



Web-Based Application for Threatened Woodland Caribou Population Modeling

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ABSTRACT Woodland caribou (*Rangifer tarandus caribou*) are threatened in Canada, with population and distribution declines evident in most regions of the country. Causes of declines are linked to landscape change from forest fires and human development, notably forestry oil and gas activities, which result in caribou habitat loss and affect ecosystem food webs. The Federal Species at Risk Act requires effective protection and restoration of caribou habitat, with actions to increase caribou survival. These requirements call for effective monitoring of caribou population trends to gauge success. Many woodland caribou populations are nearly impossible to count using traditional aerial survey methods, but demographic-based monitoring approaches can be used to estimate population trends based on population modeling of vital rates from marked animals. Monitoring programs have used a well-known simple population model (the Recruitment-Mortality [R/M] equation) to estimate demographic rates for woodland caribou, but have faced challenges in managing large data streams and providing transparency in the demographic estimation process. We present a stand-alone statistical software application using open-source software to permit efficient, transparent, and replicable demographic estimation for woodland caribou populations. We developed an easy-to-use, interactive web-based application for the R/M population model that uses a Bayesian estimation approach and provides the user flexibility in choice of prior distributions and other output features. We illustrate the web-application to the A la Pêche Southern Mountain (Central Group) woodland caribou population in west-central Alberta, Canada, during 1998–2017. Our estimates of population demographics are consistent with previous research on this population and highlight the utility of the application in assessing caribou population responses to species recovery actions. We provide example data, computer code, the web-based application package, and a user manual to guide installation and use. We also review underlying assumptions and challenges of population monitoring in this case study. We expect our software will contribute to efficient monitoring of woodland caribou and help in the assessment of recovery actions for this species. © 2019 The Authors. *Wildlife Society Bulletin* Published by Wiley Periodicals, Inc.

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Several ecotypes of woodland caribou (*Rangifer tarandus caribou*) are threatened across Canada, with many populations of southern mountain, central mountain, and boreal woodland caribou assessed as being in decline, typically in

association with anthropogenic landscape change (Wittmer et al. 2010; Festa-Bianchet et al. 2011; Environment Canada 2012, 2014). Nowhere is the decline of woodland caribou more pressing than in western Canada's boreal forest, where combined effects of energy development and forest harvesting have dramatically altered ecosystems (Hebblewhite 2017). Landscape changes have reduced the availability of caribou habitat, and altered food-web relationships by enhancing habitat for early seral ungulate species such as moose (*Alces alces*) and white-tailed deer (*Odocoileus virginianus*), which then support increased densities of predator populations such as wolves (*Canis lupus*; Seip 1992, Festa-

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Bianchet et al. 2011, Latham et al. 2011, DeCesare 2012a). Landscape change also facilitates predation through increased predator search efficiency and encounter probability with caribou related to predator use of linear features (Festa-Bianchet et al. 2011, DeCesare 2012b, DeMars and Boutin 2017). Across Canada, jurisdictions are required to comply with the Federal Species at Risk Act and woodland caribou recovery strategies (Environment Canada 2012, 2014), which require caribou and habitat protection, including habitat restoration activities to improve critical habitat. Rigorous population monitoring of woodland caribou is critical to understanding the status of individual populations and informing and enabling adjustments to species recovery actions.

With the exception of some southern mountain caribou populations that can be effectively counted by traditional aerial surveys in alpine environments in British Columbia, Canada, woodland caribou populations are challenging to monitor (Serrouya et al. 2017). Most boreal woodland caribou inhabit dense boreal forests where enumerating animals to monitor population trend by aerial surveys is ineffective because of low detectability. Like other difficult-to-monitor species, such as grizzly bears (*Ursus arctos*; Harris et al. 2011), demographic rates have been used across the country to monitor woodland caribou populations by estimating annual population growth. Many jurisdictions use a simple unstructured demographic model first proposed by Hatter and Bergerud (1991; the R/M equation, see Methods) to estimate population growth rates, and thus, population trend. The R/M model relies on estimates of adult female survival from radiotelemetry and recruitment rates from aerial surveys of radiocollared females, which can be detected effectively. For example, by monitoring survival of 1,337 radiocollared adult female caribou and classifying 20,872 caribou during 158 recruitment surveys, Hervieux et al. (2013) estimated a mean population growth rate of 0.918 across 14 caribou populations. Other jurisdictions across Canada similarly use this demographic approach to estimate caribou population trend (e.g., British Columbia, Serrouya et al. 2017; Quebec, Fortin et al. 2017). Woodland caribou are high-profile and costly to conserve (Schneider et al. 2010), so scientific methods used by researchers and governments are often under scrutiny (e.g., Harron 2015, but see Hervieux et al. 2015 and DeCesare et al. 2016).

There is a growing appreciation of the benefits of automated computer analyses to support both transparency and replicability in wildlife science and management (Lewis et al. 2018, Nowak et al. 2018). Wildlife science has a long history of developing customizable software to ease complex, yet routine, analyses such as population modeling. Program MARK, for example, built upon earlier software such as CAPTURE, transformed the field of wildlife demographic estimation (White et al. 1978, White and Burnham 1999). Yet development of new statistical methods usually requires customized analyses, which may disconnect continuity with database management, creating a bottleneck for effectively automating routine analyses (Urbano and Cagnacci 2014).

With the recent advances in open-source software such as Program R (R Core Team 2017) and PostgreSQL, it is now possible to consider software development as a seamless flow from raw field data to automated analyses and reporting (Lewis et al. 2018). For example, Nowak et al. (2018) developed a powerful web-based data analysis platform to support monitoring of wildlife populations in the western United States. Their approach automates the routine analysis of population trends of several species of mammals for harvest setting from monitoring data (e.g., counts, recruitment surveys, harvest data) using web-based interfaces with state wildlife agency databases on secure web-based servers (Nowak et al. 2018). Similar applications to enhance the rigor and replicability of population monitoring has the potential to be of great benefit to woodland caribou recovery across Canada.

We describe a stand-alone statistical software application (hereafter, “app”) that was specifically developed to automate routine demographic estimation for woodland caribou populations in Alberta, Canada. Although developed with Alberta in mind, and presented with an Alberta case study, our approach could be easily used by any jurisdiction collecting similar survival and recruitment data as Hervieux et al. (2013). Given that many other jurisdictions in Canada use a similar R/M equation to estimate caribou demography, which we describe below, our approach will be broadly applicable. We first provide a description of the transition from traditional demographic estimation methods (Hatter and Bergerud 1991, DeCesare et al. 2012) to a Bayesian approach to estimate woodland caribou population growth rate. We then illustrate the application of this software to a caribou population in Alberta, the A la Pêche caribou herd.

METHODS

Traditional Population Analysis

Typically, woodland caribou monitoring programs across Canada monitor adult female survival and recruitment of calves (~9 months of age) to estimate population growth rates (λ). This demographic-based monitoring requires a random sample of radiocollared adult female caribou within a population. Adult female survival is tracked by either movement data via Global Positioning System (GPS) satellite upload or using aerial telemetry to regularly monitor signals of Very-High-Frequency collars. A collar that is immobile for a 1–2 days indicates a potential mortality or that the collar was dropped. Recruitment surveys are typically conducted in late winter and rely on the same sample of collared adult females (because of very low detection probabilities of woodland caribou under dense coniferous forest cover) to locate and observe calves per adult female from as many groups as possible.

Simple derivations from Leslie matrix models usually represent λ as a function of recruitment and survival (e.g., Unsworth et al. 1999, Caswell 2001). In an algebraically equivalent formulation, Hatter and Bergerud (1991) formulated a simple equation to derive λ_t using annual estimates of recruitment rate per breeding age adult female

(R_t) and adult female survival rate (S_t) for a given year $t = 1 \dots T$:

$$\lambda_t = S_t / (1 - R_t) \quad (1)$$

This formulation makes many assumptions, foremost of which is the assumption that the age at first breeding is 2 years and the population is at stable stage distribution (Hatter and Bergerud 1991, DeCesare et al. 2012, Mills 2013). We address assumptions of this demographic monitoring approach below and elsewhere (DeCesare et al. 2012, Hervieux et al. 2013). However, because recruitment observations from aerial composition surveys include both male and female juveniles, the recruitment term (R_t) is divided by 2 to arrive at a female-only recruitment estimate, and thus, a female-only estimate of λ_t . Using a female-only estimate of λ is practical for many mammalian species, especially for polygynous ungulates such as caribou where males contribute little to population growth. Hatter and Bergerud (1991) developed the R/M equation for species such as moose, but there are 2 specific considerations to be accounted for when modeling woodland caribou developed by DeCesare et al. (2012) that are included in our software application.

The first consideration for caribou is that both females and young males can have antlers at the time of recruitment surveys, and so special care must be paid to distinguishing sexes (e.g., observing black vulva patches on females). If sexes cannot be discerned, such as in our case study, then researchers have used an additional adjustment factor to account for the expected number of males; for example, assigning unknown adults as 65% female and 35% male in constructing the denominator of the recruitment rate (Edmonds 1988, Smith 2004). A second consideration for caribou is the delayed age at first reproduction, which is conservatively 3 years (DeCesare et al. 2012). However, the R/M equation is appropriate for this situation because the recruitment rate is adjusted to a ratio of the number of juveniles per total number of females (rather than the usual juveniles per breeding-aged adult females). Without this adjustment, recruitment is overestimated and estimates of λ are overly optimistic (DeCesare et al. 2012). Thus, the adjusted (female-based) annual recruitment rate ($R_{adj,t}$) is estimated for year $t = 1 \dots T$ with the following equation:

$$\widehat{R}_{adj,t} = \frac{\widehat{R}_t}{1 + \frac{\widehat{R}_t}{2}} \quad (2)$$

Annual estimates of adult female survival (S_t) are informed by known-fate collar data (i.e., either a 1 = die or 0 = live or censored) and estimated using the Kaplan–Meier (KM) estimator (Pollock et al. 1989). The KM estimator provides nonparametric survival estimates (i.e., no distribution is assumed for the underlying hazard function) and is given by the following equation:

$$\widehat{S}(j) = \prod_{i: j_i \leq j} \left(1 - \frac{d_i}{r_i} \right) \quad (3)$$

where survivorship starts at 1.0 and is multiplied by the product of 1 minus the hazard of mortality at failure time i (i.e., the

number of deaths observed at time i (d_i) divided by the number at risk at time i (r_i)). Thus, the KM estimator provides the probability that survival is longer than failure time j within a given year. The Greenwood variance estimator is commonly used to estimate the standard error (SE) for annual and monthly survivorship rates (Greenwood 1926). Many jurisdictions in Canada, including Alberta, commonly use Excel spreadsheet approaches to estimate adult female survival and recruitment for many individuals and years of data, in many cases requiring dozens of hours of manual spreadsheet analyses to summarize population trends.

Data Automation and Management

We developed automated data-processing code in the R computing language (R Core Team 2017) to create a young-to-adult female ratio data set to estimate recruitment rates and a time-to-event data set to estimate adult female survival following equations 2 and 3 above. We used data from late-winter composition surveys in the recruitment estimates, and assumed that calf survival was the same as adult female survival from the time of survey (on average 1 Mar) to the end of the biological year (30 Apr), following Hervieux et al. (2013). Similar to previous methods, the automated data processing code for the time-to-event data set uses left-staggered entry and a recurrent survival origin (1 May), and allows for interval censoring (e.g., an individual whose collar went off-air and was then recaptured at a later date; DeCesare et al. 2016). Given the frequency of monitoring (i.e., real-time for satellite radiocollars and every 3 months for standard radiocollars), the survival timescale was based on monthly intervals, and individuals entered into the risk set during the month they were captured and were right-censored in the month after they were last heard live (DeCesare et al. 2012). DeCesare et al. (2016) found that the timing of mortality and censoring from the risk set due to monthly survival intervals caused no appreciable bias in KM survival estimates.

Bayesian Population Analysis

In general, Bayesian population analysis allows for a flexible framework to estimate demographic parameters and can be easily parameterized for the R/M equation (Hatter and Bergerud 1991, Hatter et al. 2017). Bayesian estimation methods are also advantageous over frequentist methods used to estimate woodland caribou demographic rates because they can easily share information across years to provide parameter estimates in years with missing data or provide shrinkage estimates when accurate estimates are difficult to obtain (Kéry and Schaub 2012). We used a Bayesian approach to estimate the means and uncertainty of demographic parameters, and included the option of using vague priors (i.e., beta(1,1)) or sharing information across years using random year effects for adult female survival and recruitment rates. We first specified the recruitment probability with a binomial likelihood (here given without the binomial coefficient) that described the observed number of calves (c_t) as a function of the recruitment probability (R_t) and the number of adult female caribou (af_t) in year t as

$$L(c_t | R_t, af_t) \sim R_t^{c_t} (1 - R_t)^{af_t - c_t} \quad (4)$$

We then derived the adjusted recruitment probability in the model following equation 2 above.

Second, we used KM estimates of annual adult female survival probability (\hat{S}) and SEs that were estimated using the survival package in R (Therneau 2017) to match moments to the alpha (α) and beta (β) parameters of the beta distribution, which is used to model continuous parameters (here given as θ) bound between 0 and 1:

$$\theta \sim \text{beta}(\alpha, \beta) \quad (5)$$

We specifically matched the moments of a normal distribution (i.e., μ , σ^2) that we parameterized with \hat{S} and SE (converted to variance; i.e., SE^2) to the α and β parameters of beta distributions using the following moment matching expressions (Hobbs and Hooten 2015):

$$\alpha = \left(\frac{1 - \mu}{\sigma^2} - \frac{1}{\mu} \right) \mu^2 \quad (6)$$

$$\beta = \alpha \left(\frac{1}{\mu} - 1 \right) \quad (7)$$

However, we had to parameterize KM estimates as the mean and variance of a truncated normal distribution ($\mu \in [0,1]$) to share survival information across years using random effects, which was not possible by matching moments to beta distribution (Kéry and Schaub 2012, Hobbs and Hooten 2015). The truncated normal distribution is not as accurate as matching KM estimates to the beta distribution, especially when survival estimates are near the boundary of 0 or 1, but the effects on λ are negligible. In most cases, sharing information across years will not be necessary for annual demographic reporting, but we included the functionality for cases of missing data and when sampling

variances were relatively large, which is common for aerial recruitment surveys.

When no mortalities were observed in a year for a given population, leading to a KM survival estimate of 1.0, we deterministically set these estimates to 1.0 in the model, which resulted in a posterior standard deviation of zero, consistent with previous frequentist approaches (DeCesare et al. 2012, Hervieux et al. 2013). However, this parameterization overestimates the contribution of these years to the environmental variance in survival probability. Moreover, in a Bayesian context, this approach is not possible when sharing survival information across years due to the estimation of random year effects. Therefore, we used a Bayesian approach to estimate the posterior standard deviation of these survival estimates from a simple binomial likelihood (estimated in a separate model; see R code for details), where \hat{S}_t and the posterior standard deviation were estimated by setting the number of successes and trials to the maximum number of collared animals at risk of mortality within these years. This avoided arbitrarily assigning a zero variance for these years when no mortalities were observed, and instead allowed the variance to be based on the sample size of these finite populations. We used these parameterizations for adult female survival because our goal was to have the estimates closely agree with those from the traditional methods, while allowing for the option of using informative priors by estimating a random year effect.

When the user desires to share information across years to estimate annual parameters (θ_t), we estimated the grand mean ($\bar{\mu}$) and the environmental (i.e., spatiotemporal) variance (σ_ε^2) of a normally distributed random year effect (ε_t) on the logit scale using equation (8).

$$\text{logit}(\theta_t) = \bar{\mu} + \varepsilon_t \quad (8)$$

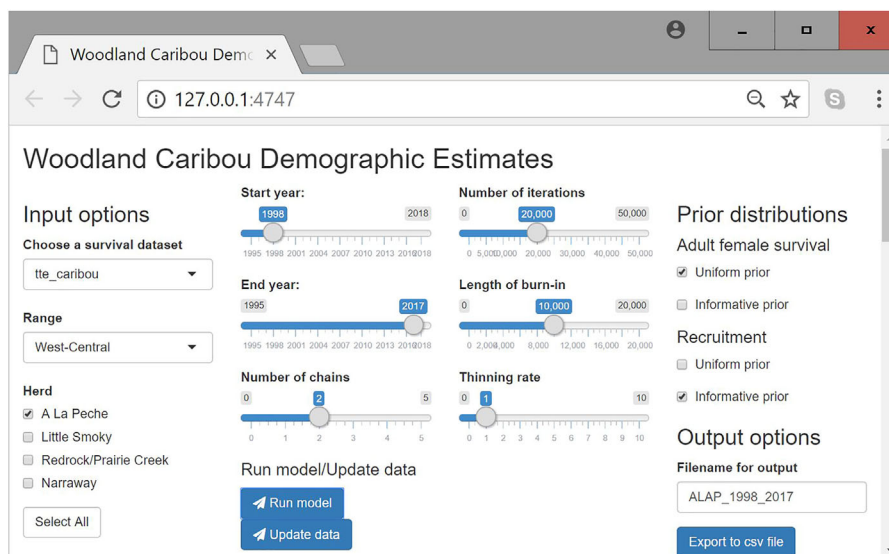


Figure 1. Woodland caribou demographic modeling web-application interface based on the shiny package in the open-source program R (R Core Team 2017) opened in web browser showing control console and web address 127.0.0.1:4747. The web-interface allows the user to select a survival data set, caribou local population (i.e., range), start and end years for the population modeling, set various Markov Chain Monte Carlo controls, whether random effects will be used for missing data, and output options.

We used a normal(0,2) prior for $\bar{\mu}$, rescaled σ_e^2 to the standard deviation (σ_e), and applied a uniform(0,5) prior using equation (9):

$$\varepsilon_t \sim \text{normal}(0, \sigma_e^2) \quad (9)$$

Parameters are estimated on the logit scale; therefore, we derived the grand mean of vital rates ($\bar{\theta}$) and their environmental variance (σ^2) on the probability scale using equations 10 and 11 (Kéry and Schaub 2012):

$$\bar{\theta} = \exp(\bar{\mu}) / [1 + \exp(\bar{\mu})] \quad (10)$$

$$\sigma^2 = \sigma_e^2 \times \bar{\theta}^2 \times (1 - \bar{\theta})^2 \quad (11)$$

Thus, the grand mean and temporal variance of each parameter will inform years of missing data and improve estimates when sampling variance is high because of, for example, small sample sizes (Kéry and Schaub 2012). Using a random effect will shrink estimates toward the grand mean of the vital rate and have less influence or weight on the parameter estimates as the precision of the annual vital rate estimate increases. Nonetheless, we provide the option in the app to use vague (the default option) or informative priors (i.e., random effects) and illustrate their application in our case study below (Fig. 1), but caution users to invest effort into understanding Bayesian methods or consult with practicing Bayesian statisticians. We review common kinds of error messages in our user manual (Appendix B; see Supporting Information online). Finally, we derive λ_t in the model using the exact formulation in the R/M equation as described in equation 1.

Web-Based Demographic Application

We developed a web-based software application using the shiny package (Chang et al. 2017) in RStudio version 1.1.447 (R Studio Team 2016) to provide annual estimates of adult female survival, recruitment, and λ for 15 woodland caribou populations in Alberta. Here, we present a simplified version of this software application that can be generalized to any woodland caribou population. Although the application

could eventually be housed in a web-based server (e.g., Nowak et al. 2018), the version we present here only requires communication between RStudio and a web browser on a personal computer, and so we refer to it also as a stand-alone software app. Along with several other R packages and RStudio (see Supporting Information available online), the application depends on the open-source software JAGS (Plummer 2015), which conducts the Markov Chain Monte Carlo (MCMC) sampling. Full details on the web-based demographic application (Appendix C), including a user manual (Appendix B) and source R code (Appendix A), are available online in Supporting Information (online supplemental materials).

The interactive console (Fig. 1) contains controls for the MCMC settings including the number of MCMC chains to initiate, number of sampling iterations, length of the burn-in period, and rate of thinning for the MCMC samples. The default settings are: 20,000 for the “Number of iterations”; 10,000 for the “Length of burn-in”; 2 for the “Number of chains”; and 1 for the “Thinning rate”. This combination of settings yields 20,000 posterior samples for each parameter ($[20,000 - 10,000] \times 2/1$).

Data summaries including tabular and graphical output are automatically provided by the app (Fig. 2). The tabular and graphical output includes a summary tab and plots of all vital rates and the output from the R package R2jags (Su and Yajima 2015) called “JAGS output” (see User Manual in Appendix B available online in Supporting Information). Convergence can be checked by inspecting plots of the marginal posterior distributions and convergence statistics (see Fig. 2a). Note that ≥ 2 chains must be initiated to estimate the Brooks–Gelman–Rubin convergence statistic (Brooks and Gelman 1998); some authors suggest using ≥ 2 chains for especially complex data sets. Finally, the app automatically generates either a Hypertext Markup Language (HTML), Word, or Portable Document Format (PDF) report (see an example report as Appendix D available online in Supporting Information). Note the entire assortment of files needed to run the app and generate the

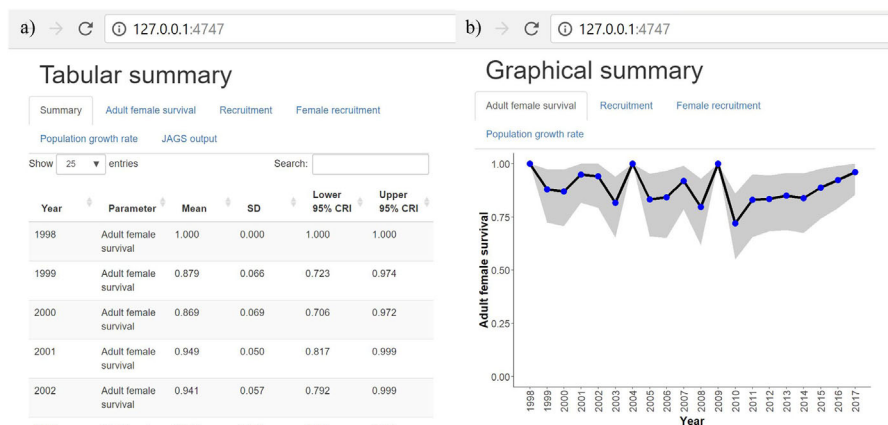


Figure 2. Example of the summary of woodland caribou demographic modeling obtained from the Program R Shiny app for the A la Pêche woodland caribou population, Alberta, Canada, 1998–2017, showing a) tabular output for each parameter (e.g., adult female survival, mean, SD, 95% credible intervals), and b) graphical outputs.

results reported here (Appendix C) can be downloaded from Supporting Information, available online.

Case Study

We demonstrate our web-based application by estimating vital and population growth rates for the A la Pêche southern mountain woodland caribou population in west-central Alberta. The A la Pêche population annually migrated between alpine summer range in Jasper National Park and Willmore Wilderness Park and some adjacent areas in British Columbia, and forested foothills winter range east of the park boundaries. Forested habitats included upland lodgepole pine (*Pinus contorta*), spruce (*Picea* spp.), and aspen (*Populus tremuloides*) forests, and lowland black spruce (*Picea mariana*) wetlands. Industrial land use occurred throughout the winter range. Previous studies documented this population as declining at approximately 5%/year (see DeCesare et al. 2012 and Hervieux et al. 2013 for more details). Following recommendations of provincial and federal recovery strategies, and signs of the reversal of population declines in the adjacent Little Smoky boreal caribou range, the Government of Alberta introduced wolf management on just the winter range in 2013 and 2014, and on the full annual range in 2016 as one strategy to recover caribou populations (Hervieux et al. 2014, Government of Alberta 2017). This provided a valuable applied case study to evaluate our demographic app, which we expand on below. Sample data input files for adult female survival and recruitment are provided (Appendix D and E available online in Supporting Information).

RESULTS

Case Study: A la Pêche Woodland Caribou Population

The adult female telemetry data set for the A la Pêche woodland caribou herd in Alberta included 136 individuals monitored for 1–16 years each during 1998–2017, representing almost 515 caribou risk-years. The minimum and maximum number of individuals at risk during a given month was 17 and 32, respectively. Recruitment data included 21 aerial composition surveys with 1–2 spring surveys/year during 1999–2017 (note that surveys were not conducted during 1998 and 2002). Overall, 238 male and female calves and 1,533 adult females (which included 65% of unknown adults) were recorded in 265 group observations.

The adjusted (female-based) recruitment rate varied from a low of 0.03 (95% Bayesian credible interval [BCI] = 0.01, 0.07) in 2005 to a high of 0.20 (95% BCI = 0.16, 0.25) in 2016 (Table 1, Fig. 3b). This corresponded to unadjusted recruitment rates (including both female and male calves and without the adjustment for total no. of females of all age classes) of 0.07 (95% BCI = 0.02, 0.14) and 0.51 (95% BCI = 0.37, 0.65), respectively. The geometric mean adjusted recruitment rate was 0.09 (95% BCI = 0.07, 0.10) with a vague prior, and declined by <1% when recruitment information was shared across years as estimates in the 2 years of missing data decreased from 0.19 (95% BCI = 0.01, 0.33) to 0.09 (95% BCI = 0.03, 0.18; Fig. 3b).

Adult female survival probability was relatively constant as expected for large ungulates, having a low of 0.72 (95% BCI = 0.55, 0.86) in 2010, but otherwise ranging from 0.80 to 1.00 (Table 1, Fig. 2B). The Bayesian estimates of adult female survival were near identical to those derived from a Kaplan–Meier estimator (see Appendix G, Table S1, available in online Supporting Information). The geometric mean adult female survival probability was 0.88 (95% BCI = 0.85, 0.91), and increased to 0.92 (95% BCI = 0.88, 0.96) when survival information was shared across years. This highlights the strong influence of sharing adult female survival information across years, which was mainly driven by years that had a high survival rate of 1.0 (Table 1). For instance, sharing adult female survival information across years resulted in a 5% increase in the annual adult female estimate for 2006, increasing from 0.84 (95% BCI = 0.65, 0.97) to 0.89 (95% BCI = 0.76, 0.98).

The A la Pêche woodland caribou herd was declining ($\lambda < 1$) in most years (Table 1). The population was estimated to be increasing when recruitment data were missing in 1998 and 2002 and a vague prior was used for recruitment. The population was also estimated to be increasing during 2016 and 2017, after the geographic extent of wolf-population reduction program delivery was increased from only the caribou winter range to both winter and summer (on provincial lands) ranges (Table 1, Fig. 4; Alberta Government 2017). Overall, the geometric mean population growth rate (λ_G) was near stable at 0.98 (95% BCI = 0.94, 1.02). Prior to the expansion of the wolf management program, λ_G was declining by 3.5%/year on average (0.97, 95% BCI = 0.92, 1.00); however, sharing recruitment information across years prior to expansion of wolf management resulted in a λ_G of 0.95 (95% BCI = 0.91, 0.98). In contrast, λ_G was 1.14 (95% BCI = 1.03, 1.21) following the geographic expansion of wolf program delivery, owing to slightly greater adult female survival rates and significantly greater recruitment rates (Table 1). Sample reports from our app are provided in Appendix C available in online Supporting Information.

DISCUSSION

Our web-application successfully combined telemetry data on adult female survival and recruitment from population composition surveys to estimate λ of woodland caribou in a replicable, transparent, and easy-to-use manner. In our case study, the caribou population was estimated to be declining at a rate of about 5%/year before wolf management, consistent with previous estimates (though our results span more years) by DeCesare et al. (2012) and Hervieux et al. (2013). As such, our software will be of great interest to wildlife managers and researchers across Canada working toward woodland caribou recovery, and possibly for other ecotypes or subspecies of caribou and reindeer. The underlying R code and algebraic formulation of the R/M equation is transparent and output generated by our software could be easily integrated into annual reporting. There are also several options for customizing analyses and,

Table 1. Adult female survival, female-only recruitment rate (female calves/total no. of females), and population growth rate estimates from an automated, Bayesian modeling approach with vague priors using a web-based application for woodland caribou in the A la Pêche woodland caribou population in Alberta, Canada, during 1998–2017; BCI is Bayesian credible interval.

Year	Adult female survival			Recruitment			Population growth rate		
	S	Lower 95% BCI	Upper 95% BCI	R_{female}	Lower 95% BCI	Upper 95% BCI	λ	Lower 95% BCI	Upper 95% BCI
1998 ^a	1.00	1.00	1.00	0.19	0.01	0.33	1.25	1.01	1.49
1999	0.88	0.72	0.97	0.11	0.09	0.14	0.99	0.81	1.10
2000	0.87	0.71	0.97	0.11	0.08	0.15	0.98	0.79	1.11
2001	0.95	0.82	1.00	0.08	0.05	0.11	1.03	0.89	1.11
2002 ^a	0.94	0.78	1.00	0.19	0.01	0.33	1.18	0.89	1.45
2003	0.82	0.65	0.94	0.09	0.05	0.13	0.90	0.71	1.04
2004	1.00	1.00	1.00	0.07	0.04	0.11	1.08	1.04	1.13
2005	0.83	0.66	0.95	0.03	0.01	0.07	0.86	0.68	0.99
2006	0.84	0.65	0.97	0.11	0.06	0.16	0.95	0.73	1.10
2007	0.92	0.79	0.99	0.06	0.03	0.10	0.98	0.84	1.07
2008	0.80	0.62	0.93	0.07	0.04	0.11	0.86	0.66	1.01
2009	1.00	1.00	1.00	0.06	0.03	0.09	1.06	1.03	1.10
2010	0.72	0.55	0.86	0.13	0.09	0.17	0.83	0.63	1.00
2011	0.83	0.65	0.95	0.05	0.02	0.08	0.87	0.68	1.00
2012	0.83	0.68	0.94	0.12	0.07	0.17	0.94	0.77	1.08
2013	0.85	0.69	0.96	0.08	0.05	0.11	0.92	0.74	1.04
2014	0.84	0.67	0.95	0.09	0.05	0.14	0.92	0.74	1.06
2015	0.89	0.74	0.98	0.07	0.03	0.12	0.96	0.80	1.07
2016	0.92	0.79	0.99	0.20	0.15	0.25	1.16	0.98	1.28
2017	0.96	0.86	1.00	0.14	0.09	0.19	1.12	0.99	1.21

^a Note that recruitment estimates were not available for these years and the adjusted, female-only estimates of 0.19 (95% BCI = 0.01, 0.33) are estimated from a vague prior; thus, the population growth rates are not reliable for these years.

with some R programming background, users could add advanced capabilities beyond what we have presented (e.g., integration of aerial count data) or expand our approach to be applicable to species that potentially start breeding earlier than caribou (e.g., deer species).

This application provides an efficient means to estimate annual population growth for Alberta’s province-wide monitoring program that annually assesses all 15 woodland caribou populations under provincial jurisdiction. Within a Bayesian framework, each year, new information on parameter uncertainty can contribute to estimating parameters for years that have missing data through a random effect. Furthermore, regular estimation of population parameters is necessary to help evaluate the efficacy of many management actions. For example, in Alberta, annual

wolf population reductions are being implemented in and adjacent to some woodland caribou ranges as an interim measure while habitat recovers from disturbance (human-caused, or fire), to avoid near-term caribou population extirpation (Hervieux et al. 2014). The potential positive result of this management action for the A la Pêche population is apparent in our demographic estimates, with increases in population growth rates following geographic expansion of wolf population management. At the same time, other long-term habitat protection and restoration initiatives may take longer to achieve demographic results, but will still require an efficient and rigorous demographic monitoring system to evaluate caribou population trends. We anticipate that our population modeling application will help woodland caribou managers track demographic responses to

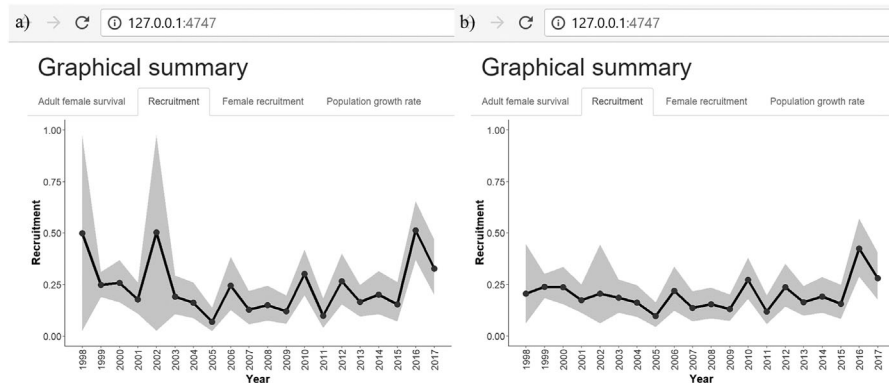


Figure 3. Recruitment probability estimates from Bayesian population model using a vague prior (a) and an informative prior (b) for the A la Pêche woodland caribou population, Alberta, Canada, during 1998–2017.

a variety of recovery actions, including predator and habitat management, throughout Canada.

Our approach requires thoughtful review of data collection, storage, and management procedures that would benefit any caribou monitoring program. As the field of wildlife biology has become more data-intensive, increased attention is needed to the management and flow of data into analyses (*sensu* Lewis et al. 2018 and Urbano and Cagnacci 2014, for an example with GPS radiocollars). For example, while developing this application, we worked collaboratively with wildlife managers to consistently apply decisions such as when to censor adult females from the data set, when they entered the capture records, etc. Separate spreadsheets of capture date, telemetry, and mortality records may lead to errors or discrepancies between years of data. Automating these data flows from the field to application can help standardize estimates and reduce the chance of human-caused errors. Another consideration that jurisdictions will have to address is database management (i.e., where to store field-survey data). In the case of Alberta, the provincial woodland caribou monitoring program had already established a functional database in Microsoft Access, which helps to eliminate the need for data manipulation by personnel that saves time with reduced risk of human-caused processing errors. R interfaces easily with such databases, facilitating automated data management. Given the increasing importance of population monitoring as woodland caribou recovery efforts ramp up across Canada, these improvements in database management and data flows could help standardize population estimates across space and time. Although a customized version of the Shiny application we developed links seamlessly with the Alberta database, the open-source application we provide here could easily be modified to integrate with other database programs in R.

It is also important in any population monitoring design to pay attention to assumptions to increase accuracy and minimize bias. We have previously reviewed key assumptions of the underlying simplified demographic model, the R/M

equation, as well as the point estimates for adult female survival and recruitment to consider (Hervieux et al. 2015, DeCesare et al. 2016). Earlier, we acknowledged the assumption that the R/M equation approach explicitly assumes the population is at a stable age distribution, a challenging assumption for declining or fluctuating populations of long-lived animals (Caswell 2001). However, because of legitimate animal-care concerns about the effects of pulling teeth from ungulates to obtain ages (Festa-Bianchet et al. 2002), there are no age-specific studies of woodland caribou population demography in the literature. This highlights a need to explore consequences of age structure to woodland caribou populations (*sensu* Prichard et al. 2012). Assumptions involved in estimating demographic rates include the randomized capture of representative animals and aerial surveys for recruitment that are randomized and systematically designed. For radiotelemetry-based estimates, these assumptions mean that new samples of animals should be radiocollared each year to avoid what is known as viability selection over time, where the individual quality of a single-year captured cohort increases over time because of differential mortality (Vaupel et al. 1979, Prichard et al. 2012). To estimate adult female survival, we must first assume the marking process does not adversely affect survival. Second, known-fate type survival models assume that detection probability is 1—that is, fate is known with certainty. If this is not true, then it may be necessary to consider interval truncation (DeCesare et al. 2016). Timing of death is also assumed to be known with certainty, which is increasingly realistic when using GPS radiocollars. One important consideration with any sampling design is power analysis; prospective power analysis based on expected adult female survival rates should guide sample sizes (White and Garrott 1990). For adult ungulates with near-constant, high survival rates, sample sizes may need to be >30–50/year to reliably detect trends in the face of binomial sampling variation of the survival process (White and Garrott 1990). Practically, if no mortalities are observed in a particular year in a sample, this strongly suggests low power

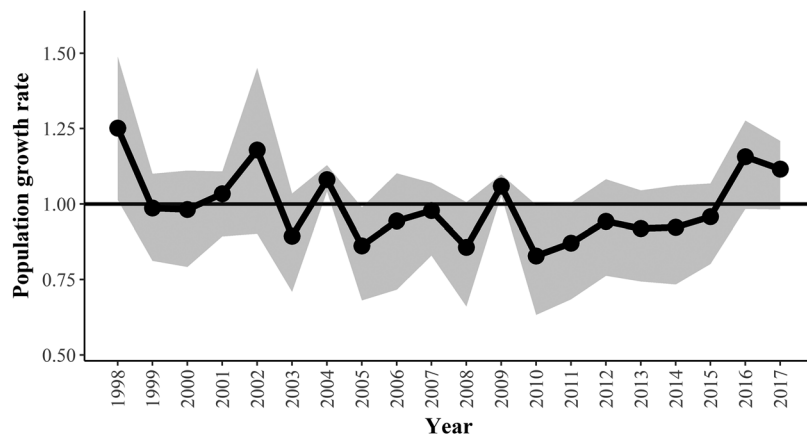


Figure 4. Population growth rate estimates from Bayesian population model using a random effect for recruitment probability for the A la Pêche woodland caribou population, Alberta, Canada, during 1998–2017. Note that the geographic extent of wolf population reduction program delivery was expanded in winter 2013–2014, and that the black horizontal reference line at 1.0 represents stable population growth.

to detect changes in survival, and that increased sample sizes for adult females are needed. Finally, the R/M equation also assumes that adult males have no direct effect on population growth rates, which is a reasonable assumption for polygynous mammals. Careful review of sampling protocols and assumptions of the components of the R/M equation will be critical for rigorous use of our application.

Our Bayesian formulation of the R/M equation offers several advantages over traditional approaches. For example, Hervieux et al. (2013) and others (McLoughlin et al. 2003) faced the challenge of how to integrate estimates of uncertainty from 2 very different parameters, survival and reproduction, into estimates and uncertainty of the derived parameter, population growth rate. They opted to use Monte Carlo-based sampling procedures, which resemble Bayesian methods in their application, but without the formalization and flexibility of a fully Bayesian approach. Our Bayesian approach provides the user with options to consider information sharing across years for missing data, through a random effect for missing data, which is a common feature of wildlife studies. This may be desirable when estimates were biologically unrealistic, perhaps due to sampling variance, or in our case, during years when no mortalities were observed in the sampled female caribou. Other methods exist to address these common but vexing statistical challenges, but they are usually beyond the reach of practicing wildlife managers. Although there have been criticisms of Bayesian methods on philosophical grounds, practically, they are easy to implement and use; as our results demonstrate here, they are functionally equivalent to more cumbersome frequentist methods.

We believe a distinct advantage of our Bayesian approach is the ability to improve estimates with new data over time. There is a temptation to treat estimates as fixed once estimated for a previous year, for example, but this overlooks the huge effect of binomial sampling variance on telemetry-based survival estimates. During development of the application, we heard the criticism that our previous estimates had changed with new information (years), which frustrated some managers. However, we maintain this is good statistical practice to be reminded that point estimates from Kaplan–Meier (or other approaches) should always be viewed as uncertain, bounded within some confidence interval (which is often wide). For example, comparing point estimates of λ for 1998–2009 presented by Hervieux et al. (2013) using frequentist methods to our Bayesian estimates for the same years, shows an average absolute difference of <0.03 and a correlation >0.89 . Of course, this ignores that both are point estimates, neither are the true population growth rate, and in all cases, the 95% CI and 95% Bayesian credible intervals had high overlap. Thus, managers should be reminded to focus on the distribution of the estimates of λ , and not be overly concerned about minor differences in point estimates. If users adopt the informative prior option with a random effect for year, each additional year of data adds information about the overall distribution of a vital

rate, which may lead to small changes in previously published or reported estimates of λ . There might also be differences between our approach, which uses a Bayesian estimator, and Kaplan–Meier estimates, which are still commonly used. Minor differences in adult female survival rates are evident in Appendix G Table S1 (Supporting Information) between Kaplan–Meier and Bayesian estimators. The average absolute difference was 0.0003 between the 2 approaches. These differences may compound with similar differences in recruitment, and thence to point estimates of λ ; however, these differences would still be expected to be similarly trivial and bounded by wide uncertainty. This is not a weakness of the approach, but a constant and important reminder that truth is unknown, wildlife biology can only imperfectly estimate the truth, and with new information and additional years of data, there may be minor changes in previously published point estimates when random effects are used.

An additional advantage of Bayesian models can be the integration of other datatypes into such a web-application. Although it is rare for woodland caribou managers to be able to obtain rigorous estimates of population size, in some areas, these estimates may be possible. For example, Serrouya et al. (2017) compared estimates of λ from aerial surveys versus those obtained by the R/M equation from estimates of adult female survival and recruitment for southern mountain woodland caribou in British Columbia. They treated these 2 estimates as independent in regression, when in reality, they are 2 imperfect observation estimates of the same underlying and unobserved biological process. Eacker et al. (2017) demonstrated how to integrate count-based information on population size into such a vital rate-based integrated population model. Eacker et al. (2017) and other results of similar models always demonstrate improvement in precision of parameter estimates when integrating multiple data types. As it stands, the simple R/M equation represents a simple unstructured population model, but it could be expanded to be a fully age- or stage-structured matrix model that could integrate well with more comprehensive data sources for other populations. Future initiatives could thus easily integrate count-based trend monitoring into a Bayesian integrated population model. Even in the boreal forest, where aerial surveys will remain impractical, alternative, noninvasive genetic methods to estimate population size of woodland caribou from mark-recapture studies could also easily be integrated into a Bayesian population modeling framework (Hettinga et al. 2012).

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's website. This includes Appendix A: Shiny Application for R, including all R code; Appendix B: User manual for caribou app. Appendix C: example user report from the Shiny Application in .html format; Appendix D: data input files for adult female survival for the A la Pêche caribou population, 1998–2017; Appendix E: data input files for recruitment for the A la Pêche caribou population, 1998–2017; Appendix F: a single, self-contained .zip compressed file consisting of all of the above plus JAGS model code for adult female survival and recruitment using uninformative and informative priors, an R markdown report generation code and associated files; Appendix G: Table S1 comparing estimates for adult female survival, recruitment probability, and population growth rate (λ) for the A la Pêche caribou population.