to the projection period.

$$\overline{R}_{t} \sim Beta(\mu_{t}^{R}, \phi^{R}); log(\mu_{t}^{R}) = \dot{\beta}_{0}^{R} + \dot{\beta}_{a}^{R}A_{t} + \dot{\beta}_{f}^{R}F_{t},$$
(4)

$$\overline{S}_t \sim \left(46 \times Beta(\mu_t^S, \phi^S) - 0.5\right) / 45; \log(\mu_t^S) = \dot{\beta}_0^S + \dot{\beta}_a^S A_t.$$
(5)

 $\phi^{R} \sim \text{Normal}(19.862, 2.229)$ and $\phi^{S} \sim \text{Normal}(63.733, 8.311)$ are precisions of the Beta distributed errors (Ferrari and Cribari-Neto, 2004). At the beginning of a simulation for an example population, regression coefficient values are sampled from Gaussian distributions (see Table 2) and the population is assigned to quantiles of the Beta error distributions for survival and recruitment. The population remains in these quantiles as disturbance changes over time, so there is substantial persistent variation in recruitment and survival among example populations (Fig. 2).

In our simulated example populations the number of collared cows at the time of the composition survey \hat{T}_t depends on the true survival rate \dot{S}_t and the number of collared cows at the beginning of the year \hat{I}_t : $\hat{T}_t \sim \text{Binomial}(\hat{I}_t, \dot{S}_t)$. The number of cows in the composition survey \hat{W}_t is given by the number of collared cows \hat{T}_t and the apparent number of adult females per collared female observed in the composition survey w: $\hat{W}_t = w\hat{T}_t$. The number of observed calves \hat{J}_t also depends on the

Table 2

Prior means and standard deviations of Gaussian distributed survival and reproduction model parameters. Standard deviations are calibrated so that the 95 % prior predictive intervals for survival and recruitment from the Bayesian model match the 95 % prediction intervals from Johnson et al.'s regression model (Supplement C).

Parameter	Description	Mean	SD
β_a^R β_a^R	R anthropogenic disturbance slope R fire slope	-0.0170 -0.0081	0.0060 0.0020
β_{a}^{S}	S anthro slope	-0.0008	0.0005
β_0^R	R intercept	-1.0230	0.3500
β_0^S	S intercept	-0.1420	0.0600

unadjusted apparent recruitment for the population \dot{R}_t :

$$\widehat{J}_t \sim \operatorname{Binomial}\left(\widehat{W}_t, \dot{R}_t\right).$$
 (6)

To ensure that results are comparable across monitoring scenarios and that populations remain extant through the monitoring period, all simulations are started with $N_0 = 5000$ animals 24 years prior to the start of the projection period. Realized population growth rate is $\dot{\lambda}_t = \dot{N}_t / \dot{N}_{t-1}$ Expected population growth rate (without interannual variation, demographic stochasticity, or effects of population density) is $\bar{\lambda}_t = \overline{S}_t (1 + c\overline{R}_t/2)$.

2.5. Bayesian integration of local demographic data and national disturbance-demographic relationships

Local demographic and covariate data provided as inputs to the Bayesian population model include the number of collared cows at the start of the year (\hat{I}_t) , the number of collared animals that survive the year (\hat{T}_t) , the observed number of adult females and calves in the recruitment surveys $(\widehat{W}_t, \widehat{J}_t)$, the apparent number of adult females per collared female in the composition survey *w*, and the measures of anthropogenic disturbance and fire (A_t, F_t) . Recruitment rate R_t is estimated from the observed number of calves \widehat{J}_t and adult female caribou \widehat{W}_t assuming a Binomial distribution:

$$\widehat{J}_t \sim \text{Binomial}(\widehat{W}_t, R_t).$$
 (7)

The difference between eqs. (6) and (7) is that in the simulation model an unadjusted apparent recruitment rate \dot{R}_t is selected and used to simulate observations. In the Bayesian model, in contrast, observations are provided, and used to estimate the unobserved recruitment rate R_t .

In both models, recruitment probability is a function of anthropogenic disturbance and fire with a log link and Beta distributed interannual variation (Dyson et al., 2022; Johnson et al., 2020; Stewart et al., 2023). The coefficient of variation ν_R is constant, while the mean $\tilde{R_t}$ and


Fig. 2. Examples of simulated population trajectories from a model informed only by national disturbance-demographic relationships. To highlight how variation among trajectories persists as disturbance changes, we have reduced interannual variation by 75 % in these examples ($v_R = 0.115$, $v_S = 0.02175$). Orange dots show means of 500 example trajectories. For reference, black lines and and shaded bands show means and 95 % predictive intervals from Johnson et al.'s (2020) regression models.

standard deviation $\sigma_{R,t}$ vary with disturbance:

$$\log(R_t) = \beta_0^R + \beta_a^R A_t + \beta_f^R F_t \tag{8}$$

$$R_{t} \sim \text{Beta}\left(\widetilde{R_{t}}, \sigma_{R,t}\right); \sigma_{R,t} = \min\left(\nu_{R}\widetilde{R_{t}}, \sqrt{\widetilde{R_{t}}\left(1 - \widetilde{R_{t}}\right)}\right)$$
(9)

In the simulation model (eq. (4)), regression coefficient values $(\dot{\beta}_0^R, \dot{\beta}_a^R)$ are selected for each example population and used to calculate recruitment rate. In the Bayesian model (eq. 8), unobserved regression coefficients $(\beta_0^R, \beta_a^R, \beta_f^R)$ are estimated from local recruitment survey and disturbance observations.

To account for sex ratio of calves and additional uncertainty caused by composition survey errors (Supplement B) estimated recruitment is adjusted to get expected female recruits per female $X_t = cR_t/2$. The composition survey bias term c (eq. (1)) depends on the known apparent number of adult females per collared animal w, the unknown ratio of young bulls to adult females q, the unknown probability of misidentifying young bulls as adult females and vice versa u, and the unknown probability of missing a calf z (Supplement B). Prior uncertainty about the value of the bias term c is approximated with a Log-normal distribution (Supplement B). Given the apparent number of adult females per collared animal w in each monitoring scenario (Table 1), we calculate the mean and standard deviation of 10,000 samples of logc assuming the ratio of young bulls to adult females q varies uniformly between 0 and 0.6, the adult misidentification probability u varies uniformly between 0 and 0.2, and the probability of missing a calf zvaries uniformly between 0 and 0.2.

Survival S_t is estimated from the observed number of collared cows at the beginning of each year \hat{I}_t and the number of those that survive the year \hat{T}_t assuming a Binomial distribution: $\hat{T}_t \sim \text{Binomial}(\hat{I}_t, S_t)$. Note that real known-fate radio collar data should be analyzed with a method that accounts for variation in survival rate and the number of collared animals throughout the year (e.g. Dalgarno et al., 2024; Eacker et al., 2019; Lamb et al., 2024). However, our implementation of a two-step non-parametric survival analysis method (following Eacker et al., 2019) yielded slightly biased survival estimates.

As done by Johnson et al. (2020), we model survival probability as an adjusted function of anthropogenic disturbance A_t with a log link and Beta distributed interannual variation with coefficient of variation ν_s , mean \tilde{S}_t and standard deviation $\sigma_{s,t}$ (Dyson et al., 2022; Stewart et al., 2023):

$$\widetilde{S}_t = \left(46e^{\beta_0^5 + \beta_a^5 A_t} - 0.5\right) \Big/ 45 \tag{10}$$

$$S_t \sim \text{Beta}\left(\widetilde{S}_t, \sigma_{S,t}\right); \sigma_{S,t} = \min\left(\nu_S \widetilde{S}_t, \sqrt{\widetilde{S}_t}\left(1 - \widetilde{S}_t\right)\right)$$
 (11)

Again assuming a simple demographic model with a census in late winter of surviving females and new recruits to the post-juvenile class (Hatter, 2020; Hatter and Bergerud, 1991), the expected population growth rate (without interannual variation or demographic stochasticity) is $\tilde{\lambda}_t = \tilde{S}_t \left(1 + c\tilde{R}_t/2\right)$.

All regression coefficients are assumed to be Gaussian distributed, with prior means from Johnson et al.'s (2020) regression models (Table 2). We calibrated the standard deviations of the priors so that the the 95 % prior predictive intervals for survival and recruitment from the Bayesian model match the 95 % prediction intervals from Johnson et al.'s (2020) regression model (Supplement C, Fig. 3). To show the value of informative priors, we also include a weakly informative scenario with prior means of the intercept parameters from Dalgarno et al. (2024) (
$$\beta_0^R = -0.3689, \beta_0^S = -0.2126776$$
), prior means of the slope parameters set to zero, and standard deviations for all parameters

(Table 2) multiplied by ten. For reference, all variables and parameters are defined in supplemental Table A1. Models and analysis were implemented using the R language (R Core Team, 2023) and a variety of tidyverse packages (Wickham et al., 2019). We use the open source Gibbs sampling software JAGS (Plummer, 2023) and the R2jags R package (Su and Yajima, 2021) to fit the Bayesian model. We ran 15,000 iterations of 4 chains, discarded the first 10,000 interations, and used a thinning rate of 2. We assessed convergence for a small random subset of example trajectories using a threshold for the Gelman-Rubin diagnostic (Gelman and Rubin, 1992) of r-hat <1.1, and visually inspected posterior autocorrelation and traceplots produced by the mcmcplots R package (Curtis, 2018). Code required to run analyses and reproduce figures in this paper is available at https://github.com/LandSciTech/Caribou-Demograph ic-Projection-Paper, and in the caribouMetrics R package available on GitHub at https://github.com/LandSciTech/caribouMetrics/tree/EI-pa per-submission.

2.6. Probability of correct status assessment and expected value of information

In order to assess whether a monitoring program is likely sufficient to inform decisions, it is important to select outcome measures that are



Fig. 3. Prior (a) and posterior predictions from the Bayesian model for population trajectories with informative (a,b) and weakly informative (c) priors given lower interannual variation ($v_R = 0.23$, $v_S = 0.435$) and long-term monitoring. In this example scenario anthropogenic disturbance increases by 2 % per year from 0 to 100 %. The population is monitored for 16 years with 30 collars per year, and 6 cows per collared cow in the composition surveys. The prior means and 95 % predictive intervals (a, orange lines and shading) are similar to the means and ranges between the 2.5 % and 97.5 % quantiles of 3000 simulated survival and recruitment trajectories from the national model (a, blue lines and shading). Local population data (open triangles) reduces uncertainty about demographic rates (b), though that is not needed to predict viability (population growth \leq 0.99) of highly disturbed populations (a). With weakly informative priors the model does not provide accurate or precise predictions of future viability after 16 years of monitoring in a case where anthropogenic disturbance is increasing to 90 % (c). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

relevant to decision making (Gregory et al., 2012). For boreal caribou and other endangered species, a relevant outcome is the probability of correctly predicting the true population status (increasing or decreasing) (Dunham et al., 2023). To calculate this outcome for each disturbance and monitoring scenario (Fig. 1) we simulate observations from 500 example trajectories (e.g. Fig. 2), fit the Bayesian model to each of these, and calculated the percentage of these 500 examples in which the Bayesian posterior expected population growth rate and the true expected population growth rate are both greater than 0.99, or both less than or equal to 0.99.

Following Dunham et al. (2023) we also calculate the expected value of perfect information (EVPI) and the expected value of sample information (EVSI) (Runge et al., 2011; Yokota and Thompson, 2004). We assign a value or utility of $\eta_{\alpha,\psi} = 1$ when the true state of the population ψ matches the assigned status α , and value of $\eta_{\alpha,\psi} = 0$ when the status assessment is incorrect. This is "the value ascribed by the decision-maker to the outcome, and is thus the measure of management performance" (Runge et al., 2011). The expected value of current information is the average utility of decisions informed by knowledge of the disturbance scenario τ (Fig. 1) and priors from the national model:

$$EV_{current} = max_{\alpha} \sum_{\alpha} \left[P(\psi|\tau) \eta_{\alpha,\psi} \right], \tag{12}$$

where $P(\psi|\tau)$ is the prior probability that the true state of the population is ψ , and each population is assigned a status α informed by the prior. The expected value under certainty (i.e. the expected value of a decision when the true state of the population is known) is $EV_{certainty} = 1$. The difference between $EV_{certainty}$ and $EV_{current}$ gives EVPI, a measure of the maximum possible benefit that could theoretically be gained if the system were perfectly known.

EVSI measures expected improvement from a particular monitoring strategy as the difference between the expected value with and without additional sample information:

$$EVSI_{\tau} = E_{x} \left[max_{a} \sum_{\psi} \left[P(\psi | x, \tau) \eta_{a,\psi} \right] \right] - EV_{current},$$
(13)

where *x* is the sample information from a particular example trajectory. In this study, we treat simulated observations from 500 example trajectories for each disturbance and monitoring scenario τ (Fig. 1) as samples from the distribution of possible values of *x*, and assume each of these sample results is equally probable. $P(\psi|x, \tau)$ is the posterior probability that the true state of the population is ψ , and each population is assigned a status α informed by the sample information.

To aid in interpretation of results and to highlight the advantages of





selecting a metric that is directly relevant to the management objective of stable or increasing populations, we also show how integrating local monitoring data alters the distribution of differences between true expected population growth rates and Bayesian posterior expected growth rates.

3. Results

Analysis of simulated example demographic trajectories confirms that our Bayesian model can effectively combine local demographic data with priors from a national demographic-disturbance relationships to reduce uncertainty in boreal caribou demographic projections (Figs. 3 and 5). When local data are limited (e.g. 4 years, 15 collars per year) the model with informative priors (i.e. knowledge of national relationships) yields predictions that are consistent with knowledge of observed outcomes across the country, and the model with weakly informative priors does not (Fig. 4). When there is interannual variation, increasing the duration of monitoring improves predictions of population growth rate substantially, and increasing the number of collars each year is less effective (Fig. 5). Insufficiently informative priors can yield predictions that are both imprecise and inaccurate even in a case where there are 16 vears of local monitoring data (Fig. 3), highlighting the benefits of integrating national relationships with these local data. Increasing the forecast horizon (Petchey et al., 2015) does not substantially decrease the accuracy of expected population growth projections (compare 0, 5 and 20 year projections in Fig. 5) in these scenarios.

Examining the probability of correctly assessing population status

(Fig. 6) and the expected value of information (Figs. 7 and E.1) helps clarify how the need for monitoring varies with landscape condition. When anthropogenic disturbance is high (right panels of Figs. 6, 7, and E.1), projections of population status informed only by priors from the national demographic-disturbance relationships are accurate, and adding additional local monitoring data does not improve accuracy. At lower levels of disturbance, local monitoring can increase accuracy, but there are diminishing returns as the number of years of monitoring increases (Figs. 6 and 7). Increasing accuracy is more difficult when interannual variation is high (Figs. 6 and 7). The shapes of the relationships between monitoring effort and the probability of correct status assessment depend on how anthropogenic disturbance is changing over time, but there are diminishing benefits of increased monitoring regardless of whether disturbance is increasing or decreasing (Supplement D). Acknowledging the possibility of composition survey errors reduces accuracy, but the reductions are not large for the set of parameters we investigate (Supplement F).

Averaging over the full set of example trajectories for each scenario (Figs. 6 and 7) obscures variation among them that is also important for monitoring decisions. For example, where disturbance is low but increasing, monitoring helps identify populations that are faring less well than expected now (top left of Fig. 8), and also helps identify populations that are likely to remain viable in the future when disturbance is higher (bottom right of Fig. 8). Status assessment accuracy is much higher when the 95 % credible interval for expected population growth rate does not include one (99.72 %) than when it does (81 %), and this information could be used to guide monitoring. A more nuanced



Fig. 5. The distribution of differences between true expected population growth rates and Bayesian posterior expected growth rates varies with the amount of anthropogenic disturbance (columns), the number of years projected (rows), and monitoring effort (see Fig. 1 for scenarios). Differences decrease as the number of years of monitoring and the number of collars increase. In these examples the composition survey cow multiplier *w* is 6, collars are renewed each year, and interannual variation is lower ($v_R = 0.23$, $v_S = 0.0435$).



Fig. 6. The probability of a correct status assessment varies with the amount of anthropogenic disturbance (columns), the number of years projected (rows), the amount of interannual variation (high: $v_R = 0.46$, $v_S = 0.087$, low: $v_R = 0.23$, $v_S = 0.0435$, none), and monitoring effort (see Fig. 1 for scenarios). When disturbance is high the probability of correct status assessment is high even with one year of monitoring. Where disturbance is low or moderate, increasing the number of years of monitoring increases accuracy, but there are diminishing returns on additional monitoring as the number of years increases. In these examples the composition cow multiplier *w* is 6 and collars are renewed each year; varying these parameters does not alter qualitative conclusions (Supplements D and E).

option is to recognize that the posterior probability of population viability ($P(\psi|x,\tau)$ in eq. (13)) is an indicator of error probability (Fig. 9). The probability of making an error also depends on the true (unknown) level of bias in the composition survey, but as the estimated posterior probability of viability approaches 0 or 1 accuracy increases to 100 % even when the survey is biased (Fig. 9). One could inform a decision about whether more information is needed for a particular population by selecting an error tolerance (e.g. the probability of correct status assessment should be >95 %) and using that threshold to distinguish cases where the posterior probability of viability is sufficiently certain (i.e. near enough to 0 or 1) from cases where more information is needed (Fig. 9). A key advantage of accounting for composition bias uncertainty in the Bayesian model is that when the model indicates high confidence (i.e. the estimated probability of viability very close to 0 or 1) the answer is likely to be correct (high status assessment accuracy) even when the composition survey is biased (Fig. 9).

4. Discussion

4.1. Bayesian integration of local demographic data & national demographic-disturbance relationships

The availability of boreal caribou demographic data varies widely across Canada due to large variation in habitat condition, population condition, available resources for monitoring, and remoteness. In a few regions enough data have been collected over time to characterize local demographic-disturbance relationships (Hervieux et al., 2013; Rudolph et al., 2017), but most populations have only been sparsely monitored for snapshot estimates of trend or abundance (Johnson et al., 2020). As a result, in most regions it is necessary to make assumptions informed by observed variation in demographic rates with disturbance among populations and other relevant information about impacts of disturbance on caribou. However, high observed variation in demographic-disturbance relationships alone (Dyson et al., 2022; Stewart et al., 2023). In some cases, predictions of population growth rate informed by national demographic-disturbance from local demographic data (Dyson et al., 2022; ECCC, 2011), but without formal methods of accounting for uncertainty it can be difficult to distinguish true discrepancies from stochastic variation.

We have proposed a simple Bayesian population model that helps address these challenges by acknowledging uncertainty associated with local demographic data and national demographic-disturbance relationships, and integrating these two sources of information to reduce uncertainty in projections of the impacts of changing landscape conditions. This Bayesian approach represents an important improvement over less formally integrated methods for estimating and projecting impacts of disturbance on population caribou population viability (ECCC, 2011; Johnson et al., 2020) because it reconciles and accounts for uncertainties in local demographic data and in demographicdisturbance relationships.



Fig. 7. The expected value of sample information (EVSI) varies with the amount of anthropogenic disturbance (columns), the number of years projected (rows), the amount of interannual variation (high: $v_R = 0.46$, $v_S = 0.087$, low: $v_R = 0.23$, $v_S = 0.0435$, none), and monitoring effort. When disturbance is high EVSI is low, indicating that local monitoring does not change predicted status. Where disturbance is lower, EVSI increases with the number of years of monitoring and the number of collars, but there are diminishing returns on additional monitoring as the number of years increases. See Fig. 6 for additional scenario details.

Our model assumes that increasing cumulative anthropogenic disturbance causes a log-linear decrease in caribou demographic rates (eqs. 4, 5, 8 and 10), reflecting a scientific consensus that cumulative anthropogenic disturbance has a negative impact on boreal caribou (ECCC, 2011; Gouvernement du Québec, 2021; Hervieux et al., 2013; Johnson et al., 2020; Rudolph et al., 2017; Sorensen et al., 2008). Local data can be integrated to estimate local demographic-disturbance parameters that differ from the national means, and in the absence of local data, appropriate priors lead to a range of outcomes consistent with the observed range of variation across the country (Figs. 3 and 5 in Johnson et al., 2020). Others (Dalgarno et al., 2024; Eacker et al., 2019; McNay et al., 2022; Moeller et al., 2021) have also used Bayesian models to estimate caribou demographic rates from local monitoring data, but our addition of prior information from national demographic-disturbance relationships is novel, and important for reducing the risk that lack of local data will be used as a reason to delay conservation action for highly disturbed and poorly monitored populations (Bissonnette and Teitelbaum, 2020; Boan et al., 2018). Accounting for demographicdisturbance relationships in a viability projection model clarifies that no additional local information is needed to project population decline where disturbance is high and actions to support recovery are not taken; the distribution of observed demographic rates from across the country (as summarized by the national analysis) is sufficient to predict problems for caribou on highly disturbed landscapes.

Interventions such as wolf culls, maternal penning, and restoration of linear features are intended to improve survival and reproduction of populations that are not otherwise viable (McNay et al., 2022; Serrouya

et al., 2020). Our focus in this paper is on assessing and projecting viability of populations in the absence of these interventions, to clarify when additional information is needed to reduce uncertainty about whether there is a need for action. The model we propose does not include effects of management interventions, and cannot be used to project outcomes for managed populations. There is nothing in our arguments, models or results that can or should be used to discourage monitoring of the effectiveness of conservation actions. The point we wish to emphasize is that action is also required, and lack of monitoring should not be used as a reason to delay conservation measures for highly disturbed populations.

Variation in anthropogenic disturbance across the Canadian boreal region is partially correlated with variation in climate and primary productivity (Neilson et al., 2022) because forestry occurs in higher productivity areas, and petroleum extraction activities are concentrated in Western Canada. Effects of disturbance on vegetation and foodweb dynamics vary with primary productivity (Neufeld, 2021), and some have expressed concern about confounding of demographic-disturbance relationships (Wilson et al., 2021). One option for addressing these concerns would be to develop regional demographic-disturbance relationships for populations that are ecologically similar to one another (e.g. caribou inhabiting forests that are sufficiently productive for industrial forestry in Eastern Canada) (ECCC, 2024), and to use the priors from regional demographic-disturbance relationships to inform demographic projections within the region. However, while acknowledging and allowing for regional variation, we also need to guard against risks that uncertainty will be inflated and used as an excuse to



Fig. 8. When anthropogenic disturbance is low and expected to increase (low scenario in Fig. 1) the probability of a correct status assessment varies with the true growth rate of the population (columns), the number of years projected (rows), the amount of interannual variation (high: $v_R = 0.46$, $v_S = 0.087$, low: $v_R = 0.23$, $v_S = 0.0435$, none), and monitoring effort (see Fig. 1 for scenarios). Increasing the number of years of monitoring helps identify populations with currently declining populations (top left), and to identify populations with higher than expected growth rates that fare better as disturbance increases (lower right). Increasing the number of collars more effectively increases near-term accuracy when interannual variation is low (top left). If the goal is long-term projection (bottom row) there is little advantage to increasing the number of collars. Increasing the accuracy of status assessment for populations with growth rates close to one is difficult (middle columns). In these examples the composition cow multiplier *w* is 6 and collars are renewed each year.

delay action, a tactic that has been used in this and other decision contexts (Bissonnette and Teitelbaum, 2020; Boan et al., 2018). In order to be informative and credible, regional demographic-disturbance analyses must include a sufficient number of observations spanning a range from high to low anthropogenic disturbance. Priors that lead to projections of outcomes for caribou that fall outside the observed range of variation across the country, characterized here (Fig. 2) by 95 % prediction intervals from a national analysis (Johnson et al., 2020), are implausible. In other words, if we have seen no examples of viable caribou populations at a particularly high level of disturbance, it is unreasonable to project or expect this outcome.

4.2. Allowing for composition survey errors

Another novel aspect of this work is a term that acknowledges possible bias caused by misclassification of adults and missing calves in composition surveys (DeCesare et al., 2012; Ellington et al., 2020). Lacking information about the true magnitude of these errors, we examined the accuracy and precision of a Bayesian model that includes uncertainty about composition bias using examples with biased composition surveys. Acknowledging bias did decrease overall accuracy and precision, though these decreases were not large (Supplement E). Importantly, when the Bayesian model predictions were precise they were also accurate even if the true composition survey was biased (Fig. 9). In other words, acknowledging composition bias uncertainty made predictions less confident, but in cases where predictions were confident they were also trustworthy.

A potential limitation of our analysis is that we assumed the same range of values for the probability of misclassifying adults and the probability of missing calves. Presuming that surveyed groups contain more cows than bulls, and that there is an equal probability of misclassifying cows as young bulls and vice versa, then misclassification errors cause high estimated recruitment. Missing calves causes low estimated recruitment, and together these errors tend to cancel one another out. An interesting extension of this work would be to investigate model performance over a broader range of assumptions about composition survey error rates, and to examine the implications of mismatches between the true distribution of errors and the unknown distribution in the Bayesian model. Better information about true composition survey error rates would also help assess their importance.

Alternatives to aerial composition surveys for estimating recruitment include fecal pellet analysis (McFarlane et al., 2018, 2021, 2022) and calf collaring (Ellington et al., 2020). In an analysis of fecal pellets from 14 populations of boreal and southern mountain caribou, Jones et al. (2023) found that sampled groups contained more females than males, and that cows tend to stay with their male and female offspring, while bulls do not. These results are broadly consistent with our assumption that composition survey groups include cows and younger animals of



Fig. 9. The posterior probability that the population is viable ($P(\psi|x,\tau)$ in eq. (13)) predicts the probability of a correct status assessment (estimated from the 114,000 example cases in Figs. 5 to 7 with a generalized additive model). The relationship between accuracy and the probability of viability depends on true composition survey bias (colours), but regardless of bias accuracy is high when the probability of viability is very near to 0 or 1. Cases in which there is no need for additional monitoring if one is willing to accept a 5 % error rate fall above the dashed line.

both sexes that can be difficult to classify visually. Documenting animals that are difficult to classify as "unknown" can help analysts account for classification uncertainties (Dalgarno et al., 2024; Ellington et al., 2020), as can comparing classification results from multiple independent observers. The probability of missing calves likely increases with vegetation cover, and is more difficult to quantify.

Each survey method has costs and benefits, and the reality is that monitoring everything everywhere all the time in great detail is neither feasible nor necessary. We hope that adding a bias term to the simple recruitment-mortality model that is used for many herd viability assessments (Dalgarno et al., 2024; DeCesare et al., 2012; Eacker et al., 2019; ECCC, 2011; Hatter, 2020; Hatter and Bergerud, 1991; Johnson et al., 2020; Serrouya et al., 2017) will enable and encourage practitioners to examine the sensitivity of their conclusions to plausible composition survey error rates, and help clarify thinking about where, when, and why additional information is needed.

4.3. Limitations and future possibilities

The main objectives of Johnson et al.'s (ECCC, 2011, 2020) national analysis were to inform a national disturbance policy that applies to all ranges except one in northern Saskatchewan (SK1) that is subject to very low anthropogenic disturbance and high fire disturbance, and to inform a different policy for SK1 (ECCC, 2011; ECCC, 2019). A hierarchical analysis (Leasure et al., 2019) would be better suited for estimating variation in demographic model parameters among populations, and for distinguishing that from variation among years. We have not reanalyzed the national data using different methods because the data are owned by many jurisdictions, and obtaining permission from all of these jurisdictions would be difficult and time-consuming. To move ahead with available published information we constrained our example trajectory simulations by assuming that populations remain in their quantile, so populations that are lower than or higher than average remain lower or higher than average over time. Note that the Bayesian model is not similarly constrained, and can accommodate evidence of a shift from unexpectedly low to unexpectedly high demographic rates over time, or

vice versa. Switching from low to high each year is unlikely, but there is evidence of variation in the slope of demographic-disturbance relationships among populations (Rudolph et al., 2017), so it is important that the Bayesian model allows for a greater range of possibilities than our more constrained simulated example trajectories. Although the simulated trajectories do not include all plausible possibilities, we believe they are sufficient to demonstrate how a Bayesian model can be used to integrate local data with national priors, and to show that monitoring requirements depend on landscape condition.

For this analysis we used a simple survival analysis method that does not account for variation in survival rate or the number of collared animals throughout the year. More sophisticated methods should be used for analysis of real survival data, but our implementation of a two-step non-parametric survival analysis method (following Eacker et al., 2019) yielded slightly biased survival estimates. Dalgarno et al.'s (2024) method may be a better alternative. More generally, the proof-ofconcept model presented in this paper is adequate for making general points about the integration of national demographic-disturbance relationships with local data, and for accounting for composition survey errors. However, it is a research prototype, not a fully developed analysis tool. The more fully developed and documented bboutools R package (Dalgarno et al., 2024) is likely a better starting point for development of tools to enable local decision makers to inform decisions with their existing data. Possible next steps are to extend that package to include priors from demographic-disturbance relationships and composition survey errors.

Aspatial demographic models generally assume that observed animals are a random and representative sample of a fully mixed population in which survival and recruitment rates apply equally to all animals. However, metrics derived from fecal pellet analysis such as reproductive success (McFarlane et al., 2018, 2021, 2022), age structure and pregnancy rates (Flasko et al., 2017; McFarlane et al., 2022), and motheroffspring co-occurence (Jones et al., 2023) suggest high variation in fitness among individuals (McFarlane et al., 2018) and spatial structure within populations (Jones et al., 2023; McFarlane et al., 2021, 2022). Analyses of movement data also show spatial variation in risks and benefits for caribou and variation in habitat preferences and space use among individuals (e.g. Avgar et al., 2015; DeCesare et al., 2014). It is possible to integrate complexities such as variation in demographic rates among individuals (Armstrong et al., 2021), population size information from aerial or fecal DNA surveys, and variation in demographic rates among age classes (McNay et al., 2022; Moeller et al., 2021) into Bayesian population models. However, in many contexts there are not enough data to estimate more complex model parameters, and simple models remain relevant.

Our proof-of-concept analysis shows the value of integrating national demographic-disturbance relationships with local data, accounting for composition survey errors, and assessing the value of local monitoring information. We applied the framework proposed by Dunham et al. (2023) to show that no additional local monitoring information is needed to predict whether boreal caribou populations in highly disturbed landscapes are viable in the absence of interventions such as predator control or maternal penning; viability is unlikely. There is more variation in caribou demographic rates among study areas with low to moderate disturbance, and thus more need for local data to inform demographic projections. In these places, our analysis suggests that there may be diminishing returns from increasing monitoring effort, but more information on monitoring costs, objectives, and existing local data would be required to assess the adequacy and cost-effectiveness of monitoring scenarios in particular circumstances.

Monitoring costs vary substantially with technologies used, the remoteness of herds, and the difficulty of collaring animals, which in turn depends on the number of currently collared animals, the population size, and vegetation across the landscape (NBCKC, 2021b). It is important to recognize that projecting population viability is only one possible objective for monitoring (NBCKC, 2019), and that the impacts

of monitoring on threatened animals should be considered (NBCKC, 2019). Since monitoring costs, options and goals are context specific, we believe the most effective way forward will be to use this proof-ofconcept analysis, existing local data, and the more fully developed *bboutools* R package (Dalgarno et al., 2024) as a starting point for working with interested decision makers to develop monitoring decision support tools that meet real local needs, recognizing that those needs will vary (NBCKC, 2021a, 2022b).

Data statement

Code required to create the data, run analyses and reproduce figures in this paper is available at https://github.com/LandSciTech/Caribou -Demographic-Projection-Paper, and in the caribouMetrics R package available on GitHub at https://github.com/LandSciTech/caribouMet rics/tree/EI-paper-submission. Results are available at https://osf. io/ryn59/.

CRediT authorship contribution statement

Josie Hughes: Conceptualization. Sarah Endicott: Writing – review & editing, Software, Resources. Anna M. Calvert: Writing – review & editing, Writing – original draft, Methodology, Conceptualization. Cheryl A. Johnson: Writing – review & editing, Methodology, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank two anonymous reviewers for their insightful comments and helpful suggestions. This work was informed by a variety of discussions with more people than we can name, but here are a few. Members of the Monitoring Working Group of the National Boreal Caribou Knowledge Consortium and the Scientific Assessment of Federal and Provincial Frameworks for the Conservation of Boreal Caribou in Ontario helped us understand context. Tal Avgar and Micheline Manseau encouraged us to think about composition survey errors. Comments from Joseph Bennett and Daniel Eacker on early versions of this work motivated a variety of improvements. Note that our acknowledgement of these contributions does not imply endorsement; we also acknowledge disagreement on some points, and that all remaining errors are our own. Funding for this work was provided by the Wildlife and Landscape Science Directorate of Environment and Climate Change Canada.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecoinf.2025.103095.

Data availability

Results: https://osf.io/ryn59/. Code: https://github.com/LandSci Tech/Caribou-Demographic-Projection-Paper; https://github.com/ LandSciTech/caribouMetrics/tree/EI-paper-submission.

References

Armstrong, D.P., Parlato, E.H., Frost, P.G.H., 2021. Incorporating individual variation in survival, reproduction and detection rates when projecting dynamics of small populations. Ecol. Model. 455, 109647. https://doi.org/10.1016/j. ecolmodel.2021.109647.

- Avgar, T., Baker, J.A., Brown, G.S., Hagens, J.S., Kittle, A.M., Mallon, E.E., McGreer, M. T., Mosser, A., Newmaster, S.G., Patterson, B.R., Reid, D.E.B., Rodgers, A.R., Shuter, J., Street, G.M., Thompson, I., Turetsky, M.J., Wiebe, P.A., Fryxell, J.M., 2015. Space-use behaviour of woodland caribou based on a cognitive movement model. J. Anim. Ecol. 84, 1059–1070. https://doi.org/10.1111/1365-2656.12357.
- Bennett, J.R., Maxwell, S.L., Martin, A.E., Chadès, I., Fahrig, L., Gilbert, B., 2018. When to monitor and when to act: value of information theory for multiple management units and limited budgets. J. Appl. Ecol. 55, 2102–2113. https://doi.org/10.1111/ 1365-2664.13132.
- Bissonnette, J.-F., Teitelbaum, S., 2020. Les controverses socioécologiques entourant la protection du caribou en forêt boréale : Recherche de l'acceptabilité sociale. Cahiers Géogr. Québec 65, 309–325. https://doi.org/10.7202/1093672ar.
- Boan, J.J., Malcolm, J.R., Vanier, M.D., Euler, D.L., Moola, F.M., 2018. From climate to caribou: how manufactured uncertainty is affecting wildlife management. Wildl. Soc. Bull. 42, 366–381. https://doi.org/10.1002/wsb.891.
- Buxton, R.T., Hamit, S., Geauvreau, J.J.W., Davis, S., Smith, P.A., Bennett, J.R., 2022. Balancing research, monitoring, and action to recover Canada's species at risk. Environ. Sci. Pol. 132, 198–205. https://doi.org/10.1016/j.envsci.2022.02.018.
- Courtois, R., Gingras, A., Dussault, C., Breton, L., Ouellet, J.-P., 2003. An aerial survey technique for the Forest-dwelling ecotype of woodland Caribou, *Rangifer tarandus caribou*. Can. Field-Nat. 117, 546–554. https://doi.org/10.22621/cfn.v117i4.823. Curtis, S.M., 2018. Mcmcplots: Create Plots from MCMC Output.
- Dalgarno, S., Thorley, J., Boulanger, J., Pearson, A., 2024. Bboutools: Boreal Caribou Survival, Recruitment and Population Growth. https://poissonconsulting.github. io/bboutools/.
- DeCesare, N.J., Hebblewhite, M., Bradley, M., Smith, K.G., Hervieux, D., Neufeld, L., 2012. Estimating ungulate recruitment and growth rates using age ratios. J. Wildl. Manag. 76, 144–153. https://doi.org/10.1002/jwmg.244.
- DeCesare, N.J., Hebblewhite, M., Bradley, M., Hervieux, D., Neufeld, L., Musiani, M., 2014. Linking habitat selection and predation risk to spatial variation in survival. J. Anim. Ecol. 83, 343–352. https://doi.org/10.1111/1365-2656.12144.
- Drummond, F.M., Lovegrove, T.G., Armstrong, D.P., 2018. Combining data-derived priors with postrelease monitoring data to predict persistence of reintroduced populations. Ecol. Evol. 8, 6183–6191. https://doi.org/10.1002/cce3.4060.
- Dunham, K.D., Devers, P.K., Lawson, A.J., Lyons, J.E., McGowan, C.P., Royle, J.A., 2023. Strategic monitoring to minimize misclassification errors from conservation status assessments. Biol. Conserv. 286, 110260. https://doi.org/10.1016/j. biocon.2023.110260.
- Dyson, M., Endicott, S., Simpkins, C., Turner, J.W., Avery-Gomm, S., Johnson, C.A., Leblond, M., Neilson, E.W., Rempel, R., Wiebe, P.A., Baltzer, J.L., Stewart, F.E.C., Hughes, J., 2022. Existing caribou habitat and demographic models need improvement for ring of fire impact assessment: a roadmap for improving the usefulness, transparency, and availability of models for conservation. Preprint. https://doi.org/10.1101/2022.06.01.494350.
- Eacker, D.R., Lukacs, P.M., Proffitt, K.M., Hebblewhite, M., 2017. Assessing the importance of demographic parameters for population dynamics using Bayesian integrated population modeling. Ecol. Appl. 27, 1280–1293. https://doi.org/ 10.1002/eap.1521.
- Eacker, D.R., Hebblewhite, M., Steenweg, R., Russell, M., Flasko, A., Hervieux, D., 2019. Web-based application for threatened woodland caribou population modeling. Wildl. Soc. Bull. 43, 167–177. https://doi.org/10.1002/wsb.950.
- ECCC, 2011. Scientific Assessment to Inform the Identification of Critical Habitat for Woodland Caribou (*Rangifer tarandus caribou*), Boreal Population, in Canada. Envrionment and Climate Change Canada, Ottawa.
- ECCC, 2019. Boreal Caribou Science to Inform Recovery Science Summary Sheet. Environment and Climate Change Canada, Ottawa.
- ECCC, 2024. Scientific Assessment of Federal and Provincial Frameworks for the Conservation of Boreal Caribou in Ontario. Environment and Climate Change Canada, Ottawa
- Ellington, E.H., Lewis, K.P., Koen, E.L., Vander Wal, E., 2020. Divergent estimates of herd-wide caribou calf survival: ecological factors and methodological biases. Ecol. Evol. 10, 8476–8505. https://doi.org/10.1002/ece3.6553.
- Ferrari, S., Cribari-Neto, F., 2004. Beta regression for modelling rates and proportions. J. Appl. Stat. 31, 799–815. https://doi.org/10.1080/0266476042000214501.
- Flasko, A., Manseau, M., Mastromonaco, G., Bradley, M., Neufeld, L., Wilson, P., 2017. Fecal DNA, hormones, and pellet morphometrics as a noninvasive method to estimate age class: an application to wild populations of Central Mountain and Boreal woodland caribou (*Rangifer tarandus caribou*). Can. J. Zool. 95, 311–321. https://doi.org/10.1139/cjz-2016-0070.
- Fortin, D., Barnier, F., Drapeau, P., Duchesne, T., Dussault, C., Heppell, S., Prima, M.-C., St-Laurent, M.-H., Szor, G., 2017. Forest productivity mitigates human disturbance effects on late-seral prey exposed to apparent competitors and predators. Sci. Rep. 7, 6370. https://doi.org/10.1038/s41598-017-06672-4.
- Gagné, C., Mainguy, J., Fortin, D., 2016. The impact of forest harvesting on caribou–moose–wolf interactions decreases along a latitudinal gradient. Biol. Conserv. 197, 215–222. https://doi.org/10.1016/j.biocon.2016.03.015.
- Gelman, A., Rubin, D.B., 1992. Inference from iterative simulation using multiple sequences. Stat. Sci. 7, 457–472.
- Gerber, L.R., 2016. Conservation triage or injurious neglect in endangered species recovery. Proc. Natl. Acad. Sci. 113, 3563–3566. https://doi.org/10.1073/ pnas.1525085113.
- Gouvernement du Québec, 2021. Revue de littérature sur les facteurs impliqués dans le déclin des populations de caribous forestiers au Québec et de caribous montagnards de la Gaspésie.

J. Hughes et al.

- Gregory, R., Failing, L., Harstone, M., Long, G., McDaniels, T., Ohlson, D., 2012. Structured Decision Making: A Practical Guide to Environmental Management Choices. John Wiley & Sons.
- Hatter, I.W., 2020. Revisiting the recruitment-mortality equation to assess moose growth rates. Alces 56, 39–47.
- Hatter, I.W., Bergerud, W.A., 1991. Moose recruitment, adult mortality and rate of change. Alces 27, 65–73.
- Hervieux, D., Hebblewhite, M., DeCesare, N.J., Russell, M., Smith, K., Robertson, S., Boutin, S., 2013. Widespread declines in woodland caribou (*Rangifer tarandus caribou*) continue in Alberta. Can. J. Zool. 91, 872–882. https://doi.org/10.1139/ cjz-2013-0123.
- Hettinga, P.N., Arnason, A.N., Manseau, M., Cross, D., Whaley, K., Wilson, P.J., 2012. Estimating size and trend of the north Interlake woodland caribou population using fecal-DNA and capture-recapture models. J. Wildl. Manag. 76, 1153–1164. https:// doi.org/10.1002/jwmg.380.
- Hirsh-Pearson, K., Johnson, C.J., Schuster, R., Wheate, R.D., Venter, O., 2022. Canada's human footprint reveals large intact areas juxtaposed against areas under immense anthropogenic pressure. FACETS 7, 398–419. https://doi.org/10.1139/facets-2021-0063.
- Ibisch, P.L., Hoffmann, M.T., Kreft, S., Pe'er, G., Kati, V., Biber-Freudenberger, L., DellaSala, D.A., Vale, M.M., Hobson, P.R., Selva, N., 2016. A global map of roadless areas and their conservation status. Science 354, 1423–1427. https://doi.org/ 10.1126/science.aaf7166.
- IPBES, 2019. Global assessment report on biodiversity and ecosystem services of the intergovernmental science-policy platform on biodiversity and ecosystem services. In: Brondízio, E.S., Settele, J., Díaz, S., Ngo, H.T. (Eds.), Global Assessment Report on Biodiversity and Ecosystem Services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. IPBES secretariat, Bonn, Germany. https://doi.org/10.5281/zenodo.6417333.
- Johnson, C.A., Sutherland, G.D., Neave, E., Leblond, M., Kirby, P., Superbie, C., McLoughlin, P.D., 2020. Science to inform policy: linking population dynamics to habitat for a threatened species in Canada. J. Appl. Ecol. 57, 1314–1327. https://doi. org/10.1111/1365-2664.13637.
- Jones, T.B., Manseau, M., Merriell, B., Pittoello, G., Hervieux, D., Wilson, P.J., 2023. Novel multilayer network analysis to assess variation in the spatial co-occurrences of close kin in wild caribou populations. Glob. Ecol. Conserv. 47, e02688. https://doi. org/10.1016/j.gecco.2023.e02688.
- Lacy, R., Miller, P., Traylor-Holzer, K., 2017. Vortex 10 user's Manual. Conservation Breeding Specialist Group; Chicago Zoological Society, Apple Valley, Minnesota, USA.
- Lamb, C.T., Williams, S., Boutin, S., Bridger, M., Cichowski, D., Cornhill, K., DeMars, C., Dickie, M., Ernst, B., Ford, A., Gillingham, M.P., Greene, L., Heard, D.C., Hebblewhite, M., Hervieux, D., Klaczek, M., McLellan, B.N., McNay, R.S., Neufeld, L., Nobert, B., Nowak, J.J., Pelletier, A., Reid, A., Roberts, A.-M., Russell, M., Seip, D., Seip, C., Shores, C., Steenweg, R., White, S., Wittmer, H.U., Wong, M., Zimmerman, K.L., Serrouya, R., 2024. Effectiveness of population-based recovery actions for threatened southern mountain caribou. Ecol. Appl. 34, e2965. https://doi.org/10.1002/eap.2965.
- Leasure, D.R., Wenger, S.J., Chelgren, N.D., Neville, H.M., Dauwalter, D.C., Bjork, R., Fesenmyer, K.A., Dunham, J.B., Peacock, M.M., Luce, C.H., Lute, A.C., Isaak, D.J., 2019. Hierarchical multi-population viability analysis. Ecology 100, e02538. https://doi.org/10.1002/ecy.2538.
- Legg, C.J., Nagy, L., 2006. Why most conservation monitoring is, but need not be, a waste of time. J. Environ. Manag. 78, 194–199. https://doi.org/10.1016/j. jenvman.2005.04.016.

Lindenmayer, D., Likens, G., 2018. Effective Ecological Monitoring. Csiro Publishing.

- Lindenmayer, D.B., Piggott, M.P., Wintle, B.A., 2013. Counting the books while the library burns: why conservation monitoring programs need a plan for action. Front. Ecol. Environ. 11, 549–555. https://doi.org/10.1890/120220.
 Martin, T.G., Nally, S., Burbidge, A.A., Arnall, S., Garnett, S.T., Hayward, M.W.,
- Martin, T.G., Nally, S., Burbidge, A.A., Arnall, S., Garnett, S.T., Hayward, M.W., Lumsden, L.F., Menkhorst, P., Mcdonald-Madden, E., Possingham, H.P., 2012. Acting fast helps avoid extinction. Conserv. Lett. 5, 274–280. https://doi.org/10.1111/ j.1755-263X.2012.00239.x.
- McCarthy, D.P., Donald, P.F., Scharlemann, J.P.W., Buchanan, G.M., Balmford, A., Green, J.M.H., Bennun, L.A., Burgess, N.D., Fishpool, L.D.C., Garnett, S.T., Leonard, D.L., Maloney, R.F., Morling, P., Schaefer, H.M., Symes, A., Wiedenfeld, D. A., Butchart, S.H.M., 2012. Financial costs of meeting global biodiversity conservation targets: current spending and unmet needs. Science 338, 946–949. https://doi.org/10.1126/science.1229803.
- McFarlane, S., Manseau, M., Flasko, A., Horn, R.L., Arnason, N., Neufeld, L., Bradley, M., Wilson, P., 2018. Genetic influences on male and female variance in reproductive success and implications for the recovery of severely endangered mountain caribou. Glob. Ecol. Conserv. 16, e00451. https://doi.org/10.1016/j.gecco.2018.e00451.
- McFarlane, S., Manseau, M., Wilson, P.J., 2021. Spatial familial networks to infer demographic structure of wild populations. Ecol. Evol. 11, 4507–4519. https://doi. org/10.1002/ece3.7345.
- McFarlane, S., Manseau, M., Jones, T.B., Pouliot, D., Mastromonaco, G., Pittoello, G., Wilson, P.J., 2022. Identification of familial networks reveals sex-specific density dependence in the dispersal and reproductive success of an endangered ungulate. Front. Ecol. Evol. 10. https://doi.org/10.3389/fevo.2022.956834.

- McLoughlin, P.D., Dzus, E., Wynes, B., Boutin, S., 2003. Declines in populations of woodland caribou. J. Wildl. Manag. 67, 755–761. https://doi.org/10.2307/ 3802682.
- McNay, R.S., Lamb, C.T., Giguere, L., Williams, S.H., Martin, H., Sutherland, G.D., Hebblewhite, M., 2022. Demographic responses of nearly extirpated endangered mountain caribou to recovery actions in Central British Columbia. Ecol. Appl. 32, e2580. https://doi.org/10.1002/eap.2580.
- Moeller, A.K., Nowak, J.J., Neufeld, L., Bradley, M., Manseau, M., Wilson, P., McFarlane, S., Lukacs, P.M., Hebblewhite, M., 2021. Integrating counts, telemetry, and non-invasive DNA data to improve demographic monitoring of an endangered species. Ecosphere 12, e03443. https://doi.org/10.1002/ecs2.3443.
- NBCKC, 2019. Boreal Caribou Monitoring in Canada Part I: Perspectives from the NBCKC Monitoring Working Group 2019. National Boreal Caribou Knowledge Consortium, Ottawa, Canada
- NBCKC, 2021a. NBCKC Monitoring Practices for Boreal Caribou: Telemetry in Canada. National Boreal Caribou Knowledge Consortium, Ottawa, Canada. NBCKC, 2021b. Boreal Caribou Monitoring Toolkit.
- NBCKC, 2022a. Boreal caribou conceptual ecological model technical report (DRAFT). National Boreal Caribou Knowledge Consortium, Ottawa, Canada.
- NBCKC, 2022b. NBCKC Monitoring Practices for Boreal Caribou: Aerial Surveys in Canada. National Boreal Caribou Knowledge Consortium, Ottawa, Canada.
- Neilson, E.W., Castillo-Ayala, C., Beckers, J.F., Johnson, C.A., St-Laurent, M.H., Mansuy, N., Price, D., Kelly, A., Parisien, M.A., 2022. The direct and habitatmediated influence of climate on the biogeography of boreal caribou in Canada. Clim. Change Ecol. 3, 100052. https://doi.org/10.1016/j.ecochg.2022.100052.
- Neufeld, B., 2021. A primary productivity hypothesis for disturbance-mediated apparent competition for boreal caribou in Canada (Master's thesis). University of Saskatchewan.
- Novomestky, F., Nadarajah, S., 2016. Package "Truncdist".
- Parlato, E.H., Ewen, J.G., McCready, M., Gordon, F., Parker, K.A., Armstrong, D.P., 2021. Incorporating data-based estimates of temporal variation into projections for newly monitored populations. Anim. Conserv. 24, 1001–1012. https://doi.org/10.1111/ acv.12702.
- Petchey, O.L., Pontarp, M., Massie, T.M., Kéfi, S., Ozgul, A., Weilenmann, M., Palamara, G.M., Altermatt, F., Matthews, B., Levine, J.M., Childs, D.Z., McGill, B.J., Schaepman, M.E., Schmid, B., Spaak, P., Beckerman, A.P., Pennekamp, F., Pearse, I. S., 2015. The ecological forecast horizon, and examples of its uses and determinants. Ecol. Lett. 18, 597–611. https://doi.org/10.1111/ele.12443.
- Plummer, M., 2023. JAGS: A Program for Analysis of Bayesian Graphical Models Using Gibbs Sampling.

R Core Team, 2023. R: A language and environment for statistical computing.

Rettie, W.J., Messier, F., 1998. Dynamics of woodland caribou populations at the southern limit of their range in Saskatchewan. Can. J. Zool. 76, 251–259. https:// doi.org/10.1139/z97-193.

- Rudolph, T.D., Drapeau, P., Imbeau, L., Brodeur, V., Legare, S., St-Laurent, M.-H., 2017. Demographic responses of boreal caribou to cumulative disturbances highlight elasticity of range-specific tolerance thresholds. Biodivers. Conserv. 26, 1179–1198. https://doi.org/10.1007/s10531-017-1292-1.
- Runge, M.C., Converse, S.J., Lyons, J.E., 2011. Which uncertainty? Using expert elicitation and expected value of information to design an adaptive program. In: Biological Conservation, Adaptive Management for Biodiversity Conservation in an Uncertain World, 144, pp. 1214–1223. https://doi.org/10.1016/j. biocon 2010 12 020
- Schaub, M., Abadi, F., 2011. Integrated population models: a novel analysis framework for deeper insights into population dynamics. J. Ornithol. 152, 227–237. https://doi. org/10.1007/s10336-010-0632-7.
- Schaub, M., Kery, M., 2021. Integrated Population Models: Theory and Ecological Applications with R and Jags, 1st ed. Elsevier.
- Serrouya, R., Gilbert, S., McNay, R.S., McLellan, B.N., Heard, D.C., Seip, D.R., Boutin, S., 2017. Comparing population growth rates between census and recruitmentmortality models. J. Wildl. Manag. 81, 297–305.
- Serrouya, R., Dickie, M., DeMars, C., Wittmann, M.J., Boutin, S., 2020. Predicting the effects of restoring linear features on woodland caribou populations. Ecol. Model. 416. https://doi.org/10.1016/j.ecolmodel.2019.108891.
- Sorensen, T., McLoughlin, P.D., Hervieux, D., Dzus, E., Nolan, J., Wynes, B., Boutin, S., 2008. Determining sustainable levels of cumulative effects for boreal caribou. J. Wildl. Manag. 72, 900–905.
- Stewart, F.E.C., Micheletti, T., Cumming, S.G., Barros, C., Chubaty, A.M., Dookie, A.L., Duclos, I., Eddy, I., Haché, S., Hodson, J., Hughes, J., Johnson, C.A., Leblond, M., Schmiegelow, F.K.A., Tremblay, J.A., McIntire, E.J.B., 2023. Climate-informed forecasts reveal dramatic local habitat shifts and population uncertainty for northern boreal caribou. Ecol. Appl. 33, e2816. https://doi.org/10.1002/eap.2816. Su, Y.-S., Yajima, M., 2021. R2jags: Using R to Run 'JAGS'.
- Tufto, J., Sæther, B.-E., Engen, S., Arcese, P., Jerstad, K., Røstad, O.W., Smith, J.N.M., 2000. Bayesian meta-analysis of demographic parameters in three small, temperate passerines. Oikos 88, 273–281. https://doi.org/10.1034/j.1600-0706.2000.880205.

Venter, O., Sanderson, E.W., Magrach, A., Allan, J.R., Beher, J., Jones, K.R., Possingham, H.P., Laurance, W.F., Wood, P., Fekete, B.M., Levy, M.A., Watson, J.E. M., 2016. Sixteen years of change in the global terrestrial human footprint and

J. Hughes et al.

implications for biodiversity conservation. Nat. Commun. 7, 12558. https://doi.org/ 10.1038/ncomms12558.

- Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L.D., François, R.,
- Grolemund, G., Hayes, A., Henry, L., Hester, J., Kuhn, M., Pedersen, T.L., Miller, E., Bache, S.M., Müller, K., Ooms, J., Robinson, D., Seidel, D.P., Spinu, V., Takahashi, K., Vaughan, D., Wilke, C., Woo, K., Yutani, H., 2019. Welcome to the tidyverse. J. Open Source Softw. 4, 1686. https://doi.org/10.21105/joss.01686.
- Wilson, S.F., Nudds, T.D., Vries, A., 2021. A causal modelling approach to informing woodland caribou conservation policy from observational studies. Biol. Conserv. 264. https://doi.org/10.1016/j.biocon.2021.109370.
- Wintle, B.A., Runge, M.C., Bekessy, S.A., 2010. Allocating monitoring effort in the face of unknown unknowns. Ecol. Lett. 13, 1325–1337. https://doi.org/10.1111/j.1461-0248.2010.01514.x.
- Wintle, B.A., Cadenhead, N.C.R., Morgain, R.A., Legge, S.M., Bekessy, S.A., Cantele, M., Possingham, H.P., Watson, J.E.M., Maron, M., Keith, D.A., Garnett, S.T., Woinarski, J.C.Z., Lindenmayer, D.B., 2019. Spending to save: what will it cost to halt Australia's extinction crisis? Conserv. Lett. 12. https://doi.org/10.1111/ conl.12682.
- Yokota, F., Thompson, K.M., 2004. Value of information analysis in environmental health risk management decisions: past, present, and future. Risk Anal. 24, 635–650. https://doi.org/10.1111/j.0272-4332.2004.00464.x.