Research Article

Modeling Cumulative Effects of Climate and Development on Moose, Wolf, and Caribou Populations

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ABSTRACT Wildlife models focused solely on a single strong influence (e.g., habitat components, wildlife harvest) are limited in their ability to detect key mechanisms influencing population change. Instead, we propose integrated modeling in the context of cumulative effects assessment using multispecies population dynamics models linked to landscape-climate simulation at large spatial and temporal scales. We developed an integrated landscape and population simulation model using ALCES Online as the model-building platform, and the model accounted for key ecological components and relationships among moose (*Alces alces*), grey wolves (*Canis lupus nubilus*), and woodland caribou (*Rangifer tarandus caribou*) in northern Ontario, Canada. We simulated multiple scenarios over 5 decades (beginning 2020) to explore sensitivity to climate change and land use and assessed effects at multiple scales. The magnitude of effect and the relative importance of key factors (climate change, roads, and habitat) differed depending on the scale of assessment. Across the full extent of the study area (654,311 km^2 [ecozonal scale]), the caribou population declined by 26% largely because of climate change and associated predator-prey response, which led to caribou range recession in the southern part of the study area. At the caribou range scale (108,378 km^2), which focused on 2 herds in the northern part of the study area, climate change led to a 10% decline in the population and development led to an additional 7% decline. At the project scale (8,331 km^2), which was focused more narrowly on the landscape surrounding 4 proposed mines, the caribou population declined by 29% largely in response to simulated development. Given that observed caribou population dynamics were sensitive to the cumulative effects of climate change, land use, interspecific interactions, and scale, insights from the analysis might not emerge under a less complex model. Our integrated modeling framework provides valuable support for broader regional assessments, including estimation of risk to caribou and Indigenous food security, and for developing and evaluating potential caribou recovery strategies. © 2021 The Wildlife Society.

KEY WORDS caribou, cumulative effects assessment, landscape simulation, moose, population dynamics, regional assessment, wolf.

Wildlife conservation management in pursuit of a population objective is a complex endeavor because of the numerous mechanisms by which a population can change. A

diversity of land uses and ecological processes operating through space and time can affect a population through changes to habitat, fecundity, mortality, and dispersal. The potential list of influencing factors (i.e., stressors) is long, and includes extractive resource development (e.g., forestry, mining, energy, agriculture), human settlement and transportation networks, utility lines, recreational activities, wildlife harvest, natural disturbance, and climate change. The effect can be direct, as in the case of degradation of habitat, or indirect, as in the case of changes to interspecific

interactions like predation. Because of the diversity of potential influencing factors and mechanisms, wildlife management typically considers cumulative effects where small but numerous incremental effects can accumulate through space and time to cause major change (Theobald et al. 1997). In the absence of a small number of well-delineated influencing factors, effects on wildlife populations can be difficult to detect, anticipate, and mitigate.

Given the complex and multifaceted nature of wildlife conservation, managers and researchers often focus on a portion of the overall system that is directing population response. Some level of abstraction is needed to avoid paralysis in the face of an overwhelming set of information needs and management options. The risk, however, is that over-simplification can obscure important influences and result in ineffective or at least inefficient allocation of finite management and monitoring efforts. A common simplification is to focus on habitat metrics, such as resource selection functions and habitat suitability indices, or habitat disturbance thresholds (Environment and Climate Change Canada [ECCC] 2011, 2012). Although assessing changes to habitat is an important component of wildlife management, it does not on its own provide direct evidence of wildlife abundance (Johnson and Seip 2008) and, by omitting estimation of fecundity or mortality rates, a singular focus on changes to habitat is ill-equipped to address issues such as population sinks (Falcucci et al. 2009). A related simplification that has also been identified by others as problematic is an inadequate consideration of indirect effects such as interspecific interactions (Johnson et al. 2005, 2019). Alternatively, wildlife managers may focus on managing mortality sources (e.g., hunting) without comprehensively considering habitat dynamics. Habitat alteration and mortality can affect populations additively (Symes et al. 2018) or even synergistically (Mora et al. 2007); thus, focusing on habitat or mortality in isolation can result in an underestimation of risk.

Limiting the spatial and temporal scope of assessment is also problematic, given that factors such as climate change and land use operate across large spatial and temporal scales (Gedir et al. 2015, Kimiti et al. 2018). Insufficient consideration of the full range of factors affecting wildlife populations is consistent with the tendency of natural resource management to inadequately address cumulative effects (Noble 2014). Although cumulative effects are now recognized as a problem, they have proven difficult to manage in large part because of a fragmented regulatory process (i.e., environmental assessment) that emphasizes local-scale project applications (e.g., for roads, mines, well sites) at the expense of comprehensive assessment of regional effects, which may include multiple related developments (Kennett 1999, Duinker and Greig 2006, Noble 2015). Similarly, wildlife management tends to compartmentalize planning through separate processes for habitat supply and quality (e.g., forest management planning) and mortality factors (e.g., hunting regulations), and by focusing on small spatial extents such as wildlife management units. Knowledge to support management can also be fragmented

because of a paucity of research and monitoring at large spatial and temporal scales (Council of Canadian Academies 2019). Maintaining the integrity of ecosystems, including wildlife populations, in the face of complex influencing factors requires integrated approaches at broad spatiotemporal scales that can address cumulative effects.

Strategies for increased integration include coordination of research and monitoring to support interdisciplinary knowledge at larger scales and, perhaps most importantly, a shift in emphasis from project-level to regional decision-making (Council of Canadian Academies 2019). Project-level assessments focus on effects in the local vicinity of the proposed development over limited time spans, whereas regional assessments provide the spatial and temporal scope required to carefully consider land uses, climate change, and ecological processes, all of which typically operate at broad scales. Insights from regional assessment can then provide direction to local decision-making in support of coordinated strategies that address cumulative effects (Elk Valley Cumulative Effects Management Framework Working Group 2018). The importance of regional approaches to environmental assessment is supported conceptually by governments across Canada, as evidenced by the call from the Canadian Council of Ministers of the Environment (2009) for regional cumulative effects assessments that are integrated, interdisciplinary, and strategic. Although regional assessments have been slow to materialize in practice, the legislated base for strategic and regional assessment that is provided by Canada's recent Impact Assessment Act (Bill C-69) is evidence that the shift is occurring (Doelle 2018). A decision to require a regional assessment for the Ring of Fire area has recently been made by the federal government (ECCC 2021), and discussions concerning terms of reference for involvement of the Provincial government are in progress.

To realize the benefits of integrated and regional management approaches, knowledge must be applied in a way that is inclusive with respect to scale and objectives, comprehensive with respect to the suite of factors that are assessed, and adaptive by fostering ongoing learning (Council of Canadian Academies 2019). For wildlife management, this requires decision support tools with enough complexity to assess the response of wildlife populations to a diverse set of factors at large spatial and temporal scales. Models are needed that can support integrated assessment of wildlife populations through simulation of landscape dynamics in response to land use changes and natural disturbances; population dynamics in response to changing landscapes and land use through processes such as habitat selection, fecundity, and mortality; and interspecific interactions in multispecies systems. The benefit of such models is that they provide wildlife managers with capacity to comprehensively assess risks and compare the consequences of management options. The challenge of such models is that they can be difficult to prepare because of their complexity and the range of information that is needed for model parameterization. Advances in computer applications and processing are improving the feasibility of comprehensive

modeling, and the modeling process will help address information needs by identifying knowledge gaps that should be targeted by monitoring and research.

The conservation of boreal woodland caribou (*Rangifer tarandus caribou*) in northern Ontario, Canada, is illustrative of the complexity encountered in wildlife management. The woodland caribou is a threatened species in Ontario whose range has declined by approximately 50% relative to historical levels (Schaefer 2003) in response to northwards expansion of anthropogenic development. Disturbance-mediated apparent competition is hypothesized as the primary cause of woodland caribou range recession (Serrouya et al. 2011, Fryxell et al. 2020, Neufeld et al. 2021). Woodland caribou avoid predators by inhabiting older forest and wetlands that grey wolves (*Canis lupus nubilus*) tend to avoid because of the absence of other primary prey such as moose (*Alces alces*; James et al. 2004). The location of older forest shifts through time in response to fire and succession, such that caribou require large home ranges (≤4,000 km^2; Ontario Ministry of Natural Resources [MNR] 2009) to maintain separation from predators. Early seral forest created by increased forest disturbance can support more moose and therefore wolves (Kittle et al. 2015), which can increase predation pressure beyond sustainable levels for caribou (Wittmer et al. 2007). Linear disturbances such as roads and trails also contribute to the problem by increasing the mobility and, therefore, efficiency of predators (DeMars and Boutin 2018). Given the province's woodland caribou objective of self-sustaining populations (MNR 2009), a requirement of the modeling framework is the ability to assess population response to land use and climate change on caribou habitat and mortality, including interspecific interactions, over large spatial and temporal scales.
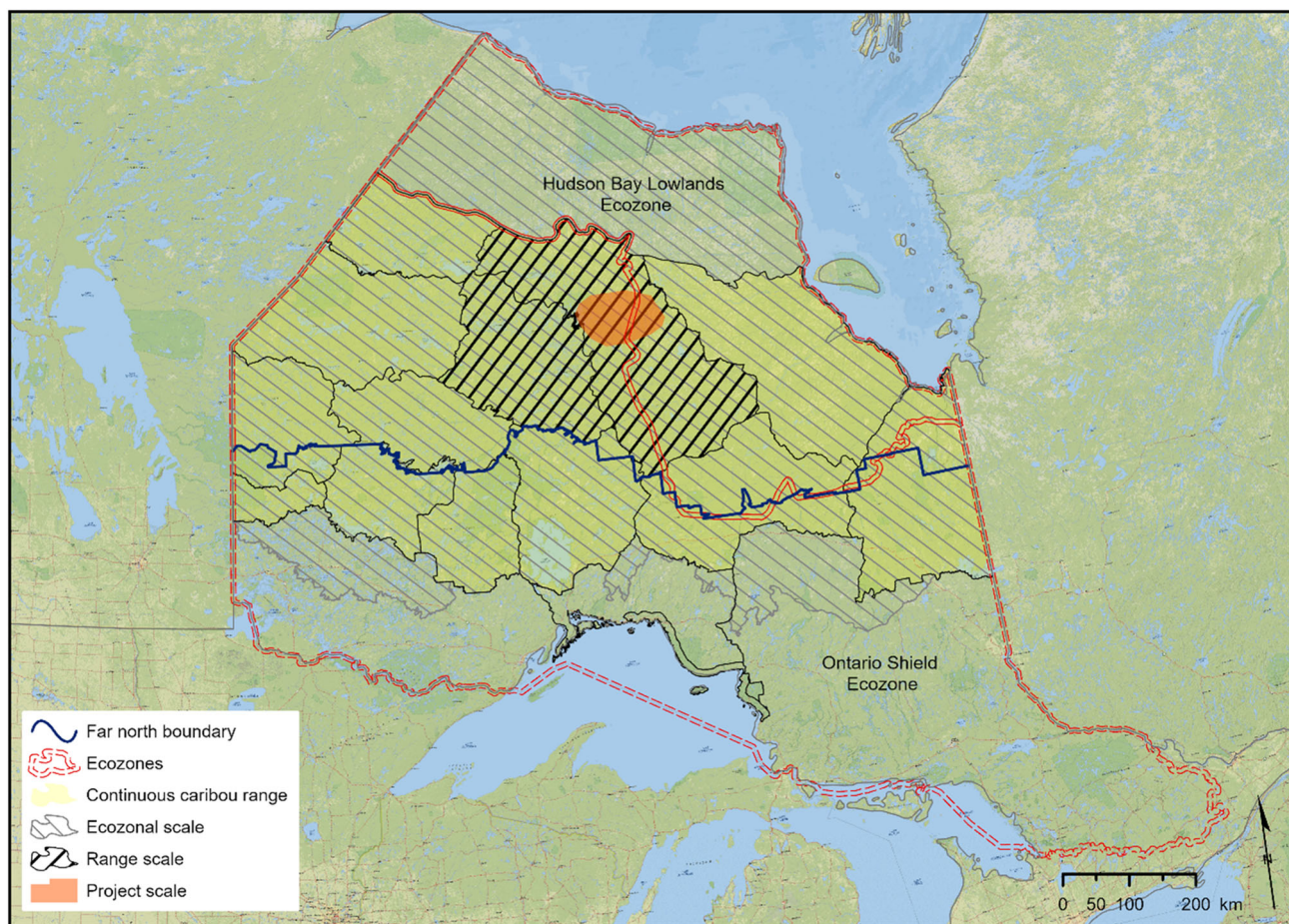
The Ontario government is engaged in research to explore and enable regional cumulative effects assessment in northern Ontario, which is home to numerous Indigenous communities, a remote region that is part of one of the largest blocks of intact boreal forest remaining globally (Far North Science Advisory Panel 2010), and of economic interest due to the presence of minerals, hydroelectric potential, and timber. The region's diverse environmental, cultural, and economic values present a planning opportunity, namely the ability to proactively plan land use to support economic development and the maintenance of ecological integrity. Realization of this opportunity requires decision support systems capable of assessing the cumulative effects of management options (Far North Science Advisory Panel 2010). To that end, a project was initiated to prototype a cumulative effects modeling framework with an initial focus on woodland caribou. The intent of the framework is to integrate available knowledge to support decision-making, and to determine priorities for ecological monitoring. Our objective was to develop and apply a decision support model capable of quantitatively demonstrating the effect of resource development and climate change on the population dynamics of moose, wolves, and caribou, and to illustrate the management insights that can be obtained through comprehensive simulation of multi-species

population dynamics in response to the cumulative effects of land use and climate change. These insights can subsequently lead to collective discussions of mitigation options to lessen detrimental effects, consideration of compensation, and strategic thinking to adjust future management decisions to better respond to a changing environment under multiple pressures. By applying this modeling framework we addressed the following research questions related to caribou conservation in Ontario's far north: How will caribou populations change under projected development and climate change scenarios? How will the sustainability of caribou populations be affected by climate change and biotic interactions? If change is detected, will the magnitude of change be the same, regardless if assessment is conducted at the ecoregional (654,311 km^2), caribou range (108,378 km^2), or local project scale (8,311 km^2)?

STUDY AREA

We explored woodland caribou population dynamics over a 654,311-km^2 region of northern Ontario (Fig. 1) encompassing the northern portion of the Ontario Shield and Hudson Bay Lowlands ecozones (Crins et al. 2009). Caribou data collection spanned the period 2009–2014. The mean annual temperature in 2010 was approximately −2°C with a mean winter (Dec, Jan, and Feb) temperature of −16°C. The study area included the Ontario Ministry of Natural Resources' Far North planning region encompassing 450,000 km^2. The Ontario Shield ecozone covers 66.2% of Ontario, with northern portions of the zone composed primarily of conifer boreal forest, and characterized by Precambrian bedrock and a cold and moist climate (Crins et al. 2009). The portion of the Shield within our study area had a mean annual temperature of approximately −2°C, with a mean winter temperature of −17°C. This area of northern Ontario is likely to warm faster than more southern areas, and effects of climate change are already becoming evident (McDermid et al. 2015). This ecozone had varied topography with eskers and complex drainage patterns that included an abundance of lakes, rivers, and wetlands such as peatlands. Fire was common, with insect and wind disturbances further influencing the landscape. The Hudson Bay Lowlands ecozone may be distinguished from the Ontario Shield by the presence of permafrost and underlying limestone bedrock. Lakes, rivers, and wetlands such as bogs and fens, were common on the landscape, and farther north the boreal forest transitioned to ridge thickets and eventually tundra (Crins et al. 2009). Further details on flora and fauna are described in Crins et al. (2009). Despite comprising 42% of Ontario's area, the far north component of the study area had a human population of approximately 32,560 (Chetkiewicz et al. 2017), representing only 0.2% of the province's population, with a composition of 90% Indigenous Peoples residing in 31 First Nations communities in traditional territories (Far North Science Advisory Panel 2010). For northern portions of the study area there is an established relationship between First Nations and governments responsible for wildlife, land use, and response to climate change determined by Treaty 9

Figure 1. Simulation extent (ecozonal scale) in northern Ontario, Canada, subregions used for finer scales of assessment (range scale and project scale), boreal woodland caribou range in 2020, the southern boundary of Ontario's Far North Planning Region, and the Hudson Bay Lowlands and Ontario Shield ecozones.

(Government of Canada 2008). Mining was the primary form of industrial natural resource development in the far north, and regulation fell under the Mining Act, including specification of mine closure requirements (Ontario Ministry of Energy Northern Development and Mines [ENDM] 2012). A large chromite deposit occurs within the area that is referred to as the Ring of Fire, for which multiple mines are potentially planned (Carlson and Chetkiewicz 2013, Chetkiewicz et al. 2017). The southern portion of the study area fell with Ontario's industrial forestry zone where managed logging occurred under Crown Forest or Sustainable Forest License agreements.

METHODS

Simulation of caribou population dynamics requires representation of the system linking caribou recruitment and mortality to landscape, climate, and interspecies dynamics. In this system, caribou recruitment is conceptualized as being controlled by habitat, which is dynamic in response to land use (forestry, mining, hydroelectric, roads) and fire. The most important source of mortality is predation by wolves, which is positively associated with a moose population that dynamically responds to climate, landscape disturbance, and hunting. We modeled the system using

ALCES Online (Alces Group 2017) because this decision support tool integrates landscape and population simulators, spatial representation of relevant influencing factors (resource development, fire, climate change, species interactions), ability to model across large spatial and temporal scales, and web-based delivery to promote collaboration across researchers and managers (Carlson et al. 2014, Adamczewski et al. 2016). The landscape simulator operates by exposing a cell-based representation of the current landscape to user-defined scenarios that differ with respect to the rate and spatial pattern of future development and natural disturbance. Changes in the abundance, location, and age of natural and anthropogenic land cover types are tracked and applied in combination with other gridded data (e.g., physical geography, climate projections) to calculate and map the performance of metrics such as wildlife habitat through space and time (Carlson et al. 2014, Carlson and Stelfox 2014, Adamczewski et al. 2016).

The population simulator is also cell-based, with each cell's population influenced by recruitment, mortality, and dispersal on an annual time step. The approach incorporates methods used in cellular autonoma models (Clarke 2014), and is linked to the geographic information system data base (Carlson et al. 2014, Cairns 2020). Simulated landscape

dynamics affect individual cells over time, which in turn influences population dynamics through processes such as the effect of land cover composition on carrying capacity. Multiple species can be simulated concurrently and linked through processes such as predation. The population dynamics simulator within ALCES Online (i.e., PopDyn) is an open-source tool coded in Python that began development in 2016 under the direction of parties in government, academia, and industry (Cairns 2020). Application of the model requires assembly of data describing current landscape composition and current and future climate; simulation of landscape dynamics in response to land use and natural disturbance scenarios; calculation of biotic relationships, including caribou and moose carrying capacity in response to landscape and climate projections; and simulation of caribou-wolf-moose population dynamics (Table 1).

Landscape and Climate Data

We prepared a data layer describing current landscape composition by integrating the Ontario Provincial Land Cover Data Base with additional data identifying the location of anthropogenic footprints (Spectranalysis 2004, Maxie et al. 2010). We aggregated the 27 classes in the land cover data base to 13 types: forest conifer, forest deciduous, forest mixedwood, tundra, rock, sand and gravel, open peatland, treed peatland, tidal wetland, water, agriculture, settlement and infrastructure, and extraction pit. We incorporated the additional anthropogenic footprint using provincial inventories of the road network, utility lines, waste sites, airports, and railways (Esri 2020, Ontario GeoHub 2020). To incorporate large (7.5 km^2) to medium (4 km^2) development sites that were missing from the land cover data base and footprint inventories, we visually scanned satellite data (Esri 2020, Ontario GeoHub 2020)

and identified 716 additional development sites. We digitized these sites and classified them into types (mines, communities, dams, other infrastructure) by overlaying identifying data layers such as the Mineral Deposit Inventory (ENDM 2021). We intersected data layers (land cover data base, footprint inventories, digitized development sites) to create a non-overlapping and contiguous representation of landscape composition for the start of the simulation period. We developed the land cover data base, which included wetlands, mature forest, and other land cover types, using the Ontario provincial land cover map, which was based on imagery from 2000 to 2002 (Spectranalysis 2004). This product had some missing pixels because of cloud cover, and we replaced these with land cover pixels using the more recent far north land cover map (Ontario Ministry of Natural Resources and Forestry [MNRF] 2014a), and then summarized the map data to 1-km resolution for modeling purposes. The summarized landscape composition layer was multivariate, such that a cell could contain multiple natural and anthropogenic cover types. We prepared data layers describing the origin (i.e., burn, cut) and age of forest using a disturbance data layer produced by the Provincial Satellite Derived Disturbance Mapping program (MNR 2012). We used these age and origin data in the model for identifying recent natural disturbance (e.g., fire, insect, weather damage) and tracking changes in land cover type due to development activities such as forestry and mining.

We used downscaled monthly temperature and precipitation projections for 2010 to 2060 from the Second Generation Earth System Model (ECCC 2017) at a 1-km resolution across the study area. We used downscaled climate data from a digital elevation model, baseline, and anomaly grids based on methods presented in Wang et al. (2016).

Table 1. Summary of input data, relationships, parameters, and simulations used in the ALCES Online landscape simulation and integrated population dynamics (PopDyn) model for a moose-wolf-caribou system in northern Ontario, Canada, 2020–2070.

Group	Description
Landscape, fire, and climate change data and simulation	
1	Historical climate and climate change predictions resulting from emission scenario representative concentration pathways 8.5 under Canadian Earth System Model 2
2	Starting landscape composition based on land cover and disturbance inventories
3	Plausible future landscape composition simulated based on land use (mining, hydroelectric, forestry, roads) and fire trajectories informed by regional planners, geologists, planning documents, and the literature
Biotic, habitat-selection, predator-prey, and carrying capacity relationships	
1	Literature-based bioclimatic model of moose and response to climate change and landscape composition (relative carrying capacity [K]) changes as function of temperature, precipitation, and age of mixedwood-deciduous forest)
2	Literature based resource selection model of caribou response to linear features and landscape configuration (relative K changes as function of linear features, age of forest, and % composition of conifer)
3	Literature-based wolf density response to moose density (relative K for wolves as a function of moose density)
4	Literature-based wolf predation rate on moose and caribou (as influenced by wolf density)
Population dynamics demographic and vital rate parameters	
1	Literature-based estimates of initial (current) moose, wolf, and caribou population levels and demographic structure (distributed spatially relative to expected habitat quality)
2	Literature-based estimates for age- and sex-specific vital rates for reproduction and mortality under density-independent conditions (for wolves, moose, and caribou)
3	Exploitation rates for recreational harvest based on analysis of Ministry of Natural Resources and Forestry data; subsistence harvest set as a fraction of recreational harvest
4	Literature-based estimates of absolute K (the number of animals the environment can support before density-dependent effects occur)
5	Population dispersal distances, including both exploratory behavior as animals seek new habitat, and as a density-dependent dispersal response as density approaches carrying capacity; estimates based on analysis of Ministry of Natural Resources and Forestry collaring data
6	Density-dependent responses for reproductive and mortality rates (rate and % of K when effects begin to manifest)

We prepared climate data for the pessimistic (representative concentration pathways 8.5) emission scenario predicted by the Intergovernmental Panel on Climate Change, in which greenhouse emissions continue to rise past the year 2100 (Iturbide et al. 2020).

Simulation of Landscape Dynamics

Landscape simulations incorporated 50-year trajectories for the region's major land use (mining, forestry, hydroelectric, roads) and natural disturbance (fire) agents using a 10-year time step. We simulated 5 scenarios to explore sensitivity of wildlife populations: stable climate and no new development (base case), changing climate but no new development, changing climate and development under high economic activity, changing climate and development under low economic activity, and changing climate and development under an alternative option for infrastructure features. Specifically, we created these scenarios by specifying 2 options for the layout of mid-term (20-yr) infrastructure based on proposed transportation routes, long-term (50-yr) mining and hydroelectric development rates under low and high levels of economic activity, and fire with and without the effect of climate change. We prepared the 2 infrastructure options in consultation with the regional planning team (R. Sitch, Ontario Ministry of Natural Resources and Forestry, personal communication) and they differed with respect to whether a western or eastern route was used to access the long-term mining and hydroelectric developments in the Ring of Fire, together with supply road and transmission line options. These options, including assumptions for other land uses, represented expert opinions at the time of scenario development. For example, the Webequie Supply Road proposal connecting the airport with proposed mine developments in the McFaulds Lake area that is now undergoing environmental assessment (Webequie First Nation 2021) was an approximate route in our scenario.

The simulated rate of forest harvest was based on 80% of the planned harvest area as specified in forest management plans for the numerous forest management units spanning the southern portion of the study area (MNRF 2020), and thus we assumed no northward expansion of harvesting. We reduced harvest level by 20% from the planned level because companies in northern Ontario are currently harvesting ≤60% of the maximum permitted (MNRF 2020). We treated simulated burned forest as salvage logged, thereby reducing planned harvest area. Timber harvest was limited to dense forest >65 years old and followed an aggregated block schedule to represent forestry guidelines for caribou range (MNRF 2018a). Regenerating stands retained their pre-harvest forest type. The model created secondary roads linking cutblocks to the road network, where 5% of harvested area was automatically converted to in-block road (i.e., temporary roads located within the harvest cutblocks). We used the linear allocation method, which uses a least cost paths approach to link cells with newly harvested forest to the existing road network. If the cell is already linked to the road network, no new road is created. In-block roads

were dispersed across newly harvested areas because the resolution of the simulations (i.e., 1 km^2) was too coarse to represent in-block roads as segments. Forest access roads in northern Ontario that were >20 years old and naturally abandoned had greater tree and shrub density on the roadbeds than comparable roads that were <20 years old (Hall et al. 2016). This increased tree and shrub density suggests that these older roads are less functional for people and predators to use, and thus provides some support for our use of a 20-year threshold for in-block roads to be reclaimed to a natural state.

We prepared mining scenarios incorporating mineral exploration and mine development under low and high rates of development in consultation with government geologists (N. Bennet, Ministry of Energy, Northern Development and Mines, personal communication). Activity was focused on the Ring of Fire mining area but also included exploration and development within other areas with mineral deposits. Our low-intensity mining scenario included 10 exploration sites/year and the development of 16 mines over the 50-year simulation period, whereas the high-intensity mining scenario included 50 exploration sites/year and development of 30 mines over the simulation period. The simulated mines target a range of minerals including chromium, diamond, gold, nickel, copper, platinum group elements, lithium, zinc, cobalt, graphite, iron, and niobium. Because of uncertainty surrounding the layout of future mines, we grew all mines outwards from a starting location to 4 km^2 or 7.5 km^2. Experts provided each mine's starting location and size class (i.e., 4 km^2 or 7.5 km^2). We created roads to link mines to the road network, and created trails to provide temporary access to exploration sites. We assumed exploration trails recovered to a natural state after 20 years, based on the assumption for in-block roads described previously. We limited exploration to within existing claims, patents, and leases, and created negligible footprint other than trails required for access from the closest road. We based hydroelectric scenarios under low and high rates of development on a previous scenario analysis exploring cumulative effects on fish populations in northern Ontario (Carlson and Chetkiewicz 2013). Our low development scenario implemented 1 planned hydroelectric project, whereas the high development scenario implemented an additional 9 potential projects. We created a transmission line footprint to link new dams to the transmission network.

To represent spatial and temporal patterns in the burn rate, we combined a regional-scale assessment of fire rate under current and potential future climate (Boulanger et al. 2014) with local-scale fire selection ratios that respond to spatial variation in cover type and age (Bernier et al. 2016). We simulated 2 fire scenarios: historical, for which the fire rate equals the observed average during 1959 to 1999, and increasing fire under the pessimistic (representative concentration pathways 8.5) emission scenarios. We obtained ratios of future relative to historical fire rates for each climate scenario (Y. Boulanger, Natural Resources Canada, personal communication) for 2011–2040 and 2041–2070 and multiplied by the historical fire rate to

derive future fire rates. We based simulated fire size on fire size class distribution observed in the study area over the past 20 years (1997–2016). We calculated fire size class distributions separately for the western and eastern portions of the study area to reflect the substantially larger fire sizes recorded in the western portion.

Simulation of Population Dynamics

We simulated moose, wolf, and caribou populations over 60 years using an annual time step. We used the first 10 years (2011–2020), during which the landscape remained constant at current conditions, to calibrate the initial population distributions to model inputs. The remaining 50 years (2021–2070), which were linked to the landscape scenarios described previously, are reported in the results. At the beginning of each time step, we used the population for each development stage from the previous time step to generate parameters, which included mortality, fecundity, and habitat carrying capacity values for each species, sex, and development stage at each cell. We calculated all mortality and births, and the resulting population size per cell for the current time step. Specified short-distance dispersal distances are then applied when the population within a cell reaches a specified threshold relative to carrying capacity, which results in populations that are susceptible to density-dependent and age-based mortality. Long-distance dispersal distances are also applied and represent the maximum dispersal distance of a population spatially expanding from its current periphery. Following the calculation of derived mortality (i.e., predation as derived from wolf density), the final population sizes and population distributions for the current time step are recorded for each species across the study region.

The PopDyn simulator required several parameter estimates for each species (Appendix A). We based our parameter estimates in part on published relevant vital rate estimates and relationship models, and in part on new analyses conducted using data from recent field studies in northern Ontario.

Relative and maximum carrying capacity.—For each species we defined region-wide carrying capacity (K) in PopDyn as the maximum population density possible across the study area, and relative K as a value ranging from 0–1 for each cell in the simulation grid. Relative K can be defined by a habitat layer, or derived from the density of other species, both of which can vary through space and time. During simulations, we computed K for each cell by multiplying region-wide K by relative K. We based relative K for moose on a bioclimatic model that relates climate (temp and precipitation), land cover composition, and percent young forest to moose density (Rempel 2011). Climate change will only affect forage in areas where soils can support browse, so we used a conditional modifier to restrict the model to cells where soil conditions supported a ≥10% proportion of mixedwood or deciduous forest. We estimated relative K for wolves as a function of moose density as simulated by PopDyn. We cast this function as an inter-species response curve based on a modeled relationship between wolf

numbers and moose density (Messier 1994), with relative K ranging from 0.12 to 1 (Appendix A). We defined relative K for caribou using season- and range-specific resource selection probability functions (RSPFs) for Ontario (Hornseth and Rempel 2016), with the assumption that a higher RSPF coefficient results in higher relative K. We developed the RSPF models using 11 land cover variables, including linear feature density, eskers, and natural burns (coefficients in Table S1 and performance statistics in Table S2, available online in Supporting Information).

We estimated region-wide K for moose and wolves in part by the 60-year study of moose-wolf dynamics on Isle Royale National Park in northern Michigan (Nelson et al. 2011). We estimated moose maximum density at 0.82/km^2, which is twice the maximum density observed from moose surveys in northern Ontario but substantially less than the carrying capacity estimate of 2/km^2 for eastern Quebec (Crête 1989). For much of the northern extents of the study area, moose have only recently occupied the area in response to climate change, or are increasing in number, so there are no good empirical estimates of maximum density for that area. Wolf maximum density more than tripled on Isle Royale as moose density increased from its lowest to highest density (Wilmers et al. 2006) so we estimated maximum possible wolf density at 17/1,000 km^2, more than triple the density observed in the Nakina, Pickle Lake, and Cochrane moose-wolf-caribou areas (Kittle et al. 2015), and slightly higher than 14/1,000 km^2 that Bergerud (1992) reported as among the highest densities found in wolf-caribou systems. Caribou maximum density was 0.096/km^2, which is the average of the 2 highest reported densities in Ontario for the Wabakimi-Brightsand-Nipigon Islands (Cumming et al. 1996) portion of our study area.

Initial distribution and demography.—We set the initial population distribution, before effects of climate change or development, to reflect the expected population across the study area (based on recent wildlife surveys), distributed by a spatial gradient of relative K as described above. This is calculated as:

$$InitPop_{i,j,s} = \left(\frac{K_i}{2}\right) \times RK_i \times ACF_{i,j,s}, \qquad (1)$$

where *InitPop* is the cell-specific initial population, i is species, j is age-class, s is sex, K is region-wide maximum density, RK is cell-specific relative carrying capacity, and ACF is the age-class fraction of the population belonging to each age-class by sex (all fractions sum to 1). As discussed above, the moose bioclimatic model is conditioned on the presence of existing mixedwood or deciduous forest. We created an age-class structure to represent the population with the minimum complexity necessary. Wolves had 3 age-classes: yearlings (0–1), mature (2–8), and old (9–12). Moose had 5 age-classes: young of year (0), yearlings (1), young adult (2–3), mature adult (4–7), and old (8–12). Caribou had 4 age-classes: young of year (0), yearling (1), mature (2–8), and old (9–15). Mortality of individuals occurred when maximum age was exceeded.

Fecundity.—We based fecundity rates for moose on an age-fecundity quadratic relationship that we modeled from Manitoba data (Critchon 1992), with estimates of 0.7, 1.0, 1.3, and 1.0 for the reproductive age classes of yearling, young adult, mature adult, and old, respectively. Fecundity was >1 for the prime breeding class because some moose give birth to twins. We based the reproductive rate for wolves (0.5) on only a single female giving birth per pack, with litter sizes of 4 to 7 pups (Harrington et al. 1983). We used caribou pregnancy and parturition rates estimated by Walker et al. (2021) for their Nakina, Pickle Lake, and Cochrane study areas, who reported 87% of caribou were pregnant. We set fecundity at a slightly lower level of 0.84 for prime breeders (to account for lower relative K in more northern areas) and 0.8 for the older age class to reflect declining breeding fitness with age.

In Ontario, the moose calf to adult female ratio decreases linearly with increasing density (Rempel 2011), so we modeled fecundity to be density dependent, with a linear decrease in fecundity beginning at an N to K ratio threshold of 0.5 and with a maximum 25% reduction in fecundity rate as moose population density approaches K. Density dependence is poorly understood in caribou and wolves, but studies on more northern Peary caribou (*R. tarandus pearyi*) suggest it is likely a subtle but important regulating factor (Tews et al. 2007), and studies in Yellowstone National Park, USA, suggest it may play an important role for non-exploited wolf populations (Cubaynes et al. 2014). We modeled caribou and wolf fecundity as density dependent with an N to K ratio threshold of 0.5 for both species and with a maximum reduction in fecundity of 25% for caribou and 20% for wolves. We added normally distributed random variation in fecundity to represent a small amount of annual variability in environmental conditions, with standard deviations of 0.01 for wolves and caribou and 0.05 for moose.

Dispersal.—We estimated 2 types of annual dispersal: short-distance dispersal responding to local populations approaching K, and long-distance dispersal that would occur under population range expansion. For long-distance dispersal, the annual movement can be substantially less than the specified distance because the value represents the maximum of a normal distribution. For moose and caribou, we used global positioning system-collar data from previous studies (Street et al. 2015, Fryxell et al. 2020) to estimate short-distance dispersal based on maximum daily movement and used maximum annual movement rates to estimate long-distance dispersal distances. Data were available for 53 female moose and 270 female caribou. Frequency distributions for both types of movement were skewed right, so we used the 90th percentile of maximum movement distance. We estimated short-distance dispersal distances of 14 km and 50 km for moose and caribou, respectively, whereas maximum long-distance dispersal estimates were 25 km and 174 km for moose and caribou. For wolves, their short-distance dispersal is analogous to within-territory movement of a pack (i.e., tracking moose availability), whereas long-distance dispersal is analogous to a cub or yearling dispersing to join a new pack. Dispersing

wolves typically establish territories or join packs within 50–100 km of the pack in which they were born (Forshner 2000), so we set maximum long-distance dispersal to 75 km for wolf yearlings (and zero for the other 2 age classes) and short-distance dispersal to 14 km (the short-distance dispersal for moose) for all wolf age classes, with the expectation that the wolf pack dispersal will track prey availability.

Mortality.—Mortality for moose had 5 sources: recreational (non-Indigenous) hunting, Indigenous hunting, wolf predation, density-independent natural mortality, and density-dependent mortality. We used moose aerial inventory and self-reporting data from 1999–2010 from northern wildlife management units to estimate recreational hunting mortality, with estimates for young of the year (YOY), yearlings, young adults, mature adults, and old adults of 0.083, 0.083, 0.113, 0.113, and 0.113 for males, respectively, and 0.083, 0.083, 0.033, 0.033, and 0.033 for females, respectively. We did not have credible estimates of hunting rates by Indigenous People, including age- and sex-specific rates, so we set a placeholder hunting rate of 0.1 for all age classes, which is approximately an average of the 0.083 and 0.113 recreational hunting rates.

We estimated natural mortality for moose from Peterson (1977) data, which separated natural mortality from wolf predation. Bears were not present in the Peterson (1977) study, so we increased natural mortality for stage classes susceptible to American black bears (*Ursus americanus*; YOY and old adults). We set natural mortality rates to 0.2, 0.02, 0.02, 0.02, and 0.16 for YOY, yearlings, young adults, mature adults, and old adults, respectively. We modeled wolf predation rate on moose as a product of the functional and numerical responses to moose density, as described by Messier (1994). We cast the response as an inter-species relationship, where moose mortality rate is a function of the modeled wolf population within a 100-km^2 cell (Appendix A). We modeled additional density-dependent mortality, separate from that of wolf predation, as a linear response to K beginning when the N to K ratio = 0.5, and increasing to a mortality rate of 0.2 at K.

Mortality for wolves included density-dependent and density-independent sources. Wolf packs have strong mechanisms that enforce density dependence resulting from food limitation, including territoriality, intra-specific strife, and reproductive inhibition in subordinate pack members (Cubaynes et al. 2014). We expected density-dependent mortality to be relatively weak because wolf pups will emigrate to other territories as populations grow (Forshner 2000, Kojola et al. 2006), so we set density-dependent mortality to a maximum of 0.2, beginning to occur when the N to K ratio exceeds 0.8. We also expected density-independent mortality to be weak, and we set this to 0.1, equally across all age classes.

Mortality for caribou had 4 sources: Indigenous hunting, wolf predation (with functional response to wolf density described under biotic interactions), density-independent natural mortality, and density-dependent mortality. We did not have credible estimates of Indigenous harvest rates, so

we set a placeholder rate of 0.1 for all stage classes. We also set natural mortality (e.g., density-independent death from disease or accidents) to a low rate of 0.05. Density-dependent mortality began at an N to K ratio of 0.6 and increased to a maximum mortality rate of 0.1 at K. We simulated predation as an inter-species dynamic based on the Bergerud and Elliot (1986) modeled relationship between wolf population and caribou mortality rate. We used a stage-based mortality factor of 1.7 to distribute the predation effect more heavily on the YOY and yearling class (Appendix A).

Simulation and assessment scales.—Although we modeled landscape and population dynamics across the full study area, we assessed outcomes at 3 scales (Fig. 1) that varied in spatial extent but shared the same resolutions for modeling landscape change (i.e., 1 km^2) and population change (i.e., 10 km^2). The ecozonal scale (654,311 km^2) included the full study area and encompassed the Hudson Bay Lowlands and Ontario Shield ecozones. The range scale (108,378 km^2) included the combined extent of 2 caribou ranges (Ozhiski and Missisa) that overlap with the Ring of Fire. The project scale (8,331 km^2) encompassed 3 proposed Ring of Fire projects (Thunder Bird, Eagle's Nest, and Butler) and the Webequie First Nation's reserve.

PopDyn model verification.—A PopDyn model has numerous parameters representing vital rates, dispersal distances, and carrying capacity. To assess if the model was calculating population changes in a manner expected under a simpler model structure, we compared PopDyn output for the moose model with output from a modified Leslie-Lefkovitch stage projection matrix model. We parameterized the stage projection model for moose using the same sex and age stages, initial population levels, and estimates for fecundity, mortality, and carrying capacity that we used in the more complex spatial PopDyn model (but with a fixed rather than variable wolf predation rate). We programmed the stage-projection model so that fecundity and mortality were responsive to population density (defined carrying capacity). To represent mortality resulting from wolf predation, we used the average level of wolf predation (0.05) over the simulation period to fix natural mortality estimates, resulting in natural mortality for the matrix model of 0.27 for young of year (YOY); 0.07 for the yearling, young adult, and mature age classes; and 0.23 for the old age class males, and likewise 0.25, 0.07, and 0.12, respectively, for females. The matrix model cannot accurately represent spatial-temporal changes in moose and wolf density resulting from climate change and expanding development, so we used the static scenario without climate change or development as the PopDyn reference model that is expected to be stable with recruitment balanced by mortality. In PopDyn, K represents the maximum moose density (carrying capacity) expected within each 10-km^2 simulation cell, whereas in the matrix model K represents the maximum moose density expected for the entire 654,310-km^2 study area. Based on moose aerial inventory data, the total number of moose expected across the study area is about 50,000 moose (0.07 moose/km^2), whereas a high moose density within an individual 25 km^2 survey block is about 0.41 moose/km^2. For both models we defined K as twice these respective values, with 0.14 moose/km^2 for the matrix model and 0.84 moose/km^2 for the PopDyn model. We calculated density-dependent responses to fecundity and mortality rates in the same linear manner as used in PopDyn, where a negative response occurs above a specified N to K ratio threshold of 50% of K, up to a maximum level of 20% additional mortality or 25% lower fecundity, as the population approaches K. For the PopDyn model, we added slight random variation in fecundity (SD of 0.01).

To verify functional biotic relationships, we plotted PopDyn output for moose density versus wolf density, and number of wolves versus wolf predation on mature and yearling caribou, pooling the full range of simulation scenarios, and verified that relationships were modeled correctly. Researchers that collected animal data used in this modeling exercise (Street et al. 2015, Fryxell et al. 2020) followed 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).
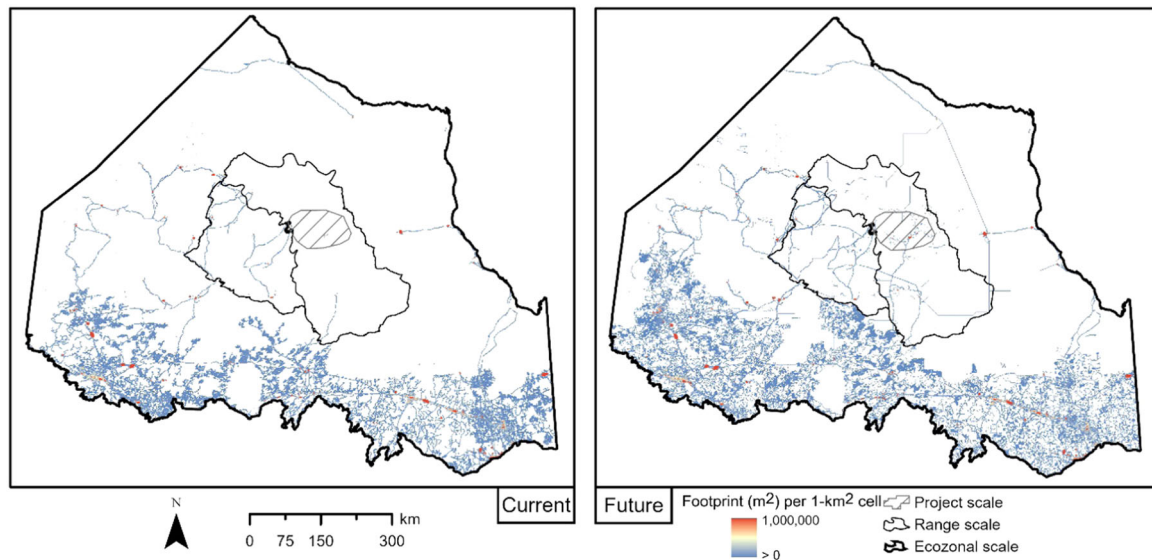
RESULTS

Landscape Simulation and Climate Change

The anthropogenic footprint (roads, transmission lines, mines, dams, and settlements) presently accounts for 4,130 km^2 (0.6%) of the study area (Fig. 2). Roads are the most prevalent footprint (1,455 km^2), followed by settlements (1,321 km^2), mines (583 km^2), and transmission corridors (176 km^2). The majority (84%) of the footprint occurs in the southern portion of the study area that is allocated to forestry. The footprint increased by 657 km^2 over 5 decades under the high development scenario, with about half of the growth occurring in the area allocated to forestry where road network expansion occurred to access timber (Fig. 2). Farther to the north, the new footprint was dominated by mines and transmission lines. Under the low development scenario, the footprint growth was about 100 km^2 less because of fewer new mines. Differences in the footprint between the 2 tactical infrastructure scenarios, which specify alternative road placements, were minor.

The average forest age decreased during the simulations, with the decline more pronounced in simulations that incorporated climate change and timber harvest. Young forest (<20 yr) nearly tripled in coverage over 5 decades from 4.8% to 12.8% of the study area, during simulations that incorporated climate change. Temperature was also responsive to climate change, with average winter temperature increasing from −17.4°C to −12.5°C and average summer temperature increasing from 15.1°C to 20.2°C over the next 5 decades.

PopDyn Model Verification

We verified that the PopDyn model was performing population calculations similar to the simplified and non-spatial stage projection model. Male and female caribou populations maintained similar levels, with an average difference between models of 6.2%, 3.6%, and 4.8% for males,

Figure 2. Current and future (50-yr) anthropogenic footprint, including roads, mines, settlements, transmission lines, and hydroelectric generating stations for the 3 assessment scales in northern Ontario, Canada, in 2020 (current) and 2070 (future).

females, and total population, respectively, over the 50-year simulation period (following the initial 10-yr calibration period; Appendix B). We also verified that functional relationships between species were appropriately calibrated and calculated as expected in PopDyn, with wolf density increasing as a function of moose density, and wolf predation rates on moose and caribou increasing as a linear function of number of wolves (Appendix B). Density and predation rates were within the range expected for the study area, with moose density varying between approximately $0.07–0.115 \, km^2$, number of wolves varying between 4.0–6.5 wolves/$1,000 \, km^2$, and wolf predation rate on mature caribou varying between 0.018–0.026 (Fig. B2).
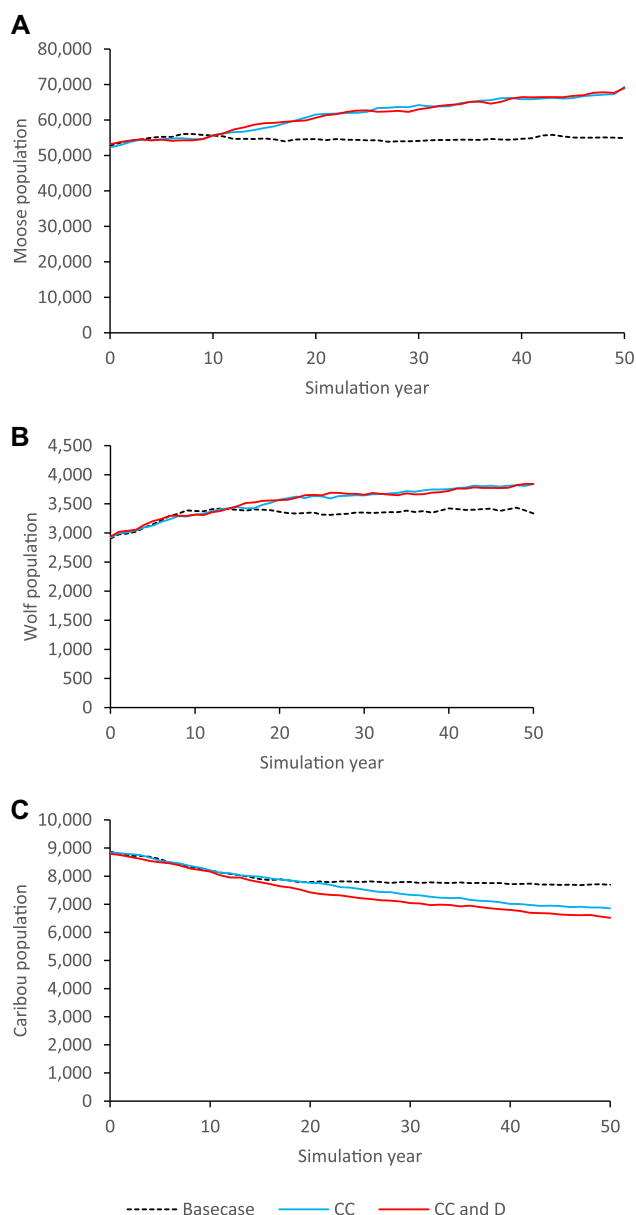
Ecozonal-Scale Population Dynamics
At the ecozonal scale, moose habitat quality was sensitive to climate change, with the average relative K index increasing by 67% during the climate change scenario. In contrast, land use had a negligible effect; the average moose relative K for the regional study area was only 1% lower after the climate change with high development scenario than the climate change without development scenario. As moose habitat increased under climate change, so too did fecundity with the number of annual offspring rising by 37% during the simulation. The ensuing 33% increase in the moose population (Figs. 3 and 4) translated into a 16% increase in wolf relative K and a 31% increase in the regional study area's wolf population during the climate change scenarios (Figs. 3 and 5). Higher wolf abundance caused the mortality rate from predation of YOY and yearling caribou to double, resulting in a 22% decline in the regional study area's caribou population during the climate change scenario without development (Figs. 3 and 6). Further contributing to the decline in the caribou population was a 4% reduction in relative K caused by development, resulting in a 26% decline in the caribou population during the climate change scenario with high development. In the absence of climate change, wolf

population growth was limited to the first decade of the simulation during which the caribou population also declined (Fig. 3). The initial decline in the wolf population under the constant climate scenario suggests a lag effect from recent moose population growth that may have already occurred because of climate change. Thereafter, the wolf population stabilized, which limited the decline in the caribou population to 13%, or half of what occurred during the climate change with high development scenario (Figs. 3 and 6).

The response of moose, wolf, and caribou populations to climate change were greatest in the southern portion of the regional study area that overlapped the Ontario Shield ecozone. In this portion of the landscape, a decline in winter severity in the predominantly forested landscape produced an increase in the modeled relative moose K, resulting in a higher increase in the southern moose population (Fig. 4). On average, this triggered a larger increase in the southern wolf population and therefore predation on caribou, resulting in larger declines in caribou. The population of herds that form the southern edge of caribou range (Sydney, Churchill, Brightsand, Nipigon, Pagwachuan, and Kesagami) exhibited a 44% decline during the climate change and high development scenario, compared to a 12% population decline across the remaining herds to the north. More rapid decline along the southern edge of caribou range is consistent with the pattern of range recession that has occurred for decades in the province (Schaefer 2003, Vors et al. 2007). Annual population growth decreased as percent anthropogenic footprint increased.

Range- and Project-Scale Population Dynamics
Compared to the ecozonal scale, caribou at the range scale displayed a more modest response to climate change (Fig. 7). The range scale is defined by the Missisa and Ozhizki caribou ranges, which overlap with the Ring of Fire mining development, and the population at this scale was stable in the absence of climate change and development,

Figure 3. Response of moose (A), wolf (B), and caribou (C) population dynamics at the ecozonal scale to landscape scenarios in northern Ontario, Canada, 2020–2070. The basecase scenario applies the current climate throughout the simulation and does not include future development. The CC scenario incorporates climate change but not future development. The CC and D scenario incorporates climate change and the high development rate in northern Ontario.

suggesting that climate change has not yet affected population dynamics through caribou habitat change. Continued warming, however, initiated a decline in the caribou population by year 10 of the simulation and resulted in a 10% population decline by year 50 due to increased predation by wolves as moose, and therefore wolves, became more abundant. By the end of the simulation, the mortality rate of YOY and yearling caribou due to wolf predation increased to 9.4% under scenarios that included climate change, compared to 7.6% without climate change. When we included development and climate change in the simulation, the population decli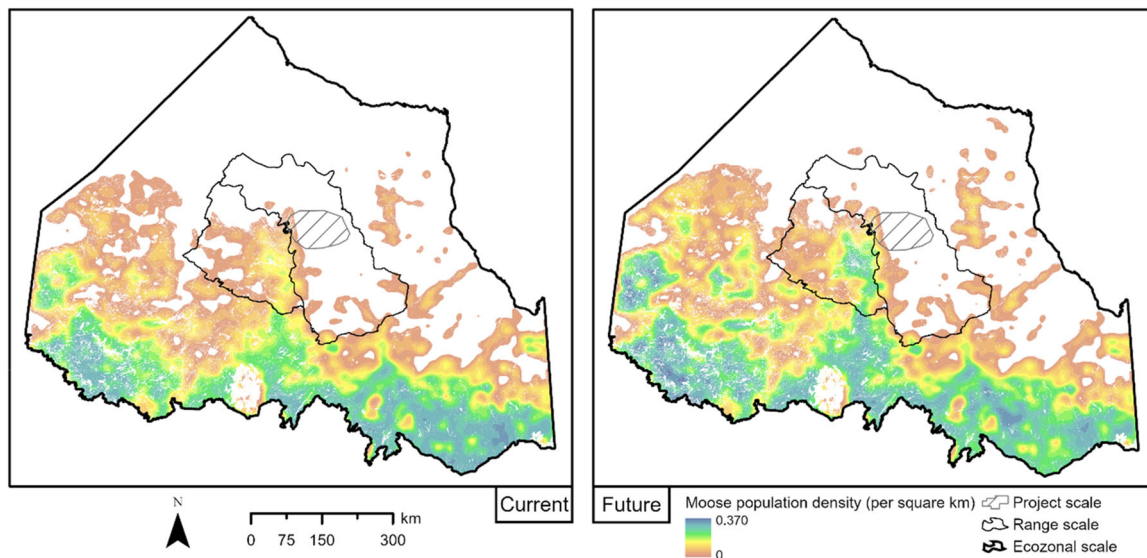ned by an additional 7% for an overall decline of 17%. The added effect of development was due to reduced habitat carrying capacity (as modeled by the RSPF), resulting in lower fecundity. The average probability of use in the ranges without development was 19%, and it declined to 17% in the presence of development. A lower rate of development reduced the overall population decline from 17% to 14% because of lower habitat disturbance. Differences in population outcomes under the 2 routing options were negligible.

At the project scale, caribou were relatively resilient to climate change, with the population decline limited to 5% (Fig. 7). This northern location has a low abundance of deciduous and mixedwood forest, resulting in a lower modeled relative K for moose. Development had a larger effect, however, given that the relatively small assessment area was projected to experience 25% of the broader region's mine development. The caribou population declined by 29% at the project scale (Fig. 7) when we included development in the simulation in addition to climate change. As was the case at the range scale, a lower rate of development moderated its effect on the caribou population, whereas the alternative infrastructure routing had minimal effect. The more pronounced temporal variation within scenarios at the project scale compared to the range and regional scales was because individual random events (e.g., fires) had a more pronounced effect on simulation outcomes owing to the smaller size of the assessment area.

DISCUSSION

We assessed the research question of how caribou populations will change under projected development and climate change. Based on our simulations, caribou populations in Ontario's far north will not remain stable over the next 5 decades under the potential development and climate change scenarios we included in our models; populations are projected to decline at all 3 scales considered. Climate change, land use change, and biotic interactions were the principal causes of the decline, but the relative importance of these factors, together with the effects of random variation and magnitude of decline, differed among scales. Although there does not appear to be an immediate risk of caribou extirpation at any scale, the sustainability of caribou populations will ultimately be threatened by potential development and climate change. Given Ontario's Range Management Policy (MNRF 2018b) to maintain range conditions that will support self-sustaining caribou populations at current or historical population densities in the absence of climate change concerns, managers should consider the potential additional threat to sustainability caused by the cumulative effects of climate change and resource development.

The holistic nature of the scenario analysis provides insights into the relative importance and cumulative effect of influences that cannot be obtained through consideration of human land use, climate change, or species interactions in isolation. This perspective, combined with map-based presentation of outcomes, are of value in diagnosing and communicating management issues. In the case of caribou in Ontario's far north, the analysis emphasizes that
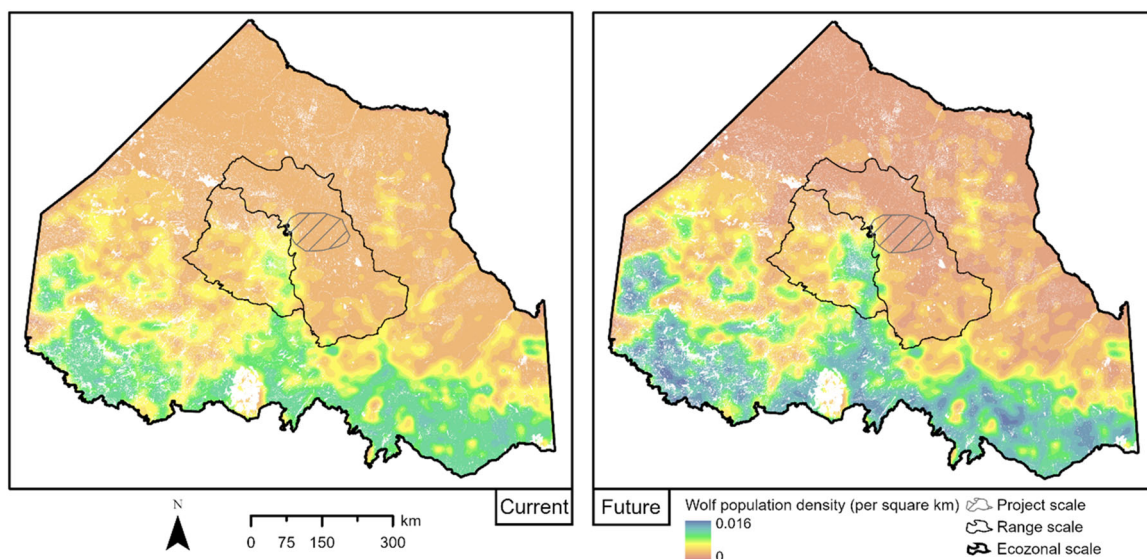
Figure 4. Current and future (50-yr) moose population distribution under the climate change with high development scenario for the 3 assessment scales in northern Ontario, Canada, 2020–2070.

managers need to address regional shifts in conditions that are likely to alter the abundance of wolves, the primary predator of caribou. Focusing on the tactical details of individual projects will not address the core issue of wolf predation facilitated by moose population growth. Rather, conservation of caribou will likely need to focus on regional development rates that influence the availability of moose habitat, and perhaps also strategies that increase moose or wolf mortality.

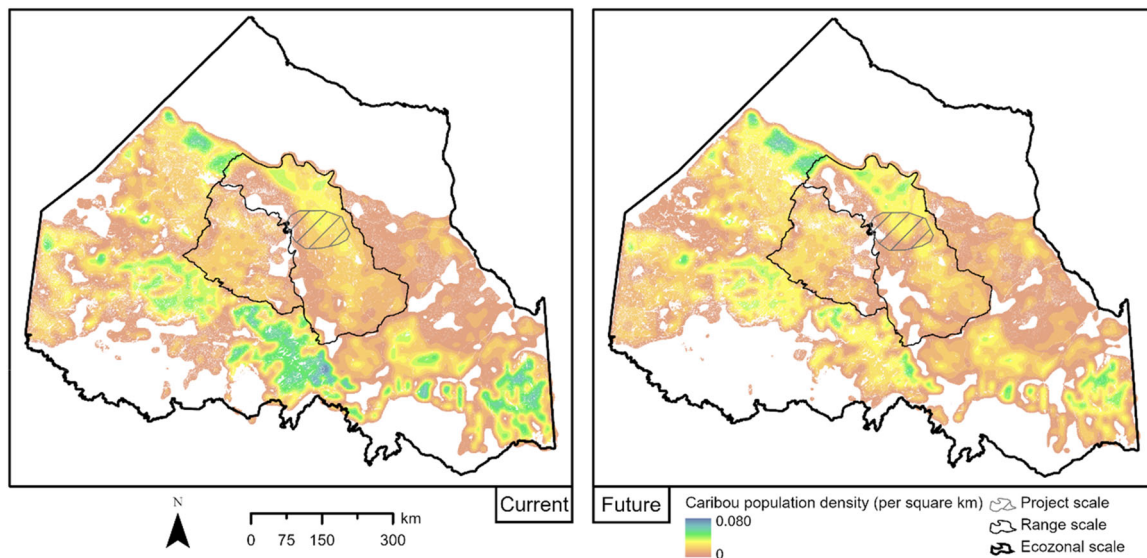## Comparing Regional-, Range-, and Project-Scale Assessments

An important issue in interpreting the model results is the scale (i.e., spatial extent) over which the simulation is applied, and assessments are made (Canadian Council of Ministers of the Environment 2009, Noble 2015, Council of Canadian Academies 2019). An important benefit of applying the simulation at the broadest scale is that it allows for a holistic assessment that can subsequently be mapped at local scales (e.g., ranges and development projects) to efficiently and realistically assess effects at those scales. In our simulation, the ecozonal scale provided insight into the effects of climate change but obscured local effects such as the Ring of Fire mine development. The project scale focused attention on localized project effects, which may be particularly relevant for nearby communities but obscured the effect of regional influences (e.g., climate change), was more sensitive to random variation in fire events, and may also obscure differences in planning options that may become more apparent at broader scales, such as zoning (e.g., protected areas networks).

Figure 5. Current and future (50-yr) wolf population distribution under the climate change with high development scenario for the 3 assessment scales in northern Ontario, Canada, 2020–2070.

Figure 6. Current and future (50-yr) caribou population distribution under the climate change with high development scenario for the 3 assessment scales in northern Ontario, Canada, 2020–2070.

Federal regional assessments will extend beyond our project-level assessment and explore the regional context to provide more comprehensive analyses that would support future project-specific assessment decisions, including cumulative effects (Impact Assessment Agency of Canada 2021). The range assessment scale we evaluated in the PopDyn wildlife model may be a good fit for a study area defined under a regional cumulative effects assessment because it strikes a balance between the scales at which climate change and land use affect caribou (MNR 2009, MNRF 2014b).

In our simulations, the percent decline in the caribou population under the climate change and high development scenario at the project scale was almost twice what occurred at the range scale and similar to what occurred at the eco-zonal scale. The large decline at the project scale, however, is mainly influenced by land use, whereas the large decline at the ecozonal scale is mainly influenced by climate change (i.e., because of increased predation rates in the southern portion of the study area). At the project scale, random simulated fire events caused relatively more variation in the population trend, weakening the ability to detect the effect of development rate and route options. In this case, the scale of the assessment affected the magnitude of the estimated effect and the relative importance of the influencing factors of climate change and land use. This leads to affirmation of an important principle for cumulative effects assessment, that selection of scale needs to consider the scale at which influencing factors affect values (Therivel and Ross 2007, Noble 2014). Given that multiple factors will likely be in play and given that these are likely to operate at different scales, the scale of assessment needs to strike a balance, and in some cases multiple scales of assessment may be required.

These results reveal an assessment conundrum in that the scale of assessment and effect size of indicators may not match the needs of all decision makers. For example, in this stud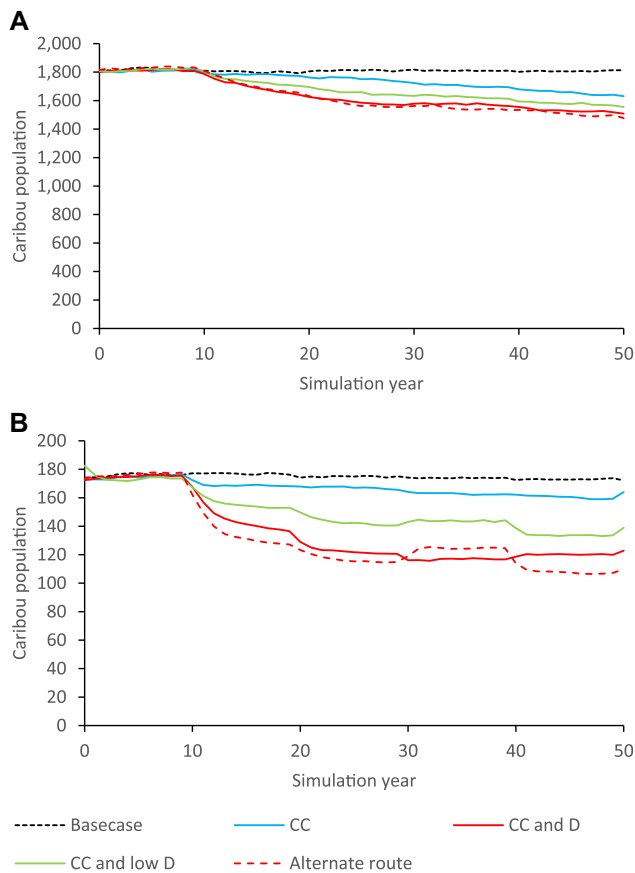y there was little difference in caribou population response between 2 tactical routing scenarios, and thus the analysis provides little insight into which option is preferred. The negligible effect of road placement may in part be because we did not include barrier effects of roads to modify outward dispersal of populations from cells, and such an addition to the model could make it more valuable for project-level planning and impact assessments. The more important reason for the similarity in outcomes, however, is that the 2 scenarios had similar implications for regional landscape composition. Both options resulted in a similar road density and facilitated substantial mine development. A strategic concern is that roads are growth-inducing over time (Johnson et al. 2020), especially because existing roads make mineral exploration more economically feasible. Simply put, the location of the access route is less important than the regional development that is likely to follow. As such, the scenario analysis provides insights that are useful at higher decision-making levels, such as the level or intensity of economic development that could be sustainably permitted within northern Ontario (in the context of climate change).

At the ecozonal scale, there is a significant risk of southern caribou range recession because of a northward shifting climate envelope for moose. Forestry can further contribute to range recession by creating younger forest and access roads. As such, conservation of the species may require conservation actions related to forestry activities to impede further range recession. Additional research into forest harvest planning strategies to balance caribou conservation and timber production in the face of increasing conservation concerns is required (Yemshanov et al. 2020).

Integrated Multispecies Modeling and Complexity

Multispecies population dynamics modeling linked to landscape and climate simulation at large spatial and temporal scales addresses limitations that have plagued cumulative effects assessments for wildlife. These limitations

Figure 7. Response of caribou population dynamics to landscape scenarios at the range scale (A) including the Ozhiski and Missisa ranges and project scale (B) in northern Ontario, Canada, from year 0 (2020) to year 50 (2070). Basecase applies the current climate throughout the simulation and does not include future development. The CC scenario incorporates climate change but not future development. The CC and D scenario incorporates climate change and the high development rate. The CC and low D scenario incorporates climate change and the low development rate. Alternate route is the same as CC and D except that an alternative route is used for roads to the Ring of Fire mining region.

include a focus on single factors such as habitat quality or harvest level, inappropriate spatial and temporal scales of simulation and assessment, and a failure to address indirect effects such as multispecies dynamics (Therivel and Ross 2007, Schultz 2010, Noble 2014, Council of Canadian Academies 2019). We sought to address these limitations, and reached conclusions that were not feasible if we had focused on habitat assessment and smaller scales. For example, the biggest stressor facing caribou viability is the indirect effect of warmer winters supporting northwards expansion of moose, resulting in higher wolf populations and therefore greater predation pressure on caribou. This stressor does not mean that direct effects (e.g., changes to habitat caused by disturbance through land use and fire) are irrelevant; on the contrary, it means that caribou are likely to be even more sensitive to habitat disturbance in future decades because its effects will be cumulative to the indirect effects of climate change. As a result, management thresholds derived from simple empirical relationships between key vital rates and disturbance (ECCC 2011) risk overestimating the amount of disturbance that can occur within

a range before the probability of caribou persistence drops below desirable levels.

Focusing solely on caribou habitat assessment would have missed the indirect effect of climate change because warmer winters have little effect on caribou habitat, except perhaps for higher fire rates and increased frequency of icing or deep snow events that could limit forage access (Vors and Boyce 2009). Therefore, our analysis demonstrates that substantially different conclusions can arise when assessments incorporate population dynamics of multiple interacting species and focus on population responses at meaningful spatial and temporal scales.

A challenge with our approach is that it encounters substantial complexity. We argue, however, that it is better to grapple with the complexity than to ignore it because it provides insights and forces us to be explicit about uncertainties that impede wildlife management. Recent studies by Johnson et al. (2019) and Fryxell et al. (2020) have also addressed caribou conservation problems by developing relatively complex, multispecies models. Although a complex model is required to account for multiple factors in the moose-wolf-caribou system, the concept of parsimony still applies, where the model should include necessary parameters and relationships but only enough complexity to sufficiently address the key questions and to gain insight into conservation options. The spatially explicit population dynamics model that we developed accounted for key ecological components and relationships in the moose-wolf-caribou system, including a northward shifting climate envelope, a spatially expanding moose population, increasing predation risk from wolves, reduced caribou carrying capacity from resource development and linear features, and response of the caribou population to these influencing factors.

Model Limitations, Sensitivity, and Critical Uncertainties

Parameters and modeled relationships are also the principal source of limitations to the model. For example, although we modeled how a changing climate and disturbance would affect moose carrying capacity, we did not directly model the effects of increasing winter tick (*Dermacentor albipictus*) infection rate or increasing exposure to brainworm (*Parelaphostrongylus tenuis*), which could decrease moose carrying capacity as climate warms, with the effects following a non-linear spatial pattern reflecting climate gradients (Jones et al. 2019, Weiskopf et al. 2019). Other parameters such as Indigenous harvest rates need further research. The effect of deer moving northward on wolf populations (Kennedy-Slaney et al. 2018) and the effect of roads on hunting mortality and caribou dispersal patterns could also be considered.

One of the important outcomes of the modeling process is to identify parameters and relationships where uncertainty is critical, and sensitivity is high (Walters 1986). Such relationships should ultimately become the focus of future research and well-targeted monitoring to better understand the cumulative effects (Johnson et al. 2005, Burton

Table 2. Annual population growth (λ) estimates of caribou in northern Ontario from the population dynamics model (PopDyn) model in this study, the State of Resource (SoR) report, and as reported by Fryxell et al. (2020).

Caribou range	Ecozone	PopDyn[a]	SoR[b]	Fryxell[c]
James Bay	Hudson Bay Lowlands	0.99	0.94	0.96
Missisa	Lowlands and Shield	0.98	0.86	0.97
Ozhiski	Northern Shield	0.97	NE[d]	0.97
Spirit	Northern Shield	0.98	0.95	0.97
Swan	Northern Shield	1.00	NE	0.97
Berens	Northern Shield	0.96	0.93	0.84
Kinloch	Northern Shield	0.94	0.95	0.96
$\bar{x}$	Northern Shield and Lowlands	0.97		0.95
Pagwachuan	Southern Shield	0.93	0.94	0.89
Churchill	Southern Shield	0.91	0.96	0.84
Kesagami	Southern Shield	0.91	0.94	0.89
Brightsand	Southern Shield	0.83	0.87	0.85
Nipigon	Southern Shield	0.88	0.98	0.85
Sydney	Southern Shield	0.92	0.98	0.96
$\bar{x}$	Southern Shield	0.90		0.88

[a] Estimated λ from PopDyn model for 2010–2060.
[b] Estimated λ as reported in the State of the Woodland Caribou Resource report (Ontario Ministry of Natural Resources and Forestry 2014b) based on averages for a 2–4-year period prior to 2012, except for James Bay (1998–2012).
[c] Estimated λ from a population viability analysis model in Fryxell et al. (2020) for 2012–2014.
[d] NE = not estimated.

et al. 2014, Winder et al. 2020). Our study revealed that small changes in recruitment and mortality rates can cascade to large changes in predicted population response. This includes the modeled relationship between wolf density and moose density that leads to changes in caribou mortality rate. Consequently, we suggest that future long-term environmental monitoring should focus on model outcomes (e.g., the overall caribou population response) but should be structured to improve estimates of key model inputs, which in this case includes survival and fecundity rates, and important modeled relationships. This focus will ultimately improve estimates of how vital rates respond to habitat change and other development pressures, predictions of population change, and overall confidence in the modeled outcomes at appropriate scales.

Model Structure and Comparisons

Recently Fryxell et al. (2020) reported on a spatially explicit individual-based model for population viability analysis that incorporated individual animal movement, and examined how the threat to caribou sustainability increases as wolf predation increases in response to anthropogenic disturbance and the related increase in moose density. In our cellular spatially explicit model, we did not model individuals (agents) but rather modeled cells as subpopulations, spatially modeling (and mapping) dispersal from a 10-km² cell as carrying capacity within the cell is approached. This adds ecological realism unaddressed in non-spatial models for which density-dependent feedback occurs only when K is approached across the entire study area. Realism is also added through age-specific dispersal, which was important when modeling wolf dynamics

because generally only the yearling age class will disperse to seek out a new wolf pack (Forshner 2000, Kojola et al. 2006). A principal outcome of the models are estimates of long-term population growth (λ) for caribou under alternative climate change and development scenarios. Estimates of λ by Fryxell et al. (2020) were similar to our model estimates at the caribou range scale, with generally <5% difference in the estimates (Table 2). The largest differences in λ were for the Berens and Churchill ranges where our estimates were 12% and 7% higher than Fryxell et al. (2020), respectively. In addition, empirical estimates of λ based on population surveys reported in the State of the Caribou Resource report (MNRF 2014b) were within a 6% difference for 8 of the 10 caribou ranges with data, and within a 10% and −12% difference for the Nipigon and Missisa ranges, respectively (Table 2; Appendix C).

The Fryxell et al. (2020) model focused on anthropogenic disturbance in northern Ontario resulting from logging; however, the authors also noted the importance for future studies to consider the effects of climate change on moose populations and wolf predation. Although our model was linked to a simulation of forest harvest conforming to the Dynamic Caribou Harvesting Scheduling strategy (MNR 2009), it was also responsive to a shifting climate envelope for moose and the resulting increased predation on caribou, and simulated development of roads and other linear features caused by forest harvest, mineral exploration, and development of mines. This responsiveness is important from a conservation planning perspective because forestry will not likely be a significant activity in low-productivity areas north of the current industrial forest, where effects related to mining development activity such as the proposed Ring of Fire will be more strongly related to an increase in anthropogenic linear features (Carlson and Chetkiewicz 2013, Rempel et al. 2016). Areas with productive soil just north of the current industrial forest, however, may experience new forestry initiatives as new northern roads are created.

MANAGEMENT IMPLICATIONS

Our model illustrates the risk to resource management of using decision support tools that represent an insufficient portion of the system, fail to address cumulative effects, or make assessments at inappropriate scales. For example, if our simulations had not considered the potential for climate warming to cause moose population growth, we would have substantially underestimated potential caribou population decline at the range scale. At the local (project) scale, however, habitat disturbance by development was a principal factor influencing the caribou population response, highlighting the need to address habitat and sources of mortality at fine scales. Our simulations suggest that Ontario's boreal woodland caribou population is likely to continue to decline in the absence of management strategies that address the cumulative effects (at multiple scales) of climate change and development to the region's moose-wolf-caribou system. The modeling framework we developed can provide resource managers, Indigenous Peoples, and stakeholders with valuable information to better understand the combined

influences of global stressors like climate change, in the context of industrial development, on risk to important values such as caribou and Indigenous food security. The framework can also support regional assessments under a risk analysis, and development of risk reduction and recovery strategies.

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LITERATURE CITED

Adamczewski, J. Z., M. J. Carlson, C. J. Daniel, A. Gunn, C. J. Johnson, J. S. Nishi, D. E. Russell, J. B. Stelfox, and D. Taylor. 2016. Development of modeling tools to address cumulative effects on the summer range of the Bathurst caribou herd—a demonstration project. <https://www.enr.gov.nt.ca/sites/enr/files/tools_address_effects_bathurst_caribou.pdf.pdf>. Accessed 25 Mar 2021.

Alces Group. 2017. ALCES online user guide. <https://alces.ca/media/files/420.pdf>. Accessed 25 Mar 2021.

Bergerud, 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, Dordrecht, Netherlands.

Bergerud, A., and J. Elliot. 1986. Dynamics of caribou and wolves in northern British Columbia. Canadian Journal of Zoology 64:1515–1529.

Bernier, P. Y., S. Gauthier, P.-O. Jean, F. Manka, Y. Boulanger, A. Beaudoin, and L. Guindon. 2016. Mapping local effects of forest properties on fire risk across Canada. Forests 7:157.

Boulanger, Y., S. Gauthier, and P. J. Burton. 2014. A refinement of models projecting future Canadian fire regimes using homogeneous fire regime zones. Canadian Journal of Forest Research 44:365–376.

Burton, A. C., D. Huggard, E. Bayne, J. Schieck, P. Sólymos, T. Muhly, D. Farr, and S. Boutin. 2014. A framework for adaptive monitoring of the cumulative effects of human footprint on biodiversity. Environmental Monitoring and Assessment 186:3605–3617.

Cairns, D. G. 2020. PopDyn Repository. <https://github.com/ieg-tech/popdyn.git.>. Accessed 25 Mar 2021.

Canadian Council of Ministers of the Environment. 2009. Regional strategic environmental assessment in Canada: principles and guidance. Canadian Council of Ministers of the Environment, Winnipeg, Manitoba, Canada.

Carlson, M., and C. Chetkiewicz. 2013. A fork in the road, future development in Ontario's far north. <https://www.wcscanada.org/Portals/96/Documents/alces-lowres.pdf>. Accessed 25 Mar 2021.

Carlson, M., and J. B. Stelfox. 2014. Alberta oil sands development and risk management of Canadian boreal ecosystems. Pages 219–244 in J. E. Gates, D. L. Trauger, and B. Czech, editors. Peak oil, economic growth, and wildlife conservation. Springer, New York, New York, USA.

Carlson, M., B. Stelfox, N. Purves-Smith, J. Staraker, S. Berryman, T. Barker, and B. Wilson. 2014. ALCES Online: Web-delivered scenario analysis to inform sustainableland-use decisions. <https://scholarsarchive.byu.edu/cgi/viewcontent.cgi?article=1276&context=iemssconference&httpsredir=1&referer=>. Accessed 25 Mar 2021.

Chetkiewicz, C., M. Carlson, C. O'Connor, B. Edwards, M. Southee, and M. Sullian. 2017. Assessing the potential cumulative impacts of land use and climate change on freshwater fish in northern Ontario. Wildlife Conservation Society Canada, Toronto, Ontario, Canada.

Clarke, K. 2014. Cellular automata and agent-based models. Springer-Verlag, Berlin, Germany.

Council of Canadian Academies. 2019. Greater than the sum of tts parts: toward integrated natural resource management in Canada. The expert panel on the state of knowledge and practice of integrated approaches to natural resource management in Canada. Council of Canadian Academies, Ottawa, Ontario, Canada.

Crête, M. 1989. Approximation of K carrying capacity for moose in eastern Quebec. Canadian Journal of Zoology 67:373–380.

Crins, W. J., P. A. Gray, P. W. Uhlig, and M. C. Wester. 2009. The ecosystems of Ontario, part 1: ecozones and ecoregions. Inventory, Monitoring and Assessment, SIB TER IMA TR-01. Ontario Ministry of Natural Resources, Peterborough, Canada.

Critchon, V. 1992. Six year (1986/87-1991/92) summary of in utero productivity of moose in Manitoba, Canada. Alces 28:203–214.

Cubaynes, S., D. R. MacNulty, D. R. Stahler, K. A. Quimby, D. W. Smith, and T. Coulson. 2014. Density-dependent intraspecific aggression regulates survival in northern Yellowstone wolves (Canis lupus). Journal of Animal Ecology 83:1344–1356.

Cumming, H., D. Beange, and G. Lavoie. 1996. Habitat partitioning between woodland caribou and moose in Ontario: the potential role of shared predation risk. Rangifer 16:81–94.

DeMars, C. A., and S. Boutin. 2018. Nowhere to hide: effects of linear features on predator–prey dynamics in a large mammal system. Journal of Animal Ecology 87:274–284.

Doelle, M. 2018. The proposed new Federal Impact Assessment Act (IAA) under Bill C-69: assessment & reform proposals. <https://doi.org/10.2139/ssrn.3134139>. Accessed 27 Apr 2021.

Duinker, P. N., and L. A. Greig. 2006. The impotence of cumulative effects assessment in Canada: ailments and ideas for redeployment. Environmental Management 37:153–161.

Elk Valley Cumulative Effects Management Framework Working Group. 2018. Elk Valley cumulative effects assessment and management report. <https://www2.gov.bc.ca/assets/gov/environment/natural-resource-stewardship/cumulative-effects/draft_elk_valley_ceam_12122018_draft.pdf>. Accessed 25 Mar 2021.

Environment and Climate Change Canada [ECCC]. 2011. Scientific assessment to inform the identification of critical habitat for woodland caribou (Rangifer tarandus caribou), boreal population, in Canada: 2011 update. <https://www.registrelep-sararegistry.gc.ca/document/doc2248p/sec2_st_caribou_e.cfm>. Accessed 25 Mar 2021.

Environment and Climate Change Canada [ECCC]. 2012. Woodland caribou (Rangifer tarandus caribou), boreal population: recovery strategy 2012. <https://www.canada.ca/en/environment-climate-change/services/species-risk-public-registry/recovery-strategies/woodland-caribou-boreal-population-2012.html>. Accessed 25 Mar 2021.

Environment and Climate Change Canada [ECCC]. 2017. Second generation Canadian Earth System Model. <https://www.ec.gc.ca/ccmac-cccma/default.asp?lang=En&n=1A3B7DF1-1&wbdisable=false>. Accessed 25 Mar 2021.

Environment and Climate Change Canada [ECCC]. 2021. Decision from the Minister of Environment and Climate Change concerning Regional Assessment. <https://www.ceaa.gc.ca/050/documents/p80468/133830E.pdf>. Accessed 25 Mar 2021.

Esri. 2020. ArcGIS World Imagery. <https://services.arcgisonline.com/ArcGIS/rest/services/World_Imagery/MapServer>. Accessed 25 Mar 2021.

Falcucci, A., P. Ciucci, L. Maiorano, L. Gentile, and L. Boitani. 2009. Assessing habitat quality for conservation using an integrated occurrence-mortality model. Journal of Applied Ecology 46:600–609.

Far North Science Advisory Panel. 2010. Science for a changing far north. <https://collections.ola.org/mon/24006/302262.pdf>. Accessed 27 Apr 2021.

Forshner, A. 2000. Population dynamics and limitation of wolves (*Cunis lupus*) in the Greater Pukaskwa Ecosystem, Ontario. Thesis, University of Alberta, Edmonton, Canada.

Fryxell, J. M., T. Avgar, B. Liu, J. A. Baker, A. R. Rodgers, J. Shuter, I. D. Thompson, D. E. Reid, A. M. Kittle, and A. Mosser. 2020. Anthropogenic disturbance and population viability of woodland caribou in Ontario. Journal of Wildlife Management 84:636–650.

Gedir, J. V., J. W. Cain III, G. Harris, and T. T. Turnbull. 2015. Effects of climate change on long-term population growth of pronghorn in an arid environment. Ecosphere 6:1–20.

Government of Canada. 2008. Treaty Texts—Treaty No. 9. <https://www.rcaanc-cirnac.gc.ca/eng/1100100028863/1581293189896>. Accessed 25 Mar 2021.

Hall, J., D. Reid, N. Buda, and L. Hunt. 2016. Regeneration along forest access roads in response to various treatments applied in northwestern Ontario. Science and Research Technical Report TR-12, Thunder Bay, Ontario, Canada.

Harrington, F. H., L. D. Mech, and S. H. Fritts. 1983. Pack size and wolf pup survival: their relationship under varying ecological conditions. Behavioral Ecology and Sociobiology 13:19–26.

Hayes, R., and A. Harestad. 2000. Wolf functional response and regulation of moose in the Yukon. Canadian Journal of Zoology 78:60–66.

Hornseth, M. L., and R. S. Rempel. 2016. Seasonal resource selection of woodland caribou (*Rangifer tarandus caribou*) across a gradient of anthropogenic disturbance. Canadian Journal of Zoology 94:79–93.

Impact Assessment Agency of Canada. 2021. Regional assessment under the Impact Assessment Act. <https://www.canada.ca/en/impact-assessment-agency/services/policy-guidance/regional-assessment-impact-assessment-act.html>. Accessed 25 Mar 2021.

Iturbide, M., J. M. Gutiérrez, L. M. Alves, J. Bedia, R. Cerezo-Mota, E. Cimadevilla, A. S. Cofiño, A. Di Luca, S. H. Faria, and I. V. Gorodetskaya. 2020. An update of IPCC climate reference regions for subcontinental analysis of climate model data: definition and aggregated datasets. Earth System Science Data 12:2959–2970.

James, A. R., S. Boutin, D. M. Hebert, and A. B. Rippin. 2004. Spatial separation of caribou from moose and its relation to predation by wolves. Journal of Wildlife Management 68:799–809.

Johnson, C. J., M. S. Boyce, R. L. Case, H. D. Cluff, R. J. Gau, A. Gunn, and R. Mulders. 2005. Cumulative effects of human developments on arctic wildlife. Wildlife Monographs 160:1–36.

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, C. J., and D. R. Seip. 2008. Relationship between resource selection, distribution, and abundance: a test with implications to theory and conservation. Population Ecology 50:145–157.

Johnson, C. J., O. Venter, J. C. Ray, and J. E. Watson. 2020. Growth-inducing infrastructure represents transformative yet ignored keystone environmental decisions. Conservation Letters 13:e12696.

Jones, H., P. Pekins, L. Kantar, I. Sidor, D. Ellingwood, A. Lichtenwalner, and M. O'Neal. 2019. Mortality assessment of moose (*Alces alces*) calves during successive years of winter tick (*Dermacentor albipictus*) epizootics in New Hampshire and Maine (USA). Canadian Journal of Zoology 97:22–30.

Kennedy-Slaney, L., J. Bowman, A. A. Walpole, and B. A. Pond. 2018. Northward bound: the distribution of white-tailed deer in Ontario under a changing climate. Wildlife Research 45:220–228.

Kennett, S. A. 1999. Towards a new paradigm for cumulative effects management. Occasional Paper No. 8 (Calgary: Canadian Institute of Resources Law). <https://prism.ucalgary.ca/handle/1880/47201>. Accessed 27 Apr 2021.

Kimiti, K. S., D. Western, J. S. Mbau, and O. V. Wasonga. 2018. Impacts of long-term land-use changes on herd size and mobility among pastoral households in Amboseli ecosystem, Kenya. Ecological Processes 7:4.

Kittle, A. M., M. Anderson, T. Avgar, J. A. Baker, G. S. Brown, J. Hagens, E. Iwachewski, S. Moffatt, A. Mosser, B. R. Patterson, et al. 2015. Wolves adapt territory size, not pack size to local habitat quality. Journal of Animal Ecology 84:1177–1186.

Kojola, I., J. Aspi, A. Hakala, S. Heikkinen, C. Ilmoni, and S. Ronkainen. 2006. Dispersal in an expanding wolf population in Finland. Journal of Mammalogy 87:281–286.

Maxie, A. J., K. F. Hussey, S. J. Lowe, K. R. Middel, B. A. Pond, M. E. Obbard, and B. R. Patterson. 2010. A comparison of forest resource inventory, provincial land cover maps and field surveys for wildlife habitat analysis in the Great Lakes–St. Lawrence forest. Forestry Chronicle 86:77–86.

McDermid, J., S. Fera, and A. Hogg. 2015. Climate change projections for Ontario: an updated synthesis for policymakers and planners. Ontario Ministry of Natural Resources and Forestry, Peterborough, Canada.

Messier, F. 1994. Ungulate population models with predation: a case study with the North American moose. Ecology 75:478–488.

Mora, C., R. Metzger, A. Rollo, and R. A. Myers. 2007. Experimental simulations about the effects of overexploitation and habitat fragmentation on populations facing environmental warming. Proceedings of the Royal Society B: Biological Sciences 274:1023–1028.

Nelson, M. P., J. A. Vucetich, R. O. Peterson, and L. M. Vucetich. 2011. The Isle Royale Wolf–Moose Project (1958-present) and the wonder of long-term ecological research. Endeavour 35:31.

Neufeld, B. T., C. Superbie, R. J. Greuel, T. Perry, P. A. Tomchuk, D. Fortin, and P. D. McLoughlin. 2021. Disturbance-mediated apparent competition decouples in a northern boreal caribou range. Journal of Wildlife Management 85:254–270.

Noble, B. F. 2014. Cumulative environmental effects and the tyranny of small decisions: towards meaningful cumulative effects assessment and management. Natural Resources and Environmental Studies Institute Occasional Paper No. 8, University of Northern British Columbia, Prince George, Canada.

Noble, B. F. 2015. Cumulative effects research: achievements, status, directions and challenges in the Canadian context. Journal of Environmental Assessment Policy and Management 17:1550001.

Ontario GeoHub. 2020. Ontario Imagery Web Map Service (OIWMS). <https://geohub.lio.gov.on.ca/datasets/101295c5d3424045917bdd476f322c02>. Accessed 25 Mar 2021.

Ontario Ministry of Energy Northern Development and Mines [ENDM]. 2012. Closure plan. <https://www.mndm.gov.on.ca/en/mines-and-minerals/mining-sequence/evaluation/advanced-exploration/closure-plan>. Accessed 25 Mar 2021.

Ontario Ministry of Energy Northern Development and Mines [ENDM]. 2021. OGSEarth. <https://www.mndm.gov.on.ca/en/mines-and-minerals/applications/ogsearth>. Accessed 25 Mar 2021.

Ontario Ministry of Natural Resources [MNR]. 2009. Ontario's Woodland Caribou Conservation Plan. <https://www.ontario.ca/page/woodland-caribou-conservation-plan>. Accessed 25 Mar 2021.

Ontario Ministry of Natural Resources [MNR]. 2012. Provincial satellite derived disturbance mapping data specifications. <https://www.sdc.gov.on.ca/sites/MNRF-PublicDocs/EN/CMID/Provincial_Satellite_Derived_Disturbance_Mapping-FarNorth.pdf>. Accessed 25 Mar 2021.

Ontario Ministry of Natural Resources and Forestry [MNRF]. 2014a. Far north land cover data specifications, version 1.4. <https://data.ontario.ca/dataset/8afe0aa1-6d6f-402f-8f7a-04f90d733432/resource/8c90d397-93e2-442c-8745-a93e5087eb65/download/far_north_land_cover_-_data_specification.pdf>. Accessed 25 Mar 2021.

Ontario Ministry of Natural Resources and Forestry [MNRF]. 2014b. State of the Woodland Caribou Resource Report. <https://www.ontario.ca/page/state-woodland-caribou-resource-report-part-2>. Accessed 25 Mar 2021.

Ontario Ministry of Natural Resources and Forestry [MNRF]. 2018a. Forest management: boreal landscapes. <https://www.ontario.ca/page/forest-management-boreal-landscapes>. Accessed 25 Mar 2021.

Ontario Ministry of Natural Resources and Forestry [MNRF]. 2018b. Range Management Policy in support of woodland caribou conservation and recovery. <https://www.ontario.ca/page/range-management-policy-support-woodland-caribou-conservation-and-recovery>. Accessed 25 Mar 2021.

Ontario Ministry of Natural Resources and Forestry [MNRF]. 2020. Sustainable growth: Ontario's forest sector strategy. <https://www.ontario.ca/page/sustainable-growth-ontarios-forest-sector-strategy>. Accessed 25 Mar 2021.

Peterson, R. O. 1977. Wolf ecology and prey relationships on Isle Royale. Department of the Interior, National Park Service, Washington, D.C., USA.

Rempel, R. S. 2011. Effects of climate change on moose populations: exploring the response horizon through biometric and systems models. Ecological Modelling 222:3355–3365.

Rempel, R. S., R. W. Mackereth, A. R. Rodgers, E. P. Iwachewski, P. D. Furlong, J. S. Hagens, J. L. Shuter, J. M. Jackson, R. S. Kushneriuk, and D. J. McCormick. 2016. Support for development of a long term environmental monitoring strategy for the Ring of Fire area. Ontario Ministry of Natural Resources and Forestry, Peterborough, Canada.

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

Schultz, C. 2010. Challenges in connecting cumulative effects analysis to effective wildlife conservation planning. BioScience 60:545–551.

Serrouya, R., B. N. McLellan, S. Boutin, D. R. Seip, and S. E. Nielsen. 2011. Developing a population target for an overabundant ungulate for ecosystem restoration. Journal of Applied Ecology 48:935–942.

Spectranalysis. 2004. Introduction to the Ontario Land Cover Database second edition (2000): outline of production methodology and description of 27 land cover classes. Ontario Ministry of Natural Resources, Peterborough, Canada.

Street, G. M., L. M. Vander Vennen, T. Avgar, A. Mosser, M. L. Anderson, A. R. Rodgers, and J. M. Fryxell. 2015. Habitat selection following recent disturbance: model transferability with implications for management and conservation of moose (*Alces alces*). Canadian Journal of Zoology 93:813–821.

Symes, W. S., D. P. Edwards, J. Miettinen, F. E. Rheindt, and L. R. Carrasco. 2018. Combined impacts of deforestation and wildlife trade on tropical biodiversity are severely underestimated. Nature Communications 9:1–9.

Tews, J., M. Ferguson, and L. Fahrig. 2007. Modeling density dependence and climatic disturbances in caribou: a case study from the Bathurst Island complex, Canadian High Arctic. Journal of Zoology 272:209–217.

Theobald, D. M., J. R. Miller, and N. T. Hobbs. 1997. Estimating the cumulative effects of development on wildlife habitat. Landscape and Urban Planning 39:25–36.

Therivel, R., and B. Ross. 2007. Cumulative effects assessment: Does scale matter? Environmental Impact Assessment Review 27:365–385.

Vors, L. S., and M. S. Boyce. 2009. Global declines of caribou and reindeer. Global Change Biology 15:2626–2633.

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

Walker, P. D., A. R. Rodgers, J. L. Shuter, I. D. Thompson, J. M. Fryxell, J. G. Cook, R. C. Cook, and E. H. Merrill. 2021. Comparison of woodland caribou calving areas determined by movement patterns across northern Ontario. Journal of Wildlife Management 85:169–182.

Walters, C. J. 1986. Adaptive management of renewable resources. Macmillan Publishers, New York, New York, USA.

Wang, X., G. Huang, and J. Liu. 2016. Observed regional climatic changes over Ontario, Canada, in response to global warming. Meteorological Applications 23:140–149.

Webequie First Nation. 2021. The Webequie Supply Road Project. <https://www.supplyroad.ca/the-project/>. Accessed 25 Mar 2021.

Weiskopf, S. R., O. E. Ledee, and L. M. Thompson. 2019. Climate change effects on deer and moose in the Midwest. Journal of Wildlife Management 83:769–781.

Wilmers, C. C., E. Post, R. O. Peterson, and J. A. Vucetich. 2006. Predator disease out-break modulates top-down, bottom-up and climatic effects on herbivore population dynamics. Ecology Letters 9:383–389.

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.

Wittmer, H. U., B. N. McLellan, R. Serrouya, and C. D. Apps. 2007. Changes in landscape composition influence the decline of a threatened woodland caribou population. Journal of Animal Ecology 76:568–579.

Yemshanov, D., R. G. Haight, R. Rempel, N. Liu, and F. H. Koch. 2020. Protecting wildlife habitat in managed forest landscapes—How can network connectivity models help? Natural Resource Modeling 34: e12286.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's website.

APPENDIX A: VITAL RATE AND DISPERSAL VALUES

We modeled the relationship between wolf density and moose predation rate as:

$$a = 3.36x/0.46 + x$$

$$Y = 0.365aw/x,$$

where Y is predation rate on moose, defined by Messier (1994) as total response (i.e., daily kill rate times wolf density, divided by moose density), a is wolf daily kill rate, w is predicted wolf density per 1,000 km², x is moose density (per km²), and 0.365 is a factor to convert daily kill rate to annual rate. We used an adjustment (Y^1) to slightly increase predation rates (converted to proportions) based on modeling results from Hayes and Harestad (2000) who reported that predation rates can be higher than rates estimated by Messier (1994) when moose densities are less than about 1 moose/km². Wolf densities in the simulation were generally <6.5 wolves/1,000 km². Our model used moose

Table A1. Fixed vital rate and dispersal values used in the population dynamics (PopDyn) model in a moose-wolf-caribou system in northern Ontario, Canada, for simulations spanning 2020–2070.

Species and parameter	Age class				
	Young of year	Yearling	Young adult	Mature adult	Old
Wolves (age range of class [yr])		0–1		2–8	9–12
Dispersal inter-habitat (km)		14		14	14
Dispersal outward (km)		75		75	75
Fecundity[a] (SE)				0.5 (0.01)	0.5 (0.01)
Fecundity reduction[b] (start, max.)				0.5, 0.20	0.5, 0.20
Mortality natural		0.1		0.1	0.1
Mortality density dependent[b] (start, max.)		0.5, 0.2		0.5, 0.3	0.5, 0.4
Moose (age range of class [yr])	0	1	2–3	4–7	8–12
Dispersal inter-habitat (km)	14	14	14	14	14
Dispersal outward (km)	25	25	25	25	25
Fecundity[a] (SE)		0.7, (0.01)	1, (0.01)	1.3, (0.01)	1, (0.01)
Fecundity reduction[b] (start, max)		0.5, 0.25	0.5, 0.25	0.5, 0.25	0.5, 0.25
Mortality natural	0.2	0.02	0.02	0.02	0.16
Morality recreational hunting (male)	0.083	0.083	0.113	0.113	0.113
Morality recreational hunting (female)	0.083	0.083	0.033	0.033	0.033
Morality Indigenous hunting	0.1	0.1	0.1	0.1	0.1
Mortality density dependent[b] (start, max.)	0.5, 0.2	0.5, 0.2	0.5, 0.2	0.5, 0.2	0.5, 0.2
Caribou (age range of class [yr])	0	1		2–8	9–15
Dispersal inter-habitat (km)	15	15		15	15
Dispersal outward (km)	174	174		174	174
Fecundity[a] (SE)				0.84, (0.01)	0.80, (0.01)
Fecundity reduction[b] (start, max.)				0.50, 0.25	0.50, 0.25
Mortality natural	0.05	0.05		0.05	0.05
Mortality Indigenous hunting	0.1	0.1		0.1	0.1
Mortality density dependent[b] (start, max.)	0.6, 0.1	0.6, 0.2		0.6, 0.3	0.6, 0.4

[a] Where stochasticity in the parameter has been included, the standard error (SE) for generating a normal random deviate is specified.
[b] Where density dependence in the parameter is included, the N to carrying capacity (K) ratio when density dependence begins (start), and the maximum proportional decrease in the parameter (max.) is specified.

Table A2. Relationship between wolf density and moose predation rate for an integrated population dynamics (PopDyn) model for a moose-wolf-caribou system in northern Ontario, Canada, 2020–2070.

Moose/km² (x)	Wolves/1,000 km² (w)	Moose predation rate (Y)	Adjusted moose predation rate (Y^1)
0.05	2.6[a]	6%	0.04
0.11	6.5	14%	0.13
0.18	10.3	20%	0.20
0.26	14.2	25%	0.26
0.37	18.1	27%	0.29
0.49	21.9	27%	0.31
0.64	25.8	29%	0.31
0.83	29.7	28%	0.31
1.08	33.5	27%	0.29
1.43	37.4	25%	0.27

[a] For the lowest moose density (0.05) the predicted wolf density was approximately 1.5, but we increased it to 2.6 based on empirical studies in Alaska reported in Messier (1994), which is consistent with wolf densities found in the areas of lowest moose density in the study area.

Table A3. Partitioning overall predation into rates for young caribou versus adults for an integrated population dynamics (PopDyn) model for a moose-wolf-caribou system in northern Ontario, Canada, 2020–2070.

Wolves/ 1,000 km² (w)	Caribou predation rate (Y)	Young of year and yearling predation rate	Mature and old predation rate
0	0	0	0
0.29	0.07	0.09	0.022
0.58	0.11	0.18	0.044
0.87	0.16	0.27	0.066
1.16	0.21	0.36	0.088
1.45	0.26	0.45	0.110
1.74	0.31	0.54	0.132
2.03	0.37	0.63	0.154
2.32	0.43	0.72	0.176
2.61	0.50	0.81	0.198

Table A4. Relationship between moose density, predicted wolf density, and relative carrying capacity (K) for wolves for an integrated population dynamics (PopDyn) model for a moose-wolf-caribou system in northern Ontario, Canada, 2020–2070.

Moose/km² (x)	Wolves/1,000 km² (w^1)	Relative K
0.020	0.00	0.12
0.044	1.06	0.22
0.089	4.23	0.32
0.133	7.01	0.42
0.178	9.57	0.52
0.222	11.84	0.62
0.266	13.91	0.72
0.311	15.85	0.82
0.355	17.58	0.92
0.400	19.22	1.00

density to determine adjusted predation rate (Y^1) for the simulation (Table A2).

We simulated predation as an inter-species dynamic based on the Bergerud and Elliot (1986) modeled relationship between wolf population and caribou mortality rate, where w is number of wolves/1,000 km² and Y is mortality (%):

$$Y = 4.766 + 0.699w^{1.275}.$$

We partitioned the predicted caribou predation rate between younger and older age classes by a factor of approximately 1.7, which increased predation rate on the young of year and yearlings and decreased it for the oldest age classes.

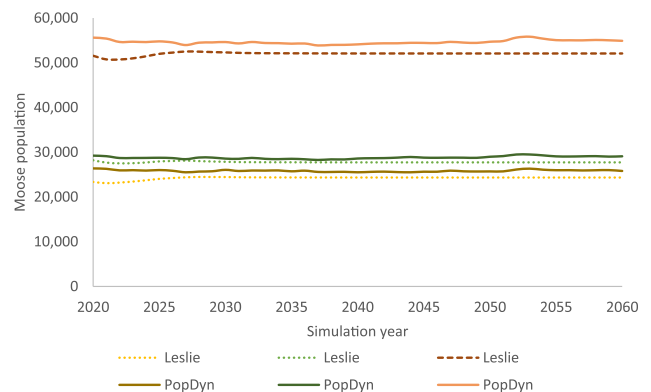Our model used wolf density (w) to determine age-group-specific predation rates in the simulation.

We modeled wolf relative carrying capacity (K) as a function of the numerical response to moose density, as described by Messier (1994), where $x =$ number of moose/km², $w =$ log number of wolves/1,000 km² based on log10-transformed modified Michaelis-Menten equation, and $w^1 = 10^w$:

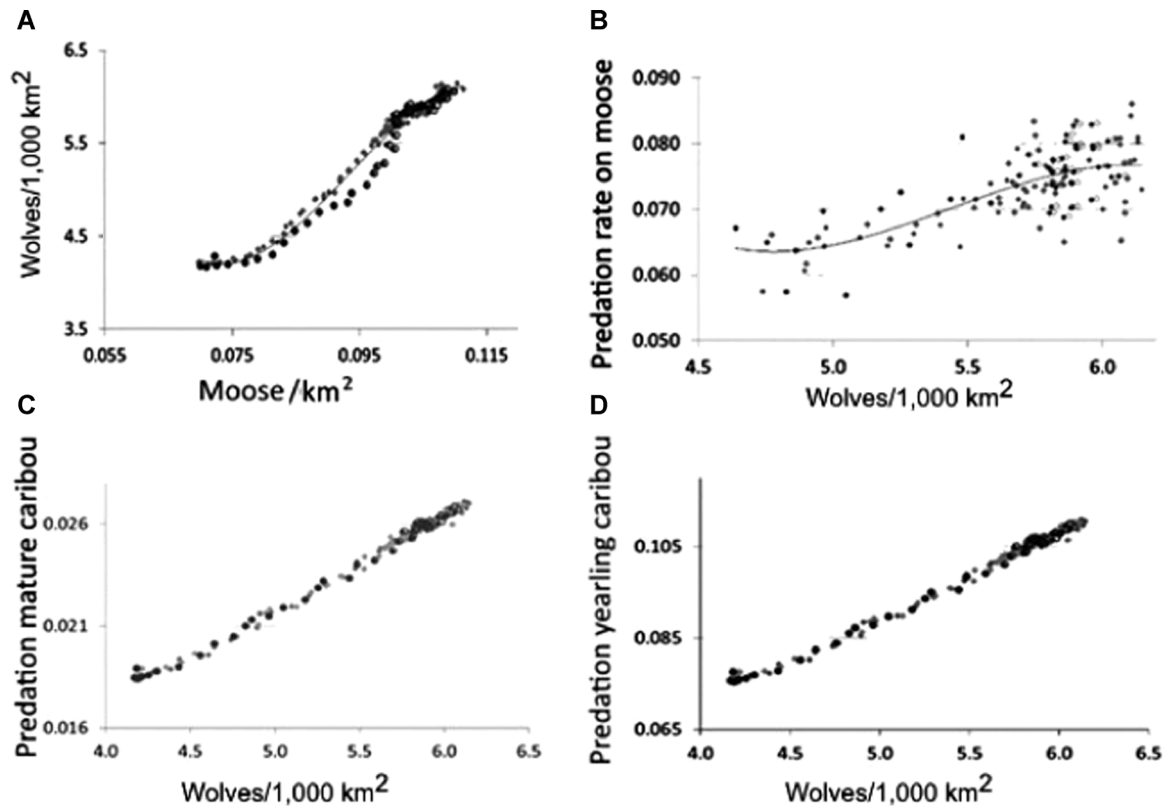$$w = log10\left(\frac{58.7(x - 0.03)}{0.76 + (x - 0.03)}\right).$$

Our model used moose density (x) to determine wolf relative K for the simulation.

APPENDIX B: MODEL VERIFICATION

Comparison of PopDyn output for the moose model with output from a modified Leslie-Lefkovitch stage projection matrix model. For this comparison only, the PopDyn model was simplified to use a static climate projection and no new development or spatial expansion of the population to allow for comparison with the simple matrix model. The PopDyn model included a slight amount of stochastic variation in fecundity rate.

Figure B1. Comparison of moose population output from a modified Leslie-Lefkovitch stage-projection matrix model versus a PopDyn model for males, females, and total population at the scale of the full study area under the scenario of no new development and stable climate in northern Ontario, Canada, 2020.

Figure B2. Density (numerical) and predation (functional) responses for wolves, moose, and caribou in northern Ontario, Canada, across a range of simulated conditions spanning 2020–2070: A) numerical response of wolf density to increasing moose density; B) functional response of wolf predation on moose to increasing wolf density; C) response of wolf predation rate on mature caribou to increasing wolf density; D) response of wolf predation rate on yearling caribou to increasing wolf density.

APPENDIX C: CARIBOU RANGES

Figure C1. Name and location of northern Ontario, Canada, caribou ranges included in the study area simulation (2020).