Boreal Caribou Can Coexist with Natural but Not Industrial Disturbances

FRANCES E. C. STEWART,1 Canadian Forest Service, Natural Resources Canada, 506 Burnside Road W, Victoria, British Columbia V8Z 4N9, Canada
J. JOSHUA NOWAK, University of Montana, 32 Campus Drive, Missoula, MT 59812, USA
TATIANE MICHELETTI,1 University of British Columbia, Faculty of Forestry, 2424 Main Mall, Vancouver, British Columbia V6T 1Z4, Canada
ELIOT J. B. McINTIRE,1 Canadian Forest Service, Natural Resources Canada, 506 Burnside Road W, Victoria, British Columbia V8Z 4N9, Canada
FIONA K. A. SCHMIEGELOW,2 University of Alberta, Department of Renewable Resources, 705A General Services Building, Edmonton, Alberta T6G 2H1, Canada
STEVEN G. CUMMING, Laval University, Department of Wood and Forest Science, 2405, rue de la Terrasse, Quebec City, Quebec G1V 0A6, Canada

ABSTRACT For species at risk, it is important that demographic models be consistent with our most recent knowledge because alternate model versions can have differing predictions for wildlife and natural resource management. To establish and maintain this consistency, we can compare predicted model values to current or past observations and demographic knowledge. When novel predictor information becomes available, testing for consistency between modeled and observed values ensures the best models are used for robust, evidence-based, wildlife management. We combine novel information on the extent of historical disturbance regimes (industrial and fire) to an existing demographic model and predict historical and projected demographics of woodland caribou (Rangifer tarandus caribou). Exploring 6 simulation experiments across 5 populations in Alberta, Canada, we identify the relative importance of industrial disturbance, fire, and population density to observed population size and growth rate. We confirm the onset of significant declines across all 5 populations began approximately 30 years ago, demonstrate these declines have been consistent, and conclude they are more likely due to industrial disturbance from the oil and gas sector within contemporary population ranges than historical fire regimes. These findings reinforce recent research on the cause of woodland caribou declines. Testing for consistency between observations and models prescribed for species recovery is paramount for assessing the cause of declines, projecting population trends, and refining recovery strategies for effective wildlife management. We provide a novel simulation method for conducting these tests. © 2020 The Authors. The Journal of Wildlife Management published by Wiley Periodicals LLC on behalf of The Wildlife Society.

KEY WORDS boreal caribou, development, disturbance, extinction, fire, population, Rangifer tarandus caribou.

Demographic models are used to understand factors affecting population growth and have a long history in biology (McIntosh 1986, Bacaër 2011). These models reflect the current knowledge of species-habitat relationships and can incorporate environmental predictors of demographic change. The application of demographic models for endangered or at-risk species has been cautioned because of the poor quality of available demographic data, associated agents of decline, and difficulties in estimating variance in demographic rates (Chaudhary and Oli 2020). As a result, testing for consistency between models and observations for species at risk when new data become available is important.

In wildlife management, demographic models commonly have a dual purpose: they aid in inferring the processes behind changing species demographics, and in recommending objectives for species recovery plans. For species with large distributions, demographic models within recovery plans have the potential to affect policy and natural resource economies within multiple jurisdictions, where alternative model structures could result in very different predicted effects of management regimes (Beissinger and Westphal 1998, Brook et al. 2000). Many species at risk are in decline because of human-induced habitat use changes (Laliberte and Ripple 2004, Ripple et al. 2014). Boreal populations of woodland caribou (Rangifer tarandus caribou), for example, are at the forefront of recovery priorities under Canada’s Species at Risk Act (Government of Canada 2019). These populations have garnered national and international attention, with only 15 of
by using simple, spatially explicit models, evaluating relative rather than absolute rates of extinction, examining all feasible scenarios, and using relevant time periods for projections (Beissinger and Westphal 1998).

Our objective was to test the consistency between predictions and observations for woodland caribou by combining an influential regional demographic model, the Sorensen model (Sorensen et al. 2008), with extensive data on Alberta’s historical disturbance regime (fire and industrial disturbances). Sorensen et al. (2008) identified 2 predictors of lambda (λ), the rate of population change, for Alberta’s boreal populations of woodland caribou: the percentage of the population’s range within buffered (250 m) industrial disturbances and the percentage of the range burned within the last 50 years. We used 6 simulations of historical industrial and fire disturbance regimes on 5 woodland caribou populations in Alberta, and compared predicted and observed population size, growth rate, and persistence. If the Sorensen model accurately describes the effects of industrial disturbance and fire on population-specific growth rates, then we predicted population growth rates were approximately stable (λ ~ 1.0) prior to the onset of industrial disturbances, and recent and intensive accumulation of industrial disturbances has a larger effect on predicted population growth rates than fire or historical population size, when compared to observed values (Vors et al. 2007, Environment Canada 2011, Johnson et al. 2020).

STUDY AREA

The study area is located in Alberta and includes the ranges of 5 of 12 extant woodland caribou populations: West Side Athabasca River, Little Smoky, Cold Lake Air Weapons Range, Caribou Mountains, and Red Earth (Fig. 1). These populations occupy both lowland and upland boreal forest comprised of black spruce (Picea mariana), white spruce (P. glauca), tamarack (Larix laricina), lodgepole pine (Pinus contorta), and jack pine (Pinus banksiana). The Albertan boreal forest occupies 381,046 km², with a mean annual temperature of 0.5°C, and mean annual precipitation of 480 mm (Alberta Parks 2006). For more details about these populations, including the geography, seasonality, movements, and other land use please see the draft Provincial woodland caribou range plan (Government of Alberta 2017).

METHODS

Simulating λ from the Sorensen Model

The Sorensen model showed that industrial disturbance (%IND) and the percentage of the range burned within the last 50 years (%BURN) were negatively associated with population-specific (i) λ for each time period (t), and their coefficients did not significantly differ:

\[ λ_{i,t} = 1.192 - 0.003x(%IND_{i,t}) - 0.003x(%BURN_{i,t}) \]

(1)

More recently, measures of industrial disturbances based on features buffered at only 250 m have been considered conservative; buffers of 250 m to 1 km have since been used in modeling caribou demographic parameters (Environment
The age-class model tracks the proportional area in 1-year age classes ($y$; 0 to the maximum age $Y$). At each time step $t$, the range $i$ is subject to a proportional area burned ($b_{i,t}$). As explained below, these values are empirically determined for 1940–2006, and otherwise sampled from a range-specific distribution fit to the empirical data. We assumed that each forest age class was equally susceptible to burning (Johnson et al. 2001) and that caribou population range boundaries did not change over the simulation period. The amount of forest that is zero years old in time $t+1$, $F_{i,t+1}(0)$, is simply the amount burned in time $t$ in that population’s range, $b_{i,t}$. The amount of 1-year-old forest at time $t+1$, $F_{i,t+1}(1)$, will be the amount that was zero in the previous year minus the fraction that was burned in the current year, $(1-b_{i,t})$, and so on. The forest age-class model may thus be written:

$$F_{i,t+1}(0) = b_{i,t}$$

$$F_{i,t}(y) = F_{i,t}(y-1) \times (1 - b_{i,t}), \text{for } y = 1, \ldots, Y-1$$

$$F_{i,t+1}(Y) = (1 - b_{i,t}) \times [F_{i,t}(Y-1) + F_{i,t}(Y)],$$

where $Y$ is the maximum, accumulating, age class. The percentage area of a population’s range $i$ that is 50 years old or younger at time $t$ is then calculated from the age structure to yield:

$$\%\text{BURN}_{i,t} = 100 \times \sum_{y=1}^{50} F_{i,t}(y)$$

Fire regime.—We characterized the natural disturbance regime within each caribou range using time-series of digital fire maps published by Alberta’s Ministry of Agriculture and Forestry, Wildfire Management Branch. The maps show the boundaries of all known human and lightning-caused fires $\geq12$ ha, for 1940–2006. Provincial authorities constructed these maps from contemporary fire management records, archival paper maps, and post-fire aerial photography; they are considered to be nearly complete for areas under forest protection (C. Tymstra, Alberta Wildfire Management Branch, personal communication), which included our 5 populations. Since the early 1960s, lightning-caused fires have predominated in this region (Cumming 2001). We overlaid all fire maps with caribou population range boundaries. From this intersection, we estimated $b_{i,t}$ for each range.

For simulation, we sampled $b_{i,t}$ for population $i$ at time $t$ from a beta distribution $b_{i,t} \sim \text{Beta}(\alpha_i, \beta_i)$. We estimated these parameters using the method of moments:

$$\hat{\alpha}_i = \frac{(1 - \bar{x}_i)\bar{x}_i^2 - \bar{x}_i\hat{\sigma}^2}{\hat{\sigma}_i^2}, \quad \hat{\beta}_i = \frac{\alpha(1 - \bar{x}_i)}{\bar{x}_i},$$

where $\bar{x}_i$ is the mean and $\hat{\sigma}_i^2$ is the variance of the annual proportional area burned for population $i$ (Table 1).
Table 1. Landscape condition, historical disturbance regime parameters, and assumed initial size for 5 caribou population ranges in Alberta, Canada. We included the herd range area (km²), estimated initial population size, mean annual proportion of caribou range burned ($\frac{\%}{\text{yr}}$), standard deviation of proportion of range burned annually ($\sigma^2$), estimates of beta distribution parameters of herd fire regimes ($\alpha$ and $\beta$, 1940 through 2006), and estimates of the proportion of a herd’s range within 250 m of an industrial feature (%IND) in 1980 and 2006.

| Population          | Area (km²) | Initial population size | $\bar{x}_i$ | $\sigma^2$ | $\alpha$ | $\beta$ | 1980 (%) | 2006 (%) |
|---------------------|------------|-------------------------|--------------|------------|----------|---------|----------|----------|
| West Side Athabasca | 15,038     | 902                     | 0.0013       | 0.0004     | 0.130    | 99.126  | 11.7     | 78.4     |
| Little Smoky        | 2,927      | 176                     | 0.0003       | 0.0002     | 0.026    | 78.202  | 29.9     | 99.0     |
| Cold Lake           | 5,402      | 324                     | 0.0090       | 0.047      | 0.030    | 3.187   | 4.2      | 79.7     |
| Red Earth           | 15,999     | 960                     | 0.0045       | 0.019      | 0.054    | 11.971  | 11.8     | 87.7     |
| Caribou Mountains   | 18,658     | 1,119                   | 0.0066       | 0.022      | 0.083    | 12.454  | 17.4     | 40.8     |

Industri al footprint.—Sorensen et al. (2008:table 1) originally calculated the percent industrial footprint for each range by buffering all industrial disturbances by 250 m, including linear features (seismic lines, roads, pipelines, and transmission corridors, oil and gas well sites), permanent clearings, and forestry cut-blocks. They counted overlapping buffers only once, and identified these industrial features from remotely sensed imagery taken from 2000. To estimate temporal trajectories over the period of record is challenging because time-series data are not available for most of the feature classes contributing to the index, except for oil and gas wells. For these, we used a comprehensive, proprietary database of energy sector infrastructure in western Canada provided by geoLOGIC Systems, Calgary, Alberta. The database records the location to the nearest quarter section and the date of completion for all exploratory and production oil and natural gas wells drilled in Alberta to the present day. At a spatial resolution of 10,000 ha, the density of drilled oil and gas wells is correlated with the densities of the linear feature classes incorporated in the Sorensen model (Cumming and Cartledge 2004), and we assumed this spatial correlation held throughout the duration of our simulations.

We calculated the annual well density ($\frac{\%}{\text{yr}}$) within range $i$ for years $t = 1940, \ldots, 2006$ as the number of wells drilled within the population range up to year $t$, divided by the range area in km². Using these values as surrogates for total industrial disturbance, we calculated:

$$\text{%IND}_{i,t} = \frac{w_{i,t}}{w_{i,2000}} \times \text{%IND}_i,$$

where %IND$_i$ are the herd level values reported by Sorensen et al. (2008). Our surrogates account for differences in development history (1940–2000) between ranges, and also allow us to extend the analysis to 2006 while accounting for development activity after 2000. We further assumed %IND$_{i,t} = 0$ for $t < 1940$ and %IND$_{i,t} = \text{%IND}_{i,2006}$ for $t > 2006$.

Simulated Caribou Population Trajectories

We applied the Sorensen model to simulate caribou population trajectories over 1656–2076. Spin-up consisted of replicate runs over 200 years (1656–1855) prior to simulation. Our simulations are split into 3 stages: pre-industrial (1856–1939), industrial (1940–2006), and future (2007–2076). In the pre-industrial stage, we simulated annual area burned using variations of the fire regime model (eq. 5) to evaluate the probability of population persistence under a natural disturbance regime in the absence of industrial development. The industrial stage used the empirical annual areas burned and the estimated developmental trajectories (eq. 6) to determine if the Sorensen model is consistent with the inferred population declines and persistence up to 2006, given our 67-year reconstruction of the historical disturbance regime. Our future stage evaluated the probability of each population’s persistence under an industrial disturbance and fire regime from 2006, with annual areas burned sampled from fitted beta distributions (eq. 5). For each simulation, we initialized the forest age structure within each population’s range to uniform values of $\frac{1}{(N+1)}$. From these covariate data, calculations, and forecasts, we predicted $\lambda_{i,t}$ from equation 1.

We know of no estimates for woodland caribou population sizes prior to 1940. We assumed an initial mean caribou population density of $\rho = 0.03$ adult females/km$^2$ (0.06 caribou/km$^2$). This value is 1.5 times higher than a contemporary woodland caribou population with limited (2%) landscape disturbance (Mealy Mountain, 0.02 adult females/km$^2$; Environment and Climate Change Canada 2019), and 7.9 times higher than an Alberta population with high (87%) landscape disturbance (Cold Lake, up to 0.0038 adult females/km$^2$; Burgar et al. [2019], Environment and Climate Change Canada 2019). This value also closely aligns with the calculated stabilizing density for forest-dwelling caribou, compiled by Bergerud (1992). We calculated average range carrying capacities as $K_i = \rho \times A_i$, where $A_i$ is the area of population $i$ (Table 1). We calculated population trajectories under a model of truncated exponential population growth as:

$$N_{i,t+1} = \min(\lambda_{i,t} \times N_{i,t}, K_i),$$

where $N_{i,t}$ is the number of adult female caribou in population $i$ at time step $t$. Equation 7 imposes a strict form of density dependence applying only to populations at or above carrying capacity.

Scenario evaluation.—We used simulation scenarios to test the consistency of the Sorensen model to observed
demographics under 6 scenarios representing different assumptions about historical disturbance regimes (Table 2). Our purpose was first to determine if the Sorensen model results in plausible outcomes given the assumptions specified as part of our model parameterization, and second to identify which parameters have the largest effect on caribou population demographics (size and growth rate).

In the first scenario (Regular), we address the compounded effect of fire and industrial activity using equations 1, 4, 5, and 6. In our second scenario (Decreased Density), we decreased the population carrying capacity to an estimate of contemporary woodland caribou population under limited landscape disturbance (Mealy Mountain, 0.02 females/km$^2$; Environment Canada 2012). The third scenario (+Fire) increased the pre-industrial (pre-1940) burn rate to 0.01 to reflect the effect of 2 possible factors creating a bias towards a low estimate of burn rate: fire suppression over the period of the empirical dataset (i.e., 1940–2006) and climate change into the future (i.e., post-2006; Boulanger et al. 2017). The observed mean annual burn rates ($\mu_i$) were all <0.009 (Table 1), which may be very low; rates $\geq 1\%$ (0.01) may be typical of this region in the long term (Larsen 1996). In the fourth scenario (++Fire), we increased the annual burn rate to 1.6% (0.016), a level equivalent to annual forest removal by the forestry industry within this region. Recommended forest harvest rates under a natural-disturbance paradigm are based on fire return intervals under the assumption that forest harvest provides a landscape disturbance similar to fire; current guidelines allow for forest harvest rotations every 50–60 years (or 0.016 of the forest each year; Hunter 1993). This scenario assumes all polygonal disturbances on the landscape are due to forest harvesting. Our fifth scenario (0Industry) separates the effects of industrial disturbance and fire by reducing industrial disturbance to zero and keeping all other parameters the same as in the Regular scenario. Our sixth scenario of no industry and very high fire (0Industry++Fire) eliminates linear industrial disturbance and assumes fire burn rates solely reflect contemporary forest harvest rotations, not a combination of existing fires and contemporary forest harvest rotations (Table 2).

Simulation scenarios ran for 220 years (pre-industrial through future stages: 1856–2076). Each simulation scenario consists of 300 replicate runs (resulting in 66,000 individual year estimates), repeated for each of the 5 caribou populations (Table 1). For each scenario, and each population, we calculated the average yearly $\lambda$ and population size. We report the mean and 95% confidence intervals where this average yearly $\lambda$ first fell below 1.0, the projected mean $\lambda$ and population size in 2017 because this was the last reported observed value provided by the Alberta Government (Government of Alberta 2017), and the range of years where the mean population size fell below a quasi-extinction threshold of 10 adult females. We conducted all analyses in R version 3.3.5 (R Core Team 2019), and present values as mean ± standard errors unless otherwise specified. We obtained animal data from Government reports and websites; no animal care approval was required for this simulation study. Analysis and manuscript code are available at https://github.com/StewartResearch/Boo2020.git.

**RESULTS**

We obtained natural and industrial disturbance data from 5 woodland caribou ranges across 67 years (1940 to 2006). On average 0.004 ± 0.0001 of each population’s area burned annually (Table 1). As of 2001, Sorensen et al. (2008) reported between 8.0% (West Side Athabasca) and 29.2% (Red Earth) of population ranges had burned, between

| Stage       | Scenario | %IND | %BURN | Max. density | Description of simulation                                      |
|-------------|----------|------|-------|--------------|----------------------------------------------------------------|
| Pre-industrial | Reg      | 0    | $\bar{\lambda} \pm \sigma$ | 0.03          | Cumulative effect of reported historical fire and industrial disturbance on rate of population change ($\lambda$). |
| Industrial  | Reg      | $%\text{IND}_{2006}$ | $\bar{\lambda} \pm \sigma$ | 0.03          | Decreased assumed population density to test the effect of carrying capacity on $\lambda$. |
| Future      | −Dens   | 0    | $\bar{\lambda} \pm \sigma$ | 0.02          | Increased burn rate from historical data to test the effect of a low historical burn rate on $\lambda$; historical burn rate may be a low estimate because of either fire suppression or climate change. |
| Pre-industrial | +Fire    | 0    | $0.01 \pm \sigma$ | 0.03          | Increased burn rate to test the effect of contemporary forest harvest rates on $\lambda$. |
| Industrial  | +Fire    | $%\text{IND}_{2006}$ | $0.01 \pm \sigma$ | 0.03          | Decreased industrial disturbance to separate the effects of industrial disturbance and fire on $\lambda$. |
| Future      | ++Fire   | 0    | $0.016 \pm \sigma$ | 0.03          | Decreased industrial disturbance and increased burn rate to separate the effects of 2 industrial disturbances, oil and gas wells and contemporary forestry, on $\lambda$. |
31.7% (Caribou Mountains) and 88.4% (Little Smoky) of population ranges had 250-m buffered industrial disturbances, population-specific rates of population change varied between 1.012 (West Side Athabasca) and 0.892 (Red Earth), and population sizes varied between 90 (Little Smoky) and 400 (Caribou Mountains). Assuming a population density of 0.03 female caribou/km², our initial population sizes (in 1940) varied between 176 individuals (Little Smoky) and 1,119 individuals (Caribou Mountains; Table 1). The historical disturbance data used here indicated 0% of all population ranges fell within a 250-m buffer of industrial disturbances as of 1940 and by 2006 this value increased on average to 77.1 ± 9.8% (Table 1).

Our Regular simulation scenario combined historical disturbance data with the Sorensen model. During the pre-industrial stage of this scenario, no population had a λ < 1.0 prior to the onset of industrial disturbance, the exception being Cold Lake whose λ may have approached 1.0 during some years because of its small population size (Fig. 2; Lande 1993). Quasi-extinction never occurred across the other 4 populations, and population size stayed within 95% of K. These same results persisted across industrial and future stages when we set industrial disturbances to zero (0Industry and 0Industry++Fire); quasi-extinction never occurred, and population sizes stayed within 11% of K (Little Smoky; Fig. 2), even with much higher fire return intervals than occurred in our period with fire data (++Fire). Importantly, prior to incorporating historical disturbance regimes, the Sorensen model appeared to be consistent with the persistence of all 5 populations.

The industrial stage represents the start of data-estimated disturbance events. Four of our 6 scenarios had declining population growth (Fig. 2); only the 2 simulation scenarios where industrial disturbances were set to zero (0Industry and 0Industry++Fire) showed no declines. During this stage, all populations had scenarios where λ values fell below 1.0 (Table 3).

The future stage represents the projection of the Sorensen model from 2007 through to 2076. Across all simulation scenarios where we set industrial disturbance to zero (0Industry and 0Industry++Fire), populations remained above the quasi-extinction threshold during this stage (Table 3). The only exception was the Cold Lake population, where quasi-extinction could have occurred as early as 1856, given stochasticity, in every scenario (Table 3); we attribute this exception to the high rates of pre-industrial fire disturbance (Tables 1 and 2) and small population size. All other scenarios indicated 2 of 5 populations were potentially quasi-extinct prior to 2017 (Little Smoky, Cold Lake; Table 3). This may be surprising, except that the projected λs for all populations in the Regular scenario were within the confidence limits reported by the latest Government of Alberta estimates for the same year (Government of Alberta 2017; Table 3); there was consistency between the Sorensen model tested with historical disturbance regimes and observed caribou populations in Alberta today. Increasing fire frequency to reflect climate change or fire suppression (+Fire scenario), current forest harvest rates (++Fire scenario), or decreasing density (Decreased Density scenario) generally decreased the

Figure 2. Trends in mean rate of population change, λ (solid line) for 5 woodland caribou populations under 6 simulation scenarios. We performed simulations in 3 stages: pre-industrial (yellow; 1856–1939; natural disturbance only), industrial (orange; 1940–2006; natural and industrial disturbance vary), and future (red; 2007–2076; natural and industrial disturbance are fixed at 2006 rates). Reg refers to our regular data scenario using historical disturbance regime data; –Dens refers to our Decreased Density scenario; +Fire and ++Fire refer to our scenarios where burn rate was increased to reflect either fire suppression, climate change, or annual forest removal; 0Ind refers to our zero industrial disturbance scenario; and 0Ind++Fire refers to our scenario with no industrial disturbance and increased burn rates that reflect contemporary forest harvesting regimes.
average date (i.e., the date was earlier) where $\lambda$ fell below zero, and population size as of 2017, and potential quasi-extinction date for all populations, with the exception of Cold Lake. Compared to the Regular scenario, +Fire and ++Fire scenarios generally had a larger effect on these values than the Decreased Density scenario (Table 3). Given stochasticity all populations may have the potential to persist past 2076, but our simulations demonstrate these probabilities were significantly reduced by industrial disturbance (Fig. 2; Table 3).

**DISCUSSION**

Our simulations indicate that all 5 Alberta caribou populations examined are able to persist under a historical natural disturbance regime of fire but not under recent cumulative effects of industrial disturbance. Woodland caribou populations were stable under simulations of a reduced carrying capacity or increased area burned by forest fires prior to the onset of industrial disturbances. This work provides a novel simulation method to test the predictability of demographic models relied upon for species recovery planning. We suggest, with similar historical data, our approach could be applied elsewhere to assess models relating demography to changing landscapes (Johnson et al. 2020).

We examined whether the Sorensen model predicted observed population demography when tested against historical disturbance regimes. We demonstrate significant consistency between observed and predicted caribou demographics in 2017 (Table 3), supporting inferences regarding causes of observed woodland caribou declines. The predicted $\lambda$ in the Regular scenario was contained within the 95% confidence intervals of observed 10-year $\lambda$ estimates (Table 3). These mean $\lambda$ estimates correspond to the observed, widespread declines of Alberta’s boreal woodland caribou populations over the last 30 years (Fig. 2; McLoughlin et al. 2003, Hervieux et al. 2013), concomitant with rapid intensification of industrial development within population ranges (Hebblewhite 2017, Fortin 2020); the estimates do not match with our only fire scenarios (+Fire, ++Fire, or 0Industry++Fire), consistent with findings for

| Population | Scenario | $\lambda$ | 95% CI | Predicted Observed |
|-----------|----------|----------|--------|-------------------|
| West Side Athabasca | Reg 2002 | 0.90 | 0.904–0.906 | 2036 | 0.88 |
| | -Dens 2002 | 0.90 | 0.907–0.908 | 2033 | 0.68–1.02 |
| | +Fire 1994 | 0.80 | 0.806–0.807 | 2021 | 0.50 |
| | ++Fire 1979 | 0.77 | 0.770–0.77 | 2016 | 0.50 |
| | 0Ind | 1.17 | 1.175–1.176 | | |
| | 0Ind++Fire | 1.02 | 1.028–1.039 | | |
| Little Smoky | Reg 1994 | 0.87 | 0.875–0.876 | 2013 | 0.99 |
| | -Dens 1994 | 0.75 | 0.756–0.757 | 1999 | 0.6–1.1 |
| | +Fire 1980 | 0.71 | 0.716–0.716 | 1995 | 0.50 |
| | ++Fire 1997 | 1.18 | 1.189–1.189 | | |
| | 0Ind | 1.02 | 1.029–1.028 | | |
| | 0Ind++Fire | 1.03 | 1.036–1.140 | 1856 | |
| Cold Lake | Reg 1856 | 0.76 | 0.757–0.762 | 1856 | 0.83 |
| | -Dens 1856 | 0.75 | 0.756–0.761 | 1856 | 0.63–0.98 |
| | +Fire 1856 | 0.73 | 0.732–0.736 | 1856 | |
| | ++Fire 1856 | 1.03 | 1.036–1.140 | 1856 | |
| | 0Ind | 1.02 | 1.022–1.026 | 1856 | |
| | 0Ind++Fire | 1.03 | 1.022–1.026 | |
| Red Earth | Reg 1998 | 0.97 | 0.934–1.01 | 2044 | 0.88 |
| | -Dens 1998 | 0.97 | 0.932–1.01 | 2035 | 0.71–1.02 |
| | +Fire 1991 | 0.90 | 0.883–0.932 | 2036 | |
| | ++Fire 1987 | 0.92 | 0.889–0.947 | 2030 | |
| | 0Ind | 1.11 | 1.059–1.140 | | |
| | 0Ind++Fire | 1.11 | 1.030–1.094 | | |
| Caribou Mountains | Reg 1997 | 0.97 | 0.976–0.982 | 2035 | 0.93 |
| | -Dens 1997 | 0.97 | 0.978–0.984 | 2040 | 0.76–1.05 |
| | +Fire 1974 | 0.92 | 0.917–0.921 | 2028 | |
| | ++Fire 1968 | 0.92 | 0.924–0.928 | 2035 | |
| | 0Ind | 1.11 | 1.105–1.110 | | |
| | 0Ind++Fire | 1.00 | 1.005–1.008 | | |

* Estimated number, actual number unknown (Government of Alberta 2017).

a Burgar et al. (2019).
woodland caribou populations in other parts of Canada's boreal forests (Schaefer 2003, Johnson et al. 2020).

Predictions from the Sorensen Model
We developed our predictions to evaluate the relative contributions of natural and industrial disturbances to the declines of Alberta's boreal populations of woodland caribou. Our results support our predictions; across populations, demographic parameters (population size and \( \lambda \)) were higher when we removed the effects of industrial disturbance. Testing the effect of our assumed carrying capacity by reducing it 1.5 times, and increasing the annual rate of disturbance by fire to 1.6% (up to a 33-fold increase over historical rates, depending on the population) had little effect on projected demographics; the time to quasi-extinction decreased by only 0–18 years. The outcomes of population extinction or persistence as of 2017 were affected most by variations to the industrial disturbance regime (Table 3; Fig. 2).

Emulating historical fire with contemporary harvesting is foundational to ecosystem-based forest management (Perera et al. 2007, but see Cyr et al. 2009 for an empirical critique). The natural range of variation (Landres et al. 1999) of forest fires in this region has been reported as up to 1.6% of the landscape (i.e., forest fires replace the forest every 60–100 yr; Hunter 1993, Andison 2013). We tested the effect of fire-remulated harvesting on woodland caribou by increasing the annual proportion of area burned through simulation scenarios while keeping industrial disturbance consistent. If these values accurately represent the natural range of variation, the Sorensen model predicts the 5 study populations may become extinct between 1995 (Little Smoky) and 2035 (Caribou Mountains). Some caribou populations might coexist with a harvest return interval of 60 years (0Industry++Fire scenario), if there are no decreases in habitat carrying capacity, additional fires, or other industrial disturbances. This situation does not reflect the current state of Canada’s boreal ecozone. Our simulations suggest that to sustain the boreal populations of woodland caribou, forest harvest rates should not exceed the historical fire regime of these Alberta populations, 0.9% annually (Table 1), or a harvest rotation of roughly 110 years.

Model Limitations and Edge Cases
Although the Sorensen model fits its data well (\( R^2 = 0.96 \)), it used only 6 data points. Previous validation against 5 years of independent demographic data suggested it generally over-predicted \( \lambda \) (Sleep and Loehle 2010). Our initial values (Fig. 2, \( \lambda = 1.2 \)) may therefore be too high, leading to overestimated times to quasi-extinction (Table 3). Sleep and Loehle (2010) also question the equal weights assigned to industrial and natural disturbances in the model, corroborated by the more recent findings of Johnson et al. (2020) that herd demography is more sensitive to industrial disturbances than to fire. This would not alter our main results; indeed, it would further emphasize our conclusion pointing to the greater importance of industrial disturbances than fire (Fig. 2; Table 3).

Our study neglected several potential sources of temporal variation in the data or in underlying processes. For example, our ability to estimate population densities may change with time (e.g., Government of Alberta [2017] vs. Burgar et al. [2019] density estimates for Cold Lake; Table 3); the effects of industrial disturbances may decrease over time as they return to a natural state, at rates that may vary by disturbance types (Dabros et al. 2018, Dhar et al. 2018); and true adult female mortality and juvenile recruitment rates may have varied with increased wolf densities because of landscape change and reduced trapping (Bergerud 1974). Neither did we account for wildlife management actions recently undertaken to conserve Alberta’s caribou (see below); however, our model’s simplicity supports rapid assessment of the relative effects of the factors that are included (Beissinger and Westphal 1998), and may be easily translated to other systems having spatially explicit disturbance histories.

Our model predicts very high pre-industrial population growth rates (\( \lambda = 1.2 \)) for some populations, under the scenario 0Industry (Fig. 2). This occurs when fire disturbance rates are very low. In that case, the predicted \( \lambda ' \)’s approach the intercept of equation 1, which is 1.192. In population ranges with higher historical disturbance rates, or scenarios with elevated disturbance rates, these high growth rates are not predicted.

Our simulations project possible quasi-extinction for the Little Smoky population from the year 2013 onwards and for the Cold Lake population as early as 1856 (Table 3). Both populations may be vulnerable because of low numbers as derived from their small range areas (Table 1; Lande 1993). Although both populations have persisted to the present day, they did exhibit substantial and consequent population declines prior to 2001 (Government of Alberta 2017). The predicted and observed declines were ameliorated by wolf cull programs undertaken in winters 2005–2006 and 2016–2017 for Little Smoky and Cold Lake, respectively (Hervieux et al. 2014, Government of Alberta 2017). Our predictions for Little Smoky corroborate a recently published simulation that reported >68% of undisturbed habitat is needed to maintain a self-sustaining population over a 20-year period (Johnson et al. 2020); this condition has not been satisfied since 1981 according to our estimated development trajectory. With respect to the Cold Lake population, possible early quasi-extinction is compounded by the relatively high rate of fire disturbance on their range and limited cross-border movement due to province-specific altered landscape change with the contiguous SK2 herd in Saskatchewan, Canada (Government of Saskatchewan 2019). We think this points to an oversensitivity of the quasi-extinction index rather than any fundamental weakness in our models.

Predictions of demographic models for species at risk will be most accurate if reliable predictor histories are obtained (Chaudhary and Oli 2020), models can be decomposed into life-stage survivorship and recruitment terms (Johnson et al. 2020), assumptions regarding historical population density estimates are tested for consistency against observed
data, and environmental stochasticity of survival and recruitment is incorporated into model predictions—all factors that are generally hard to come by (Williams et al. 2002, Lafontaine et al. 2017). In the present context, more detailed industry-specific disturbance histories would increase model sensitivity relative to the surrogate index of drilled well density that we used.

**MANAGEMENT IMPLICATIONS**

Our results suggest that many of Alberta’s woodland caribou populations in boreal ecosystems will continue to decline as a result of cumulative industrial disturbances if preventative or mitigative management actions are not taken. Our data support the need to limit industrial disturbance within caribou population ranges because caribou may persist even under fire regimes with annual burn rates higher than currently observed if industrial disturbance is absent. In other words, caribou appear resilient to fire even at the most extreme end of our fire history uncertainty. Our results are also consistent with a positive effect of existing wolf culls (Little Smoky and Cold Lake) on population persistence; our simulations imply observed persistence would be unlikely in the absence of such treatments. This further suggests there remain opportunities to conserve other caribou study populations (e.g., Red Earth, West Side Athabasca, and Caribou Mountains) through management action that limits, reduces, or mitigates the presence of industrial features within their ranges.

**ACKNOWLEDGMENTS**

Authors have no conflicts of interest to declare. We thank the Alberta Caribou Committee, G. Hauer, S. A. Boutin, E. H. Dzus, R. R. Schneider, Alberta Forest Protection, I. Eddy, C. Barros, N. Holloway, the Boreal Ecology and Economics Synthesis Team, S. Magnusson, M. Wheatley, and 2 anonymous reviewers for help with data consolidation, knowledge reference, geographic information system expertise, and discussion. Research was funded by the Natural Resources Canada Postdoctoral Research Program to E. J. McIntire, and the Service Assistant Deputy Minister’s Innovation Fund. Research Council Discovery Grant, the Canadian Forest Industry expertise, and discussion. Research was funded by the Canada Research Chairs program to E. J. McIntire and Eddy, C. Barros, N. Holloway, the Boreal Ecology and Economics Synthesis Team, S. Magnusson, M. Wheatley, and 2 anonymous reviewers for help with data consolidation, knowledge reference, geographic information system expertise, and discussion. Research was funded by the Canada Research Chairs program to E. J. McIntire and N. Bacaër, editor. A short history of mathematical population dynamics. Springer, London, United Kingdom.

**LITERATURE CITED**

Alberta Caribou Committee. 2006. Alberta Caribou Committee; Conserving northern Alberta’s woodland caribou through knowledge and planning. <http://www.albertacariboucommittee.ca>. Accessed 8 Oct 2010.

Alberta Parks. 2006. Natural regions and subregions of Alberta. Natural Regions Committee. <https://www.albertaparks.ca/media/2942026/nrscomplete_may_06.pdf>. Accessed 8 Aug 2019.

Andison, D. 2013. Wildfire patterns in Western Boreal Canada. Healthy landscapes research series, RRI Research. <https://fireresearch.ca/resource/wildfire-patternswestern-boreal-canada-healthy-landscapes-research-series-report-no-85>. Accessed 12 Nov 2019.

Bacaër, N. 2011. Verhulst and the logistic equation (1838). Pages 35–39 in N. Bacaër, editor. A short history of mathematical population dynamics. Springer, London, United Kingdom.

Beissinger, S. R., and M. I. Westphal. 1998. On the use of demographic models of population viability in endangered species management. Journal of Wildlife Management 62:821–841.

Bergen, A. T. 1974. Decline of caribou in Northern Minnesota following settlement. Journal of Wildlife Management 38:757–770.

Bergen, A. T. 1992. Rareness as an antipredator strategy to reduce predation risk for moose and caribou. Pages 1008–1021 in D. R. McCullough and R. H. Barrett, editors. Wildlife 2001: populations. Springer Science & Business Media, Stamford Sierra Camp, Fallen Leaf Lake, California, United States of America.

Boon, J. J., J. R. Malcolm, M. D. Vanier, D. L. Euler, and F. M. Moola. 2018. From climate to caribou: how manufactured uncertainty is affecting wildlife management. Wildlife Society Bulletin 42:366–381.

Boulanger, Y., A. R. Taylor, D. T. Price, D. C. Yr, E. McGarrigle, W. Rammer, G. Sainte-Marie, A. Beaudoin, L. Guindon, and N. Mansuy. 2017. Climate change impacts on forest landscapes along the Canadian southern boreal forest transition zone. Landscape Ecology 32:1415–1431.

Brook, B. W., J. J. O’Grady, A. P. Chapman, M. A. Burgman, H. R. Akçakaya, and R. Frankham. 2000. Predictive accuracy of population viability analysis in conservation biology. Nature 404:385–387.

Burgar, J. M., A. C. Burton, and J. T. Fisher. 2019. The importance of considering multiple interacting species for conservation of species at risk. Conservation Biology 33:709–715.

Chaudhary, V., and M. K. Oli. 2020. A critical appraisal of population viability analysis. Conservation Biology 34:26–40.

Cumming, S. G. 2001. A parametric model of the fire-size distribution. Canadian Journal of Forest Research 31:1297–1303.

Cumming, S. G., and P. Cartledge. 2004. Spatial and temporal patterns of the industrial footprint in northeast Alberta, 1960–2000. Sustainable Forest Management Network. University of Alberta, Edmonton, Canada.

Cyr, D., S. Gauthier, Y. Bergeron, and C. Carcaillit. 2009. Forest management is driving the eastern North American boreal forest outside its natural range of variability. Frontiers in Ecology and the Environment 7:519–524.

Dabros, A., M. Pyper, and G. Castilla. 2018. Seismic lines in the boreal and arctic ecosystems of North America: environmental impacts, challenges, and opportunities. Environmental Reviews 26:214–229.

Dhar, A., P. G. Comeau, J. Karst, B. D. Pinno, S. X. Chang, A. M. Naeth, R. Vassov, and C. Bamfylde. 2018. Plant community development following reclamation of oil sands mine sites in the boreal forest: a review. Environmental Reviews 26:286–298.

Environment and Climate Change Canada. 2019. Progress report on steps taken to protect critical habitat for the woodland caribou (Rangifer tarandus caribou), boreal population, in Canada—June 2019. <https://www.canada.ca/en/environment-climate-change/services/species-risk-public-registry/critical-habitat-reports/woodland-caribou-boreal-registry-protected-2019.html>. Accessed 8 Aug 2019.

Environment Canada. 2011. Scientific assessment to inform the identification of critical habitat for woodland caribou (Rangifer tarandus caribou), boreal population, in Canada: 2011 update. Environment Canada, Ottawa, Ontario, Canada.

Environment Canada. 2012. Recovery strategy for the woodland caribou (Rangifer tarandus caribou), boreal population, in Canada. Species at Risk Act Recovery Strategy Series. Environment Canada, Ottawa, Ontario, Canada.

Festa-Bianchet, M., J. C. Ray, S. Boutin, S. D. Côté, and A. Gunn. 2011. Conservation of caribou (Rangifer tarandus) in Canada: an uncertain future. Canadian Journal of Zoology 89:419–434.

Fortin, D., P. D. McLoughlin, and M. Hebblewhite. 2020. When the protection of a threatened species depends on the economy of a foreign nation. PLoS ONE 15:e0229555.

Government of Alberta. 2017. DRAFT: provincial woodland caribou range plan. <https://open.alberta.ca/dataset/932b6c22-3a2a-4b4e-a5f5-ch2703c52b80/resource/56363a-0924-44ab-b178-62a34d3bb157/download/draft-caribou-rangeplanandappendices-dec2017.pdf>. Accessed 23 Mar 2020.

Government of Canada. 2019. Species at risk: management plans. <https://www.canada.ca/en/environment-climate-change/services/species-risk-public-registry/methodology-plans.html>. Accessed 8 Mar 2019.

Government of Saskatchewan. 2019. DRAFT: range plan for Woodland caribou in Saskatchewan. Boreal Plain Ecozone—SK2 West caribou administration unit. <https://pubsaskdev.clob.core.windows.net/pubssaskprod/114947/Draft%252BRange%252BPlan%252BFor%252BWoodland%252BCaribou%252BIn%252BSK%252BSK2%252BW%252BWest.pdf>. Accessed 15 May 2020.
Hubblewhite, M. 2017. Billion dollar boreal woodland caribou and the biodiversity impacts of the global oil and gas industry. Biological Conservation 206:102–111.

Hervieux, D., M. Hubblewhite, N. J. DeCesare, M. Russell, K. Smith, S. Robertson, and S. Boutin. 2013. Widespread declines in woodland caribou (Rangifer tarandus caribou) continue in Alberta. Canadian Journal of Zoology 91:872–882.

Hervieux, D., M. Hubblewhite, D. Stepnisky, M. Bacon, and S. Boutin. 2014. Managing wolves (Canis lupus) to recover threatened woodland caribou (Rangifer tarandus caribou) in Alberta. Canadian Journal of Zoology 92:1029–1037.

Hunter, M. L. 1993. Natural fire regimes as spatial models for managing boreal forests. Biological Conservation 65:115–120.

Johnson, C. A., G. D. Sutherland, E. Neave, M. Leblonde, P. Kirby, C. Superbie, and D. McLoughlan. 2020. Science to inform policy: linking population dynamics to habitat for a threatened species in Canada. Journal of Applied Ecology 57. https://doi.org/10.1111/13652664.13637

Johnson, C. J., M. A. Mumma, and M.-H. St-Laurent. 2019. Modeling multispecies predator–prey dynamics: predicting the outcomes of conservation actions for woodland caribou. Ecosphere 10:e02622.

Johnson, E. A., K. Miyaniishi, and S. R. J. Bridge. 2001. Wildfire regime in the boreal forest and the idea of suppression and fuel buildup. Conservation Biology 15:1554–1557.

Lafontaine, A., P. Drapeau, D. Fortin, and M.-H. St-Laurent. 2017. Many places called home: the adaptive value of seasonal adjustments in range fidelity. Journal of Animal Ecology 86:624–633.

Laliberte, A. S., and W. J. Ripple. 2004. Range contractions of North American carnivores and ungulates. Bioscience 54:123–138.

Lande, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. American Naturalist 142:911–927.

Landres, P. B., P. Morgan, and F. J. Swanson. 1999. Overview of the use of natural variability concepts in managing ecological systems. Ecological Applications 9:1179–1188.

Larsen, C. P. S. 1996. Fire and climate dynamics in the boreal forest of northern Alberta. Canada, from AD 1850 to 1989. Holocene 6:449–456.

Latham, A. D. M., M. C. Latham, and M. S. Boyce. 2011. Habitat selection and spatial relationships of black bears (Ursus americanus) with woodland caribou (Rangifer tarandus caribou) in northeastern Alberta. Canadian Journal of Zoology 89:267–277.

Leblond, M., C. Dussault, J.-P. Ouellet, and M.-H. St-Laurent. 2016. Caribou avoiding wolves face increased predation by bears—caught between Scylla and Charybdis. Journal of Applied Ecology 53:1078–1087.

Mayer, D. G., and D. G. Butler. 1993. Statistical validation. Ecological Modelling 68:21–32.

McIntosh, R. P. 1986. The background of ecology: concept and theory. Cambridge University Press, Cambridge, United Kingdom.

McLoughlin, P. D., E. Dusz, B. Wynes, and S. Boutin. 2003. Declines in populations of woodland caribou. Journal of Wildlife Management 67:755–761.

Perera, A. H., L. J. Buse, and M. G. Weber. 2007. Emulating natural forest landscape disturbances: concepts and applications. Columbia University Press, New York, New York, USA.

R Core Team. 2019. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Ripple, W. J., J. A. Estes, R. L. Beschta, C. C. Wilmers, E. G. Ritchie, M. Hubblewhite, J. Berger, B. Elmhagen, M. Letnic, M. P. Nelson, et al. 2014. Status and ecological effects of the world’s largest carnivores. Science 343(6167):1241484.

Schafer, J. A. 2003. Long-term range recession and the persistence of caribou in the taiga. Conservation Biology 17:1435–1439.

Schneider, R. R., G. Hauer, W. L. (vic) Adamowicz, and S. Boutin. 2010. Triage for conserving populations of threatened species: the case of woodland caribou in Alberta. Biological Conservation 143:1603–1611.

Schneider, R. R., G. Hauer, K. Dawe, W. Adamowicz, and S. Boutin. 2012. Selection of reserves for woodland caribou using an optimization approach. PLoS ONE 7:e31672.

Seip, D. R. 1992. Factors limiting woodland caribou populations and their interrelationships with wolves and moose in southeastern British Columbia. Canadian Journal of Zoology 70:1494–1503.

Serrouya, R., M. Dickie, C. DeMaris, M. J. Wittmann, and S. Boutin. 2020. Predicting the effects of restoring linear features on woodland caribou populations. Ecological Modelling 416:108891.

Serrouya, R., B. N. McLellan, H. van Oort, G. Mowat, and S. Boutin. 2017. Experimental moose reduction lowers wolf density and stops decline of endangered caribou. PeerJ 5:e3736.

Serrouya, R., D. R. Seip, D. Hervieux, B. N. McLellan, R. S. McNay, R. Steenweg, D. C. Heard, M. Hubblewhite, M. Gillingham, and S. Boutin. 2019. Saving endangered species using adaptive management. Proceedings of the National Academy of Sciences 116:6181–6186.

Sleep, D. J. H., and C. Locle. 2010. Validation of a demographic model for woodland caribou. Journal of Wildlife Management 74:1508–1512.

Sorensen, T., P. D. Mcloughlin, D. Hervieux, E. Dusz, J. Nolan, B. Wynes, and S. Boutin. 2008. Determining sustainable levels of cumulative effects for boreal caribou. Journal of Wildlife Management 72:900–905.

Tattersall, E. R., J. M. Burgar, J. T. Fisher, and A. C. Burton. 2020. Mammal seismic line use varies with restoration: applying habitat restoration to species at risk conservation in a working landscape. Biological Conservation 243:108295.

Vors, L. S., J. A. Schafer, B. A. Pond, A. R. Rodgers, and B. R. Patterson. 2007. Woodland caribou: conservation and anthropogenic landscape disturbance in Ontario. Journal of Wildlife Management 71:1249–1256.

Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. Analysis and management of animal populations. Academic Press, London, United Kingdom.

Winder, R., F. E. C. Stewart, S. Nebel, E. J. B. McIntire, A. Dyk, and K. Omendja. 2020. Cumulative effects and boreal woodland caribou: how bow-tie risk analysis addresses a critical issue in Canada’s forested landscapes. Frontiers in Ecology and Evolution 8:1. https://doi.org/10.3389/fevo.2020.00001

Witmer, H. U., A. R. E. Sinclair, and B. N. McLellan. 2005. The role of predation in the decline and extirpation of woodland caribou. Oecologia 144:257–267.

Associate Editor: Steeve Côté.