



Research Article

Anthropogenic Disturbance and Population Viability of Woodland Caribou in Ontario

JOHN M. FRYXELL,¹ Department of Integrative Biology, University of Guelph, 50 Stone Road E., Guelph, Ontario N1G 2W1, Canada

TAL AVGAR,² Department of Integrative Biology, University of Guelph, 50 Stone Road E., Guelph, Ontario N1G 2W1, Canada

BOYAN LIU, Department of Integrative Biology, University of Guelph, 50 Stone Road E., Guelph, Ontario N1G 2W1, Canada

JAMES A. BAKER, Ontario Ministry of Natural Resources and Forestry, Wildlife Research and Monitoring Section, 300 Water Street, Peterborough, Ontario K9J 8M5, Canada

ARTHUR R. RODGERS, Ontario Ministry of Natural Resources and Forestry, Centre for Northern Forest Ecosystem Research, 435 James Street, Thunder-Bay, Ontario P7E 2VE, Canada

JENNIFER SHUTER, Ontario Ministry of Natural Resources and Forestry, Centre for Northern Forest Ecosystem Research, 435 James Street, Thunder-Bay, Ontario P7E 2VE, Canada

IAN D. THOMPSON, Canadian Forest Service, 1219 Queen Street East, Sault Ste. Marie, Ontario P6A 2E5, Canada

DOUGLAS E. B. REID, Ontario Ministry of Natural Resources and Forestry, Centre for Northern Forest Ecosystem Research, 435 James Street, Thunder-Bay, Ontario P7E 2VE, Canada

ANDREW M. KITTLE, Department of Integrative Biology, University of Guelph, 50 Stone Road E., Guelph, Ontario N1G 2W1, Canada

ANNA MOSSER,³ Department of Integrative Biology, University of Guelph, 50 Stone Road E., Guelph, Ontario N1G 2W1, Canada

STEVEN G. NEWMASER, Department of Integrative Biology, University of Guelph, 50 Stone Road E., Guelph, Ontario N1G 2W1, Canada

TOM D. NUDDS, Department of Integrative Biology, University of Guelph, 50 Stone Road E., Guelph, Ontario N1G 2W1, Canada

GARRETT M. STREET,⁴ Department of Integrative Biology, University of Guelph, 50 Stone Road E., Guelph, Ontario N1G 2W1, Canada

GLEN S. BROWN, Ontario Ministry of Natural Resources and Forestry, Wildlife Research and Monitoring Section, 300 Water Street, Peterborough, Ontario K9J 8M5, Canada

BRENT PATTERSON, Ontario Ministry of Natural Resources and Forestry, Wildlife Research and Monitoring Section, 300 Water Street, Peterborough, Ontario K9J 8M5, Canada

ABSTRACT One of the most challenging tasks in wildlife conservation and management is to clarify how spatial variation in land cover due to anthropogenic disturbance influences wildlife demography and long-term viability. To evaluate this, we compared rates of survival and population growth by woodland caribou (*Rangifer tarandus caribou*) from 2 study sites in northern Ontario, Canada that differed in the degree of anthropogenic disturbance because of commercial logging and road development, resulting in differences in predation risk due to gray wolves (*Canis lupus*). We used an individual-based model for population viability analysis (PVA) that incorporated adaptive patterns of caribou movement in relation to predation risk and food availability to predict stochastic variation in rates of caribou survival. Field estimates of annual survival rates for adult female caribou in the unlogged ($\bar{x} = 0.90$) and logged ($\bar{x} = 0.76$) study sites recorded during 2010–2014 did not differ significantly ($P > 0.05$) from values predicted by the individual-based PVA model (unlogged: $\bar{x} = 0.87$; logged: $\bar{x} = 0.79$). Outcomes from the individual-based PVA model and a simpler stage-structured matrix model suggest that substantial differences in adult survival largely due to wolf predation are likely to lead to long-term decline of woodland caribou in the commercially logged landscape, whereas the unlogged landscape should be considerably more capable of sustaining caribou. Estimates of population growth rates (λ) for the 2010–2014 period differed little between the matrix model and the individual-based PVA model for the unlogged (matrix model $\bar{x} = 1.01$; individual-based model $\bar{x} = 0.98$) and logged landscape (matrix model $\bar{x} = 0.88$; individual-based model $\bar{x} = 0.89$). We applied the spatially explicit PVA model to assess the viability of woodland caribou across 14 woodland caribou ranges in Ontario. Outcomes of these simulations suggest that woodland caribou ranges that have experienced

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¹E-mail: jfryxell@uoguelph.ca

²Current affiliation: Department of Wildland Resources, Utah State University, Logan, UT 84322, USA

³Current affiliation: CBS Biology Teaching/Learning, University of Minnesota Twin Cities, Room 3-133 MCB, 420 Washington Ave SE, Minneapolis, MN 55455, USA

⁴Current affiliation: Department of Wildlife, Fisheries and Aquaculture, Mississippi State University, Box 9690, Mississippi State, MS 39762-9690, USA

significant levels of commercial forestry activities in the past had annual growth rates <0.89 , whereas caribou ranges that had not experienced commercial forestry operations had population growth rates >0.96 . These differences were strongly related to regional variation in wolf densities. Our results suggest that increased wolf predation risk due to anthropogenic disturbance is of sufficient magnitude to cause appreciable risk of population decline in woodland caribou in Ontario. © 2020 The Authors. The *Journal of Wildlife Management* published by Wiley Periodicals, Inc. on behalf of The Wildlife Society.

KEY WORDS apparent competition, boreal, disturbance, forestry, growth rate, model, moose, movement, Ontario, population viability analysis, predation, survival, wolf, woodland caribou.

Range retraction and population decline characterize the recent history of many boreal woodland caribou (*Rangifer tarandus caribou*) populations across North America (Bergerud 1974, Schaefer 2003, Wittmer et al. 2005, Vors and Boyce 2009, Festa-Bianchet et al. 2011). The most widely supported hypothesis is that these demographic trends are caused by apparent competition among woodland caribou, moose (*Alces alces*), and white-tailed deer (*Odocoileus virginianus*) through enhanced rates of predation by gray wolves (*Canis lupus*) in landscapes with extensive secondary growth following commercial logging (Wittmer et al. 2005; DeCesare et al. 2014; Serrouya et al. 2015, 2017, 2019). Moose and deer thrive in early successional forests following logging, which in turn supports an increased density of wolves. Woodland caribou subsequently suffer from apparent competition (Holt 1977) when they blunder into areas preferentially used by moose and deer and, therefore, heavily used by wolves (DeCesare et al. 2014; Serrouya et al. 2015, 2017, 2019). White-tailed deer are relatively uncommon across the boreal zone of northern Ontario, Canada, occupied by woodland caribou, whereas moose are widely distributed and abundant. Previous field studies indicate that habitat use by wolves in Ontario is concentrated in regenerating conifer and mixedwood stands heavily used by moose (Cumming and Beange 1987, Cumming et al. 1994, Bowman et al. 2010, Kittle et al. 2017), whereas caribou preferentially use mature conifer stands (Ferguson and Elkie 2004, Hornseth and Rempel 2016). This suggests that predation risk to caribou might depend on the proportion of regenerating moose habitat on a given landscape and its frequency of use by caribou as they travel across heterogeneous landscapes (Cumming et al. 1994, James et al. 2004).

One way to assess the potential risk of further population decline is to link estimates of vital rates (typically survival and reproduction) to a system-specific demographic model to estimate stochastic variation in population growth rates. This class of models is often referred to as population viability analysis (PVA; Boyce 1992, Beissinger and McCullough 2002, Morris and Doak 2002, Wittmer et al. 2010). Population viability analysis models can be based on single species or a community of interactive species. Populations can be represented without any structure or with age- or size-specific parameters. Some PVA models are constructed to assess the effect of spatial variation in vital rates experienced by a collection of individuals living in different parts of a heterogeneous landscape. The latter modeling framework is often termed an individual-based PVA (Grimm and Railsback

2005) because demographic variation depends on the portion of the landscape occupied by different members of the focal population. Unlike conventional PVA models, individual-based models can yield insight into how variation in ecological conditions experienced by different animals translates into variation in individual fitness and its aggregate effect on population growth rates, enhancing the magnitude of demographic stochasticity due to other causes. Such information can be useful in exploring the potential effectiveness of alternative land use policies or management interventions (Lindenmayer et al. 2000, McCarthy et al. 2000).

We used a previously published model of facultative movement by woodland caribou in response to food availability and predation risk to predict patterns of caribou landscape use (Avgar et al. 2013, 2015) and their consequent effect on caribou survival rates for 2 study areas in northern Ontario. Four central objectives guided our efforts. First, we used the individual-based model to predict differences in predation risk between logged and unlogged study sites and tested those predictions for 122 adult females equipped with satellite global positioning system (GPS) radio-collars. Second, we used the individual-based model to evaluate whether the change in survival rates due to anthropogenic disturbance was of sufficient magnitude to cause significant reduction in population growth rates. Third, we evaluated whether the distribution of population growth rates estimated using the individual-based model was comparable to the distribution of population growth rates estimated using conventional matrix projection models equipped with identical recruitment parameters for our field study populations. Although not a model validation because we do not know what the true population change was over time, this comparison is helpful in assessing whether it might be defensible to apply the individual-based model to assess other landscapes for which we do not have demographic data. Fourth, we applied the individual-based model to estimate what proportion of woodland caribou ranges in Ontario might be at appreciable risk of decline in the near future and what risk factors are associated with caribou decline. In combination, these objectives allow us to evaluate the hypothesis that population viability of woodland caribou is threatened by apparent competition induced by anthropogenic habitat disturbance.

STUDY AREA

We compared caribou movement patterns and demography during 2010–2014 in 2 study areas in northern

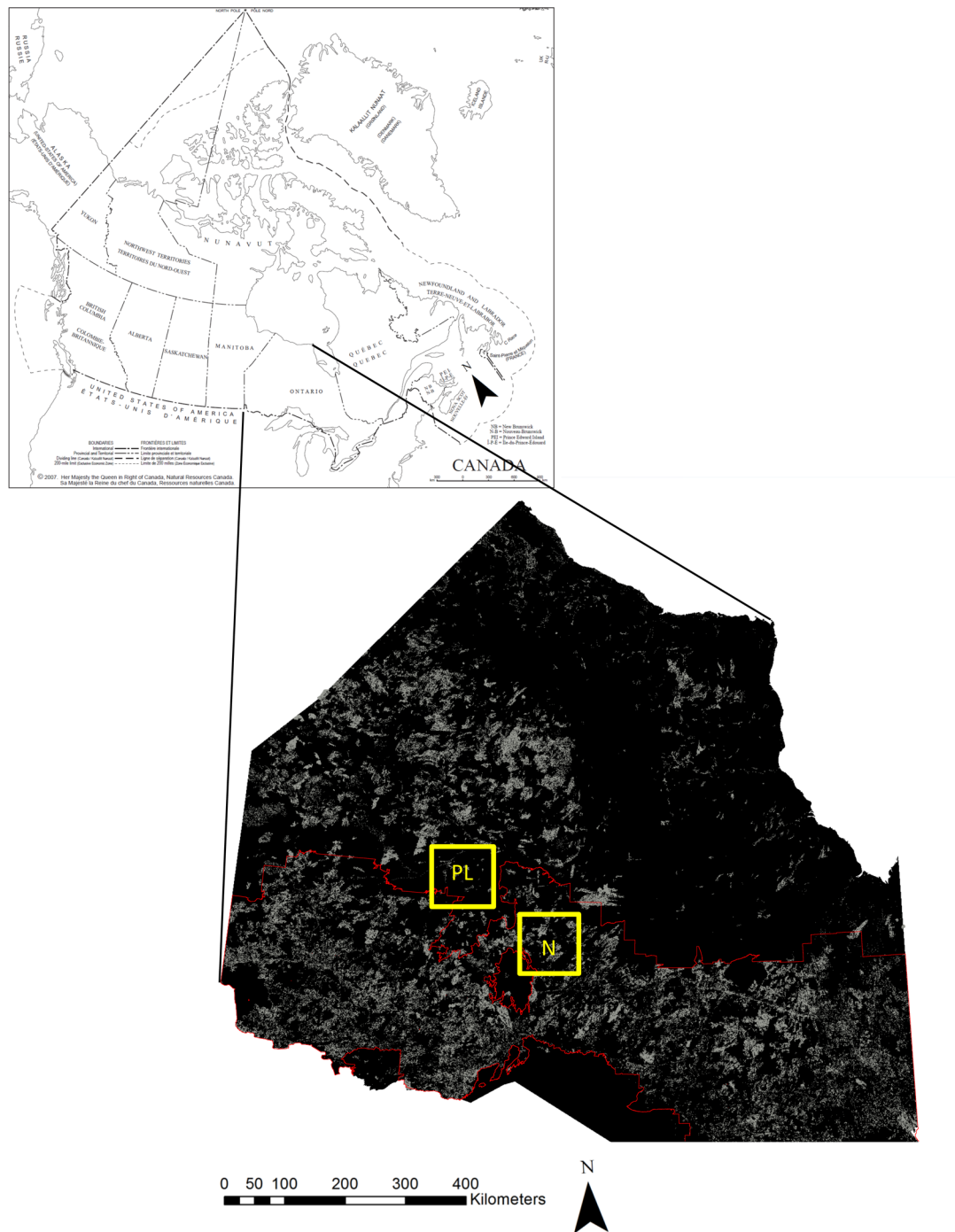


Figure 1. Natural and anthropogenic disturbance across Ontario, Canada, 2010. Gray shading represents disturbed areas. Red lines demarcate the zone within which commercial forestry activities have been permitted. Yellow squares correspond to the Pickle Lake (PL) and Nakina (N) study sites used to evaluate demography and movement of woodland caribou.

Ontario, each exceeding 22,500 km² in extent (Fig. 1): Nakina (50°N, 87°W) and Pickle Lake (51°N, 91°W). A boreal forest matrix with lakes and bogs interspersed throughout characterized both sites. Upland stands tended to be dominated by jack pine (*Pinus banksiana*) and balsam fir (*Abies balsamea*) with some deciduous broadleaf trees (poplar [*Populus* spp.] and birch [*Betula* spp.]), whereas lowland stands were dominated by black spruce (*Picea mariana*), eastern white cedar (*Thuja occidentalis*), and tamarack (*Larix laricina*). Predominant wildlife fauna in

our study areas included gray wolves, black bears (*Ursus americanus*), moose, and woodland caribou. Topography in both study sites was consistent with the Canadian Shield ecoregion, with rolling hills and little change in elevation across sites (Nakina: 230–459 m; Pickle Lake: 324–475 m). Monthly mean temperature was –19.2°C in January and 16.9°C in July (Environment Canada: Geraldton 49°46'N, 86°55'W; 1971–2000). We operationally defined the summer as 1 May–31 October and the winter as 1 November–30 April.

Our field sites spanned a strong gradient in anthropogenic disturbance and consequently differed in a number of other habitat attributes because the more northerly site (Pickle Lake) was just beyond the provincial limit for commercial forestry operations, whereas the other field site (Nakina) was immediately south of that administrative boundary (Fig. 1). Nakina had experienced considerable amounts of commercial forestry since 1970, whereas Pickle Lake had been exposed solely to natural sources of forest disturbance due to windthrow, fire, and insect outbreaks.

METHODS

We used extensive ground truthing of each land cover class from both field study sites (Fig. 2A) to estimate local variation in several key ecological variables, including food availability (Fig. 2B), moose density (Fig. 2C), and wolf density (Fig. 2D). Full details of how we derived these ecological variables and projected them across the landscapes is provided by Avgar et al. (2015). We provide a brief description of this undertaking with respect to spatial variation in the 3 key landscape variables that influence the animal movement in the individual-based PVA model: food availability, moose density, and wolf density.

We operationally defined food availability in the units of digestible energy/m² summed across all plant species that contribute to caribou diets in each land cover type during the summer and winter. We estimated local spatial variation

in food availability (F_x) at each location x (Fig. 2B) by multiplying the average standing crop of each plant species recorded during field sampling during summer (Mallon et al. 2016) by its proportion in woodland caribou diets in summer or winter (Thompson et al. 2012, 2015); then we multiplied this value by energy content and dry matter digestibility (Avgar et al. 2015).

We estimated the local density of moose (M_x) within each pixel by multiplying mean moose density across the entire study site by the resource selection coefficient for the habitat in pixel x divided by the mean resource selection coefficient for the entire landscape. We obtained parameters for the resource selection probability function from aerial transects flown during mid-winter across each study site; a detailed description of methodology is provided in Street et al. (2015) and Avgar et al. (2015). During winter survey flights, 2 observers searched for moose within a 500-m strip on either side of the aircraft. When observers located moose, the plane circled directly overhead and observers took a waypoint at the centroid of the circle. We matched each waypoint with a number of habitat variables and assessed selection by comparing used and non-overlapping unused locations uniformly sampled along the flight transects (Street et al. 2015). We multiplied probability of use by estimates of moose density obtained from winter aerial surveys conducted in each of the 2 study areas (Street et al. 2015) to derive a local estimate of moose density in each

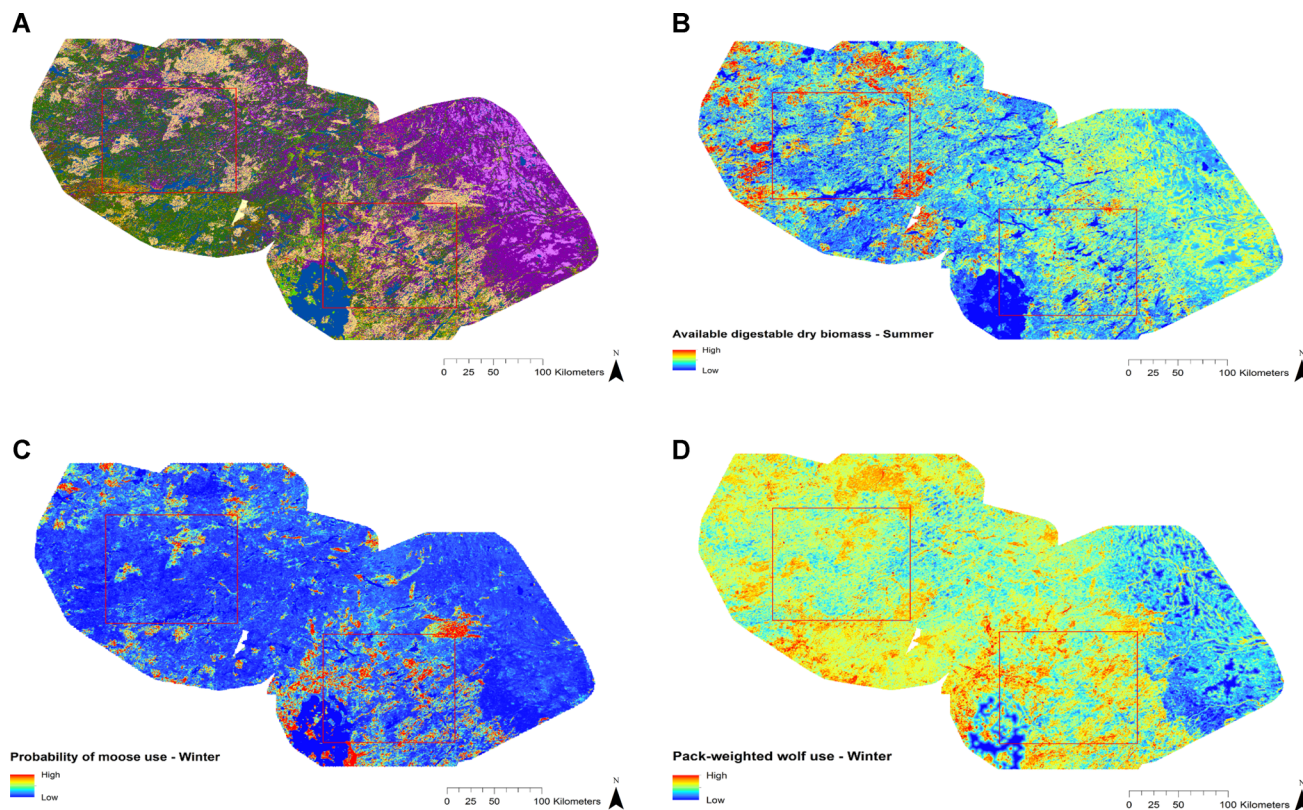


Figure 2. Estimated spatial distribution of critical habitat variables across a broad gradient in anthropogenic disturbance in northwestern Ontario, Canada, during 2010–2014. (A: land cover classes, B: food abundance, C: moose resource selection probability function, and D: wolf resource selection probability function). The commercially logged study site centered on the township of Nakina (SE corner of map) and the less disturbed study site centered on the township of Pickle Lake (NW corner) are shown in red, each with an area = 22,500 km².

hexagonal pixel ($\bar{x}$ moose density in Nakina = 0.046/km² and Pickle Lake = 0.024/km²).

Female woodland caribou from the Nakina and Pickle Lake study sites were equipped with GPS radio-collars ($n = 122$) during mid-winter 2010 and their fates monitored over the following 3 years, with capture methodology described in detail in Avgar et al. (2015) and McGreer et al. (2015). Animal captures and handling procedures were in accordance with approved animal care protocols for the Ontario Ministry of Natural Resources and Forestry (protocols 10-183, 11-183, 12-183, 13-183, and 14-183). When field teams received mortality signals, they recovered the radio-collar and assess if predation was the likely cause of death based on blood and tissue scattered widely, signs of struggle, presence and type of bone damage, and a disarticulated skeleton. We applied the nonparametric cumulative incidence function estimator method (Kalbfleisch and Prentice 1980, Heisey and Patterson 2006) to individual fate data to estimate the relative contributions of predation versus other sources of mortality for each study population.

We estimated local densities of gray wolves (W_x) from a combination of aerial counts of pack size and radio-telemetry of 49 individual wolves sampled from 34 packs widely distributed across the Pickle Lake and Nakina study landscapes; detailed methods are described in Kittle et al. (2015, 2017) and Avgar et al. (2015). We recorded GPS fixes every 5 hours and used the set of fixes over a 3-year period to estimate the Brownian bridge utilization distribution (Horne et al. 2007) for each individual. We multiplied normalized distributions by pack size to arrive at local estimates of wolf density. We then used these data to estimate wolf resource selection probability function models based on the same habitat metrics used for food availability and moose space use. Multiplication of resource selection probabilities by mean wolf density estimated across each of the study landscapes (Nakina $\bar{x} = 0.005/\text{km}^2$, Pickle Lake $\bar{x} = 0.003/\text{km}^2$) produced a spatially explicit estimate of wolf density in each hexagonal pixel.

Matrix-Based PVA Model

The matrix-based PVA model used population-wide estimates of annual survival of adult and yearling females (S) and successful offspring recruitment ($S \times B$, where B is birth rate of female offspring) in each study area to fill the elements of a Lefkovich matrix (L):

$$L = \begin{bmatrix} 0 & S_1 \times B_1 & S_a \times B_a \\ S_0 & 0 & 0 \\ 0 & S_1 & S_a \end{bmatrix},$$

where B_j = offspring recruitment rate stemming from age class j , and S_j = annual survival rate of age class j , where $j = 0, 1$, and a for new-born calves, yearlings, and adults. We used standard matrix algebra identities to estimate the asymptotic rate of population growth from the largest eigenvalue of the Lefkovich matrix (Fryxell et al. 2014).

Our field data were only sufficient to estimate site-specific vital rates for yearling and adult individuals because we did not radio-collar calves. We accordingly parameterized the

Lefkovich matrix model with pregnancy rates for yearling (43%) and 2-year-old individuals (90%) recorded by Parker (1981) from a field sample taken from the rapidly increasing George River herd of woodland caribou in Ungava-Labrador, Canada. We then set the survival rate of calves in the matrix model to 30% to yield an asymptotic yearling recruitment rate of 12% (the maximum ratio of female yearlings to reproductive-age females in social groups recorded during helicopter counts conducted in mid-winter). We used the same yearling recruitment rate for the individual-based PVA model, ensuring that it would have a similar mean level of productivity as the matrix model. We used the maximum eigenvalue of the Lefkovich matrix to estimate the asymptotic annual growth rate (λ ; Fryxell et al. 2014). For each of the 10,000 replicates, we incorporated demographic stochasticity through Monte Carlo simulation of survival and recruitment events drawn from a binomial distribution (Wisdom et al. 2000). Computer code used to estimate the stochastic matrix simulations is provided in Supporting Information.

Movement Trajectories from the Individual-Based Model

Our spatially explicit PVA model had 2 distinct components: the first phase was designed to simulate annual movement trajectories across an inputted landscape and the second phase predicted a demographic response (e.g., survived or died) for each for each individual, which was then scaled up to a population response (e.g., annual survival rate). Computer code for the movement and demography simulations is provided in Supporting Information.

In the first phase, we generated simulated movements by 1,000 adult female caribou across heterogeneous landscapes populated with 0.22-km² hexagons whose centroids were separated by 500 m from the nearest neighboring hexagons, based on movement parameters derived using the methodology described in Avgar et al. (2013) and Avgar et al. (2015). Geographic information system data clipped to each hexagon quantified local features of ecological importance, including local wolf density, moose density, food availability, roads, streams, and power lines superimposed on 29 land cover types from the Ontario Land Cover Database (Fig. 2A). This landscape remained constant across all simulations. The movement model incorporated perceived variation in resource quality and predation risk as exponentially decaying functions of distance from the current location, memory of past experiences at the same locations, and an overall background expectation of fitness based on the previous 365 days of movement experience. We used this movement model as a subroutine to simulate a set of 1,000 individual movement trajectories over 730 days, with each trajectory starting from the centroid of the study site. The last 365 days of the simulated trajectory were the only values used for the individual-based PVA model. Two years of simulation were nonetheless required so that simulated movements during the last 365 days would have the benefit of memory derived over the course of the previous year (Avgar et al. 2015). Facultative patterns of movement

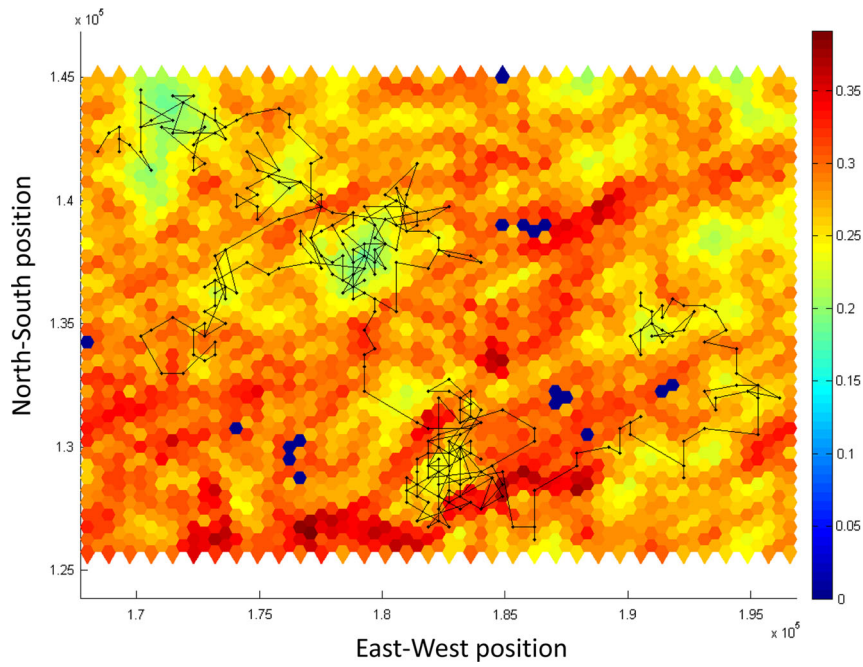


Figure 3. Simulated movement path by a woodland caribou individual in northwestern Ontario, Canada, in relation to wolf predation risk, based on the cognitive movement model of Avgar et al. (2015). The color bar indicates relative predation risk due to wolves.

derived from the model resulted in simulated individuals partially reducing their use of land cover types associated with pronounced risk of predation (Fig. 3).

We chose to simulate movement from first principles, rather than simply estimating probabilities of habitat use from caribou resource selection functions, because local composition and configuration of habitat have strong bearing on patterns of habitat selection by woodland caribou (McGreer et al. 2015), as typically observed in other resource selection studies (Beyer et al. 2010). Mechanistic movement modelling allowed us to estimate how variation in caribou fitness might be shaped by landscape configuration (Semeniuk et al. 2012, 2014). Assessment of the effect of such variation is a key feature of individual-based PVA models needed for application across multiple jurisdictions for which field data are missing or inadequate for one reason or another (Semeniuk et al. 2012, 2014).

Survival Prediction from the Individual-Based Model

In the second component of the individual-based PVA, we used the set of 1,000 simulated movement trajectories to provide a stochastic sample of vital rates that might arise because of different movement patterns experienced by different individuals. Each caribou alive at the beginning of each year in the simulated PVA time series was supplied with a movement path randomly drawn with replacement from the full set of 1,000 possible trajectories. We then calculated the subsequent fate of each individual based on the habitat characteristics experienced over each 5-hour interval over 365 days. Because individual location was updated in our movement simulation every 5 hours, the number of time steps per year ($j_{\max}$) in the PVA simulation was 1,752 ($365 \text{ days} \times 24 \text{ hours/day} \times 1 \text{ step/5 hours}$) and the time unit for each step of the model = $1/1,752 \text{ years} = 5 \text{ hours}$.

We combined local estimates of the probability that an individual yearling or adult caribou encounters a hunting wolf at each step along the simulated movement path with an estimate of risk of mortality due to other causes to estimate the probability of survival for each individual. We estimated the probability that a female caribou would be killed by wolves using a type-II multi-species functional response (Holling 1959):

$$p = \frac{a\bar{W}}{1 + ab_C\bar{C} + ab_M\bar{M}}, \quad (1)$$

where a = the area searched per year by wolves in km^2 , $\bar{W}$ = mean wolf density per km^2 averaged across the entire landscape, b_C = the time (in yrs) required by wolves to handle each caribou prey item encountered, $\bar{C}$ = mean woodland caribou population density per km^2 averaged across the entire landscape, b_M = the time (in yrs) required by wolves to handle each moose prey item encountered, and $\bar{M}$ = mean moose density per km^2 averaged across the entire landscape.

Messier's (1994) review of several moose-wolf studies throughout North America suggested that the maximum rate of consumption = 12.3 moose/wolf/year. In our formulation, the maximum rate of consumption = $1/b_m$, where $b_m = 1/12.3 = 0.081 \text{ years}$. Messier (1994) estimated that wolf consumption was half its maximum value at a moose density of $M = 0.47 \text{ individuals/km}^2$. The maximum rate of consumption in a Holling type II functional response = $1/b_m$, so algebraic rearrangement of the functional response formula yields an estimate of the area of search coefficient $a = 1/b_m M = 26.17 \text{ km}^2/\text{year}$. This value is similar to the value of $a = 33 \text{ km}^2/\text{year}$ used by Serrouya et al. (2015) for a

similar model of multi-species predation in boreal forest environments. In the absence of reliable parameter estimates for wolves feeding solely on woodland caribou in heavily forested boreal environments, we assumed that the rate of wolf encounter with caribou would be identical to that with moose if they occurred at a similar density. Given that moose outnumbered caribou, the wolf encounter rate with moose would be substantially higher than that of caribou, even though the *per capita* risk would be lower (Fryxell et al. 2014). The estimated handling time for each caribou (10 days) is a third of the time required to handle a moose (30 days) based on data recorded in subarctic Alaskan ranges (Dale et al. 1994: figure 2), similar to the handling time estimate from Serrouya et al. (2015) of 13 days.

Wolves are assumed to target moose, the predominant prey in our system, by hunting in particular land cover types in direct proportion to their attractiveness to moose, as reported by Kittle et al. (2015, 2017). Our boreal landscapes differed in the amount of anthropogenic disturbance they had experienced and consequently the amount and spatial distribution of early succession forest stands preferentially used by moose. We accordingly scaled the basic predation rate such that the probability of a predation event occurring during time step j was calculated by $p_j = pR_j/\bar{R}$, where R_j is the resource selection coefficient by moose for the land cover type occupied by a caribou individual at time step j (Fig. 4). Scaling the probability of predation events to behavioral preference through a coefficient is common practice in behavioral ecology (Fryxell and Lundberg 1998). Combining the rates of background mortality (μ) and predation (p_j), we calculated

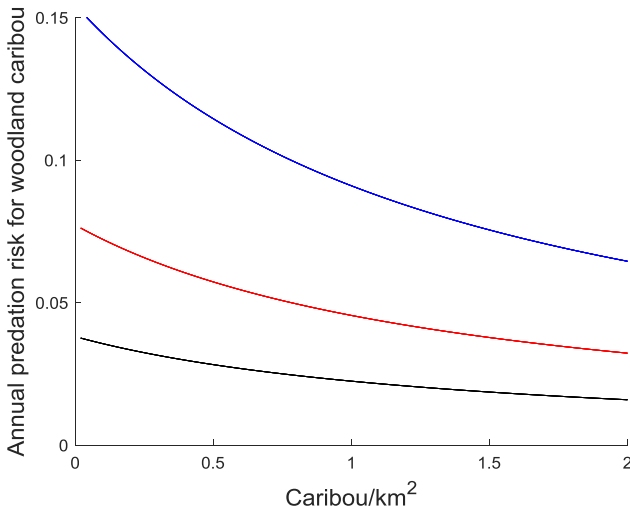


Figure 4. Estimated risk of predation for woodland caribou in Pickle Lake, Ontario, Canada during 2010–2014, in relation to caribou density and local moose density (M) relative to mean moose density ($\bar{M}$) across the entire landscape (black line: $M = \bar{M}/2$, red line: $M = \bar{M}$, blue line: $M = 2 \times \bar{M}$). Other parameters were constant for each curve ($a = 26.17$, $h_c = 0.028$, $h_m = 0.081$, $\bar{M} = 0.024$, $\bar{W} = 0.0031$), where a = the area searched per year by wolves in km^2 , h_c = the time (in yrs) required by wolves to handle each caribou prey item encountered, h_m = the time (in yrs) required by wolves to handle each moose prey item encountered, and $\bar{W}$ = mean wolf density per km^2 averaged across the entire landscape.

the probability of mortality for individual i during time step j according to the following formula:

$$m_{ij} = 1 - (1 - \mu - p_{ij})^{1/j_{\max}}. \quad (2)$$

We calculated the probability that individual i survives $j_{\max}$ sequential time steps over the course of the year according to the following formula:

$$s_i = \prod_{j=1}^{j_{\max}} 1 - m_{ij}. \quad (3)$$

We treated the fate of each simulated caribou individual i over the course of the year (ψ_i) as a binary state variable (valued 0 or 1), obtained by comparing the unique survival probability of that individual against a random number ranging between 0 and 1 (σ) drawn from a uniform distribution:

$$\psi_i = \begin{cases} 0 & \text{if } \sigma_i > s_i \\ 1 & \text{if } \sigma_i \leq s_i \end{cases}. \quad (4)$$

Recruitment Prediction from the Individual-Based Model

For each simulated individual that survived the year, we scaled the *per capita* recruitment of yearlings (y) to the average level of food availability experienced by a given individual over the course of the year (F_i) relative to food availability averaged across the entire study area (F):

$$y_i = y_{\max} F_i / F, \quad (5)$$

where $y_{\max}$ represents the *per capita* rate of recruitment of yearlings under excellent environmental conditions (12% based on the max. yearling/female ratio recorded from helicopter counts in mid-winter). The yearling recruitment rate we used is similar to the exponential rate of increase (0.11) recorded for the George River woodland caribou herd in Canada as it recovered from a population crash in the mid-1900s (Messier et al. 1988), but it is lower than exponential rates of increase ($\bar{x} = 0.25$) recorded for barren-ground caribou (*Rangifer tarandus groenlandicus*) herds re-introduced onto Arctic islands and lower still than the theoretical maximum of 0.31 that would occur if there was 100% pregnancy of each female ≥ 1 year of age and no mortality (Heard 1990). We then obtained the reproductive fate of each agent (ω_i) by comparing the probability of successful recruitment against a random number ranging between 0 and 1 (ζ) drawn from a uniform distribution:

$$\omega_i = \begin{cases} 0 & \text{if } \zeta_i > y_i \text{ or } \psi_i = 0 \\ 1 & \text{if } \zeta_i \leq y_i \text{ and } \psi_i = 1 \end{cases}. \quad (6)$$

This procedure allowed us to evaluate the effect of demographic stochasticity stemming from spatial variation in forage availability through its effect on the probability of offspring recruitment and spatial variation in predation risk through its effect on the probability of survival by each individual in the population.

By depicting stochastic survival and offspring recruitment events in this manner, the simulated abundance of woodland caribou would be expected to vary stochastically across different replicates, with a population increase occurring during Monte Carlo replicates in which individual trajectories led many animals by chance to visit many food-rich patches and few predation-risky patches and decline in simulation runs in which the opposite occurred:

$$N_{t+1} = \sum_{i=1}^{N_t} \psi_i + \omega_i. \quad (7)$$

Hence, our spatially explicit PVA model translated spatial heterogeneity in food availability and predation risk into demographic stochasticity mediated by the paths followed by individuals across the landscape. We ran each of the 10,000 replicates of the spatially explicit PVA for a population of 200 yearling and adult caribou in each of the study areas for a single year and used these 10,000 replicates to estimate the distribution of annual growth rates ($\lambda_t = N_{t+1}/N_t$) one might expect from logged versus unlogged boreal landscapes. We chose a caribou population of 200 for our simulations to be roughly consistent with averaged field estimates of minimum number alive ($\bar{x} = 172$ in Nakina vs. $\bar{x} = 332$ in Pickle Lake) obtained from aerial surveys in our study areas conducted during 2008–2013.

RESULTS

Survival rates of radio-collared females differed between subpopulations ($t = 2.90$, $P = 0.022$), with caribou living in the commercially logged landscape at Nakina exhibiting an average annual survival rate of 0.76 ± 0.034 (SE) compared with an annual survival rate of 0.90 ± 0.032 across the much less disturbed landscape in Pickle Lake (Table 1). This difference in average survival rates across landscapes was echoed by estimates for each year of field study. In each landscape, most recorded mortality events were due to predation (Fig. 5), with the annual risk of predation mortality averaging 14% in the logged Nakina landscape and 7% in the unlogged Pickle Lake landscape. Black bear predation of

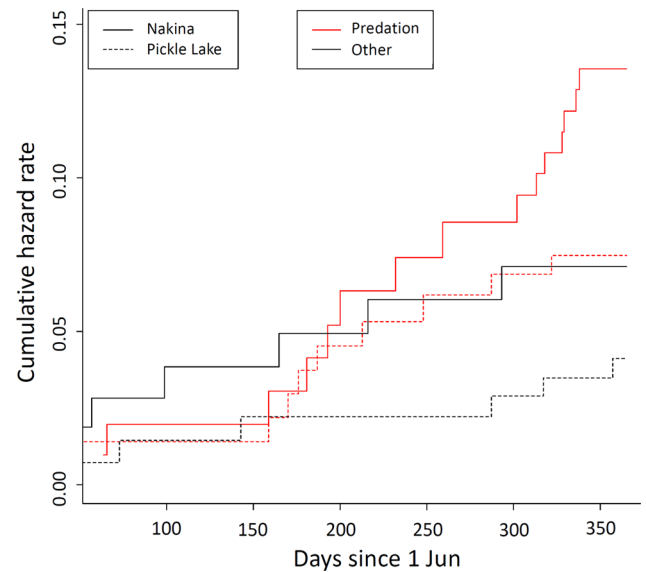


Figure 5. Cumulative probability of mortality during 2010–2014 of 122 woodland caribou due to predation and other sources of mortality in the control (Pickle Lake) and disturbed (Nakina) study sites, Ontario, Canada. We estimated probability of mortality for each cause of death using the nonparametric cumulative incidence function estimator approach (Heisey and Patterson 2006). We modeled cause-specific hazards using an annual 365-day time scale (i.e., a recurrent time scale; Fieberg and DelGiudice 2009), with time = 1 set to 1 June, to represent the start of the biological year for caribou.

adult caribou was much less important than wolf predation in both of our study sites. Of 25 predation-related deaths recorded in Pickle Lake and Nakina, 22 were probable wolf kills and only 3 were probable bear kills (2 in Nakina vs. 1 in Pickle Lake).

Although there was substantial overlap in the distributions of survival predicted by the individual-based model for Pickle Lake and Nakina (Fig. 6; $P[\text{overlap}] = 0.81$), the mean probability of adult survival in Pickle Lake ($\bar{x} = 0.88$) was 9% higher than that for Nakina ($\bar{x} = 0.79$). Adult survival rates predicted by the individual-based model were consistent with field estimates in both Pickle Lake ($\bar{x} = 0.90 \pm 0.032$, $t = 0.63$, $P = 0.53$) and Nakina ($\bar{x} = 0.76 \pm 0.034$, $t = 1.00$, $P = 0.32$).

The stochastic matrix PVA model constructed from observed vital rates in the field indicated that the asymptotic rate of population change in Pickle Lake ($\bar{x} = 1.01$, $SD = 0.022$, $n = 10,000$) was considerably higher than that in the logged landscape in Nakina ($\bar{x} = 0.88$, $SD = 0.031$, $n = 10,000$). Based on the distribution of values of λ projected from the stochastic matrix (Fig. 7), there was negligible probability that the annual growth rate in Nakina would be sustainable ($P[\lambda > 1] < 0.001$), whereas the estimated growth rate in Pickle Lake would be more likely to be sustainable ($P[\lambda > 1] = 0.67$), albeit with an appreciable residual risk of decline ($P[\lambda < 1] = 0.33$).

Output from the individual-based PVA model predicted that the average rate of population increase in the commercially logged Nakina landscape would be 0.89, suggesting that there is substantial risk of population collapse ($P[\lambda > 1] < 0.001$) if vital rates do not improve (Fig. 7). Output from

Table 1. Survival data for radio-collared female woodland caribou from the commercially logged (Nakina) and less disturbed (Pickle Lake) landscapes, Ontario, Canada, 2010–2014. We present the minimum number of individuals at risk for a given mortality event per year (min. number at risk/event) and the number of individuals (n) that entered into the risk set per year.

Year	$\bar{x}$	SE	95% CI	Min. number at risk/event	n
Nakina					
2010–2011	0.74	0.17	0.47–1.00	5	49
2011–2012	0.83	0.06	0.72–0.95	33	56
2012–2013	0.73	0.08	0.60–0.90	24	44
2013–2014	0.64	0.19	0.36–1.00	5	22
$\bar{x}$	0.76	0.03	0.69–0.83		
Pickle Lake					
2010–2011	0.96	0.03	0.90–1.00	45	53
2011–2012	0.87	0.05	0.77–0.97	38	56
2012–2013	0.86	0.06	0.75–0.98	27	41
$\bar{x}$	0.90	0.03	0.83–0.96		

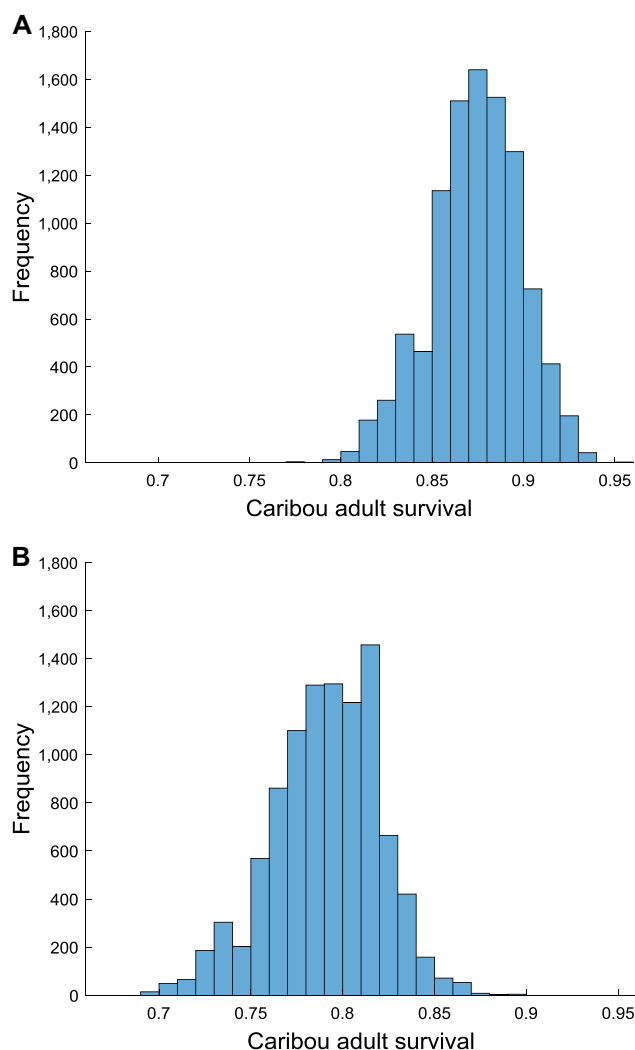


Figure 6. Stochastic variation in annual probability of survival during 2010–2014 by woodland caribou based on field data for the individual-based population viability assessment model simulated 10,000 times for 2 landscapes in northern Ontario, Canada: the unlogged landscape at Pickle Lake (A) and the commercially logged landscape at Nakina (B).

the individual-based PVA model indicated that populations of woodland caribou in the unlogged boreal landscape of Pickle Lake would have an average annual growth rate of 0.98 (Fig. 7). As a result, although reduction risk of wolf predation due to changes in land cover composition was associated with substantial improvement in the probability of population viability ($P(\lambda > 1) = 0.29$), there would still be appreciable risk of decline ($P(\lambda < 1) = 0.71$).

The simulated variance in λ for the stochastic matrix model was lower than that of the individual-based model for both Pickle Lake ($F = 2.39$, $P \leq 0.001$) and Nakina ($F = 1.52$, $P \leq 0.001$) because stochastic variation in individual risk induced by differential movement patterns across a heterogeneous landscape would inevitably lead to increased variability in population growth rates beyond the level expected if all individuals had equal probability of mortality. This can be readily demonstrated by substituting the mean and variance in both adult survival and offspring recruitment derived from the individual-based model into

the stochastic matrix model. This resulted in increased variance in estimated λ (Nakina: $SD = 0.035$; Pickle Lake: $SD = 0.030$) relative to the values estimated on the basis of a simple binomial distribution. The fact that the variance in the fitted version of the stochastic matrix did not match the individual-based PVA likely stems from the fact that there is additional covariation in the landscape features controlling survival and recruitment, so these demographic parameters are not independent.

Application of the individual-based PVA model to 14 management jurisdictions (Fig. 8) across Ontario indicated that caribou in 7 ranges (James Bay, Kinloch, Missisa, Ozhiski, Spirit, Sydney, and Swan) had annual rates of growth exceeding 0.96. Although there is no evidence they are thriving, they are not severely threatened with imminent collapse under current conditions. These more northerly ranges have not experienced appreciable levels of commercial forestry, although they are all subject to natural sources of landscape disturbance, such as insect outbreaks, windthrow, or fire. On the other hand, all 7 of southern ranges were estimated to have annual rates of growth (λ) < 0.89 , suggesting that these more southerly ranges are considerably less capable of sustaining viable populations of woodland caribou under current conditions (Table 2). Not surprisingly, given the structure of the prediction model, mean population growth rates estimated by the individual-based PVA were strongly related to average wolf densities across caribou ranges (Fig. 9; $F_{1,12} = 1,047$, $P < 0.001$, $R^2 = 0.99$).

DISCUSSION

Our field results suggest that increased wolf density in the study site that had received substantial commercial forestry activity was associated with reduced adult survival rates of woodland caribou, as predicted by the individual-based model. We specifically chose our study landscapes because they straddle a pronounced gradient in anthropogenic disturbance primarily caused by commercial logging. About a third of the Nakina site was logged 30–50 years ago, resulting in a higher proportion of mixed forest stands and a dense network of remnant logging roads compared to the Pickle Lake landscape. Given their spatial proximity, we presumed major differences between landscapes had arisen from their divergent disturbance histories. The logged landscape (Nakina) had a larger fraction of mixed and deciduous stands than the unlogged Pickle Lake landscape (Mallon et al. 2016), much higher road density (Kittle et al. 2015), higher density of moose (Street et al. 2015), and higher population density of wolves (Kittle et al. 2017). We conjecture that all of these features probably contribute to some degree to increased predation risk because movement trajectories of caribou in our system were shaped by spatial variation in projected moose density, wolf density, and food abundance (Avgar et al. 2015).

One of the key goals of movement ecology is to clarify how patterns of space use by mobile organisms as they traverse heterogeneous landscapes influences demographic parameters, behavioral interactions within and among species, and population dynamics (Morales et al. 2010, Owen-Smith

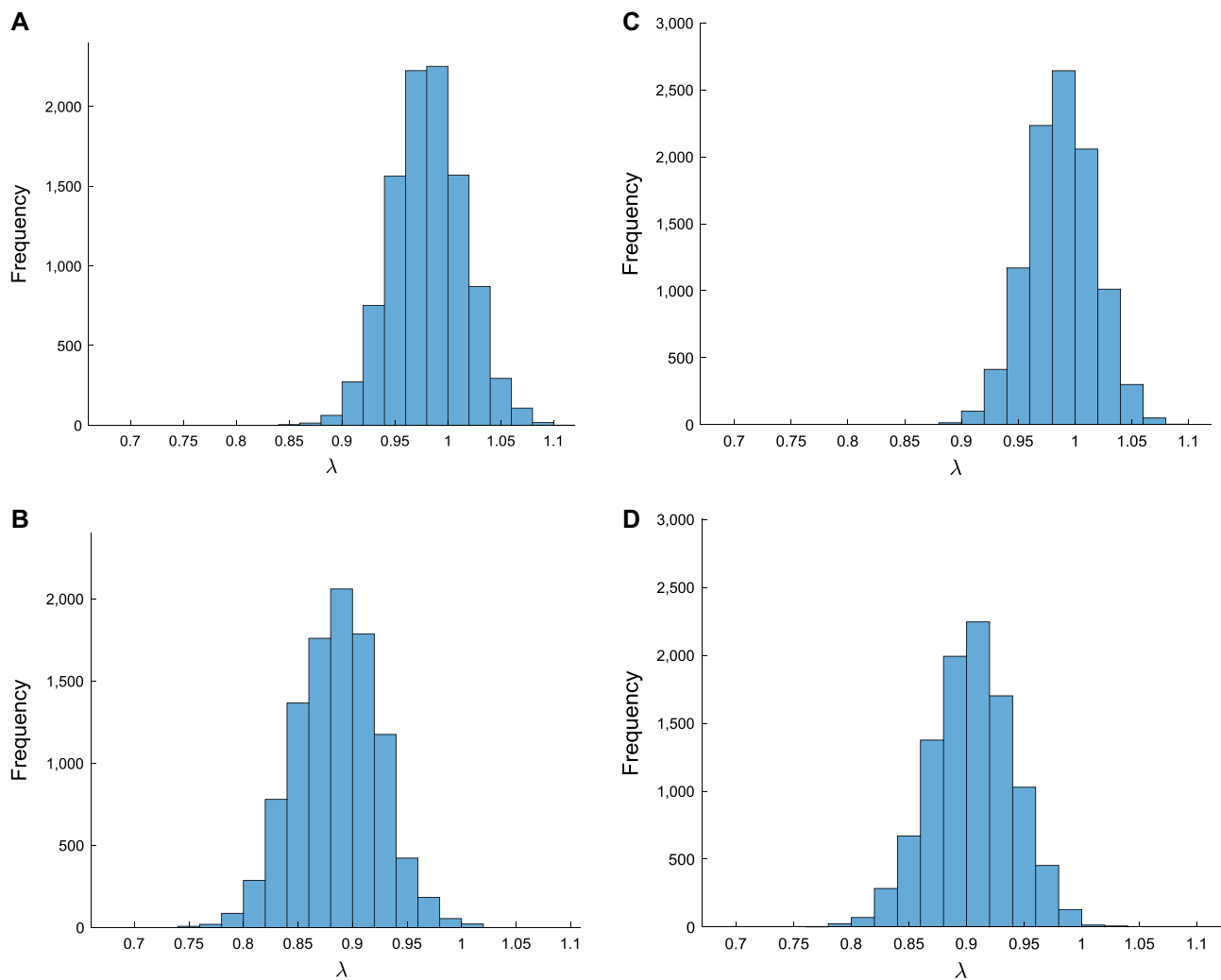


Figure 7. Stochastic variation in annual growth rate (λ) during 2010–2014 by woodland caribou based on field data, Ontario, Canada, estimated using the individual-based population viability assessment model for the unlogged landscape at Pickle Lake (A) and the commercially logged landscape at Nakina (B) and using the matrix model for the unlogged landscape at Pickle Lake (C) and the commercially logged landscape at Nakina (D).

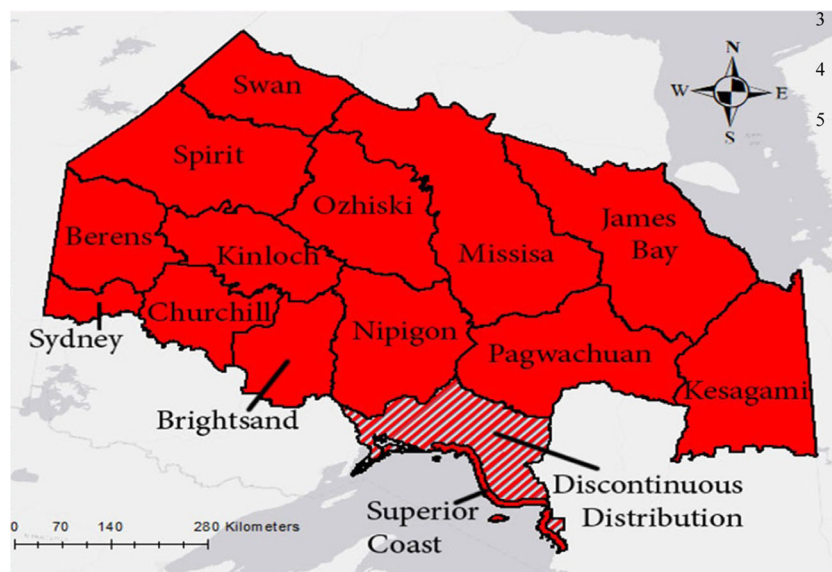


Figure 8. Woodland caribou ranges in Ontario, Canada, 2018.

Table 2. Mean and standard deviation of 10,000 annual growth rate (λ) values estimated using the spatially explicit population viability assessment model for 14 woodland caribou ranges in Ontario, Canada, 2010–2014.

Range	$\bar{x}$	SD	$P(\lambda > 1)$
Berens	0.835	0.0419	<0.001
Brightsand	0.850	0.0406	<0.001
Churchill	0.837	0.0406	<0.001
Discontinuous	0.769	0.0431	<0.001
James Bay	0.964	0.0351	0.161
Kesagami	0.887	0.0378	0.002
Kinloch	0.958	0.0349	0.122
Missisa	0.971	0.0343	0.216
Nipigon	0.846	0.0400	<0.001
Ozhiski	0.965	0.0347	0.179
Pagwachuan	0.885	0.0382	0.001
Spirit	0.966	0.0346	0.179
Swan	0.966	0.0341	0.177
Sydney	0.964	0.0348	0.169

et al. 2010). Although clearly of central importance to this rapidly growing field, examples of successful application of movement modeling at the individual level to understand population dynamics at a higher level of biological organization are rare (Morales et al. 2010, Matthiopoulos et al. 2015). This is a matter of considerable practical concern because many conservation issues hinge on the role of habitat fragmentation, habitat loss, and their manifold effect on organismal fitness (Andren 1994, Fahrig 2003). Without a clear understanding of how organisms respond to patterns of habitat transformation, loss, or fragmentation across broad landscapes and their effectiveness in minimizing environmental hazards, identification of useful conservation measures for remediation will no doubt prove to be elusive.

Our model suggested that adaptive decision-making by individual caribou, demonstrated in the earlier analyses of McGreer et al. (2015), Avgar et al. (2015), and Viejou et al. (2018), was insufficient to completely compensate for fundamental differences in fitness across sites. A similar pattern

was suggested by DeCesare et al. (2014) in their analysis of spatial risk of woodland caribou in British Columbia relative to patterns of habitat selection. Despite the demonstrated capacity by woodland caribou for adaptive movement, vital rates in our study sites differed to a demonstrable degree between sub-populations. This was particularly the case for annual survival rates, which varied considerably between the heavily disturbed Nakina and less disturbed Pickle Lake landscapes.

Both the individual-based PVA and stochastic Lefkovich matrix outcomes predicted that woodland caribou in the landscape recovering from commercial forestry operations several decades ago would have asymptotic population growth rates well below the level required for persistence ($\lambda < 1$), whereas caribou in the part of the landscape not yet exposed to commercial forestry show less evidence of rapid declining (i.e., λ not significantly different from 1). Without further information on population trend, it is impossible to tell whether this means that caribou in the unlogged landscape (Pickle Lake) were thriving and close to their carrying capacity or whether caribou in this less disturbed landscape were in much more gradual decline. Regardless, caribou in the more disturbed landscape were faring considerably worse, based on the individual-based PVA and matrix projection models. Similarity in the outcomes from the matrix and individual-based models suggest that both modeling approaches offer a useful perspective for understanding potential threats to woodland caribou populations.

Efforts to develop a sound conservation strategy for woodland caribou in Ontario have been hampered by a lack of validated diagnostic tools to predict which caribou herds are under greatest threat (Ministry of Natural Resources and Forestry 2014) and a lack of rigorous evaluation of the relative effectiveness of alternative policy options for remediation (Serrouya et al. 2017, 2019). Viability assessment of woodland caribou in Ontario ranges on the basis of critical thresholds for cumulative disturbance (Environment Canada 2012) has identified several southern ranges as being at significant risk of decline (Berens, Brightsand, Kesagami). Our model outcomes corroborate this assessment by Environment Canada (2012) but also identified several other ranges that have similarly high probability of decline (Churchill, Discontinuous, Nipigon ranges). Both perspectives suggest that high levels of anthropogenic disturbance may be incompatible with long-term viability of woodland caribou in Ontario. The most secure conservation measure would be to set aside extensive tracts of boreal forest with natural patterns of disturbance to sustain viable caribou sub-populations (Ministry of Natural Resources and Forestry 2014). In areas where such conservation measures are impractical for social, economic, or historical reasons, there is urgent need to identify effective alternative solutions.

The most obvious short-term strategy to counter this worrisome situation would be through reduction in wolf density. This could be achieved via many different management options, including direct culls, incentives for additional wolf harvest by licensed trappers, increased harvest

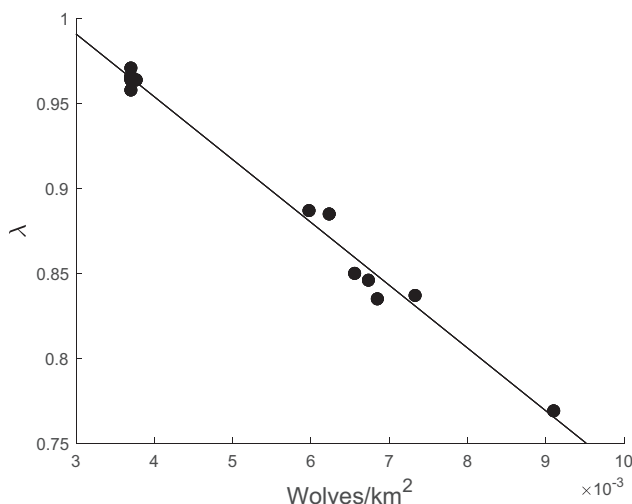


Figure 9. Mean annual growth rate (λ) by woodland caribou based on field data recorded during 2010–2014 in relation to wolves/km² for 14 woodland caribou ranges in Ontario, Canada, estimated using the individual-based population viability assessment model.

of moose combined with wolf control, or habitat modification to discourage moose and wolf occurrence. As a first step towards identifying the potential effectiveness of reducing wolf or moose abundance as a management step, we re-ran our individual-based model for the Nakina landscape and substituted moose and wolf abundance with the levels recorded in the unlogged Pickle Lake site. The individual-based PVA model suggests that reducing wolf abundance in Nakina to the level seen in the unlogged Pickle Lake landscape would improve caribou annual growth rates in the short term from 0.884 to 0.947 (Fig. 10). Reducing wolf and moose abundance to levels recorded in Pickle Lake would produce little additional benefit (Fig. 10).

Our conclusions reinforce a growing consensus that predation is the most pressing demographic challenge facing woodland caribou in Canada living in boreal landscapes (Festa-Bianchet et al. 2011; Serrouya et al. 2017, 2019). Before the arrival of Europeans, woodland caribou in boreal ecosystems lived in landscapes dominated by fire as the primary form of disturbance (Bergerud 1974). The resulting mosaic of forest stands of varying age created ample opportunity for caribou to space themselves out from gray wolves and black bears, their primary predators (Bergerud 1974; Seip 1992; Courbin et al. 2009, 2014), by migrating among patches of muskeg for calving and mature upland coniferous forest during other periods of the year. The same logic suggests that predators would be maintained at low densities because of limited prey availability.

In more recent times, however, commercial logging has displaced fire as the dominant form of landscape disturbance in boreal ecosystems, with cascading consequences of crucial importance to caribou. Many boreal forests regenerating from commercial logging have a large fraction of stands at an early seral stage, in many cases dominated by broadleaf deciduous shrub species and poplars and aspen. Such early

successional stands are favored by moose and white-tailed deer, supporting both species at much higher densities than is typical of unlogged forests (Rettie and Messier 1998; Fisher and Wilkinson 2005; Courbin et al. 2009, 2014; Bowman et al. 2010). Although white-tailed deer were not an important contributor to apparent competition in our study area, rapid northward expansion of deer populations, such as that seen in Alberta, Canada (Latham et al. 2011a, b), is to be expected. With an increased prey base, wolf densities are typically higher in disturbed landscapes than those that have had little recent disturbance (Bergerud 1974; Kittle et al. 2015; Serrouya et al. 2015, 2017, 2019), with resultant increases in mortality risk for caribou. As a territorial species, however, density-dependent responses by wolves might be expected to eventually cap their demographic response to superabundant prey.

The size distribution of harvested forest stands often differs considerably from that in fire-dominated systems (Perera et al. 2004, Fisher and Wilkinson 2005), bringing caribou into more frequent contact with wolves as they travel across highly fragmented landscapes (Courbin et al. 2009, 2014; Fortin et al. 2013, 2017), despite the preference of woodland caribou for habitats infrequently used by moose, deer, or wolves (Courtois et al. 2008, Fortin et al. 2008, Avgar et al. 2015, McGreer et al. 2015). Unlike fire-dominated systems, commercial logging often leaves highly reticulated networks of roads, which are heavily used by wolves as they travel across their communal territories (James and Stuart-Smith 2000, Kittle et al. 2017, Newton et al. 2017) and sometimes bringing them into higher than expected proximity to caribou despite their road avoidance (Fortin et al. 2013).

There are a number of ways that our individual-based model could be improved. Delayed onset of reproduction in some caribou herds can substantially reduce population growth rates (DeCesare et al. 2012). Hence, the simplified transition matrix (3 stages to represent a long-lived ungulate species) we have employed could well overestimate asymptotic values of λ if significant numbers of females delay the onset of reproduction beyond their second year of life. In the absence of more detailed age-specific estimates of vital rates, there is no obvious remedy and this remains a potentially important source of uncertainty in our growth rate projections. We currently have no reliable field estimates of offspring survival or yearling recruitment, so our projections of population growth rate are hampered accordingly. Setting calf recruitment to the maximum level recorded during the study (12%) was also an optimistic choice.

We also cannot be sure that our estimate of background mortality of adults is not influenced by food availability, although we feel confident that by visiting carcasses as soon as possible after death that we correctly identified predation events. We chose to incorporate a simple type-II multi-species functional response largely because there is no empirical evidence that wolves make more complex decisions around diet breadth and time series data on variation in caribou predation risk with respect to changes in caribou and moose density is rudimentary at best in all jurisdictions. At low population

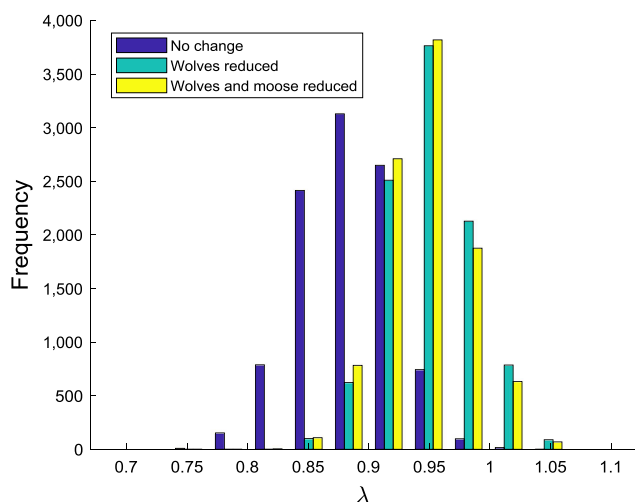


Figure 10. Stochastic variation in annual growth rate (λ) by woodland caribou based on field data using the individual-based population viability assessment model simulated 10,000 times across the commercially logged landscape at Nakina but assuming that wolf abundance or both wolf and moose abundance have been reduced to levels seen in the unlogged landscape at Pickle Lake, Ontario, Canada, 2010–2014.

densities, Allee effects due to challenges in locating suitable mates or through compensatory effects on hunting efficiency could well occur (McLellan et al. 2010).

Our model also does not allow assessment of the effect of black bear predation. Although field evidence from our study sites indicated that bear predation on adult caribou was relatively uncommon, studies in other landscapes have demonstrated substantial effects of bear predation on recruitment of young caribou (Latham et al. 2011a,b; Rayl et al. 2015; Leblond et al. 2016). Spatially explicit assessment of bear predation is undoubtedly an important feature to build into future generations of our spatially explicit PVA model. It would probably require massive field effort in its own right, hence was simply not possible in the current study.

It would also be useful to clarify how patterns of understory plant recruitment vary across forest stand types following disturbance and how future patterns of climate change will influence successional pathways in understory plants and the effect of future climate change on moose populations. Such information, coupled with realistic scenarios for landscape disturbance due to both natural and anthropogenic causes, would be needed to reliably assess long-term prospects for persistence of woodland caribou populations. In the meantime, our approach to incorporating spatial processes into estimates of population growth rates provides a useful starting point for discussing the utility of alternative management scenarios.

Many of these model details could lead to further reductions in projected growth rates by woodland caribou. As dire as our model predictions might be, it is accordingly conceivable that we may actually represent an overly optimistic view of population viability of woodland caribou across Ontario. In spite of these limitations, our work suggests that individual-based, spatially explicit PVA modeling provides a useful tool to address these challenges. Because spatial variation in food availability and predation risk in our model are linked with land classes in provincial databases and broad gradients in wolf and moose abundance are well established across the province, we have shown that it is possible to simulate patterns of movement, vital rates, and long-term viability of caribou in any boreal landscape in Ontario. Spatially explicit PVA models such as ours offer a potentially useful engine for conducting thought experiments to evaluate alternative conservation or management measures (Lindenmayer et al. 2000, McCarthy et al. 2000). In the case of woodland caribou, a short list of possible conservation candidates might include changes in cut rotation, road decommissioning, predator control, and moose and deer harvest enhancement. As an example of this approach, we altered parameter values in our model to demonstrate that reduction of wolf abundance may be useful in preventing rapid decline in woodland caribou numbers in a heavily disturbed landscape. Given the enormous cost of such policy changes, complex ethical and societal concerns, and logistical difficulty in modifying ecological interactions across vast boreal landscapes, such thought experiments represent a useful intermediate step to evaluate the cost-effectiveness of possible changes to landscape management practices.

Balanced against this intriguing potential, spatially explicit models are particularly data hungry, demanding enormous amounts of time and energy to estimate variation in fitness variables across space (Reed et al. 2002). Moreover, any such model is plagued by fundamental concerns about the accuracy and precision of vital rate estimates and meaningful assessment of their long-term variability in systems subject to stochastic environmental variation and long-term changes in underlying climatic and biotic variables (Coulson et al. 2001, Reed et al. 2002). We nonetheless submit that there can be appreciable benefits in understanding and improved efficiency in evaluating alternate conservation plans provided by an explicitly spatial perspective on fitness variables that is well justifiable when the conservation and societal concerns are as complex as those currently facing woodland caribou in Canada (Festa-Bianchet et al. 2011).

MANAGEMENT IMPLICATIONS

Habitat management combined with wildlife harvest policies to discourage high densities of moose and wolves are essential components of a robust long-term plan for conservation of boreal woodland caribou in Ontario. This calls for the development of new tools to fully assess the social, economic, and conservation implications of alternative management plans. Such plans might include a wide range of options, including population control in the short term combined with longer-term enhancement of protected area networks, long-term cutting rotation, and perhaps even triage assessment if population viability for woodland caribou is not achievable any other way. In assessing any of these options, computer simulations like those presented here can be invaluable in assisting informed discussion among stakeholders with divergent points of view.

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