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Effects of climate change on moose populations: Exploring the response horizon through biometric and systems models

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ABSTRACT

Interest in the response of moose to climate change has increased because of the potential role they play in the conservation of woodland caribou, and threatened loss to recreational and economic opportunities. The objective of this study is to develop a plausible, parsimonious, systems-level model of moose population dynamics that will be useful in exploring the response of moose populations to climate projections. The study begins with a statistical model of moose carrying capacity, which is then integrated into a systems-level model that predicts moose density based on explicit causal factors. Scenario analysis was conducted using a variety of assumptions concerning biotic and abiotic interactions, and under the A2 climate scenario all model scenarios predict a decline of moose density at the southern limits of the Ontario distribution and an increase at the northern extents. Predicted declines are a result of lower carrying capacity and higher heat stress, parasite loads and wolf predation. Given the sensitivity of the model to density-dependent factors, the indirect effect of parasites on decreased recruitment may have greater impact on moose than the direct effect of increased death rate. Results indicate that conservation planning for woodland caribou populations should account for possible increases in moose and wolf populations.

1. Introduction

The response of moose to possible climate change has important consequences both from ecosystem services and ungulate conservation perspectives, as moose continue to provide ecological, cultural, economic, and social benefits to society (Ontario Ministry of Natural Resources, 2009). Interest in the response of moose to climate change has increased because of the potential role they play in the conservation of woodland caribou. Increasing numbers of moose may bring along higher densities of wolf populations, resulting in higher predation rates on threatened caribou (Courtois and Ouellet, 2007). Climate affects moose both directly and indirectly. Temperature and precipitation influence the productivity of browse, the energy required to thermo-regulate in both winter and summer, and may also affect predator numbers and the influence of pests and disease on survivorship (Kelsall and Telfer, 1974; Thompson et al., 1998).

Exploring future change to moose populations is necessarily a modeling exercise, and there are three broad modeling approaches that can be taken: statistical inferential, matrix projection, and mechanistic systems modeling. A variety of statistical techniques, including parametric regression, generalized additive models, and maximum entropy modeling, have all been used to create climate envelope models (Hijmans and Grahm, 2006). The statistical approach is essentially an attempt to fit the data to the model, or if using Bayesian techniques, the model to the data. Causal relationships are inferred, but never explicitly stated in the covariance matrix (Shipley, 2000). Past environmental relationships are used to model the *fundamental* niche (or climate envelope), but because relationships are based on data collected under past conditions, using statistical models to guide future management has been likened to "driving down a road using your rear-view mirror to navigate" (Kimmins et al., 2007).

Matrix algebra techniques, such as age- or stage-specific projection models directly model mortality and fecundity rates, but each of these are essentially black-boxes that express a variety of processes influencing mortality and fecundity. Matrix models represent a static process-based modeling approach, and while the models can directly and elegantly estimate λ (finite rate of increase) from the matrix eigenvalue (e.g., Lenarz et al., 2010), dynamic feedback-loops that result from numerical and functional response of predators cannot easily be incorporated into the modeling framework.

In contrast, the dynamic systems approach attempts to model ecological processes as mechanistic causal relationships, and does not explicitly attempt to fit model-output to test observations. In

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this dynamic approach, moose population density emerges from processes such as recruitment, predation, and disease-induced death. The motivation is to define the *realized* niche of the species, where species interactions ultimately constrain the broad fundamental niche of the species. Model-fitting activities occur at the component level, where individual relationships are often established through statistical modeling and hypothesis testing (e.g., relationship between moose density and recruitment). From this perspective, systems-modeling is an extension of, not an alternative to statistical modeling. When extending the systems-model to a spatial-context, matrix algebra is employed for computational simplicity, but no analytical characteristics of the matrix are derived.

It is important to view all modeling results with appropriate scepticism, recognizing the insight of G.E.P. Box that even though all models are wrong, some models are useful. The objective of this study is to develop a plausible, parsimonious, systems-level model of moose population dynamics that will be useful in exploring the response of moose populations to future climate projections. This requires key processes be expressed with sufficient detail to explore model scenarios, while factors with less importance relative to the model objectives be omitted or specified with less detail. The study begins with development of a statistical model that estimates moose density as a function of broad climatic and vegetative variables, and then integrates this component into a systems model that predicts moose density based on a combination of density dependent and independent limiting factors. The model is then used to explore scenarios depicting different assumptions of biotic and abiotic interactions with climate change, and the consequences to moose distribution and abundance.

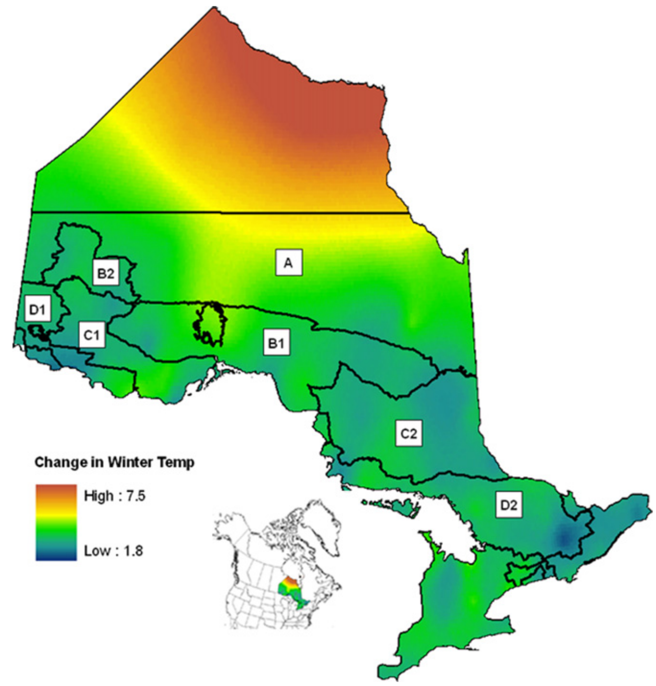

Fig. 1. Change in average winter temperature (AWT) (°C) from period 1971–2000 to period 2041–2070, with overlay of CEZ boundaries.

2. Methods

Moose density data was collected in Ontario using standard moose aerial inventory (MAI) procedures (Oswald, 1997) during two time periods: 2000–2006 for model development (2557 plots) and 1990–1999 for model testing (3284 plots). Plots are flown using helicopters or fixed-wing aircraft, and are generally north–south oriented plots 10 km by 2.5 km. Sex, age, and track aggregates are identified, but I used only total number of moose seen as the response variable for regression analysis. Plots are randomly assigned, with the exception that plots flown in the previous survey period are removed from the selection pool. Only 7.4% of the plots overlapped spatially between the two time periods, so the test data was largely independent from model development data in both time and space.

Two groups of explanatory variables were used for regression analysis: biotic (landcover) and climatic (temperature and precipitation). Through review of literature and discussion with experienced moose and forestry researchers and initial collinearity analysis, variables were selected based on their potential causal link to moose bioenergetics and productivity of browse. Selected biotic variables were (i) percent mature and immature mixed conifer and deciduous (MIXCD), generally 20–60 years of age, (ii) percent mature and late seral stage dense conifer (MC), generally >60 years old, and (iii) percent young forest (YNG), generally <20 years old. Young forest provides high levels of twiggy browse required to meet moose bioenergetic demands, mature conifer provides escape cover from predators, snow interception during winter, and thermal cover in summer, and mixed conifer and deciduous is used as late winter habitat by providing a mix of snow interception and twiggy browse supply (Allen et al., 1987).

Landcover variables were derived from a Landsat-TM based landcover map for the period 1999–2002. In general, forest types are classified with a high level of confidence, but there is some confusion between treed wetlands and sparse forest classes (Spectranalysis, 2004). Forest disturbance is classified with a high level of confidence; however, bedrock outcrops may be confused with recent clearcuts if the two classes occur in close proximity (Spectranalysis, 2004).

Climate variables used in the models were average winter temperature (°C) over period December–February (AWT); average summer temperature (°C) over months June–August (AST); and total rain and water-equivalent snow precipitation (mm) during the cold period over months October–March (TCP). Higher late winter temperatures improve survival of the parasite winter tick (*Dermacentor albipictus*) and increase survival of deer, consequently increasing spread of the meningeal brain worm (*Parelaphostrongylus tenuis*) (Lankester and Samuel, 1998) and liver fluke (*Fascioloides magna*) (Murray et al., 2006). Higher precipitation (rain) in late winter and early spring may increase stress when moose condition and thickness of the coat are lowest (Lankester and Samuel, 1998). Higher summer temperatures may increase summer heat stress in moose by reducing the ability to thermo-regulate body temperature (Schwartz and Renecker, 1998).

Climate projections were made with version 2 of Environment Canada's climate model, the Canadian Coupled Global Circulation Model (CGCM2). The CGCM2 model was interpolated to a finer spatial resolution by the Landscape Analysis and Applications Section (LAAS) at the Canadian Forest Service in Sault Ste. Marie (Colombo et al., 2007; Ontario Ministry of Natural Resources, 2007). Climate projections were based on the A2 climate scenario, where greenhouse gases reach 1320 parts per million by volume (ppmv) in CO_2 equivalents by 2100 (IPCC, 2000). Relative to other scenarios, this represents a large increase in CO_2, a population increase to 15 billion by 2100, and only a moderate emphasis on environmental protection. The A2 scenario predicts about a 2–3 °C increase in average summer temperature in Ontario's far north between the current time period (1971–2000) and the 2041–2070 time period, a 5–6 °C increase in average winter temperature (Fig. 1), and about a 15–17 mm increase in cool period precipitation north and west of Lake Superior. The model also predicts a substantial decrease