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Factors driving range expansion of white-tailed deer, *Odocoileus virginianus*, in the boreal forest of northern Alberta, Canada

by

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Abstract

A large suite of species, across numerous taxa, are expanding their geographic ranges, with potential impacts on species, communities and ecosystems. This has increased interest in understanding the mechanisms driving range change and anticipating future changes in species' distributions. White-tailed deer have expanded their range into the boreal forest in North America. For northern ungulates, energy expenditure for thermoregulation and movement in winter can exceed energy gain from limited resources, leading to mortality. Substantial changes in climate and land use over the last half of the 20th century may have decreased winter energy loss or increased resource abundance, facilitating range expansion. The objective for this dissertation was to determine the relative importance of climate change and land use as drivers of white-tailed deer range expansion in northern Alberta and to predict how the range may change during the first half of the 21st century. I developed a method to calculate a winter severity index for white-tailed deer using widely available data, and used this mechanistically relevant metric of winter climate in a species distribution model analysis. White-tailed deer presence in the 2000s was explained by a positive relationship with land use footprint, deciduous forest, and growing season length and a negative relationship with winter severity and wetland. The only important land use footprints were agriculture, forestry, and well pads. Model predictions for the northern Alberta boreal region had relatively good accuracy, according to assessments with independent data from the 1970s, 1980s, 1990s, and 2000s decades. Climate was found to be the most important factor driving range

expansion in this region. If the shifts toward less severe winters and longer growing seasons continue at the rate observed, white-tailed deer will be able to occupy the majority of the northern Alberta boreal by the 2050s. This increases concern for northern caribou populations and suggests wildlife managers in Alberta face big challenges now and into the future.

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Dissertation introduction

Understanding what limits a species range is among the most fundamental questions in ecology. Interest in the drivers of species ranges has re-emerged recently as species ranges across the globe have been changing (Holt and Keitt 2005, Parmesan et al. 2005). The study of species' ranges is inherently tied to the concept of ecological niches, population ecology, meta-population dynamics, evolution and adaptation, trophic interactions, competition and facilitation (Caughley et al. 1988, Holt and Keitt 2005). It is the culmination of these processes on survival, reproduction, and dispersal that ultimately leads to species range boundaries (Brown et al. 1996, Holt and Keitt 2000). Recent focus has been on empirical rather than theoretical approaches to understanding range boundaries, as ecologists have been tasked to anticipate changes in species ranges and potential ecosystem consequences (Miller et al. 2004, Holt et al. 2005).

MacArthur (1972) stated that at the northern extent of a range, species tend to be limited by abiotic factors (i.e. climate). Climate change can release species from physiological limitations on reproduction and survival, allowing increased abundance and expansion beyond their historic range. Numerous authors have linked range expansion to changes in temperature (Crozier 2004, Battisti et al. 2005, Walther et al. 2007), and precipitation regimes (Gray et al. 2006) and there is an abundance of recent literature attempting to predict future distributional changes as a result of projected climate changes (Morrison et al. 2005, Urban et al. 2007, Jensen et al. 2008, Reygondeau and Beaugrand 2011). Disturbance from human land use, however, changes biotic factors associated with range boundaries and may be a more important driver of range expansion for some species. The effects of human land use on the success of invasive species have been long recognized by invasion ecologists (Davis et al. 2000, Elton 2000, With 2004). Human land use facilitates invasion by creating niche opportunities through increased availability of resources, and/or decreased competition or predation (Petren and Case 1996, Davis et al. 2000, Shea and Chesson 2002). The same can occur when land use changes occur at a species range margin (Kanda et al. 2009). To date, few studies have attempted to tease apart biotic and abiotic mechanisms for range expansion (but see (Hersteinsson and Macdonald 1992, Melles et al. 2011, Rubidge et al. 2011).

White-tailed deer (*Odocoileus virginianus*) have been expanding their range into the North American boreal forest over the last half of the 20th century (Webb 1967, Veitch 2001). At the start of the 20th century, the northern range edge for white-tailed deer roughly followed the southern edge of the boreal forest from Alberta to New Brunswick, Canada (McCabe and McCabe 1984). By 1960, white-tailed deer occurred in agricultural areas in northwestern Alberta and along the Athabasca River running between Athabasca and Fort McMurray (Webb 1967). Charest (2005) showed an increase in white-tailed deer occurrence in the northeastern part of Alberta in 2001 as compared to 1969 and there was a 17.5

fold increase in white-tailed deer abundance in that region between 1990s and 2000s (Latham et al. 2011). The northern extent of sightings now extend as far north as Norman Wells, North West Territories, and Dawson, Yukon (65.17° and 64.04° latitude, respectively) indicating that the range has changed substantially (Figure 3.1) (Veitch 2001).

The consequences of white-tailed deer expansion could include increases in invasibility of ecosystems to exotic plant species (Parker et al. 2006), increased human-wildlife conflict (White and Ward 2010), and increased disease spread (Bar-David et al. 2006, Oyer et al. 2007). Where overabundant, deer herbivory also affects nutrient cycles (Bardgett and Wardle 2003), vegetation community structure (Potvin et al. 2003, Côté et al. 2004), and successional pathways (Hobbs 1996). Of particular concern is the effects of increased presence and abundance of white-tailed deer on native species. Particularly in Alberta, the expansion and subsequent population increase of white-tailed deer has been associated with major changes in the predator-prey system. Increased abundance of white-tailed deer has been correlated with increases in wolf numbers and subsequent elevated predation on woodland caribou (*Rangifer tarandus caribou*) populations, which are listed as threatened by the Committee on the Status of Endangered Wildlife in Canada (Dale et al. 1994, COSEWIC 2002, Latham et al. 2011). Understanding the mechanisms leading to white-tailed deer expansion into the boreal forest is of immediate management concern.

Chapter 1: Introduction

Northern ungulates rely on stored body fat to survive winter, which is often a period of net energy loss due to deep snow, cold temperatures, and limited forage intake (Schmidt 1993, Dumont et al. 2005, Lima and Berryman 2006). Abiotic or biotic changes may have shifted this energy balance toward increased survival and reproduction. Warmer, shorter winters with less snow may increase deer survival at the edge of their typical range by decreasing energy loss (Moen 1976). Longer growing seasons may increase food resources by increasing forest productivity, or may increase the frost free period for accumulating fat reserves, leading to better body condition at the start of winter, which is a key predictor of over winter survival (Mautz et al. 1976, Taillon et al. 2006, Parker et al. 2009). Alternatively, increased abundance of and/or access to resources (i.e. through more forage or browse biomass or reduced competition for available resources) may decrease fat loss during winter or improve body condition heading into winter. Industrial activities, such as agricultural production of forage crops and forest harvesting leading to early successional forests, can increase forage abundance (Augustine and Jordan 1998, Fisher and Wilkinson 2005). Energy sector activities could also positively affect deer survival and distribution by providing increased forage (planting of legumes on well pads, seismic lines, and pipelines, and/or increased shrub growth on seismic lines) or by facilitating access to patches of favorable habitat that were previously inaccessible (upland patches in peatlands for example). Alberta has an intensive land use footprint that developed rapidly over the last half of the 20th century and continues to increase (Hamley 1992, Schneider 2002, Smith et al. 2003). There has also been substantial change in climate in Northwestern North America during that period (Jarvis and Linder 2000, Stone et al. 2002, Nemani et al. 2003, Lemke et al. 2007, Strong et al. 2009). Either or both of these changes may have led to the observed changes in white-tailed deer distribution.

The objective for this dissertation was to determine the relative importance of land use and climate change as drivers of white-tailed deer range expansion in northern Alberta during the last half of the 20th century and to predict how the range may change during the first half of the 21st century. To better understand the effects of climate on species distributions, it is helpful to use mechanistically informed climate variables covering large spatial extents and small spatial grain (Rödder et al. 2009, Elith et al. 2010). White-tailed deer have behavioural mechanisms to mitigate the direct impacts of temperature and precipitation fluctuations on survival (Telfer and Kelsall 1984, Humphries 2009). Instead of using these variables directly, I use an energetically based index of winter severity that has been shown to predict over-winter survival in white-tailed deer (DelGiudice et al. 2002). Snow depth is an important component of the index; however snow depth data are available at relatively few climate stations across Canada and for limited time periods. In chapter two, I develop a method to replace the snow depth component of the established white-tailed deer winter severity index with snow water equivalent (SWE) data, which is the amount of water that would result from melting a column of snow (Geiger et al. 2009). SWE data are available from multiple sources that typically provide fine grained data across multiple years, allowing for analyses at small spatial grains across time. In chapter three, I develop a species distribution model to understand the factors determining recent (2002 – 2009) distribution, applying the index from chapter one as my measure of winter climate. In chapter four, I use that species distribution model to predict distributions in the 1970s, 1980s, 1990s, and 2000s across the northern boreal forest of Alberta and test the predictions in each decade using independent data. I assess the drivers of change between decades by investigating the difference in predicted probabilities when climate or land use footprint is held constant between decades. Finally, in chapter five I predict changes in climate during the first half of the 21st century based on observed changes in modeled climate variables during the 20th century. I then predict future decadal white-tailed deer distributions up to the 2050s.

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Chapter 2: A winter severity index using widely available weather information

Introduction

To understand mechanisms driving changes in species distributions, climate variables that describe yearly climate variation at large spatial extents and small spatial grain are helpful. Large scale climate indices (such as Pacific Decadal Oscillation, North Atlantic Oscillation and El Nino Southern Oscillation) have been increasingly related to species population change but these indices fail to provide the spatial resolution necessary to address questions related to changes in species distribution. Both Elith et al. (2010) and Rödder et al. (2009) highlight the importance of incorporating mechanistically informed variables in species distribution models, particularly if interest lies in understanding species range shifts. Thus, a climate index based on known mechanistic relationships would increase our ability to assess how changing climate may affect changes in species ranges.

Northern ungulates experience a net negative energy balance in winter when energy demands increase with increasing snow depth and decreasing temperature (Ammann et al. 1973, Mautz et al. 1976, Moen 1976, Parker et al. 1984) and energy inputs are reduced as a result of low availability and quality of browse (Gray and Servello 1995, Jensen et al. 1999). Both the Wisconsin and Minnesota Department of Natural Resources uses energetic relationships as thresholds in a

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winter severity index to predict yearly deer population trends (DelGiudice et al. 2002, Jacques 2008). Mattfeld (1974) showed that energy expenditure for white-tailed deer in snow increases as snow depth increases, with a sharp increase after 30cm sinking depth. Between depths of 7 and 37 cm deer could adjust their behaviour and distance moved to maintain constant energy expenditure, however beyond this, movement required a plunging gait which has a very high energy expenditure/unit distance moved, and greatly reduces speed of travel. Parker et al. (1984) also found energy expenditure in elk and mule deer to be dramatically increased once snow depths exceeded front knee height. Increased energy expenditure also occurs when animals experience temperatures below the lower critical point of their thermoneutral zone, where increased metabolic heat production is required to compensate for heat loss. This point has been cited as -11.2 °C for white-tailed deer fawns (Jensen et al. 1999), and -20°C for non-fasting adults (Moen 1968). Thus, the Department of Natural Resources index adds the number of days between November and May with more than 38 cm of snow on the ground to the number of days with minimum temperature below -17.7°C (DelGiudice et al. 2002, Jacques 2008).

Winter die offs in deer populations are common (Severinghaus 1947, Edwards 1956, Kelsall and Prescott 1971, Verme and Ozoga 1971, Roper and Lipscomb 1973) and recent research has linked snow depth, temperature, and/or duration of winter to fawn survival and fetus production (Patterson and Power 2002, Garroway and Broders 2007), fetus sex (Patterson and Power 2002, Garroway and

Broders 2007), body condition (Garroway and Broders 2005), and initiation of migration (Fieberg et al. 2008). Notably, DelGiudice et al. (2002) found the index described above significantly predicted the risk of adult white-tailed deer death from natural causes. To understand the effects of changing winter climate on deer populations across the northern extent of their range, this index must be calculated at a relatively small spatial grain size, across a large extent, and over multiple decades. Snow depth data are available at relatively few climate stations across Canada, however, and for limited time periods; for example, less than half of the 625 stations operating in Alberta in 2002 collected data other than air temperature and precipitation. Of the stations that did collect detailed weather data, only a few collected snow depth data (Chetner 2003). In Northern Alberta, only four stations report snow depth data for more than 20 years. Thus, a surrogate for snow depth is needed to achieve the spatial and temporal resolution needed for studying distribution change.

Snow water equivalent (SWE) is the amount of water that would result from melting a quantity of snow and is a function of snow depth and snow density (Geiger et al. 2009). Daily SWE data are available through multiple sources from which snow depth data are not; among these, passive microwave satellite data (Derksen and MacKay 2006), and interpolation from climate stations (McKenney et al. 2006). These sources typically provide fine grained data across multiple years, allowing for analyses at small spatial grains across years. For example, the National Snow and Ice Data Center (NSIDC) provide satellite derived SWE data at a 25 km cell size covering more than 8 years (Tedesco et al. 2004) and Natural Resources Canada (NRC) provides SWE data interpolated from climate stations at a spatial resolution of 300 arc s of latitude and longitude for over 43 years (Hutchinson et al. 2009). Daily precipitation, which in winter is SWE of fallen snow, is also reported for many Canadian climate stations at which snow depth are not reported. The increasing availability and broad coverage of SWE data make SWE a good candidate for developing a model for snow depth which would be useful for studying how changing snow depths might affect species range shifts.

The snowpack is not just an accumulation of daily snowfall, however. Interception of snow by forest canopies, wind forced redistribution of snow, and sublimation during each of these processes can have marked influences on snow depth at any location (Woo and Marsh 2005). Snow density changes with age of the snow pack, snow depth, and exposure to wind (Pomeroy and Gray 1995, Jost et al. 2007). Melt increases the density of the snow pack (Hock 2005) and is a function of energy components such as net radiation, sensible heat flux, latent heat flux, ground heat flux, and sensible heat flux supplied by rain. Despite this complexity, melt models based on air temperature tend to be highly correlated to more complex energy balance models due to strong relationships between temperature and several of the energy components. Studies have also found that elevation, northing, and forest cover explain much of the variation in both snow accumulation and snow melt, likely through their links to air temperature (Jost et al. 2007). Although others have developed models for snow depth (eg Brasnett 1999), these are difficult to apply broadly as they require local energy parameters, or data at temporal scales that are less generally available (eg 6-hourly data). Here, I use SWE to develop a method for calculating the snow depth portion of the white-tailed deer winter severity index (WSI). Because of the complexity and variability inherent in snow models, I aim only to ensure the model performs well in calculating this index, rather than to model snow depth per se.

Methods

Environment Canada (EC) data

Environment Canada's Climate Data Online (2010) is a publicly available database of hourly, daily, or monthly weather data. I acquired daily climate data from this database for weather stations in northwestern Canada that included temperature data, daily snow depth and SWE of daily snowfall, and had greater than 20 years of data. I limited my calculations to November 1 through April 30, as only one station registered the threshold values for snow depth during May and in only two years. Snow water equivalent data are estimated from daily snowfall, assume a snow density of 100 kg m^{-3}, which is the generally accepted average density of freshly fallen snow (Pomeroy and Gray 1995), and are reported as total daily precipitation. When daily mean temperature was below 0°c, precipitation was taken as SWE, when it was at or above 0°c it was taken as rainfall.

Missing data

In cases when more than six days of data were missing for any variable for one station within the same winter season, that year of data was removed from the analysis. If fewer than six days of data were missing, temperatures values were estimated by averaging measurements from the day before and the day following the missing data. Snow depth and SWE were taken to be the lowest non-zero value of the day before or the day following the missing data. None of the estimated missing temperature values were near threshold values used in calculating the WSI and a single day of SWE data has little effect on the overall index.

Accumulation of daily swe of snowfall

To estimate the SWE of the snowpack (CUMLT), SWE of daily snowfall was added to the previous day's total if mean temperature was below 0°C, but if mean temperature was at or above 0°C a melt parameter was subtracted from the previous day's total. The melt parameter, used by Environment Canada and adapted here by removing the constant was given by the United States Army Corps of Engineers (1956) for forested areas. The constant is meant to account for changes in the individual energy components across space and time. Variability in this constant does not show consistent relationships by region due to the multitude of factors that influence it in different directions, and thus must be calculated using locally specific data (Hock 2003, 2005). A constant was not applied here because it limited use of the WSIswe to areas where a constant has been or could be calculated. I aimed to test whether a general model could predict the WSI to allow application across the range of deer distributions. Although weather stations tend to be in non-forested areas, I aim to apply this index across forested landscapes, making the parameter for forested areas more appropriate. I recognize that melt will likely be underestimated as a result. The melt parameter is defined as:

Eqn 1 $MELT = (1.88 + 0.007\ R)*(1.8\ T) + 1.27$

where MELT = snowmelt in mm snow water equivalent, and

R = daily rainfall in mm, and

T = mean temperature in °C

The CUMLT calculation is given by:

Eqn 2 CUMLT = IF mean temp < 0, THEN SWE_f + CUMLT (day-1),

IF $T \geq 0$ & MELT > CUMLT (day-1), THEN 0,

IF $T \geq 0$ & MELT ≤ CUMLT (day-1), THEN CUMLT (day-1) – MELT

where CUMLT = cumulative snow water equivalent of the snowpack in mm,

CUMLT (day-1) = the previous day's CUMLT, and

SWE_f = daily snow water equivalent of snowfall (mm)

Counting snow index days and calculating the index

Simple empirical model

The relationship between snow depth and snow water equivalent of the snow column is given by:

Eqn 3 $CUMLT = 0.01\, d_s\, \rho_s$ (Lundberg et al. 2006)

where d_s = snow depth in cm, and

ρ_s = density of snow in kg m^{-3}.

Lundberg et al. (2006) found that snow density increased with snow depth. In shallow snowpacks (mean depth < 60cm), this relationship can be accounted for using the following equation (Pomeroy and Gray 1995):

Eqn 4 $CUMLT = 0.01(\rho_s\, d_s + C)$

where C is the covariance between snow depth and snow density and all values are means.

To count the number of index days contributed by snow, I need to convert CUMLT to snow depth. To calculate snow depth from CUMLT using equation 3, a value for snow density is required. I can avoid assumptions or locally informed parameters however, if equation 4 is used. This equation also avoids the over-simplifying assumption that density is constant over time and snow depths.

We calculated equation 4 by regressing snow depth on CUMLT. The intercept represents the covariance between snow depth and density and the slope is the empirically estimated mean density multiplied by 0.01. I solved each regression equation with snow depth equal to 38 cm to find the CUMLT value that represents the threshold for counting snow contributed index days, SWE index days. I did this at the station level (i.e. ran 13 separate regressions), as this would give the best approximation of the index and was a first test as to whether the approach would work at all. Temperature index days were calculated the same way for both indices. I used the coefficient of determination (R^2) to test the ability of SWE index days to predict the count of snow index days, and WSIswe to predict WSI.

Time variable density model

We tested whether including locally informed parameters for density in equation 3 could provide better predictions than the simple empirical model. Density, and thus SWE, of the snow pack increases as winter progresses. The extent to which density changes depends, in part, on the temperature gradient in the snow pack, which is influenced by regional variation and snow depth (Pomeroy and Gray 1995). To count the number of index days contributed by snow, I used the densities reported by Pomeroy and Gray (1995) figure two, page five, to set monthly snow density assumptions for each station (Table 2.1).

Rewriting equation 3 to calculate snow depth from CUMLT gives:

Eqn 5 $d_s = CUMLT\ (0.01\rho_s)^{-1}$

Equation 5 was calculated for each day of the data set, and estimated snow depth was regressed on actual snow depth for each station. I solved each station regression equation for actual snow depth equal to 38 cm to determine the threshold for counting SWE index days from estimated snow depth. The rest of the index was calculated as above and I compared the ability for each model, the empirical and the variable density model, to predict SWE index days and WSI for each station.

Generalizing the model

Station specific thresholds for counting the number of index days contributed by snow are likely not informative for the regions between stations. To calculate this climate index at large spatial extent and small grain using interpolated data or satellite collected surfaces of temperature and precipitation, a common threshold value for calculating SWE index days is needed across a study region. I tested whether a common threshold for calculating SWE index days calculated from station data combined across a climate region could still give good predictions for each station. The climate regions, identified in Table 2.1, are defined by common temperature and precipitation patterns and similar geography. If the common or averaged threshold predicts each station well, I gain confidence that it would also predict the inter-station region well, provided the inter-station region is within the same climate region. I did this for the northwest forest climate region (nwf) because I have the largest sample size from that region (Table 2.1) and I used the empirical model for this test because it is the simplest approach.

Equation 4 was calculated by regressing snow depth on CUMLT for the combined data set (i.e. one regression equation for the entire nwf). I solved the regression equation with snow depth equal to 38 cm to find the CUMLT value that represents the nwf averaged threshold for counting SWE index days for that region. I then added the temperature index days to calculate WSIswe for this case. Because latitude and elevation are important factors in between-station variability (Jost et al. 2007), I calculated a regression model (WSInwf) relating WSIswe to WSI that included latitude and elevation. Latitude was measured in decimal degrees in North American Datum 1983 and elevation, also in North American Datum 83, was in meters above mean sea level. I compared the models with and without these topographical variables using AIC (Akaike 1974).

Finally, I tested the limits of WSInwf by applying it to stations in the Northern and Southern BC mountains and the prairie climate region and comparing the R^2 values to those from the station specific models.

Results

There were 13 weather stations in Northwestern Canada included in this analysis (Figure 2.1). They represented four major climate regions, prairie, northwestern forest, southern British Columbia mountains, and northern BC and Yukon mountains (Climate Research Branch 2009). For some stations, there were years that did not accumulate any index points for snow. Of the years that did include snow as part of the index score, snow accounted for an average of 40% of the index, with its contribution ranging from <1% to 97% (Table 2.1).

Empirical versus time variable density model

Ten of the 13 stations had an R^2 of 0.70 or higher (Table 2.2). The empirical relationship between SWE and snow depth provided the best prediction of WSI (average R^2 across stations = 0.71 versus 0.63 for the regional density model) however the regional density model was superior for two stations (Table 2.2). Stations that accumulated more snow and more snow index days tended to have lower predictability. The R^2 for WSIswe, calculated using the empirical model, increased as the ratio of years that did and did not accumulate snow index points decreased ($R^2 = 0.77$, $F_{1, 10} = 33.06$, $p = <0.001$), if the High Level station was removed. Likewise as the overall mean of the yearly maximum snow depth at each station increased, the R^2 for the snow index days compared to SWE index days decreased ($R^2 = 0.50$, $F_{1, 10} = 9.89$, $P = 0.01$). High Level was an outlier because the model predicts the snow index days and the WSI very well, despite most years in the data set including snow index points and the mean maximum snow depth being high (Table 2.1, Table 2.2). Very little variation in the R^2 for the regional density model was explained by these variables (ratio comparison $R^2 = 0.27$, $F_{1, 10} = 3.78$, $p = 0.08$; snow count $R^2 = 0.01$, $F_{1, 10} = 0.15$, $p = 0.71$).

Generalizing the model

Including latitude and elevation in the generalized model substantially improved prediction of WSI. The ΔAIC between models with and without topographic variables was 60.3, with the WSInwf being the standout top model. The WSInwf predicted well for all nwf stations except Thompson (Figure 2.2A). The regression equation (with standard errors) for WSInwf is:

$$-325.13\,(44.13) + 0.79\,(0.03) * \text{WSIswe} + 6.43\,(0.8) * \text{lat} - 0.03\,(0.01) * \text{elev}$$

WSInwf tends to overestimate WSI in lower severity years and underestimate WSI in higher severity years (Figure 2.2A). All commission errors (overestimates) come from days when snow depth is less than 38cm, and omission errors (underestimates) occur when more than 38cm of snow is on the ground, thus this bias is an inherent quality of the threshold approach.

The WSInwf predicted comparatively well for stations from other climate regions (Figure 2.2B). Although the R^2 values for Dease Lake and Smithers are low, all models predicted poorly for these stations (Table 2.2).

Discussion

The winter severity index calculated using SWE provides a good measure of relative winter severity across space and time. Because snow depth only accounts for one portion of this index, prediction of winter severity is high despite lower prediction of snow index days from SWE. Also, much of the variability stemming from accumulation of daily SWE of snowfall and the melt parameter is reduced to either above or below the threshold. Only when the snowpack depth varies around 38 cm, does error in CUMLT result in an over or underestimate of snow index days. While the use of that threshold results in a systematic bias, the direction of the errors makes estimating trends from the data, which are of interest when studying distribution change, conservative. The systematic bias does raise caution if interested in an absolute measure of winter severity, however.

My goal to develop a general model that does not rely on detailed local parameters to relate SWE to snow depth was supported here. WSInwf predicts WSI well for all but three stations, even when they are from different climate regions. The three stations with poor predictions from this model also had poor predictions from the station specific calculations. The poorer predictions when using the regional density estimates from Pomeroy and Gray (1995) suggest that making assumptions about local parameters, such as snow density and how that density varies over a winter season, can increase rather than decrease error. The density change reported for the British Columbia Trench may have more closely reflected changes in the snowpack for Dease Lake and Prince George, however, as the regional density model improved the predictions at these two stations. Dease Lake has the deepest snowpack of the stations studied, so accounting for changes in density as depth increases is likely more important.

All models for Dease Lake, Smithers and Thompson predict poorer than for other stations. This may be due to a stronger influence of density variation or to the suitability of the melt parameter to adequately model SWE of the accumulated snowpack in these locations. The Dease Lake and Thompson stations represent the longitudinal extremes of the dataset which could result in different characteristics of the prevalent weather, or the atmospheric conditions in which the snow formed. For example, lower snow densities are expected in dry, cold conditions, compared with the higher densities in wet snow that falls in warmer temperatures (McKay and Gray 1981). Continental climates tend to follow the former pattern, while coastal conditions follow the later (McKay and Gray 1981). Conditions during snowfall and metamorphosis as well as the temperature gradients at the snow-soil interface and land conditions on which the snow falls, also affects snow retention and ablation (McKay and Gray 1981). Each of these factors will affect the ability of my methods to predict snow depth from SWE of snow fallen across a broad landscape. Alternatively, climate stations placed in locations with excessive wind loss of snow (eg. airports) may also affect the ability of the general model to predict the snow depth at that location. To gain confidence in the predictions when applying this model elsewhere, I suggest authors make use of local station data to determine a study region derived threshold value for calculating SWE index days, as I show here and test that the method predicts reliably across the stations in the study region. Only then should the method be applied to continuous coverage SWE data for that study area.

The WSIswe index could be easily adapted for use with other ungulates by adjusting the threshold values for counting index days to recognize the lower thermal tolerance and approximate front knee height of the species. The new threshold would have to be calculated using a local source of both SWE and snow depth data, as reported here. The approach taken here to incorporate SWE in place of snow depth can also be followed by other researchers or managers working on any species for which a mechanistic link to snow depth is known, and for which a generalized index can be built. The benefit of this approach is a comparatively simple method to maximize on the greater availability of SWE data at varying spatial and temporal scales compared to snow depth data.

Table 2.1: Station data description. Prov designates Canadian Provinces which are: BC (British Columbia), AB (Alberta), SK (Saskatchewan), and MB (Manitoba). Abbreviations under both climate and density region are N (northern), S (southern), BC (British Columbia), Mtn (mountains), NW (northerwestern), E (eastern), and MB (Manitoba). The density region refers to the regions given by Pomeroy and Gray (1995) in figure two, page five. The number of snow years is the number of years that snow index points were counted in the actual snow depth index. Max is the mean of the annual maximum snow depths for each date range.

Model Stations	Prov	Climate Region	Density Region*	Date Range	N yrs	snow yrs	Mean max (cm)
Dease Lake	BC	N BC Mtn	British Columbia trench	1955 - 1993	38	38	70.55
Smithers	BC	S BC Mtn	British Columbia trench	1955 - 2007	50	35	52.37
Prince George	BC	S BC Mtn	British Columbia trench	1957 - 2007	50	29	46.15
Fort Nelson	BC	NW forest	Southern Boreal Forest	1955 - 2007	52	45	65.42
Fort St John	BC	NW forest	Southern Boreal Forest	1955 - 2007	52	37	56.11
High Level	AB	NW forest	Southern Boreal Forest	1970 - 2007	34	32	56.39
Peace River	AB	NW forest	Southern Boreal Forest	1960 - 2005	42	20	40.81
Grande Prairie	AB	NW forest	Eastern Rockies	1955 - 2006	47	28	46.24
Edmonton	AB	Prairie	South Canadian Prairies	1961 - 2007	45	14	33.98
La Ronge	SK	NW forest	Southern Boreal Forest	1967 - 2007	35	26	49.85
Prince Albert	SK	NW forest	Southern Boreal Forest	1955 - 2006	50	14	34.52
Las Pas	MB	NW forest	Northern Manitoba	1955 - 2007	52	37	55.87
Thompson	MB	NW forest	Northern Manitoba	1967 - 2007	39	35	57.29

Table 2.2: Coefficients of determination for the count of SWE index days compared to snow index days (R^2 snow) and for WSIswe compared to WSI (R^2 index) using a threshold calculated under a simple empirical model (Empirical) and one calculated using time variable density assumptions given by Pomeroy and Gray (1996) for different regions (Regional density). Bolded numbers highlight the top model for each station. The threshold is the value used for each station to count SWE index days. For the empirical model this was used on the CUMLT values, and for the regional density model, the threshold was applied to estimated snow depth. See table 2.1 for province (prov) designations.

		Empirical			Regional density		
Model Stations	Prov	threshold	R^2 snow	R^2 index	threshold	R^2 snow	R^2 index
Dease Lake	BC	48.94	0.50	0.53	26.81	0.67	**0.68**
Smithers	BC	52.94	0.41	**0.60**	31.98	0.31	0.47
Prince George	BC	74.66	0.53	0.71	43.46	0.59	**0.74**
Fort Nelson	BC	46.93	0.49	**0.70**	25.49	0.42	0.61
Fort St John	BC	49.84	0.53	**0.70**	37.11	0.28	0.49
High Level	AB	60.26	0.78	**0.86**	29.52	0.71	0.78
Peace River	AB	58.03	0.64	**0.79**	31.19	0.52	0.68
Grande Prairie	AB	65.94	0.52	**0.73**	41.12	0.29	0.52
Edmonton	AB	70.73	0.73	**0.88**	32.99	0.63	0.81
La Ronge	SK	59.05	0.59	**0.72**	30.28	0.49	0.61
Prince Albert	SK	69.40	0.67	**0.83**	30.81	0.53	0.71
Las Pas	MB	56.43	0.59	**0.71**	43.08	0.58	0.68
Thompson	MB	70.93	0.40	**0.50**	50.95	0.37	0.45

Figure 2.1: Station locations. See tables for full station names. NWF is northwest forest climate region. Table 2.1 gives the climate regions for those stations marked 'other' here. The top of the dark outline runs along the 60th parallel (60° N).

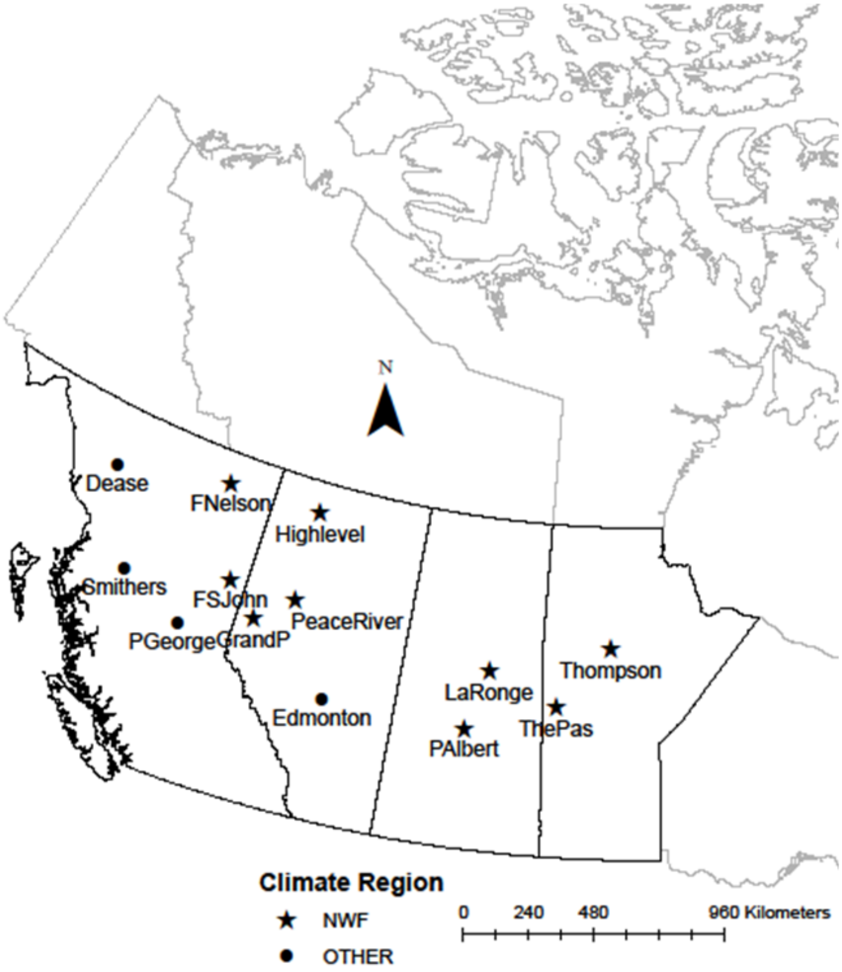

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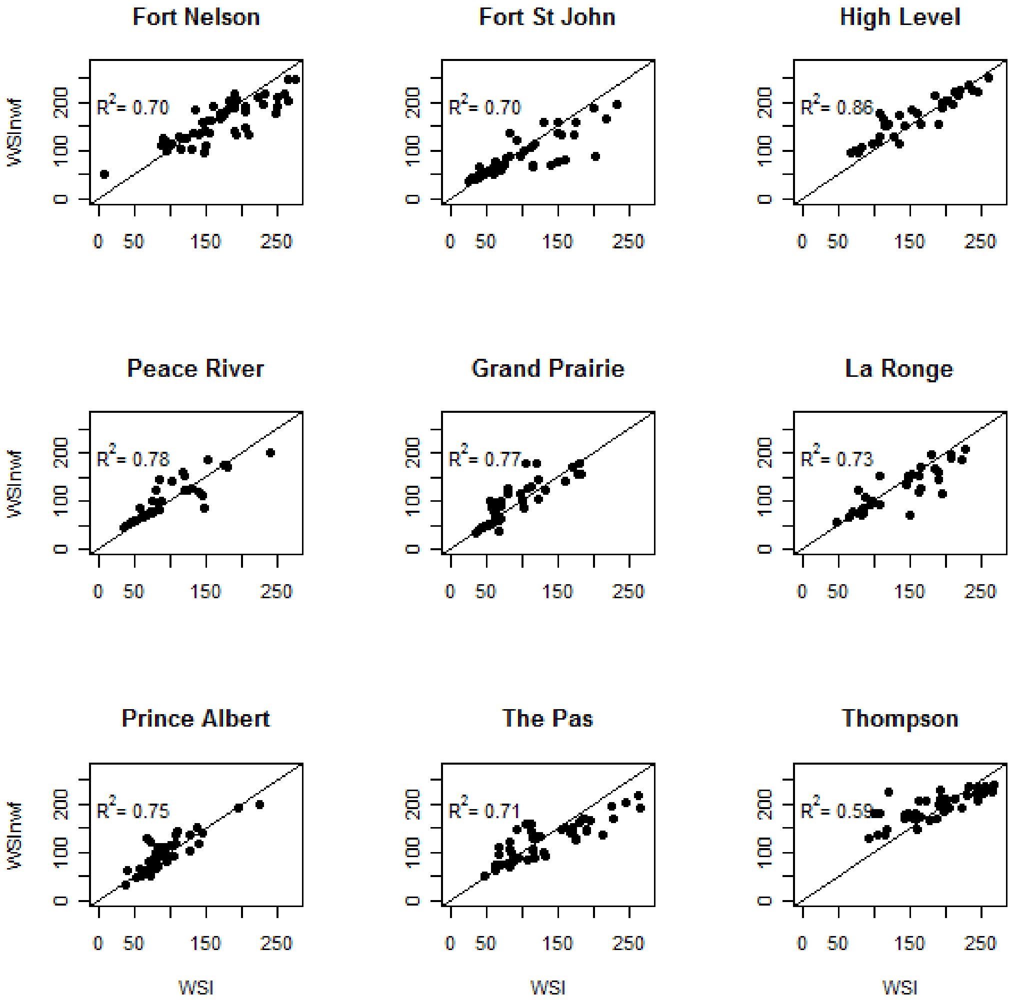
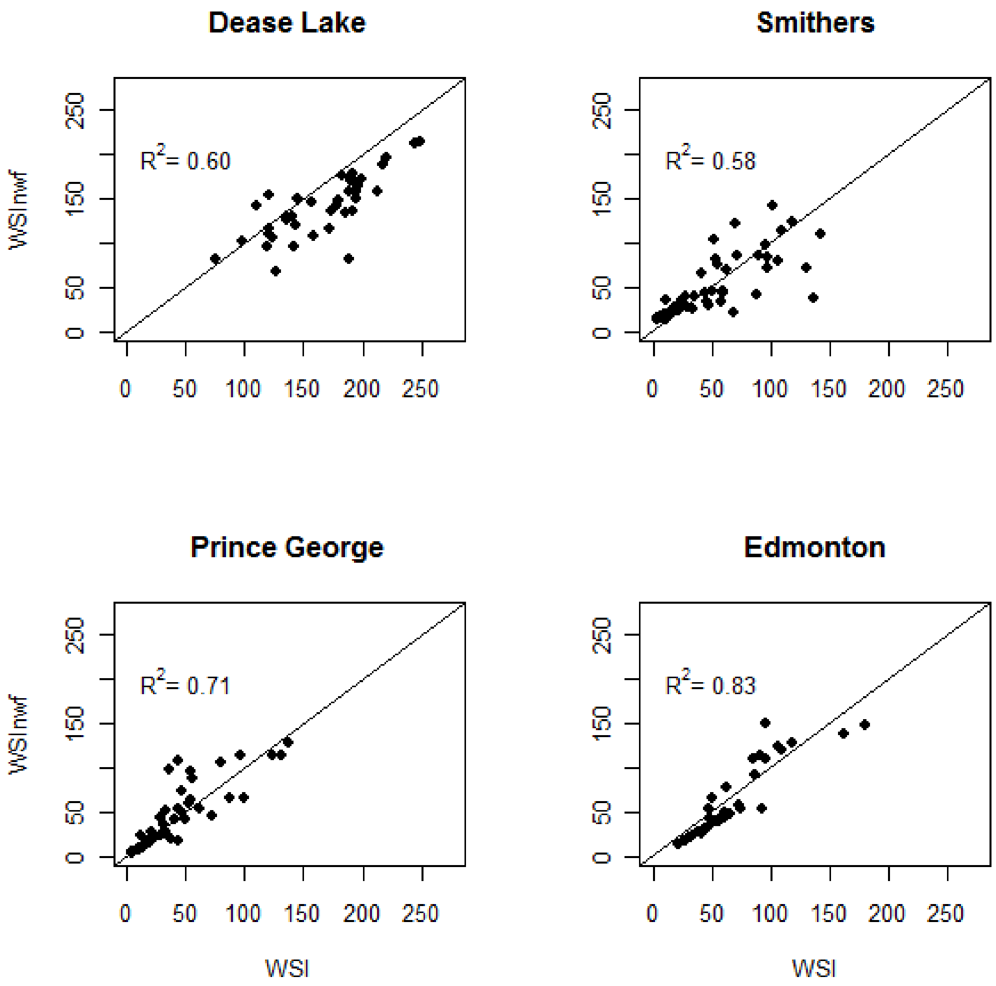
Figure 2.2: Correlation of WSInwf to WSI for stations in the northwest forest climate region (A) and for stations from other climate regions (B). The line represents the point where WSInwf and WSI are equal. The threshold for counting SWE index days from CUMLT used in this analysis was 57.82. Coefficients of determination (R^2) are shown in each plot.

A.



B.


Dease Lake
Smithers
Prince George
Edmonton
R^2= 0.60
R^2= 0.58
R^2= 0.71
R^2= 0.83
WSInwf
WSInwf
WSI
WSI
0
50
150
250
0
50
100
150
200
250

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Chapter 3: Long-term climate and land use determine white-tailed deer, *Odocoileus virginianus* distribution in a newly invaded range: implications for range expansion

Introduction

Species range limits across numerous taxa have been shown to be expanding (Hughes 2000, Peterson et al. 2001, Parmesan and Yohe 2003, Wardle et al. 2011). Range expansion, in this context, refers to the process of colonization of novel habitats from adjacent regions (Davis and Thompson 2000). It occurs in response to increased habitat availability at the range edge, which is otherwise limited by unsuitable biotic or abiotic factors (MacArthur 1972, Caughley et al. 1988). Abiotic and biotic factors can interact to limit species ranges yet, until recently, models developed to predict or explain changes in species range boundaries were largely parameterized by climate variables (Caughley et al. 1988, Parmesan et al. 1999, Araújo et al. 2005, Melles et al. 2011, Reygondeau and Beaugrand 2011, Rubidge et al. 2011). Land cover change through land use development has been implicated in the expansion of introduced invasive species for some time (With 2004, Hulme 2008) however, and can facilitate expansion by allowing species to overcome energetically based climate limitations where resources are increased (Kanda et al. 2009). Ultimately, species distributions are determined by multiple factors and changes in any of those could lead to range expansion. Investigating species' distributions in relation to environmental gradients in recently occupied range offers insight into potential factors that may be driving range expansion (Küster et al. 2011).

Expansion of species into new regions can have profound impacts on native communities (Thomas et al. 2004, Clout and Russell 2007, Jepsen et al. 2008, Ling 2008). Jepsen et al (2008) recorded more northerly outbreaks of two forest pest species, and Ling (2008) showed the loss of 150 taxa in a macro algal bed after range expansion of the sea urchin (*Centrostephanus rodgersii*). Several members of the deer family, Cervidae, are expanding their ranges in North America, and may have large ecosystem impacts (Darimont et al. 2005, Van Dyke 2007, Humphries 2009, Latham et al. 2011). Invasion ecology provides some high profile examples of biodiversity loss (Atkinson 2006) and trophic cascades (Croll et al. 2005) as a consequence of mammalian invasions. Nentwig et al (2010) also ranked artiodacts, to which the cervids belong, among the orders of mammals whose invasions have had the greatest environmental and economic impacts in Europe. Cervids are known to have large ecosystem impacts, even within their native range, and have been implicated as facilitators to plant invasions (Côté et al. 2004, Parker et al. 2006, Spear and Chown 2009). Understanding the factors determining the distribution of these expanding species is critical for targeting management and conservation initiatives in response to range change.

White-tailed deer (*Odocoileus virginianus*) have expanded their range into northern boreal regions, which are atypical for this species (Côté et al. 2004). At the start of the 20th century, the northern range edge for white-tailed deer roughly followed the southern edge of the boreal forest from Alberta to New Brunswick, Canada (McCabe and McCabe 1984). By 1960, white-tailed deer had established an intermittent distribution in the northwestern developed part of Alberta and along the Athabasca River running between Athabasca and Fort McMurray (Figure 3.1) (Webb 1967). Charest (2005) showed that the expansion has continued in the northeast since that time. Although the continuous range for white-tailed deer is likely still in northern Alberta, the northern extent of sightings extends as far north as Norman Wells, North West Territories, and Dawson, Yukon (65.17° and 64.04° latitude, respectively) indicating that the range has changed substantially (Figure 3.1) (Veitch 2001). In Alberta, this expansion and subsequent population increase of white-tailed deer has been associated with major changes in the predator-prey system. Increased abundance of white-tailed deer has led to increases in wolf numbers and subsequent elevated predation on woodland caribou (*Rangifer tarandus caribou*) populations, which are listed as threatened by the Committee on the Status of Endangered Wildlife in Canada (Dale et al. 1994, COSEWIC 2002, Latham et al. 2011). These, as well as other potential impacts to native communities, increase the importance of understanding factors determining white-tailed deer spatial distribution in Alberta (Côté et al. 2004, Spear and Chown 2009).

A number of changes on the landscape may have facilitated white-tailed deer range expansion in northern Alberta. Northern ungulates often suffer a negative energy balance in winter due to deep snow, cold temperatures, and limited forage intake (Schmidt 1993, Dumont et al. 2005, Lima and Berryman 2006). They rely on stored body fat to survive until spring arrives. A shift toward warmer, shorter winters with less snow may have increased potential for deer survival and reproduction in the boreal by decreasing energy loss (Moen 1976). Lengthening of the growing season may have increased forest productivity leading to higher food resources or increased the frost free period for accumulating fat reserves. Alternatively, industrial activities such as agricultural production of forage crops and forest harvesting leading to early succession forests can increase forage or browse abundance in summer and winter (Mautz et al. 1976, Augustine and Jordan 1998, Brinkman et al. 2005). Alberta has an intensive land use footprint that developed rapidly over the last half of the 20th century and continues to increase. The footprint includes the most northern agricultural development in Canada (Hamley 1992) and close to 20 million m^3 of annual forest harvesting by the forest industry (Smith et al. 2003). Unique to Alberta, compared to the rest of the northern range, is an extensive energy sector footprint comprised of a matrix of seismic lines and well pads which are linear tracts of land cut during exploration phases and patches of land cleared for oil well establishment, respectively (Schneider 2002). Practices from the early 1950s to 1970s resulted in double the amount of early seral forest where both energy sector and forest industry operated on the same land base (Schneider 2002, Smith et al. 2003). The extensive industrial footprint in Alberta may have increased the quality or quantity of habitat available for white-tailed deer in this part of their range; which may have increased survival and reproduction by improving fall fat stores or reducing fat loss in winter. Finally, white-tailed deer distribution may be explained by a combination of these factors.

The objective of this study was to determine which of these factors correlate with white-tailed deer distribution in northern Alberta and to infer potential drivers of the range expansion that has been on-going since the second half of the 20th century. I use a species distribution model approach with winter presence and absence data to test among multiple *a priori* models to explain current winter deer distribution. Population processes that limit the ability of species to track changes in habitat availability, such a dispersal limitation, can lead to spatial distributions that are not strongly associated with environmental factors, however (Guisan and Thuiller 2005). Investigating these spatial dependencies is an essential component of species distribution modeling (Elith and Leathwick 2009), so I compared environmental models to spatial models describing the distance from potential source populations, latitude and longitude and tested model residuals for spatial autocorrelation, which is a similarity in observations due to proximity (Elith and Leathwick 2009). This analysis is an important step toward understanding white-tailed deer spatial distribution in this recently occupied boreal region and separating the competing mechanisms to explain why range expansion has occurred.

Methods

Study region

The study region (Figure 3.1), from 53.9° N to 59.8° N latitude and from 119.8° W to 110.0° W longitude, covers much of the Alberta boreal forest. Uplands in this region are characterized by aspen (*Populus tremuloides*) and balsam poplar (*Populus balsamifera*) dominated deciduous forest, white spruce (*Picea glauca*) and jack pine (*Pinus banksiana*) dominated conifer stands, and mixed wood stands. These gently undulating uplands are interspersed with extensive peatlands composed of black spruce (*Picea mariana*) bogs and shrub or sedge wetlands (Downing and Pettepiece 2006). The region experiences long cold winters and short warm summers. Mean temperature from the warmest and coldest month are 15.7°C and -19.2°C respectively, and mean annual precipitation is 469 mm (Downing and Pettepiece 2006).

Sample site selection

Sampling for this study was conducted by two linked organizations between 2002 and 2009 to monitor biodiversity: the Integrated Landscape Management (ILM) lab at the University of Alberta and the Alberta Biodiversity Monitoring Institute (ABMI), a not-for profit organization composed of government, environmental, industry, and university governors with an independent, international science committee to ensure scientific rigor in data collection (Figure 3.1). The western Canada land description system divides Alberta into a grid of 9.7 km x 9.7 km townships (McKercher and Wolfe 1986). Sample sites selected by the ILM group were townships, stratified by total amount of human footprint. Equal numbers of sites were selected randomly from each strata to sample a gradient of land use disturbances (Bayne et al. 2008). Sampling was conducted between December 15 and March 15 from 2002 to 2004. Sample sites selected by the ABMI were part of a systematic grid of permanent 10 km x 10 km sites the organization monitors across the province, over a 5 year cycle. Sites were sampled between November and February from 2005 to 2009. In 2006 the ILM and ABMI groups collaborated on sampling, based on the ILM site selection protocol, in the northwest region of the province (Figure 3.1). During that year, due to funding sources, sampling by ABMI personnel was conducted at grid points in the Conoco-Philips/Opti-Nexen development region in the northeastern region of the province, instead of following the ABMI site rotation cycle (Figure 3.1) (Bayne et al. 2006). In total, there were 151 sites sampled by ILM, 21 sampled through the ILM/ABMI collaboration in 2006, and 127 sites sampled by ABMI for a total of 299 sites. All sites were selected at random with respect to land cover type.

White-tailed deer presence/absence

White-tailed deer presence/absence data were collected by snow tracking using triangle (N = 174) and transect (N = 125) sampling schemes. Triangles were sampled from 2002 – 2005 and arranged with the center of an equilateral triangle at the center of the sample site and one apex pointing north. Each side of the triangle was 3 km long. Triangles were sampled on snow shoes 3 – 10 days after a track obliterating snow fall (considered to be > 1 cm) (Bayne et al. 2008). A single score of presence or absence was recorded for the entire triangle according to whether or not a track crossed the sample path. Transects were sampled from 2006 – 2009 and were established with the transect center as close as possible to the sample site center point. Transects were 10 km long and oriented east-west for as long as possible, however they bent, where necessary, to accommodate travel routes. Like triangle sampling, data collection on transects occurred 3 – 7 days after the last track obliterating snowfall. The 10 km transects were driven on snow mobile to break the trail, then immediately driven a second time to record species presence or absence. Presence or absence was recorded based on tracks within 1 meter of transect travel routes (Bayne et al. 2006). The method changed from triangle to transect to reduce the time required for sample collection.

Climate variables

Climate variability affects ungulate populations through both direct effects of recent winter weather on survival, and indirect effects through longer term impacts on fecundity and life-history traits (Saether 1997, Post and Stenseth 1998, Post E. and Stenseth 1998). I calculated long-term and recent winter severity and long-term growing season length for each sample unit. Long-term measures averaged the variables over the last half of the 20th century, where data were available, and recent measures accounted for the two years prior to sampling. To measure long-term winter severity, I used the winter severity index developed in chapter 1. This index (WSIswe) uses snow water equivalent (SWE) data, the amount of water obtained from melting a quantity of snow, in place of snow depth data to build a winter severity index for white-tailed deer that has been shown to be negatively related to survival (DelGiudice et al. 2002). It is based on thresholds in temperature and precipitation beyond which white-tailed deer must drastically increase energy expenditure for thermoregulation and movement (Mattfeld 1974, Parker et al. 1984, DelGiudice et al. 2002). I used interpolated temperature and precipitation data from Natural Resources Canada (NRC) at a 10 km spatial grain for boreal Alberta, spanning 1961 – 2002 (Hutchinson et al. 2009). I intersected the center point of each triangle or transect with WSIswe for each year in a Geographic Information System (GIS) and calculated the mean from 1961 – 2002. I also calculated WSIswe in one and two years prior to white-tailed deer data collection using Environment Canada’s climate data on-line (2010) for the station nearest the sample location.

Length of the growing season for 1950 – 1999 was obtained from the NRC and was developed using the same interpolated temperature data used for the WSIswe, however these data were at an 8.363 km spatial grain. The growing season started when the mean daily temperature was equal to or greater than 5°C for at least five consecutive days, beginning March 1. It ended when the minimum temperature reached -2°C after August 1. This closely corresponds to the frost free period, which would best represent the growing season for browse species (Meehl et al. 2007). I intersected the center point of each triangle and transect with the yearly growing season length in a GIS and calculated the mean growing season length from 1950 – 1999.

Landscape variables

All land use and land cover variables were calculated as the proportion of a 500 m buffer place around each triangle and transect. The transect or triangle and its 500 m buffer are referred to as the sampling unit throughout the rest of this chapter.

Land use

The proportion of five land use variables were calculated for each sampling unit; agriculture, cut blocks, seismic and pipelines lines, well pads, and roads. Three composite variables were also calculated: total footprint, which is the sum of all land uses, total forested footprint, which is the total footprint minus agriculture, and total non-linear footprint, which is the sum of agriculture, cutblocks and well pads. Agriculture data were acquired from the National Land and Water Information Service (NLWIS) prairie agricultural classification which uses Landsat images from 2000 to distinguish agricultural lands from surrounding forested lands. The data have a 30 m resolution and an overall accuracy of 89%. Cut block data were obtained from ABMI in the form of Alberta Vegetation Inventory (AVI) data, based on 1987 – 2009 1:20 000 scale aerial photos, with some field verification (Nesby 1997). The AVI is reported as GIS shapefiles with minimum polygon size ranging from 2 ha to 20 ha. These data have position accuracy of plus or minus 20 m. Digital data on seismic lines, pipelines, roads, and well pads were obtained from the Alberta Base Features Dataset from 2008, which is the digital representation of the 1:20 000 maps for the region. Linear footprints were assigned a width of 6 m, 40 m, and 8 – 80 m, depending on the road type, to enable calculation of proportions. Well pad point locations were expanded to 100 m^2 to account for the size of forest clearing associated with well establishment (Hird et al. 2009).

Land cover

Alberta Ground Cover Classification (AGCC) (Sanchez - Azofeifa *et al.* 2004) data were used to calculate the proportion of five vegetation communities within each sampling unit: deciduous, mixed wood, shrub, wetland, and bog. Deciduous forests were defined as greater than 80% occurrence of deciduous species, mixed wood stands contained 20 – 80% mixed coniferous and deciduous species occurrence, and shrub land was characterized by more than 25% shrub cover and less than 6% tree cover (Sanchez - Azofeifa *et al.* 2004). The AGCC data were developed using Landsat Thematic Mapper and Landsat 7 Enhanced Thematic Mapper satellite imagery with images acquired in 1999 – 2002. The data describe patches of 57 m or greater in diameter with an accuracy of approximately 75% (Sanchez - Azofeifa *et al.* 2004).

Natural vegetation change through fire disturbance can also increase resource availability in the boreal through growth of herbaceous under story and early seral stage vegetation communities. Digital fire data were obtained from Alberta Sustainable Resources Development (ASRD) historical wildlife database spanning 1970 to 2006. For areas burned more than once during this time period, the most recent burn year was retained. Prior to 1998, only fires greater than 200 hectares (class 4 fires) were recorded in the spatial database. From 1998 onward, fires that were 12 hectares or greater were included in the database.

Spatial variables

Latitude, longitude, and distance from agriculture were recorded for the center point of each transect and triangle. To delineate the agricultural boundary, I used the white zone boundary, which is a government of Alberta designated region that distinguishes land available for cultivation from that designated as forest resources. Digital data from Agriculture and Agri-foods Canada were used to adjust the white zone boundary to reflect actual cultivated and hayed lands (Speiss 1997). These data were developed by satellite remote sensing of images from 1993 – 1995, at a grain size of 0.5 ha (Speiss 1997).

Modeling

In total there were 22 climate, land use, and land cover variables established for modeling white-tailed deer distribution (Table 3.1). Using these variables, I ran 31 *a priori* generalized linear models with a binomial family and logit link. Sampling method was included in all models to account for differences between triangle and transect sampling designs. Models were selected using AIC model selection where models with a ΔAIC less than 4 were considered to be competing as best models (Anderson 2008, Burnham et al. 2011).

Models were selected in a hierarchical fashion. The 31 models were divided into one of five categories: climate, land use, land cover, combinations of these three, and spatial. Within the climate category the top model describing the relationship between white-tailed deer distribution and recent winter severity was determined first, because there were multiple variables describing this relationship. This was included in models with long term winter severity and/or growing season to determine the top climate model. The top model for the land use and land cover categories were also identified (Table 3.2). Models of combinations of climate, land use, and land cover were run using the variables in the top model from each individual category to represent climate, land use, and land cover (Table 3.2). If there were multiple competing models in any of the categories, the model with the fewest parameters was selected for inclusion into combined models. I did this to minimize risk of multicollinearity and over parameterization. Combined models with terms describing interactions among factors in different categories were also tested (Table 3.2). I determined the best spatial model as a null model with which to compare environmental models. I used AIC model selection to determine the overall best model across the full model set. I assessed fit using AIC weights, which give the probability that a model is the best given the data (Anderson 2008, Burnham et al. 2011).

Although multicollinearity does not influence AIC values, it can cause imprecise estimation of coefficients and inflated standard errors which could increase type II error (Graham 2003, Zuur et al. 2010). I tested for multicollinearity by determining variance inflation factors (VIF) for all *a priori* models. Following the methods suggested by Zuur et al (2010), if VIFs were greater than 2, I removed the variable with the highest VIF, re-ran the model without that variable and recalculated the VIF scores. Finally, spatial autocorrelation can result from dispersal driven distributions, missing environmental predictors, or species behavior (i.e. yarding in white-tailed deer populations) (Dormann et al. 2007, Elith and Leathwick 2009). I tested for autocorrelation in the top model residuals using Moran's I in PASSaGE 2.0.10.18, at a spatial lag of 10 km (Rosenberg and Anderson 2011). I assessed significance for each distance class using permutation tests. Although this does not allow us to distinguish the cause of autocorrelation, detecting it warns that further investigation is necessary before inferences can be made from the model.

Results

Of the 299 sampling sites, 73% had white-tailed deer present. The range in WSIswe spanned 127 index points for the long-term mean and 175 index points for the WSIswe for years prior to sampling (Table 3.1). The growing season length varied across 35.5 days (Table 3.1). Total footprint varied from 0 to 95%, with agriculture comprising the majority of the footprint (Table 3.1). Deciduous and bog land cover types were the most prevalent, and the amount of burns in the sampling units varied from 0 to 100% (Table 3.1).

Model selection

There were two competing top climate models. Both models included long term winter severity and growing season, and one also included the winter severity two years prior to sampling (Table 3.2). The total non-linear footprint was the top land use model (Table 3.2). Although a model of forestry and agriculture individually was also in the top set, parameter estimates for each term were very similar, suggesting that deer respond to these footprints in a similar way (Table 3.2). Seismic lines and roads were not included in either of the top competing land use models. The proportion of deciduous forest and wetlands described deer distribution just as well as the proportion of these two variables plus the proportion of shrubs, bogs, and mixed wood forest (Table 3.2). Burns were not an important factor describing the distribution. The best combined model of white-tailed deer distribution, according to ΔAIC, included climate, land use, and land cover (Table 3.2). The latitude plus longitude and latitude only models were equally plausible geographic models. The latitude and longitude geographic model described distribution better than land use or land cover alone (ΔAIC of 16.45 and 18.08 respectively), however it was not better than climate alone (ΔAIC = -19.71) or the combined model (ΔAIC = -68.35) (Table 3.2). The VIF scores for variables in all models were less than 2.

The combined climate, land use and land cover model had a 93% probability of being the top model given the data (Table 3.2). There was no spatial autocorrelation in the residuals for this final model (Moran's I correlogram bonferroni corrected significance = 1.0; for all distance classes $p > 0.12$). Climate was the most important factor explaining white-tailed deer distribution in Northern Alberta. The change in AIC when climate was dropped from the top model was 59.85, compared to 18.07 for land use, and 19.73 for land cover. Of the climate variables, winter severity was more important than growing season with a change in AIC of 37.28 when it was dropped from the top model compared to 1.37 for growing season.

Model description

For each unit increase in WSIswe, the odds of deer presence decreased by 7% (odds ratio = 0.93, CI = 0.91 – 0.94) and for each 1% increase in total non-linear land use footprint the odds of deer presence increased by 10% (odds ratio = 1.10, CI = 1.03 – 1.18). A 1% increase in the amount of deciduous forest increased the odds of presence by 5% (odds ratio = 1.05, CI = 1.02 – 1.08). For each day increase in the mean length of the growing season, the odds of white-tailed deer being present increased by 12%. A 1% increase in proportion of wetland decreased the odds of occurrence by 3%. The confidence interval for these odds ratio spanned 1, however (odds ratio growing season = 1.12, CI = 0.99 - 1.26; odds ratio wetlands = 0.97, CI = 0.94 – 1.0). The triangle sampling method was 7 times more likely to record deer as present than the transect sampling method (odds ratio = 7.10, CI = 3.00 – 16.78). I conducted post-hoc analysis to ensure inclusion of the method term represented a difference in the methods themselves, rather than spatial or sampling design biases. Firstly, sampling by the triangle method occurred only in the northeast portion of the study area. To ensure the difference in likelihood of presence was not related to this bias, I compared prevalence from triangle samples to prevalence on transects sampled in the northeast region (N = 72). Only 54% of transects sampled in that region had white-tailed deer present, while 89% of triangles sampled had white-tailed deer present. Secondly, the majority of sampling sites selected for transect sampling were selected by systematic design (83%), while the majority of sampling sites selected for triangle sampling were selected by stratified random design (87%). To ensure the stratified design did not bias site selection to areas with higher presence, I compared prevalence on transects in the northwest portion of the study area where sites were selected by both designs (N = 19 for stratified design, N = 34 for systematic design). Only 21% of transect sites selected by stratified design recorded white-tailed deer present, while 59% of those selected by systematic design recorded presences.

When land use was absent and all other model variables were at their means, the probability of observing a white-tailed deer track was 0.66 (Figure 3.2). The probability of presence is less than 10%, once mean WSIswe exceeds 160 (Figure 3.3). When all model variables are at their means (Table 3.1), the predicted probability of presence is 0.86 (Figure 3.2). This effectively reaches 1 (probability > 0.995) when the proportion of nonlinear footprint is 0.5 (Figure 3.2). The probability of deer presence was estimated at 0.88, under the worst climate conditions, where the nonlinear footprint was 0.91, which was the maximum found at the study sites (Table 3.1, Figure 3.2).

Discussion

White-tailed deer have expanded their range into the northern boreal forest. My analysis indicates that climate, and in particular, long term winter severity is the most important factor determining current white-tailed deer distribution in Northern Alberta. Land cover is as important as land use at describing white-tailed deer distribution. Drivers of land cover change in the boreal forest include climate change leading to changes in productivity, land use, and natural disturbances such as fire (Jarvis and Linder 2000, Nemani et al. 2003, Wang and Cumming 2010). I explicitly modeled those here, so assume there has been no additional change in the amount of deciduous or wetland land cover types at the sample sites. White-tailed deer were not in these communities historically so inclusion of land cover in the final model suggests a factor limiting the presence of white-tailed deer has shifted. This supports the importance of climate in driving the white-tailed deer range change, as a land use only hypothesis for range expansion would predict that boreal land cover types, without land use disturbance, would also lack white-tailed deer. Land use was an important driver of the distribution, as well, however suggesting that changing climate and changes in land use may have both contributed to the range expansion of this species into boreal Alberta.

Species that are expanding their ranges pose problems for distribution modeling, as critical model assumptions may be violated. Firstly, assumptions that the species is at equilibrium, or pseudo-equilibrium, with its environment may be violated so that absences can occur in unsuitable environments or suitable environments that the species has been unable to colonize by the time of sampling. In extreme cases this could lead to inability to elucidate species relationships with environmental factors when using static distribution models (Guisan and Zimmermann 2000, Elith et al. 2010). Secondly, distance limitations on dispersal, environmental connectivity, competitive exclusion or spatially patterned predation pressure, and missing covariates that are themselves spatially patterned, are among the factors that can lead to spatial patterning in the species data, or spatial autocorrelation (Dormann et al. 2007, Elith and Leathwick 2009, Elith et al. 2010). Spatial autocorrelation inflates type I errors, potentially leading to misplaced importance on model variables (Legendre 1993, Dormann et al. 2007). In both of these cases, spatial models describing species locations rather than a suite of environmental variables would better describe the distribution.

Several pieces of evidence suggest that my model is not plagued with these problems. Firstly, the distance to agriculture model, representing dispersal from a potential source, was out competed by the latitude and longitude, land use only, and land cover only models. Secondly, although latitude and longitude are correlated with climate variables, they also represent dispersal from a southern or southeastern source for spread into the northern boreal, so these variables are proxies for two potential phenomenon affecting distribution. Even so, the latitude and longitude model was refuted by the climate only model as well as the combined model. Finally, there was no spatial autocorrelation in the residuals from the top combined model suggesting that the environmental variables have sufficiently described the species distribution.

Many authors advocate for the use of more functionally relevant predictors to improve recent approaches to species distribution modeling in light of the limitations outlined above (Guisan and Zimmermann 2000, Elith et al. 2010). My attempt to do this has likely lead to the success of this analysis. Large mammals and white-tailed deer in particular, have behavioural mechanisms to mitigate the direct impacts of temperature and precipitation fluctuations on survival (Telfer and Kelsall 1984, Humphries 2009). Instead of using these variables directly for the winter climate metric, I included them in an energetically based index of winter severity that has been shown to predict survival in white-tailed deer (DelGiudice et al. 2002, Chapter 1). My summer climate metric, growing season length, has linkages to forest productivity and length of the winter energetic bottleneck, which also makes it more closely related to function for white-tailed deer than temperature alone (Jarvis and Linder 2000, Nemani et al. 2003). Humphries et al (2002) suggested that seasonal energetic bottlenecks are the key factor determining which environments mammals can occupy. Specifically they suggested that the energy stores leading into that bottleneck, the rate of energy loss during the bottleneck, and the length of the period of energy loss all determine whether the mammal survives (Humphries et al. 2002). My results support this assertion in that factors related to the severity of the energetic bottleneck: winter severity, growing season length, and land use to the extent that it increases resources, all increase the probability of white-tailed deer presence in the study area.

A commonly suggested improvement for species distribution models is to include biotic interactions (Elith and Leathwick 2009). I did not investigate competition or predation as potential drivers of the spatial distribution or range change. Both competition and predation affect species through complex pathways. Theoretically, predators can induce range limits through direct mortality, and reduction in predation could then facilitate expansion (Holt and Barfield 2009). Alternatively, a species' range can be affected by interactions between competitors and predators, through a process called apparent competition (Holt and Lawton 1994). Predation rate may be reduced on the species of interest because of an abundance of alternate prey or alternatively, competition may be reduced due to predation on competitor species (Holt and Barfield 2009). Some species distribution models have been improved by including variables describing potential competitor's distributions or abundance (Leathwick and Austin 2001, Ritchie et al. 2009, Rubidge et al. 2011); however there have been fewer attempts to include effects of predation. Incorporating species interactions is one of the greatest challenges for species distribution modeling because of the complexity of the relationships and the correlation between environment and biotic factors (Guisan and Thuiller 2005, Elith and Leathwick 2009).

Moose (*Alces alces*) and white-tailed deer co-exist across their range. Telfer (1970) found that moose and white-tailed deer selected different habitats within sympatric winter range, and although Ludewig and Bowyer (1985) found diet overlaps between the species, they found significant differences in their use of white spruce and balsam fir which reduced competition. Other ungulates in northern Alberta include mule deer (*Odocoileus hemionus*), elk (*Cervus elaphus)*, and wood bison (*Bos bison athabascae*) and woodland caribou (*Rangifer tarandus caribou*). Patchy distribution, low abundance, and preference for peatland communities in the boreal suggest these species likely did not limit white-tailed deer (Alberta Environmental Protection 1991, Alberta Sustainable Resource Development 1993, Alberta Sustainable Resource Development 2009). The main predator for white-tailed deer in Alberta is the gray wolf (*Canis lupus*). This species has undergone two periods of low abundance during the 20th century, the first during the 1920s, from which they recovered and were abundant in the northern and western portions of the province by the 1940s; and the second was during a rabies control effort between 1952- 56. Upon ending the rabies control program, wolf populations increased again and by the early 1970s there were numerous complaints from farmers and hunters regarding high wolf numbers (Alberta Environmental Protection 1991, Gunson 1992). The population was estimated at 4200 through 1975 – 1985, close to the maximum historical population estimate of 5000, and wolf numbers appear to have continued to increase through the 1990s (Alberta Environmental Protection 1991, Gunson 1992, Webb 2008, Robichaud and Boyce 2010, Latham et al. 2011). While I cannot rule out that current or historical competition or predation affected white-tailed deer distributions, the effect of these processes may be more important at local scales rather than broader distributional extents (Pearson and Dawson 2003, Guisan and Thuiller 2005). The results suggest the model is not missing critical covariates and the relationships with land use and climate are well supported. It is also possible that biotic interactions may be mediated by environmental factors already included in the model (i.e. land use and/or land cover relationships); however I am unable to detect those relationships with these modeling methods.

Management implications

Land use alone cannot explain white-tailed deer distribution in Alberta. Climate is more strongly related to distribution, and land cover explains distribution just as well as land use. The influence of land use footprints does have important management implications, however. Based on the current landscape, forestry cutblocks and well pads could account for 66% of the sampling unit area, although the mean footprint amount was much less than this. If development were to increase, my model suggests that the odds of deer presence would also increase. This is particularly important for local level management in regions of high concern, such as in and around caribou ranges. White-tailed deer have already been linked to elevated predation on woodland caribou populations in the

West Side of the Athabasca caribou range in Northeast Alberta, which are listed as threatened in this range (COSEWIC 2002, Latham et al. 2011). Latham et al. (2011) suggested prey reduction programs may be necessary to manage increasing white-tailed deer numbers in order to conserve caribou. Managing white-tailed deer access to land use footprints on a local scale may help reduce increasing problematic populations.

Ungulate populations undergo large population fluctuations due to climate variability (Saether 1997). This occurs through both direct effects of recent winter weather on survival, and indirect effects through longer term impacts on fecundity and life-history traits (Sæther 1997, Post and Stenseth 1998). Extending my model to situations with severe winters and high footprint suggests that there would be presence in these locations even when winter is most severe. This means that even after population die-backs in severe winters, reservoirs of white-tailed deer may persist in highly developed landscapes. These reservoirs could then serve as sources allowing for spread into surrounding landscapes during milder winters. This may be particularly true in agricultural landscapes where there is extensive land conversion, and high quality and quantity of resources (Augustine and Jordan 1998, Brinkman et al. 2005, Stewart et al. 2007). Because agriculture extends almost to the northern extent of Alberta, this suggests that white-tailed deer will continue to be part of the boreal ecosystem in this province, particularly if the climate becomes less severe.

Conclusions

The combined climate, land use, land cover model was supported above all others tested here and did not show any evidence of poor fit suggestive of missing critical covariates. It suggests that changes in climate and land use footprint may be important factors driving the range expansion of white-tailed deer. Investigating how these factors have changed through time and space is necessary to strongly relate these results to range expansion, however. There is a need for innovative approaches to address the complexities associated with species range changes in light of rapid landscape and climate change (Parmesan et al. 2005). I must understand the relationships between species and their current environments, understand drivers of change, develop predictive models and test those models before predicting future changes. The lack of time series in species data makes this task challenging. Here I used a correlative approach to elucidate factors describing the current distribution and factors that may be driving changes in white-tailed deer distributions in northern Alberta. This is a first step toward understanding the causes and consequences of this ungulate's expanding range.

Figure 3.1: Map of study area in relation to northern-most sightings of white-tailed deer. Inset shows the sampling sites. Small grey sites were sampled by ILM between 2002 and 2004, large grey sites were sampled by the combined ILM-ABMI effort in 2006, and black sites were sampled by ABMI between 2005 and 2009.

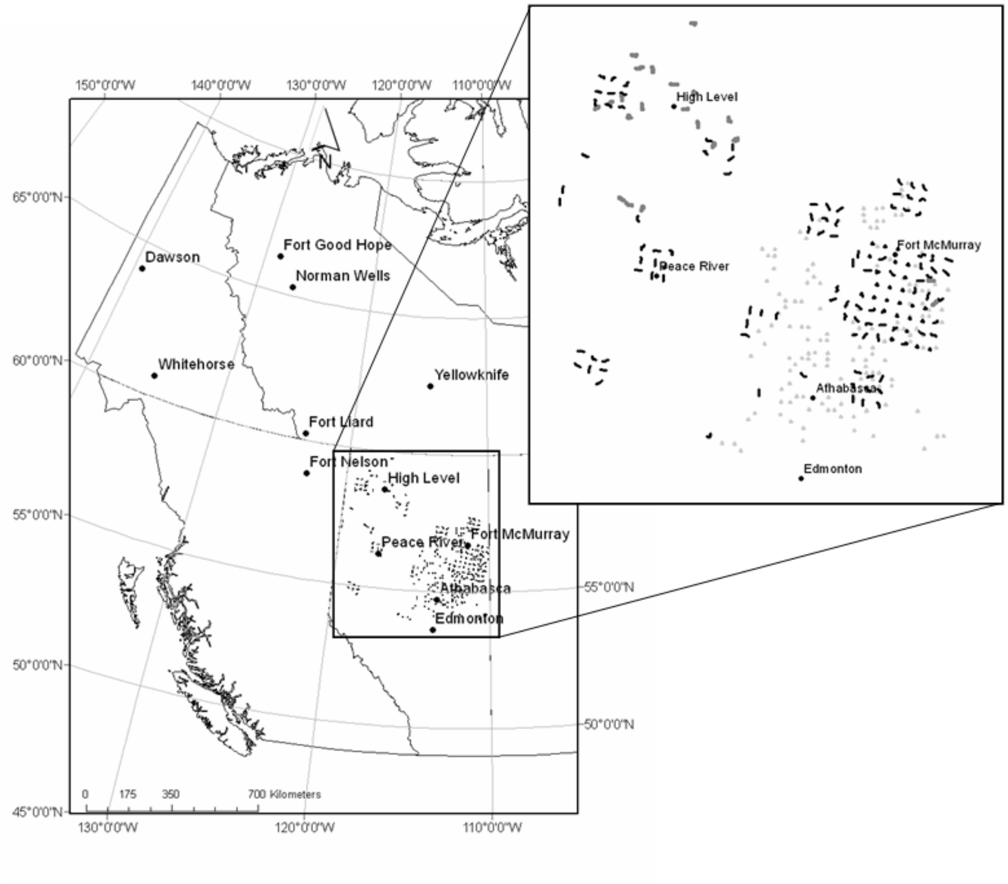


Table 3.1: Variable summary.

Variable Description	code	min	max	mean	SD
presences/absence white-tailed deer		P = 218	A = 81		
method	method	Tran = 125	Tri = 174		
Latitude	lat	53.93	59.76	56.16	1.2
Longitude	long	-119.9	-110	113.20	2.5
proportion burned	pburn	0	1	0.11	0.27
proportion deciduous	pdecid	0	0.9	0.24	0.2
proportion mixed forest	pmixed	0	0.32	0.04	0.05
proportion shrubland	pshrub	0	0.39	0.02	0.04
proportion wetland	pwetl	0	0.13	0.02	0.11
proportion bog	pbog	0	0.6	0.16	0.13
proportion cutblocks	for	0	0.53	0.03	0.08
proportion linear features	lin	0	0.28	0.06	0.05
proportion roads	rd	0	0.1	0.01	0.02
proportion wellpads	well	0	0.13	0.02	0.02
proportion agriculture	pag	0	0.89	0.08	0.19
distance to agriculture (km)	dis2ag	0	279	83.30	76.17
mean growing season 1950 - 1999	sg50_99	142.6	178.1	163.70	5.16
mean WSI 1961 - 2002	m1961_02	66.87	193.94	119.26	24.8
WSI year previous to sampling	pywsi	26	201	86.46	35.3
WSI two years previous to sampling	p2yrwsi	26	201	91.63	44.04
proportion agriculture+ cutblocks + wellpads	tot_ag_for_well	0	0.91	0.12	0.2
proportion cutblocks+ wellpads + linear features + roads	tot_for_eng_rd	0	0.6	0.11	0.1
proportion agriculture + cutblocks + wellpads + linear features + roads	tot_ag_for_eng_rd	0	0.95	0.19	0.21

Table 3.2: *A priori* model set. The model that was included in combined models for each category is bolded. The top model of the entire set is in bold and italics. ΔAIC is the change in Akaike Information Criteria, and w_i is the weight of evidence for that model.

Category	Model	AIC	Within category ΔAIC	Within category wi	Across model set ΔAIC	Across model set wi
geography	lat + long	239.74	0.00	0.55	68.36	0.00
	lat	240.15	0.40	0.45	68.76	0.00
	dis2ag	261.99	22.25	0.00	90.60	0.00
habitat	pdecid + pwetl	**257.82**	**0.00**	**0.70**	86.43	0.00
	pdecid + pmixed + pshrub + pwetl	260.90	3.08	0.15	89.52	0.00
	pdecid + pmixed + pshrub + pwetl + pbog + prop_burn	262.18	4.36	0.08	90.79	0.00
	pwetl + pbog	262.56	4.74	0.07	91.17	0.00
	pdecid + pmixed + pshrub	279.83	22.01	0.00	108.44	0.00
	pburn	297.45	39.63	0.00	126.06	0.00
land use	tot_ag_for_well	**256.19**	**0.00**	**0.80**	84.80	0.00
	pag + for	259.92	3.73	0.12	88.53	0.00
	pag + for + lin + well	262.05	5.86	0.04	90.66	0.00
	pag + for+ lin + well + rd	263.28	7.09	0.02	91.89	0.00
	pag + tot_for_eng_rd	265.18	8.99	0.01	93.79	0.00
	tot_ag_for_eng_rd	265.61	9.42	0.01	94.22	0.00
Climate	m1961_02 + sg50_99	**220.03**	**0.00**	**0.65**	48.64	0.00
	m1961_02 + sg50_99 + p2ywsir	221.91	1.88	0.25	50.52	0.00
	m1961_02	224.41	4.38	0.07	53.02	0.00
	m1961_02 + p2ywsir	226.32	6.29	0.03	54.93	0.00
	sg50_99	266.35	46.33	0.00	94.97	0.00
	p2ywsir	269.78	49.76	0.00	98.40	0.00
	pywsir + p2ywsir	271.71	51.68	0.00	100.33	0.00
	pywsir	286.48	66.46	0.00	115.10	0.00
combined	climate + land use + habitat	***171.39***	***0.00***	***0.93***	***0.00***	***0.93***
	pdecid+ pwetl * lin + sg50_99 + m1961_02 * tot_ag_for_well	176.57	5.18	0.07	5.18	0.07
	pdecid+ pwetl * lin + sg50_99 + m1961_02 * for + pag	181.92	10.53	0.00	10.53	0.00
	climate + habitat	189.46	18.07	0.00	18.07	0.00
	climate + land use	191.12	19.73	0.00	19.73	0.00
	pdecid + pmixed + pshrub + pburn + for + lin + rd + well + pag	218.92	47.53	0.00	47.53	0.00
	land use + habitat	231.24	59.85	0.00	59.85	0.00

Figure 3.2: Predicted probability of deer presence according to footprint from the best AIC selected model. The solid black line shows the change in probability at increasing footprint when all other variables are set to their means. The solid grey line shows the change at increasing footprint when land cover variables are set to their mean value, and climate is at its worst: WSIswe is at its maximum value and growing season is at its minimum value (see Table 3.1). Dashed lines show 95% confidence intervals. The diamond indicates the probability when all variables are at their means. The X indicates the probability for the maximum proportion of land use in study sites.

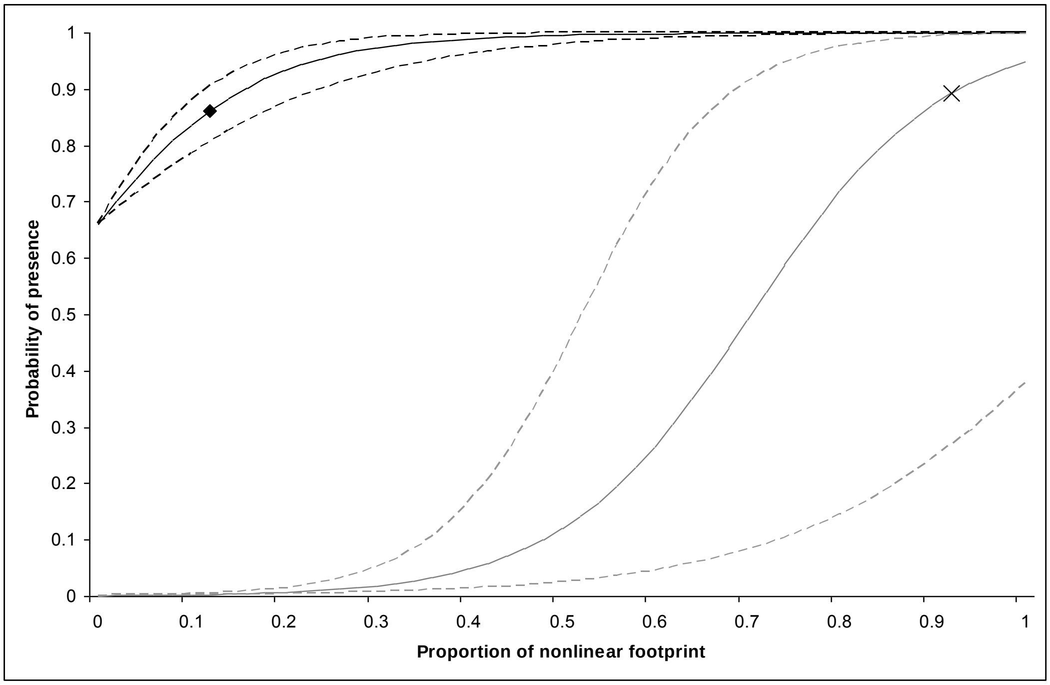
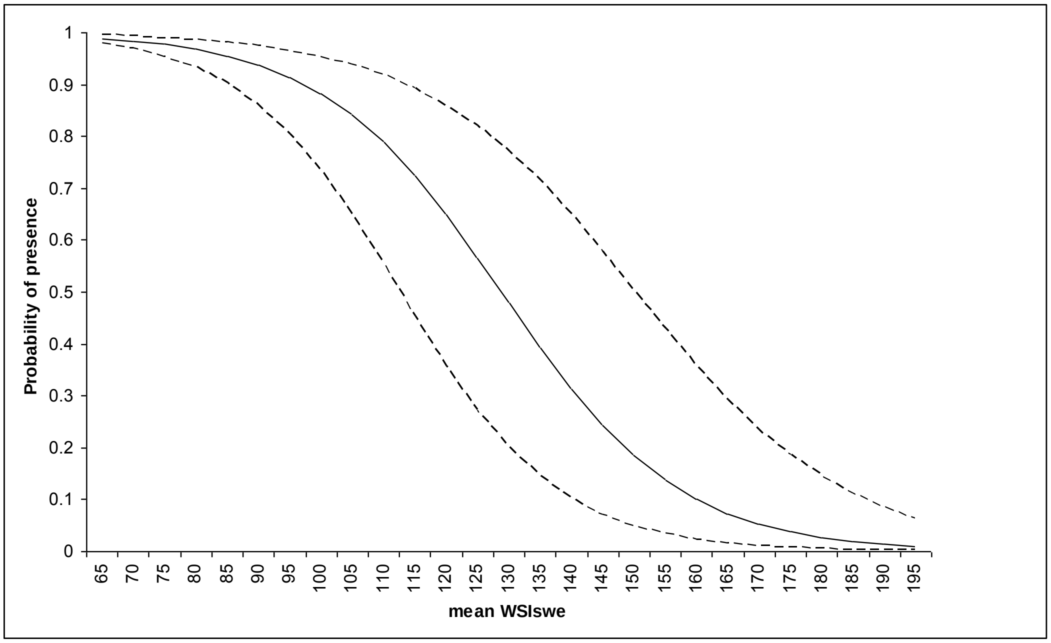


Figure 3.3: Predicted probability of deer presence based on long term mean WSIswe when growing season length, proportion of deciduous forest, and proportion of wetland are at their means (Table 3.1) and land use footprint is absent.



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Chapter 4: Climate change drives white-tailed deer range expansion in Alberta's industrial landscape

Introduction

Understanding the mechanisms driving range change has become one of the key questions in ecology. Parmesan and Yohe (2003) recorded an average poleward range expansion of 6.1 km per decade across 99 species in response to twentieth century climate change. However, 19% of changes at the polewards and upper elevational range boundaries studied shifted in a direction that was inconsistent with changing climate (Parmesan and Yohe 2003). Hockey et al (2011) found that 12.8% of South African bird species that expanded their ranges shifted in a direction consistent with climate change, while 13.1% shifted in a direction more consistent with land use change. Range boundaries are shaped by abiotic (e.g. temperature, growing season length, precipitation) and biotic (e.g. predators, competition, resource availability) factors and changes in either of these can facilitate range changes (MacArthur 1972). Recent emphasis has been on the impact of climate on range boundaries (examples include: (Peterson et al. 2002, Parra and Monahan 2008) however changes in biotic factors as a result of human land use could be an equally or more important driver of species range expansion. To date, few studies have attempted to tease apart biotic and abiotic mechanisms for range expansion (but see (Melles et al. 2011, Rubidge et al. 2011).

Chapter 4: Range expansion

Environmental models describing current species distributions in relation to climate variables are used extensively to predict range changes under projections of climate change (Pearce and Ferrier 2000, Peterson et al. 2001, Beaumont and Hughes 2002, Carvalho et al. 2010). This approach has the implicit assumption that species ranges will track changes that occur in those climate variables. The ability of static models to predict distributions through time and space is suspect, however, as current distributions are not only influenced by environmental gradients, but also past environmental variability, population processes, interactions with other species, and movement dynamics (Guisan and Thuiller 2005). New spatial or temporal landscapes may have ranges of variables beyond those used to fit the model or have unique combinations of those variables, which could limit model predictions (Thuiller et al. 2004). Testing the predictive ability of static models is important, particularly if the predictions will be used for decision making in the context of management or conservation (Araújo et al. 2005). For species that are already expanding their range, the past provides an opportunity to test the predictions of static species distribution models through time and under changing conditions. Without such verification, we cannot be confident that we understand the mechanisms influencing species range expansion and thus cannot confidently predict how future changes will affect species range.

White-tailed deer (*Odocoileus virginianus*) have been expanding their range into the North American boreal forest over the last half of the 20th century (Webb 1967, Veitch 2001). Alberta, Canada likely represents the northern extent of the continuous range, although occurrences have been recorded in the Northwest Territories and the Yukon (Figure 4.1) (Webb 1967, Veitch 2001). According to the species distribution model (SDM) developed in chapter 3, long-term climate, land use, and land cover are important factors describing the current spatial distribution of white-tailed deer in northern Alberta. Winter severity, in terms of the duration and frequency of cold temperatures and deep snow, increases energy expenditure for white-tailed deer (Mattfeld 1974, Mautz et al. 1976, Parker et al. 1984) and the long term mean winter severity (averaged over 1961 - 2002) was negatively associated with presence of white-tailed deer. The probability of white-tailed deer presence was also higher where long term mean growing seasons (averaged over 1950 - 1999) were longer, potentially due to higher forest productivity or a longer frost-free period at these locations (chapter 3). The total amount of agriculture, forestry cut block, and well pad footprint also increased the probability of white-tailed deer presence (chapter 3). Finally, higher proportion of deciduous forest and lower proportions of wetlands surrounding sampling sites led to higher probability of white-tailed deer presence. The influence of these factors on the observed changes in white-tailed deer distribution depends on the spatial and temporal pattern and magnitude of changes that have occurred. I assume there have been no changes in vegetation communities during the last half of the 20th century that were not due to natural or anthropogenic changes explicitly modeled in chapter 3 (i.e. land use, fire, climate changes affecting productivity), as these are the typical drivers of change in boreal vegetation communities (Jarvis and Linder 2000, Nemani et al. 2003, Wang and Cumming

2010). However, there has been substantial change in climate and land use in Alberta. Temperature, precipitation, date of snow melt, and length of the growing season have changed in northwestern North America since 1908 (Jarvis and Linder 2000, Stone et al. 2002, Nemani et al. 2003, Lemke et al. 2007, Strong et al. 2009). Northern Alberta has also undergone rapid industrial development in the last half of the 20th century. Agriculture quickly extended through northwestern Alberta reaching 58.31 ° latitude by the late 1950s, which is the most northern agricultural development in Canada (Hamley 1992). It continues to expand east and westward within the arable land in northern Alberta (Hamley 1992). Forest harvesting more than tripled in Alberta from 1984 to 2000, with harvest going from 6.5 million m^3 to 21.9 million m^3 (Smith et al. 2003). Oil and gas discoveries were made in the province in the late 1940s, with large production increases occurring in the 1970s and early 1990s. The number of well pads in the province has increased from approximately 2000 in 1975 to almost 160000 in 2000 (Schneider 2002). Either climate or land use, or both may have facilitated spread of white-tailed deer.

My objective was to determine the relative importance of land use and climate change as drivers of white-tailed deer range expansion from 1970 – 2000. I use the SDM from chapter 3 to predict past distributions of white-tailed deer in northern Alberta and test those predictions in each decade with independent data. To determine the drivers of range change I predict distributions in the 1980s, 1990s, and 2000s using first the climate, then the land use variables from the previous decade, which would give predictions under a scenario of no change in climate, then no change in land use between decades. I compare these ‘no change’ predictions with the predictions under observed changes in land use and climate to determine which factor was responsible for the greatest changes in predicted probability. By spatially and temporally delineating the changes driven by these competing mechanisms, I better define locations where we need to monitor the species (i.e. areas where climate has changed the most and might continue to change), to manage the land (i.e. areas where land use footprint reclamation should be a priority), and to implement conservation actions (i.e. areas of higher probability of presence).

Methods

Study region

The study region covered the Alberta boreal forest natural region within the boreal and taiga plains ecozones of Alberta, approximately 380000 km^2 (Figure 4.1). The region is a mosaic of upland forests composed of white spruce (*Picea glauca*, jack pine (*Pinus banksiana*), trembling aspen (*Populus tremuloides*), and balsam poplar (*Populus balsamifera*), and peatland complexes composed of shrub and fen wetlands, and black spruce (*Picea mariana*) and tamarack (*Larix larcina*) bogs. Climate in the area is characterized by short cool summers and long cold winters, particularly at the northern extent of the region.

Species distribution model

I used the SDM developed in chapter 3 to predict distributions of white-tailed deer in northern Alberta for 1970, 1980, 1990 and 2000s. This is a generalized linear model with binomial family and logit link. The response data for the SDM, called the training data hereafter, was presence and absence data collected during 2002 – 2009 between 53.9°N and 59.8°N latitude and 110.0° W and 119.9° W longitude, in the boreal and taiga plains of Northern Alberta (Figure 4.1). Data were collected by snow tracking from 299 sample sites. Sampling was conducted by the Alberta Biodiversity Monitoring Institute (ABMI) (N = 127), the Integrated Landscape Management (ILM) lab at the University of Alberta (N = 151) or a combined effort between these groups (N = 21) to monitor biodiversity. Sample sites were selected according to a stratified random or systematic design, depending on the organization conducting sampling. Two methods were used to collect the data: a 9km triangle shaped sampling unit traveled on snow shoes, and a 10 km transect traveled on snow-mobile. Methodology changed from triangles to transects to decrease time spent collecting each sample (see chapter 3 for further details).

The top model describing white-tailed deer distribution was selected from an *a priori* set of 31 models, according to the lowest AIC score and highest weight of evidence (Anderson 2008). There was no autocorrelation in the residuals of this model and the weight of evidence over all others in the *a priori* set was 0.93. The final model, with standard errors was:

$$\text{p/a (deer)} \sim -10.12\ (10.83) + 1.96\ (0.45) * \text{method} + 4.98\ (1.44) * \text{Dec} - 3.11\ (1.72) * \text{Wetl} + 9.79\ (3.4) * \text{land use} - 0.07\ (0.01) * \text{WSIswe} + 0.11\ (0.06) * \text{SG}$$

where p/a (deer) is the presence or absence of white-tailed deer at each sampling unit (transect or triangle) and method refers to the sampling method, comparing the triangle method to the transect method. Dec and Wetl are the proportion of deciduous forest and wetland communities, respectively, within a 500 m region around the sampling unit, and land use refers to the cumulative proportion of agriculture, forestry cut blocks, and well pads within that 500 m buffer. WSIswe is the 41 year mean winter severity and SG is the length of the growing season averaged over 50 years, each calculated at the center of the sampling unit. Long term climate means averaged the variables over the last half of the 20th century. They differ due to data availability.

Environmental data

To make past predictions, I established decadal landscapes for each of the SDM variables using time specific data similar to that used for the SDM (see chapter 3 for details). Using GIS analysis, I placed a 10km x 1 km grid across the boreal and taiga plains ecozones of northern Alberta. This is the same scale as transect data used to calibrate the SDM. Climate variables were calculated for the center of each grid cell and land use and land cover variables were calculated as the proportion of each grid cell.

Climate

To calculate WSIswe, daily temperature and precipitation data interpolated from climate stations using thin-plate smoothing splines, were obtained from Natural Resources Canada (NRC) (Hutchinson *et al.* 2009). These data were at a spatial grain of 10 km. The SDM included a term for the overall mean WSIswe from 1961 up to the start of data collection, which was 2002. I calculated the running mean from 1961 to the beginning of the decade of interest for hind casting analyses. I calculated the mean from 1961 to maintain the full history of winter severity for each region. Long term averaged climate variables have been found to have higher predictive power then shorter term climate variables in ecological models (Hallett et al. 2004, Melles et al. 2011).

The start of the growing season is defined as the point when the mean daily temperature is equal to or greater than 5°C for at least five consecutive days, beginning on March 1. The end is defined as the point when the mean minimum temperature across a region reaches -2°C after August 1. I obtained data on the length of the growing season from NRC. The NRC developed this metric using the same temperature data used for calculation of the WSIswe, but at an 8.363 km grain size. Growing season length was included in the SDM as the mean for years 1950 - 1999. For each past decade, I used the mean from 1950 to the beginning of the decade of interest for model calculation.

Land Use

Agriculture, forestry cut blocks and well pad data was acquired from three different sources. Well pad data were obtained from the 2010 Alberta Sustainable Resources Provincial Digital Base Map. Each point representing a well was buffered by a 50m radius circle to account for the area of forest clearing associated with each well. The spud date, or date ground was broken, was available for more than 99% of the wells on the landscape. For the wells missing spud date, I used license date to assign the development of the footprint to a decade. The well pad data covered all wells from 1900 – 2010. There is no regulation requiring re-forestation on abandoned well sites, and natural regeneration is hindered by these disturbances (Osko and MacFarlane 2001, Schneider 2002). For this reason, I used the cumulative total of wells for subsequent decades.

Cut block data were obtained from Alberta Vegetation Inventory covering development from 1940 – 2008 (Nesby 1997). These data are derived from 1987 – 2009 1:20 000 scale aerial photos, with some ground truthing, and have position accuracy of 20 m. Thirty percent of the cut blocks were missing year of cut information. Although their footprint could be reliably attributed to the 2000s decade, I could not assign them to any other decade with confidence. I calculated the probabilities for each decade using the minimum cut block footprint based on all cut blocks known to be cut in each decade and the maximum cut block footprint based on all known cutblocks in each decade plus the cut blocks with unknown year of cut. Cut blocks developed prior to 1970 were not included in the 2000s footprint because after approximately 30 years, browse available in cutblocks would likely have grown to similar heights as the surrounding forests.

Spatially and temporally explicit agriculture data are limited. I used agricultural ecumene data for 1991 and 2006 from Statistics Canada (Werschler 1995) to represent the change in agriculture through time. These data summarize the agricultural landscape according to areas with high levels of agricultural products produced for sale. To be included in the spatial representation of agriculture, census coverage areas are ranked according to the aerial ratio of developed to undeveloped land and added to the ecumene from highest to lowest ranking until the total area of improved and unimproved land for the region is reached (Werschler 1995). This removes small isolated farms from the ecumene (Werschler 1995). The ecumene data align spatial boundaries with other geographic features rather than mapping boundaries by GPS coordinates, so may have inaccuracies in spatial boundaries (Statistics Canada 2006). I removed any regions from the ecumene data that fell outside the Alberta white zone boundary, which delineates the region available for agricultural development. I also assumed that agricultural footprint from 1991 would remain on the landscape in 2006, even if not under production so regions developed in 1991 were included in the total agriculture footprint for the 2000 decade. I used the 1991 agriculture ecumene to describe the 1970s and 1980s agricultural footprint, and the adjusted 2006 ecumene data to describe the 1990s and 2000s agricultural footprint (Werschler

1995, Statistics Canada 2006). There was only a 4% increase in the area of occupied farmland between 1971 and 1991 in Alberta (Stelfox accessed 2011, Statistics Canada 2007) and the change in agricultural area between the 1991 and 2006 ecumene only accounts for 4% of the study region. Although the coarse temporal resolution of the agricultural data may reduce predictive accuracy in the regions that experienced agricultural expansion, this uncertainty is for a small proportion of the study area so should not affect overall inferences.

The proportion of each land use was calculated for each grid cell, and these proportions were added to give the total footprint. I accounted for areas where land uses overlapped to ensure total land use proportion could not add to more than one.

Land cover

Land cover data were derived from the 2002 Alberta Ground Cover Classification (AGCC) Geographic Information Systems data layer (Sanchez - Azofeifa *et al.* 2004). The AGCC data were developed using Landsat Thematic Mapper and Landsat 7 Enhanced Thematic Mapper satellite imagery with images acquired in 1999 – 2002. Deciduous forest was defined as having greater than 80% occurrence of deciduous species, and all wetlands other than black spruce bogs were included in the wetland variable. The data are at a spatial grain of 25 m. Patches of 57 m or greater in diameter are described with an accuracy of approximately 75% (Sanchez - Azofeifa *et al.* 2004).

Differences in resolution of GIS layers led to total proportions of land use and land cover that exceeded one in some cases. In this case, land cover variables were reduced because the AGCC data were at coarser resolution than the land use data and likely led to the errors. The total proportion of land use and land cover in a grid cell was reduced to 1. The amount by which it was reduced was then subtracted from the proportion of deciduous and wetland land cover proportional to their coverage in the grid cell.

Predictions

I fit a 0 for the method term so the reference condition for all predictions was the transect method. I calculated the SDM equation above for all grid squares and converted the outcome to probabilities using the inverse logit: (exp(model))/1+ (exp(model)).

Independent data

We tested the predictions of the SDM using two independent data sets, called validation data hereafter. The first, aerial survey data collected in winter 2007 tested the predictions in the same decade for which the model was developed. The second, aerial surveys conducted by Alberta Sustainable Resource Development during the 1970s – 1990s, tested the predictions of the model in past decades.

Sites for the recent aerial surveys, collected in 2007, were selected in two regions of Alberta: High Level, 58° 31' 0" North, 117° 8' 0" West and Athabasca, 54° 43'

0" North, 113° 16' 0" West (Figure 4.2). In each region, sites measuring 10km x 10km, were selected in the agricultural zone at random and in the forested zone. Forested sites were stratified by high and low forestry footprint and I used Alberta Vegetation Inventory data in a GIS analysis to ensure all sites had >39% total upland land cover with deciduous forest or deciduous dominated mixed wood covering between 30 and 60% of the site. This was done to maximize our ability to view white-tailed deer, which can be obscured by closed canopy forests. In total there were 23 agriculture sites (5 in High Level and 18 in Athabasca) and 49 forested sites (13 and 36 in High Level and Athabasca respectively). Three 10 km transects were selected to be flown within each site, using visual inspection of GIS maps to maximize the amount of open canopy forest sampled. Aerial surveys were conducted using a Cessna 206 with two observers from December 10, 2007 – January 5, 2008. Altitude and speed were maintained at approximately 400 ft (120m) and 80 knots (150km/hr) respectively. Wind did not exceed 20 knots during flight times and temperatures ranged from -20 – 0 °C. Sampling of sites from forested and agricultural zones was balanced across time of day to account for differences in white-tailed deer activity patterns. Transect lines were buffered by 300m, to cover the approximate area that could be surveyed from the aircraft, and intersected with the predicted landscape for the 2000s decade. For each site, which consisted of three transects, I compared the average predicted probability of white-tailed deer presence from the model to observed presence or absence.

Model predictions in past decades were tested using 76 aerial ungulate surveys conducted by Alberta Sustainable Resource Development between 1971 and 1997 (Charest 2005). I only included surveys conducted using rotary aircraft to standardize potential false negatives related to non-detection between surveys and decades. The Western Canada land description system divides Alberta into a grid of 100km^2 townships (McKercher and Wolfe 1986). Survey design followed random or directed paths to target expected concentrations of white-tailed deer or sampled sections of townships using transect or full coverage surveys of polygons stratified by land cover or expected density. For all surveys, a township was scored with a presence if any portion of that township had a presence recorded; otherwise it was scored as an absence. Once a township was scored with a presence, absences from subsequent surveys in the same township were considered false absences and the township remained as a presence for the analysis. I formed three independent data sets according to the decade of the surveys to compare to decadal predictions (Figure 4.2). The 10km x 10km sites covered several of the predicted grid squares for the model so I took the average of predicted grid square values for each township.

Prediction accuracy

To provide comparable statistics to other studies and to show explicit tradeoffs in error rates for the predictions, I used three metrics to test the predictive ability of the SDM. Calculations from logistic regression models are predicted probabilities of occurrence, whereas validation data is observed presence or absence of the species. To determine whether model predictions agree with these binary states, a probability threshold must be set to convert predictions to presence or absence. The area under the receiver operator curve (ROC) is currently the most widely used metric to test the predictions of SDMs as it summarizes performance over a range of threshold values (Lobo et al. 2010). An ROC curve is developed by plotting the pairs of true and false positives generated from incrementally increasing the decision threshold. The area under this curve (AUC) is a summary statistic estimated as the proportion of the total square in which the curve is drawn. AUC measures the model's ability to estimate a higher probability of occurrence for a randomly selected site with the species present compared to a randomly selected site with the species absent; as such, it tests the discrimination ability of a model (Fielding and Bell 1997). The discrimination ability of models producing AUC values between 0.5 and 0.7 is considered poor, between 0.7 and 0.9 is considered good, and above 0.9 is considered very good (Pearce and Ferrier 2000). I used the ROCR package in R 2.11.1 to calculate AUC, and use the predicted probabilities as the list of threshold values for calculating the ROC curve.

Prevalence is the number of occurrences/the number of observations. Prevalence is positively related to the probabilities from a logistic regression model and so affects all performance statistics (Liu et al. 2005). The prevalence in the training data, then, has been suggested as one of the best thresholds for converting probabilities of occurrence to presence or absence data as other fixed thresholds would vary performance dependant on prevalence (Liu et al. 2005). I used prevalence in the training data as the threshold to assign presence or absence to predicted probabilities for further analysis. For any given threshold value, sensitivity is the proportion of correctly predicted presences and specificity is the proportion of correctly predicted absences (Pearce and Ferrier 2000). Examining the trade-off between sensitivity and specificity is important when training or evaluation datasets have uncertainty in the absences, which is common with ecological data (Lobo et al. 2008). If training data include imperfect absences due to detection error the model may predict absences where there are actually species present (false negatives, decreased sensitivity in the model) (Lobo et al. 2008). Alternatively, if evaluation data were collected by methods with imperfect detection, then the model may predict presences where independent evaluation data have recorded absences due to non-detection (false positives, showing the model as having decreased specificity, when it actually does not). I compare the sensitivity and specificity for predictions using prevalence in the training data as the threshold for calculating these statistics (Liu et al. 2005).

Finally, I calculated the true skills statistic (TSS), which is the sensitivity + specificity – 1 (Allouche et al. 2006). This statistic has been shown to overcome dependency issues on prevalence found in the commonly used cohen's kappa and is gaining use for testing SDM predictions (Allouche et al. 2006, Rubidge et al. 2011). TSS values range from -1 to +1, with a 0 meaning prediction is no better than random, and a value above 0.5 is considered to show high predictive power (Allouche et al. 2006, Rubidge et al. 2011).

Another component of predictive ability is calibration. The model probabilities indicate the proportion of sites at that probability that should be occupied across the region (Pearce and Ferrier 2000). For example, 20% of grid cells with a predicted probability of 0.20 should be occupied. While a well calibrated model will usually have good discriminatory power, the opposite is not true (Pearce and Ferrier 2000). I ran a generalized linear model with a binomial family and logit link using observed presence and absences from the validation data as the dependent variable, and the associated predicted probabilities as the independent variable. The fitted values from this model were plotted against the predicted probabilities at those sites. I visually investigated how well the model accurately predicted the proportion of occupied sites for each decade. Perfect calibration would result in a plotted line with slope 1 and intercept 0. Points falling above or below this line indicate the model under or over estimates the proportion of occupied sites, respectively (Pearce and Ferrier 2000).

Spatially and temporally explicit change

To determine where land use was responsible for a change in probability between 1970 and 1980, I calculated the predicted probabilities in the 1980s using the land use footprint from the 1970s and the climate data from the 1980s. The new probability, which assumes no change in land use between 1970 and 1980, was then subtracted from the original 1980s probabilities. Conversely, to determine where climate was responsible for a change in probability between 1970 and 1980 I calculated the predicted probabilities for the 1980s using the land use footprint from 1980 and the climate data from the 1970s. The new probability, which assumes no change in climate between 1970 and 1980, was subtracted from the original 1980s probabilities. Where subtracted values equaled zero in both cases, there was no change in probability between decades. Where the absolute value of the difference in probabilities was greatest for climate, climate was the driver of change for that grid cell, and where the absolute value of the difference in probabilities was greatest for land use, land use was the driver of change for that grid cell. This series of calculations was repeated for the changes between 1980 and 1990, and 1990 and 2000. To determine where changes resulted in the probability crossing the 0.73 threshold, signifying a change from absence to presence, I identified locations where the calculated decadal probability was greater than 0.73, and the probability with the land use of the previous decade, or the climate of the previous decade was lower than 0.73, for land use and climate changes respectively. The minimum footprint, excluding the uncertain cut block data, was used for all of these calculations.

Results

The range of climate variables and the proportion of deciduous forest were similar for the validation data sets and the training data (Table 4.1). The validation data sets contained higher total footprint and higher proportions of wetland land cover than the training data, however (Table 4.1). Testing the predictions under these extrapolated conditions helps determine how robust the model is to conditions expected across the rest of the landscape and through time.

Prediction accuracy

The model had very good discrimination power in the 2000s and the discrimination power was good for the 1980s and 1990s. However the SDM had poor discrimination power in the 1970s, based on AUC. If sensitivity and specificity are weighed as equally important, then the TSS suggests that the model has high predictive power for only the 1990s and 2000s decades. In fact, there is a temporal trend in the accuracy of the SDM predictions where the model performs better when predictions are made closer to the time period in which the model was built (Table 4.2). The loss in predictive power may occur because the model predicts presences where the validation sets have absences (lower specificity) (Table 4.2). The sensitivity, or ability of the model to correctly predict presences in the validation data, remains high and relatively stable across decades (Table 4.2).

All regression models testing calibration have significant positive slope parameters indicating that high model predictions over-estimate the proportion of occupied cells, and predictions of low probability under-estimate the proportion of occupied cells (Figure 4.3). There is also a significant negative intercept for 1980 – 2000 decades which indicates a bias toward over estimating occurrence over all (i.e. there are more absences than the model predicts). This can arise as a result of lower prevalence in the validation data compared to the training data (Pearce and Ferrier 2000). This is consistent with the error found in the discrimination statistics.

Spatially and temporally explicit change

The predicted probability of white-tailed deer presence increased in 40% or more of the study area between each decade (Figure 4.4). The greatest change occurred between 1980 and 1990 (54%), compared to the previous decade (42%) and the one that followed (40%). The change in predicted white-tailed deer distribution was driven mainly by changes in climate (Figure 4.4). Between 1970 and 1980, climate, rather than land use, increased probability of presence in 96% of the area that predicted an increase in white-tailed deer presence. Similarly, the increased probability of white-tailed deer presence in 89% and 90% of the grid cells was driven by changes in climate between 1980 and 1990 and 1990 and 2000 respectively. Climate was also the driver responsible for 75 – 80% of the cases where changes in probability of presence crossed the 0.73 threshold, which would change the interpretation from an absence to a presence (1970-1980 = 420 grid cells/527 grid cells that changed, 1980 – 1990 1626 grid cells/ 1950 grid cells, 1990 – 2000 = 536 grid cells/668 gird cells that changed).

Substantially more change in predicted presence of white-tailed deer has occurred in the northeast part of the province compared to the northwest. Based on a threshold of 0.73 to signify presence, since 1970 the distribution has moved approximately 50 to 250km north in the eastern part of the study area (Figure 4.5). Fingers of distribution increase coincide with major rivers and deciduous forest (Figure 4.6).

Uncertainty

The missing year for harvest data for 30% of the cut block data had little effect on the interpretation of predictions. Adding the undated cut blocks in any decade only changed 1% of the grid cells from below 0.73 to above 0.73 (Figure 4.5). For this reason, I included the undated cutblocks in calculations of predictions for all tests. The uncertainty in the boundary of agriculture could not be quantified; however predicted probability of occurrence was high on both sides of the boundary for all decades, so slight shifts in that boundary likely would not affect interpretation of the predictions (Figure 4.5).

Discussion

In chapter 3 I showed that both climate and land use were important for describing the current distribution of white-tailed deer. Here I show that the predicted distribution of white-tailed deer changed substantially in northern Alberta from 1970 – 2000, particularly in the NE region of the province and that changes in climate increased the probability of presence across substantially more of the landscape than did land use change in all decades. Climate changes also resulted in probability increases suggestive of a change from absence to presence more frequently than land use change.

It is interesting to note that the predicted distributions appear as an extension of the distribution pattern shown by Webb (1967) for the 1960s, developed from interviews with homesteaders and people who worked in the region (i.e. surveyors, guides, trappers and Fish and Wildlife Officers). Webb (1967) showed the distribution starting to move north along the Athabasca River in the northeast part of the province, and the provincial management plan for white-tailed deer mentions white-tailed deer were often sighted around the Peace River Alberta (Figure 4.6) (Alberta Environmental Protection 1991). There are fingers of higher probability moving north along the Peace, Loon, Wabasca, Athabasca and Christina rivers. The most northerly occurrence record of white-tailed deer was also along a major river, the MacKenzie River near Fort Good Hope in Northwest Territories and two other sightings were reported further south in that river valley (Veitch 2001). Some studies have found that white-tailed deer disperse along river corridors, although others have not found any association (Sparrowe and Springer 1970, Long et al. 2010). The pattern shown here appears to be a result of more deciduous forest being located nearer to the rivers. As climate becomes more favorable, the predicted distribution change follows the pattern of existing favorable habitat.

The predictions from the SDM were validated in each decade and matched closely with the observed presences and absences from independent validation data. Although the validation data sets were sampled from similar regions as the training data, they were collected using different methodology, in different time periods, and at different spatial scales than the training data, so offer a good test of the predictive ability of the SDM. The WSIswe and growing season length for the validation data was within the range of climate variables modeled in the SDM so I could not test predictions under extrapolation of climate variables. The training data covered a wide range of values for these climate variables, however, so extrapolation may not be necessary for this landscape for some time. Predictions were robust to a higher amount of land use and wetland land cover in the validation data than were modeled with the training data. The accuracy of the predictions suggests the model is adequate for predicting white-tailed deer spatial distribution through time and space for northern Alberta.

Predictive power decreased as predictions were made further from the decade in which the model was built. Araujo et al (2005) suggested this is because temporal autocorrelation in predictions is reduced the further apart in time the predictions are made. For my study, the problem appears to be related to the ability of the model to predict absences. While lower prevalence in the validation data may lead to more absences than predicted by training data, 1970 had the lowest specificity in this analysis but nearly the same prevalence as the training data. In 1970, only 38% of absences in validation data were predicted to be absences. This means

62% of actual absences were predicted to have white-tailed deer present. This may indicate inaccuracy in the model, a problem with the validation data, or both. Tests of accuracy assume perfect detection for validation data, which is rarely possible with ecological data (Lobo et al. 2008). Although methods have been developed to estimate detection probability and adjust observations (Royle et al. 2005), it is difficult to incorporate them when using historic data sampled under different survey techniques. If population size was smaller in past decades, as would be expected given the range was expanding, the ability to detect presence would be reduced compared to later decades when population size would be expected to be higher. Absences resulting from non-detection would lower the apparent specificity of the predictions. The AUC was also seen to decrease through time however, suggesting model related inaccuracies exist regardless of issues with detection. Lag times in species' responses to climate changes, interactions with predators or competitors, or seasonal fluctuations in abundance, survival, and reproduction could all result in species being absent from otherwise suitable locations (Araújo et al. 2005, Mitikka et al. 2008). These processes link the pattern of species distribution to the process of range expansion. Attempts to incorporate some of these processes into species distribution models have been some of the recent advances in this field (Elith and Leathwick 2009, Melles et al. 2011).

Accuracy in prediction of absences is less important for some applications of species distribution models than for others (Araújo et al. 2005, Allouche et al.

2006, Lobo et al. 2008). White-tailed deer are already having negative impacts in northern Alberta by increasing grey wolf (*Canis lupus*) abundance and subsequently increasing predation on woodland caribou (*Rangifer tarandus caribou*) populations, which are listed as threatened by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2002, Latham et al. 2011). The consequences of the white-tailed deer SDM over predicting the absolute probabilities of occurrence (calibration error) by under predicting absences (low specificity in past predictions) are arguably lower than the consequences of expecting them to be absent when they are in fact present.

It is difficult to monitor white-tailed deer in the boreal forest using aerial survey techniques, which are the traditional method for monitoring ungulate populations, because sightability is hampered by closed canopy forests. Ground sampling methods are expensive and labor intensive making them inadequate for monitoring changes across the species range in this region. This analysis illustrates the likely current distribution of white-tailed deer in northern Alberta, allowing managers to prioritize regions for conservation where impacts of the species presence may be greatest on native populations. I indicate locations where land use has driven the changes in distribution which may be important for local management. I also indicate where climate change has driven changes in the distribution and suggest these areas should be monitored to assess future changes and to further validate the predictions of this model.

Conclusion

Species distribution models are relatively simple approximations of a more complex ecological process occurring on the landscape. While I see evidence of some of the uncertainties related to using static species distributions models to predict distributions through space and time, the model is performing relatively well. It provides predictions of distributions that make ecological sense and match closely to changes noted in the past (Webb 1967), and occurrences observed on the landscape. Provided limitations of such models are made explicit, they can be useful for management and conservation planning while also providing insight into the drivers of range expansion.

Here I indicated that white-tailed deer distribution changes in northern Alberta, Canada have been driven largely by changes in winter and summer climate, despite extensive industrial development occurring in the region. To the best of my knowledge, this is the first attempt to test predictions of a species distribution model through multiple time steps. Although these predictions remain useful within the limitations of such modeling approaches, I illustrate a declining predictive accuracy of an SDM at time periods further from the model development decade. This illustrates the importance of species monitoring, informed by the model predictions, to improve the model itself. An iterative modeling – monitoring approach could greatly increase our ability to anticipate impacts of future climate change on ecological communities.

Figure 4.1: Study area. Dark black outline indicates the two ecozone boundaries in the study area. The light grey lines show major rivers. Black dots are sampling locations for the training data. Stars show the location of towns mentioned in the text. The northern border of the study area follows 60° north latitude, the western border follows 120° west longitude, and the eastern border follows 110° west longitude.

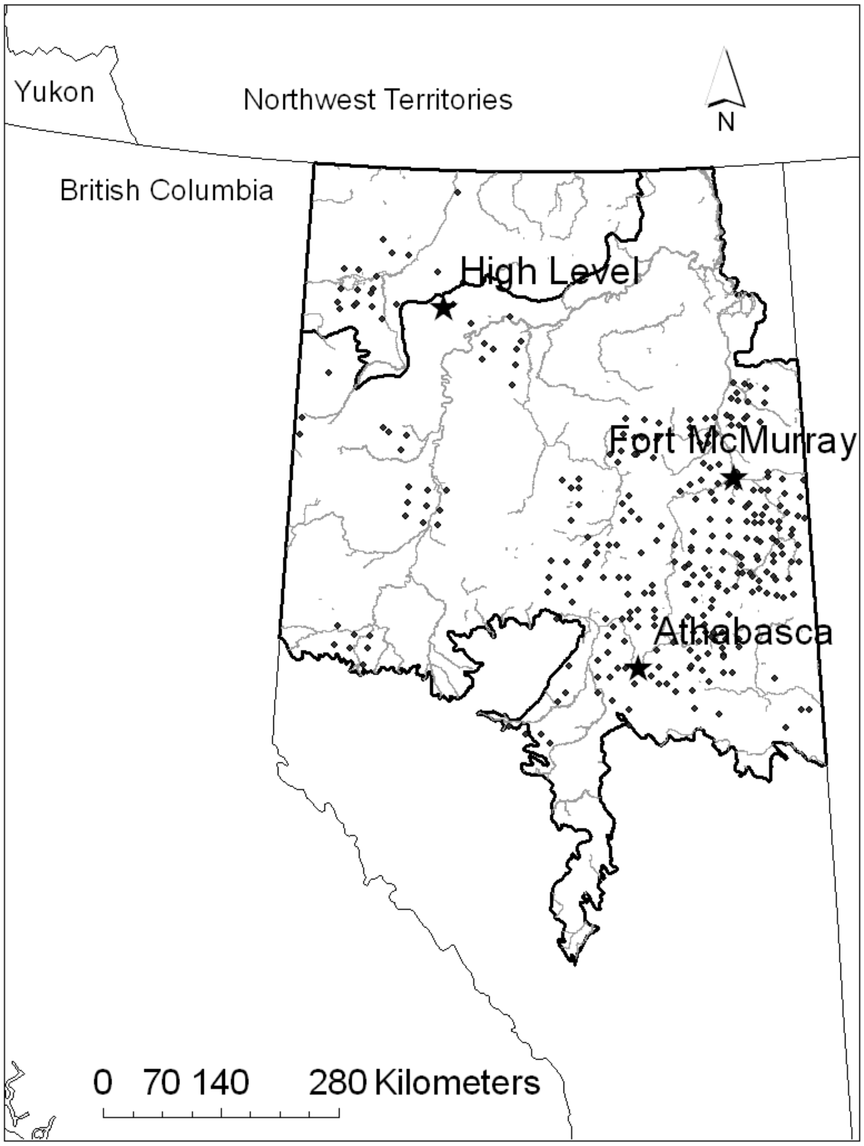

Figure 4.2: Validation data sets for the 1970s (A), 1980s (B), 1990s (C), and 2000s (D). Dark blue indicates presence of white-tailed deer and light blue indicates absence. The numbers correspond to the Peace (1), Wabasca (2), Loon (3), Athabasca (4), Clearwater (5), and Christina (6) Rivers.

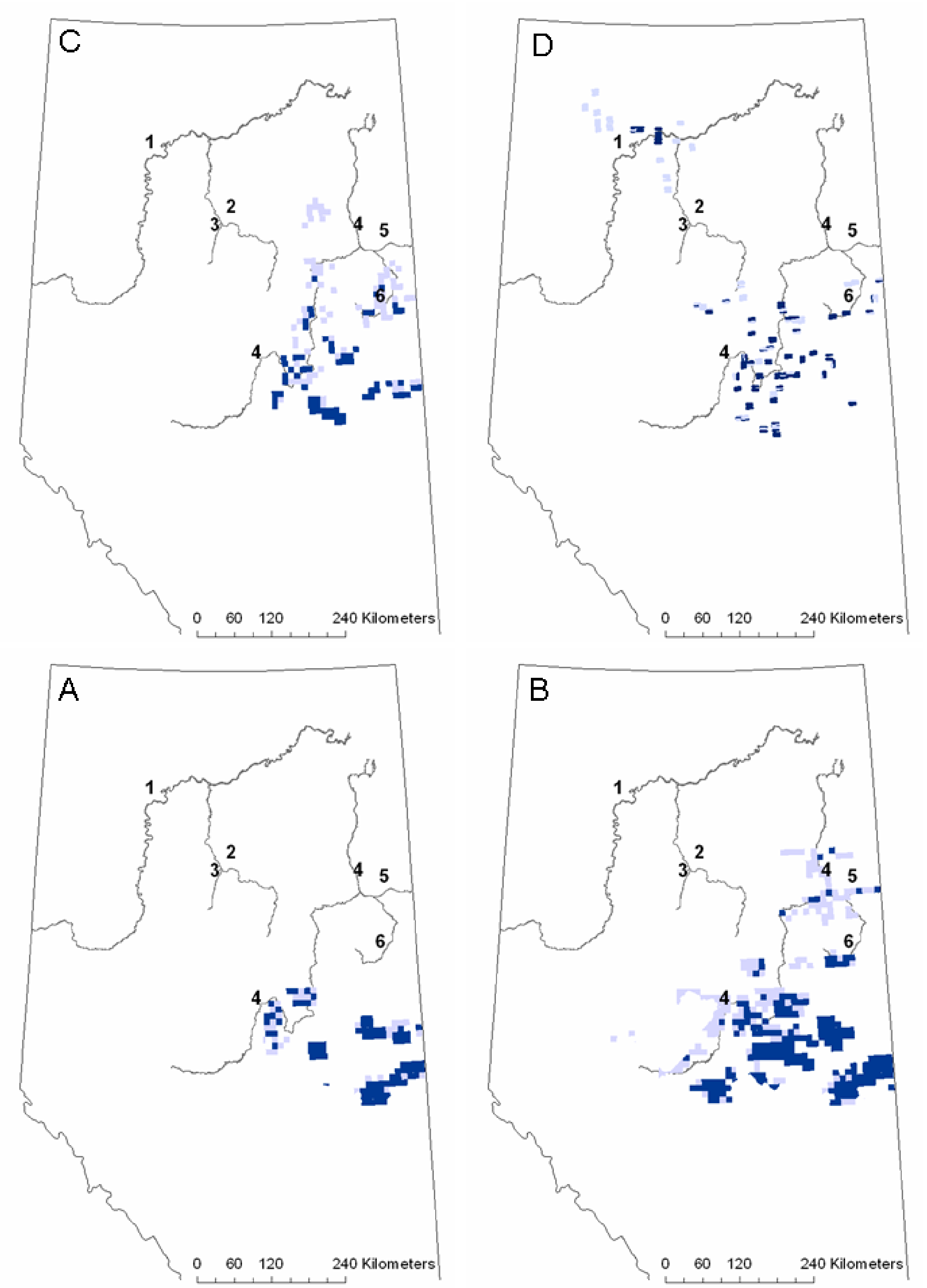

Table 4.1: Variable ranges for model parameters.

	Training Data			Aerial Surveys 00s			Aerial Surveys 90s			Aerial Surveys 80s			Aerial Surveys 70s		
Variable Description	min	max	mean	min	max	mean	min	max	mean	min	max	mean	min	max	mean
growing season	142.60	178.10	163.70	148.40	173.40	164.50	150.50	170.90	165.00	153.70	172.30	165.60	157.80	168.90	163.30
winter severity	66.87	193.94	119.26	78.80	180.20	117.30	84.40	172.80	112.50	74.70	170.30	113.10	87.90	129.60	108.20
total footprint	0.00	0.91	0.12	0.00	1.00	0.32	0.00	1.00	0.31	0.00	1.00	0.36	0.00	1.00	0.41
proportion deciduous	0.00	0.90	0.24	0.00	0.60	0.23	0.00	0.62	0.16	0.00	0.74	0.20	0.00	0.74	0.23
proportion wetland	0.00	0.13	0.02	0.00	0.34	0.08	0.00	0.49	0.09	0.00	0.34	0.06	0.00	0.25	0.04

Table 4.2: Accuracy Statistics. N is the sample size, N(p) is the number of presences. Prev is the prevalence (N(p)/N) and sd is standard deviation.

Data Set	N	N (p)	prev	AUC	TSS	sensitivity	sd	specificity	sd
training	299	218	0.73	0.94	0.68	0.83	0.03	0.85	0.04
2000	72	51	0.71	0.90	0.61	0.80	0.06	0.81	0.09
1990	136	78	0.57	0.82	0.57	0.78	0.05	0.79	0.05
1980	354	209	0.59	0.75	0.39	0.85	0.02	0.54	0.04
1970	113	81	0.72	0.64	0.21	0.84	0.04	0.38	0.09

Figure 4.3: Model predictions compared to the actual proportion of occupied sites in validation data sets for decades 1970 - 2000. Points on the diagonal line indicate perfect calibration. m is the slope of the regression between actual presence and absence and predicted probabilities of presence and b is the regression intercept.

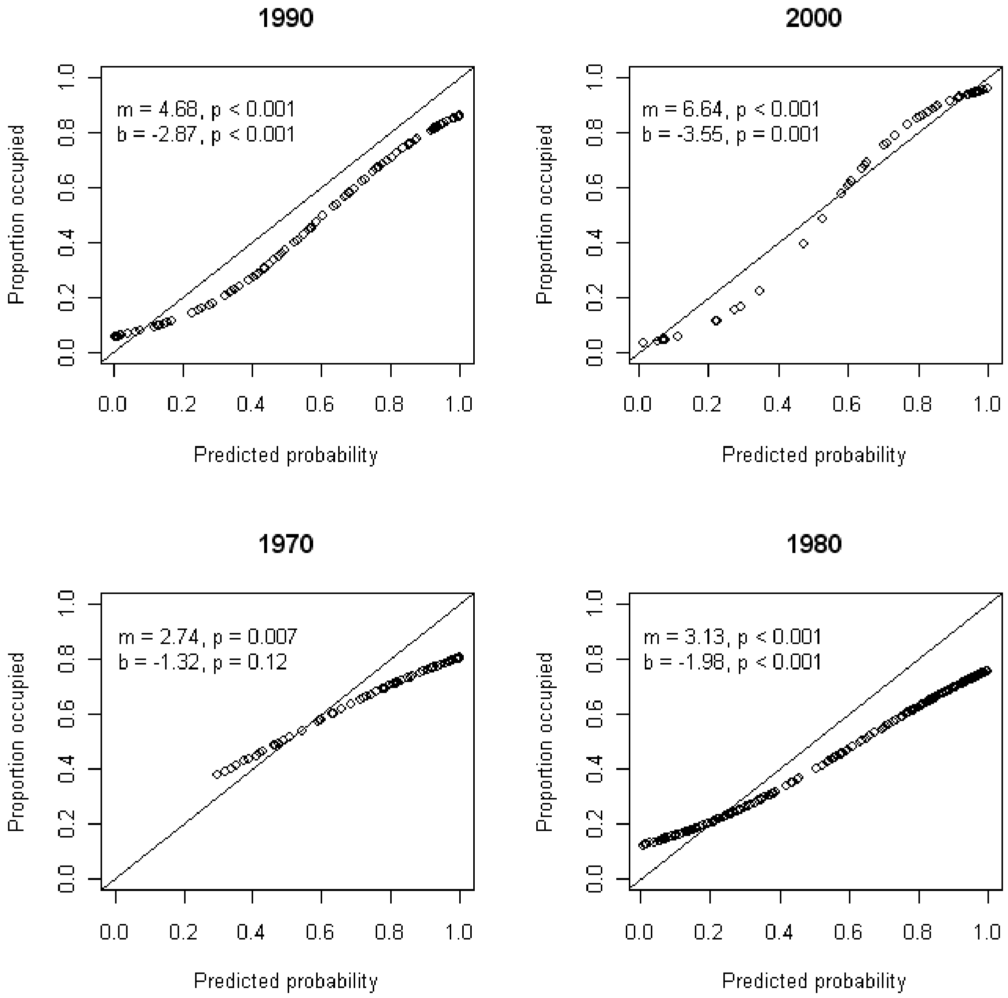

Figure 4.4: Drivers of white-tailed deer range change between 1970 and 1980 (A), 1980 and 1990 (B), and 1990 and 2000 (C) decades. Colors indicate the variable that changed and had the largest impact on the predicted probability of white-tailed deer presence.

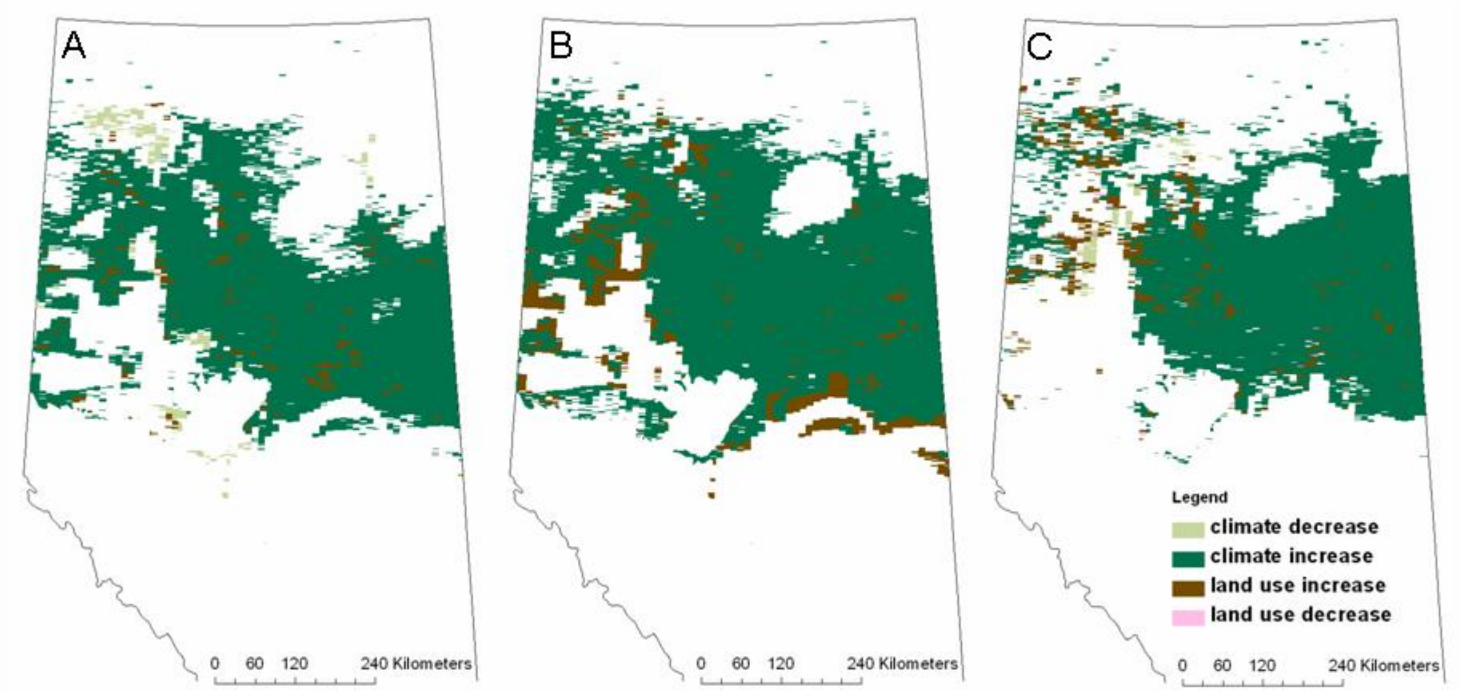

Figure 4.5: Predicted distribution of white-tailed deer for 1970 (A), 1980 (B), 1990 (C), and 2000 (D) decades. Blue designates where probability of white-tailed deer presence is greater than or equal to 0.73 (dark blue), between 0.37 and 0.72 (medium blue), or less than 0.37 (light blue). The numbers correspond to rivers as listed in the caption for figure 4.2. The agricultural boundary is outlined in black. Yellow indicates where inclusion of undated cut blocks would change the probability of presence from < 0.73 to ≥ 0.73.

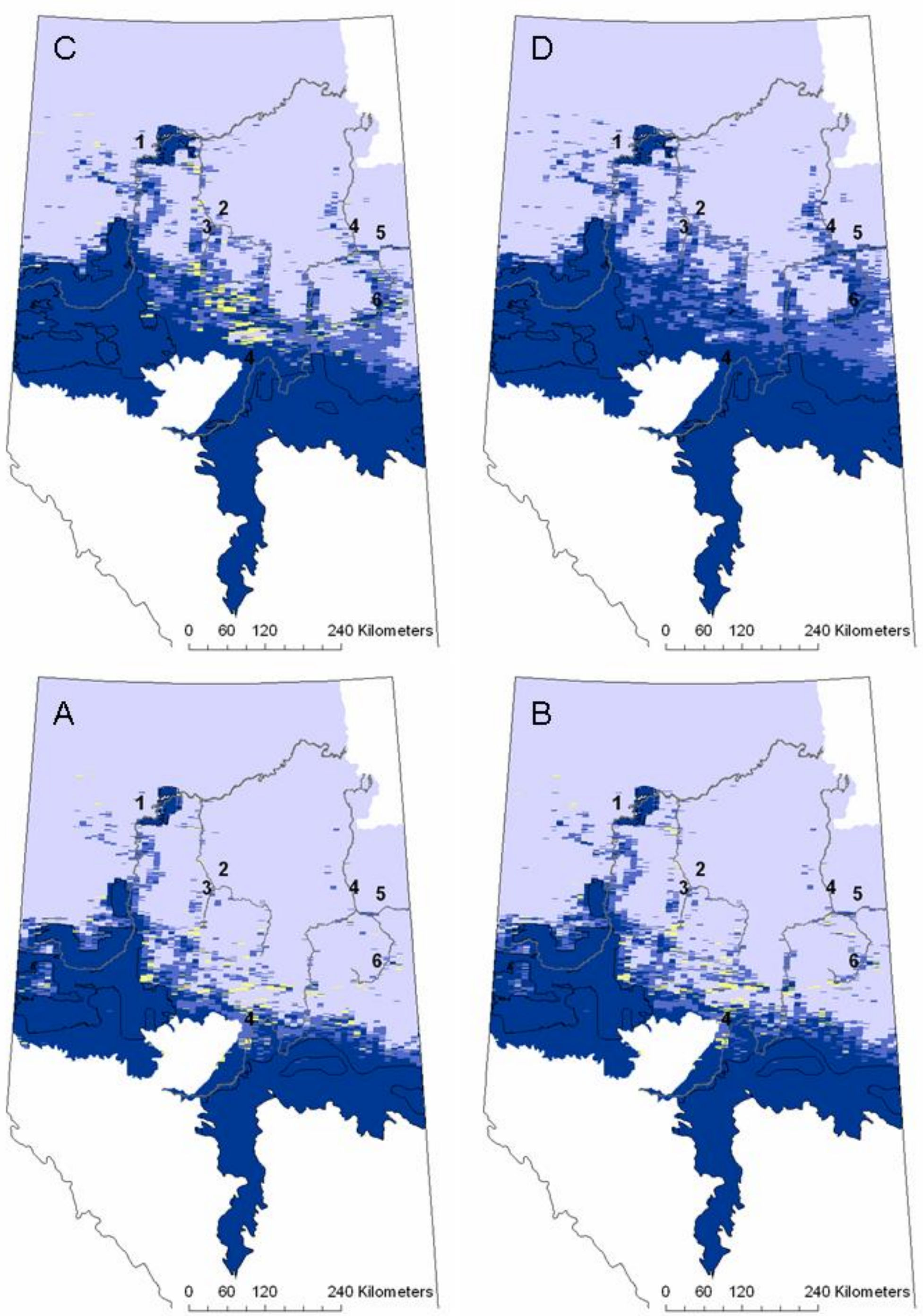
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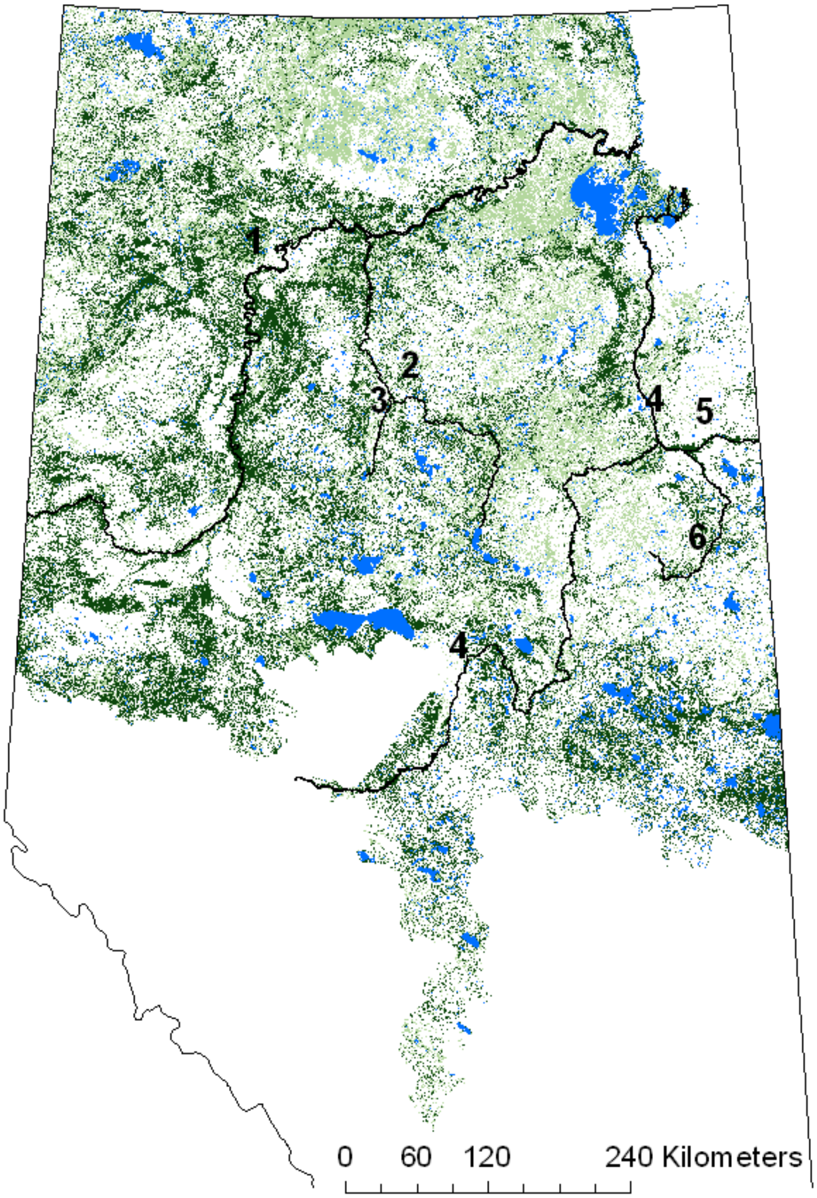
Figure 4.6: Boreal vegetation communities included in the SDM. The dark green indicates deciduous forest and the pale green is wetland. Blue is water. Numbers designate rivers as described in the figure 4.2 caption.



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Chapter 5: White-tailed deer range expansion under future climate change

Introduction

Substantial changes in climate are expected to occur in North America by the end of the 21st century (Christensen et al. 2007). Temperature increases may exceed 5°C and precipitation is also expected to increase, although the proportion of precipitation falling as snow, the length of the snow cover period and the depth of the snow pack are expected to decrease (Hayhoe et al. 2004, Christensen et al. 2007). Snow melt is already occurring 8 days earlier in northern-Alaska compared to pre-1960 periods due to decreased snow fall and warmer springs; a trend that has likely occurred across northwestern North America (Stone et al. 2002, Lemke et al. 2007). Concurrent changes in the length of the growing season have also led to earlier plant growth in North America and higher productivity (Jarvis and Linder 2000, Nemani et al. 2003). These changes are having, and are projected to have substantial impacts on species' distributions (Parmesan and Yohe 2003, Field et al. 2007). In turn, changes in species composition and diversity within communities as a result of species range expansion may change ecosystem function and have substantial impacts on native species (Chapin et al. 1997, Clout and Russell 2007). It is important to anticipate changes in species distributions to manage potential ecological impacts on communities and ecosystems.

White-tailed deer (*Odocoileus virginianus*) have expanded their range into northern boreal ecosystems over the last half of the 20th century (Webb 1967, Charest 2005). Based on the species distribution model developed in chapter 3, the current predicted distribution covers the northwestern agricultural region and has fingers of higher probability of presence along northeastern rivers (chapter 4). There is low probability of presence past 58.55° latitude (chapter 4). Although current distribution in the invaded range can be explained by land use, land cover and climate variables, 89 - 96% of the increases in probability of presence of white-tailed deer from 1970 – 2000 were explained by decreases in winter severity and increases in growing season length (chapters 3 and 4). Changes in these climate variables will likely lead to further changes in white-tailed deer distribution in this province. The population increase and expansion of white-tailed deer has already led to increased grey wolf (*Canis lupus*) abundance and elevated predation on at least one northern Alberta herd of threatened woodland caribou (Rangifer tarandus caribou) (Dale et al. 1994, COSEWIC 2002, Latham et al. 2011). Understanding the likely temporal and spatial pattern of future expansion will allow for potential mitigation of impacts to other threatened caribou herds and native species in northern Alberta.

Our objective was to predict decadal changes in white-tailed deer distribution in northern Alberta from the 2000s – 2050s, based on projected changes in climate. Projections of climate change reported by the Intergovernmental Panel on Climate Change, are based on general climate models (GCMs) developed at grid cell sizes ranging from 125 km – 400 km and over monthly time periods (Christensen et al. 2007). These are not relevant for some ecological applications and there have been conflicting results when projections from different GCMs were considered (Beaumont et al. 2007, Ashcroft et al. 2009, Seo et al. 2009, McKenney et al. 2011). A tradeoff also exists when including mechanistically informed climate variables in species distribution models because the variables may not be included in GCM projections under future climate scenarios. According to the species distribution model (SDM) developed for white-tailed deer in northern Alberta, daily temperature and precipitation data are required to calculate winter severity (chapter 3). Data at a small spatial grain is also necessary to capture the spatial variability within this region. Projections from GCMs are not at the spatial or temporal resolution needed for climate variables in the white-tailed deer distribution model. Instead, I calculated the linear change in winter severity and growing season length observed for this region from 1961 – 2002 and 1950 – 1999, respectively, and extrapolated this to predict potential changes in these variables up to 2049. Several authors have modeled change in climate variables over past decades using linear relationships (Stone et al. 2002, Rikiishi et al. 2004, Mote et al. 2005, Ashcroft et al. 2009). Although projections from GCMs are based on varying parameterizations and complexity of atmospheric and ocean circulation systems (Randall et al. 2007, Heffernan 2010), rates of change in recent decades closely match those predicted for the near future. Temperature increases of 0.2°celsius/decade have been observed for 1990 – 2005 (IPPC 2007). This rate of change is expected to continue under all emissions scenarios until the 2030s, when predictions under different emissions scenarios begin to diverge, according to multimodel averages (Meehl et al. 2007). The most conservative estimates for future climate change follow the B1 emissions scenario, which assumes global solutions to economic, social and environmental sustainability (IPPC 2007). The linear increase in mean temperature continues under this scenario to approximately 2060, when the rate of change slows. That scenario also predicts a linear increase in growing season length from 1960 – 2060 (Meehl et al. 2007). Although here I use a more simplistic approach to projecting changes in climate, I see this as justification for using linear extrapolation. I applied predictions for winter severity and growing season length to the SDM from Chapter 3 to predict potential future distributions of white-tailed deer.

Methods

Study region

I wished to predict white-tailed deer distribution for the Alberta boreal forest natural region within the boreal and taiga plains ecozones of Alberta, approximately 380000 km^2. A mosaic of upland forests and peatland complexes cover this area and climate is characterized by short cool summers and long cold winters. Dominant tree species in the uplands include white spruce (*Picea glauca*, jack pine (*Pinus banksiana*), trembling aspen (*Populus tremuloides*), and balsam poplar (*Populus balsamifera*). Peatlands are composed of shrub and fen wetlands, and black spruce (*Picea mariana*) and tamarack (*Larix larcina*) bogs.

Climate predictions

Winter severity was calculated by combining temperature and precipitation data according to the index and thresholds described in Chapter 2. When air temperatures drop below the lower thermoneutral zone for white-tailed deer, approximately -17.7°C, individuals must expend energy to increase body temperature (Moen 1968, Jensen et al. 1999). Similarly, energy expenditure for movement is substantially increased once snow depth exceeds front knee height, approximately 38cm (Mattfeld 1974, Parker et al. 1984). The index (WSIswe) calculated here, summed the number of days between November 1 and April 31 that were below the temperature threshold and the days that were above the snow depth threshold, adjusted according to the snow water equivalent of snow depth (Chapter 2). Daily temperature and precipitation data, interpolated from climate stations using thin-plate smoothing splines, were obtained from Natural Resources Canada (NRC) (Hutchinson et al. 2009). These data covered the period from 1961 – 2002. They were at a spatial grain of 10 km in grid format in a geographic information system (GIS), with 3775 cells covering the study area. I calculated WSIswe for each cell in each year available in the data set. To determine the pattern of change for WSIswe, I regressed WSIswe on year for each cell, with year coded as an integer so the intercept of the regression was equal to the WSIswe estimate for 1961. To predict the WSIswe for future years, I calculated the WSIswe for each year from 2003 to 2049 for each cell using the regression equation developed for that cell. Any calculated values that were negative were set to zero.

The growing season began when mean temperature was greater than or equal to 5°C for five consecutive days after March 1 and ended after August 1 when minimum temperature reached -2°C. Growing season data were obtained from NRC covering the period from 1950 – 1999 (Hutchinson et al. 2009). They were at a spatial grain of 8.363 km in grid format in GIS, with 8028 cells covering the study area. To determine how growing season length has changed, I regressed growing season length on year for each cell in the GIS layer and coded year so the regression intercept was equal to the growing season length for 1950. I calculated the length of the growing season for each year from 2000 to 2049 for each cell using the regression equation developed for that cell.

Distribution predictions

I used the white-tailed deer SDM developed in chapter 3 to predict future decadal distributions of white-tailed deer in northern Alberta. The SDM was a generalized linear model with binomial family and logit link, selected as the lowest AIC model from a suite of *a priori* climate, land use, land cover, and spatial models (w_i = 0.93). Presence and absence data were collected between 53.9° N to 59.8° N latitude and 119.8° W to 110.0° W longitude in the Alberta boreal forest from 2002 to 2009 by the Alberta Biodiversity Monitoring Institute and the Integrated Landscape Management lab at University of Alberta (chapter 3). Sample sites were selected by stratified random or systematic design, depending on the organization conducting sampling. Data from 299 sampling sites were collected by snow tracking on foot along 9 km triangle transects, or on snowmobile on 10 km straight transects; sampling methods changed to decrease sampling time (chapter 3).

The model, describing predictors of distribution for the 2000s decades, included parameters for method, climate, land use, and land cover. There was a higher probability of presence when sampling was conducted by triangle method rather than transect method. Probability of white-tailed deer presence increased with decreasing WSIswe and increasing growing season length, measured as the 40 and 50 year means, respectively. Land use and land cover variables were calculated as the proportion of each type within a 500 m region of the sampling unit. As the total proportion of nonlinear land use footprint increased, probability of presence increased as well. Nonlinear footprint consisted of agriculture, forestry cutblocks, and well pads. Probability of white-tailed deer presence increased with increasing proportion of deciduous forest, and decreasing proportion of wetland land cover.

To predict future distributions, a 10km (east – west) x 1 km grid was established across the study region and variables were derived for each cell. I fit a zero for the method variable, basing calculations on the transect method. The mean WSIswe from 1961 to the beginning of the decade of interest and the mean growing season length from 1950 to the beginning of the decade of interest were calculated. I maintained the land cover and land use footprint for the 2000s decade for future predictions. Agriculture data were obtained from Statistics Canada agricultural ecumene and the Alberta Sustainable Resources white zone boundary designating the agricultural zone (Werschler 1995, Statistics Canada 2006, chapter 4). Cut block data were derived from Alberta Vegetation Inventory (Nesby 1997) and included any blocks cut from 1970 – 2010. Well sites were set as a circular footprint with a 50m radius to account for forest clearing associated with well establishment. These data were obtained from the Alberta Base features GIS data set. There is no regulation requiring re-forestation on abandoned well sites, and natural regeneration is hindered by these disturbances (Osko and MacFarlane 2001, Schneider 2002) so all wells established from 1900 – 2010 were included in the footprint. Alberta Ground Cover Classification data were used to calculate land cover proportions (Sanchez - Azofeifa et al. 2004). Although the spatial pattern of the land use footprint will change over time, I was interested only in climate driven changes of future distribution. Agriculture has reached its northern limit in Alberta and is expected to expand only east and west from existing margins (Hamley 1992), and forestry sector cutting will occur within already established forest management areas. Energy sector developments are projected to intensify within the oil sands regions over this time period (National Energy Review Board 2006). None of these should affect predictions of northward expansion, however where land use developments occur, the probability of presence of white-tailed deer will be higher than predicted by this analysis.

I compared future distributions to the predicted distribution calculated for the 2000s decade across the same grid in chapter 4. To quantify predicted changes between decades, I assumed a probability of presence of 0.73 or higher designated an occurrence of white-tailed deer. This was the prevalence (number of presences/number of samples) for the data used to build the SDM (chapter 3) and has been recommended as a threshold to convert model probabilities to presence or absence (Liu et al. 2005).

Results

Climate predictions

Overall change in climate variables was toward warmer winters and longer growing seasons (Figure 5.1). WSIswe change ranged from a decrease of 0.155 - 2.248 index points per year and was greatest in the northeast portion of the study area, near Fort McMurray (Figure 5.2A). The largest changes in length of the growing season occurred in the northeast and far north of the study region and ranged from a shortening of 0.059 days per year to a lengthening of 0.375 days per year (Figure 5.2B).

Distribution predictions

The decadal mean WSIswe, averaged over the study region, was predicted to drop by 31 index points from 2000s to 2050s and the mean growing season length, averaged over the study region, was predicted to increase by 5.17 days (Table 5.1). The changes in these variables led to an 80900 km^2 increase in predicted white-tailed deer range size in the northern Alberta boreal (Table 5.1, Figure 5.3F). Over the next decade, white-tailed deer are predicted to continue expanding along the Loon, Wabasca, Athabasca, and Christina Rivers where range expansion was predicted to have occurred during the last half of the 20th century (chapter 4, Figure 5.3A). By the end of the 2020s, the area east of Christina River to the border of Saskatchewan is predicted to be occupied (Figure 5.3B). Over the 2030s and 2040s the distribution is predicted to extend east and west from these rivers, essentially filling in between the fingers of distribution formed by the rivers mentioned. By the end of the 2050s, white-tailed deer are predicted to occupy most of the region south of Fort McMurray, as well as agricultural regions and major river valleys north of Fort McMurray. The quadrant formed by the southern edge of the boreal shield, the Athabasca and Christina Rivers and the Saskatchewan border is also predicted to be occupied. This is the same region that has experienced the greatest change toward less severe winters (Figure 5.2). The distribution in the northeast is predicted to extend approximately 100km further north along the Athabasca River, reaching the northern extent predicted for the High Level area during the 2000s decade. The predicted probability of white-tailed deer presence north of High Level remained low throughout the first half of the 21st century (Figure 5.3).

Discussion

I predict substantial changes in the white-tailed deer distribution across the northern Alberta boreal forest over the first half of the 21st century. Most of these changes will be in the northeast portion of the province, where changes in winter severity and growing season have been the greatest. Although I assumed the rate of change in winter severity and growing season length would remain the same for the next five decades as for the last half of the 20th century, changes in the 21st century climate may "very likely" exceed changes observed in the past if global emissions continue at current rates, according to the Intergovernmental Panel on Climate Change (Meehl et al. 2007). In this case, the predictions presented here are conservative and areas predicted to have low probability of white-tailed deer presence in this analysis may actually have higher probability. Alternatively, in figure 5.1 of this chapter it appears that the growing season length was decreasing, on average, for the first part of the time series. If such changes occurred in the future this may lead to lower probabilities of presence than predicted here. The direction of change of WSIswe has been more consistent; however it is possible that the rate of change may decrease as the WSIswe approaches zero. This is because the index is based on the number of days that temperature and precipitation values cross a threshold value. As these variables decrease, they will cross the threshold less frequently; however even under substantially warmer temperatures and low snow fall, the occurrence of extremes of low temperature or high snow fall may still lead to the accumulation of some WSIswe index points. Although this would violate my assumption of a linear decrease, it would have little effect on the predicted probabilities because once WSIswe is below 95 units, in the absence of land use and at moderate values for other model variables, predicted probability or presence is already greater than 90% (chapter 3).

Predictions from species distribution models provide insight on potential distributions (Pearson and Dawson 2003). Whether the predicted distribution changes are realized will depend on population factors such as dispersal rate and distance, competition, and predation (Pearson and Dawson 2003, Guisan and Thuiller 2005). In chapter 4 I found that there were more absences in actual species occurrence data than were predicted by the SDM, and this was a bigger issue for predictions made longer in time from the decade for which the model was built (chapter 4). This suggests, not surprisingly, that movement processes and/or biotic interactions likely affect the ability of white-tailed deer to exploit all suitable habitats. Nevertheless, the SDM used here was found to have reasonable accuracy in predicting past distributions, which lends confidence to the predictions for future distributions (chapter 4). There is always uncertainly associated with ecological predictions (Miller et al. 2004). The value of distribution predictions under predicted climate change is that they can direct monitoring, and alert managers to potential impacts on native species and ecosystems.

We have not considered changes in land cover or land use in this analysis. Schneider et al (2009) modeled potential land cover changes in the Alberta boreal forest according to predicted changes in climate; based on the caveat that forest disturbance (fire or cutting) must occur to allow land cover change in the direction predicted by changing climate. They predicted shifts toward more deciduous forest stands in the boreal, mainly through a change in the relative abundance of existing species after disturbance events (Schneider et al. 2009). Although the amount of deciduous forest increases the probability of white-tailed deer presence, based on the SDM, white-tailed deer presence is already predicted to be high where those land cover changes are most likely to occur (see Schneider et al 2009 for predicted land cover map). This means the predicted changes in land cover should have little effect on the predictions for white-tailed deer distribution. Further, changes in climate led to high predicted probability of occurrence throughout the study area, despite occurrence of wetland land cover, which is negatively related to presence in the SDM. Once climate variables are more favorable (low WSIswe and long growing season length), the effects of climate variables on predicted presence is stronger than that of land cover variables (chapter 3).

While land use may increase the predicted probability of white-tailed deer presence, its effect will only be important where predicted presence due to future climate changes is low. In chapter 4 I showed that a maximum of 11% of the increase in predicted probability of white-tailed deer between past decades was due to land use changes. Subsequent changes in climate would have led to increased probability of presence in those locations, even in the absence of the land use (figure 5.3 and figure 4.5). Temporal changes in suitability leading to expansion of white-tailed deer are important from a management perspective, however. At a local level, managers can expect increases in agriculture, forestry cut blocks, or well pad footprint to increase the probability of white-tailed deer presence above that predicted here.

Conclusion

If the shifts toward less severe winters and longer growing seasons continue at the rate observed in recent decades, white-tailed deer will be able to occupy the majority of the Alberta boreal by the 2050s. Large changes are expected for the northeast region south of the Peace River, in particular, where the West Side of the Athabasca caribou herd has already suffered high predation rates due to increases in white-tailed deer in and around their range (Latham et al. 2011). Several other herds occupy ranges in the northeast, south of the Peace River; suggesting wildlife managers in Alberta face big challenges now and into the future.

Figure 5.1: Change in mean winter severity index and growing season length for the entire study area. Calculated are based on NRC interpolated temperature and precipitation data (years before the dotted line) and extrapolated from regression equations for the years before the dotted lines.

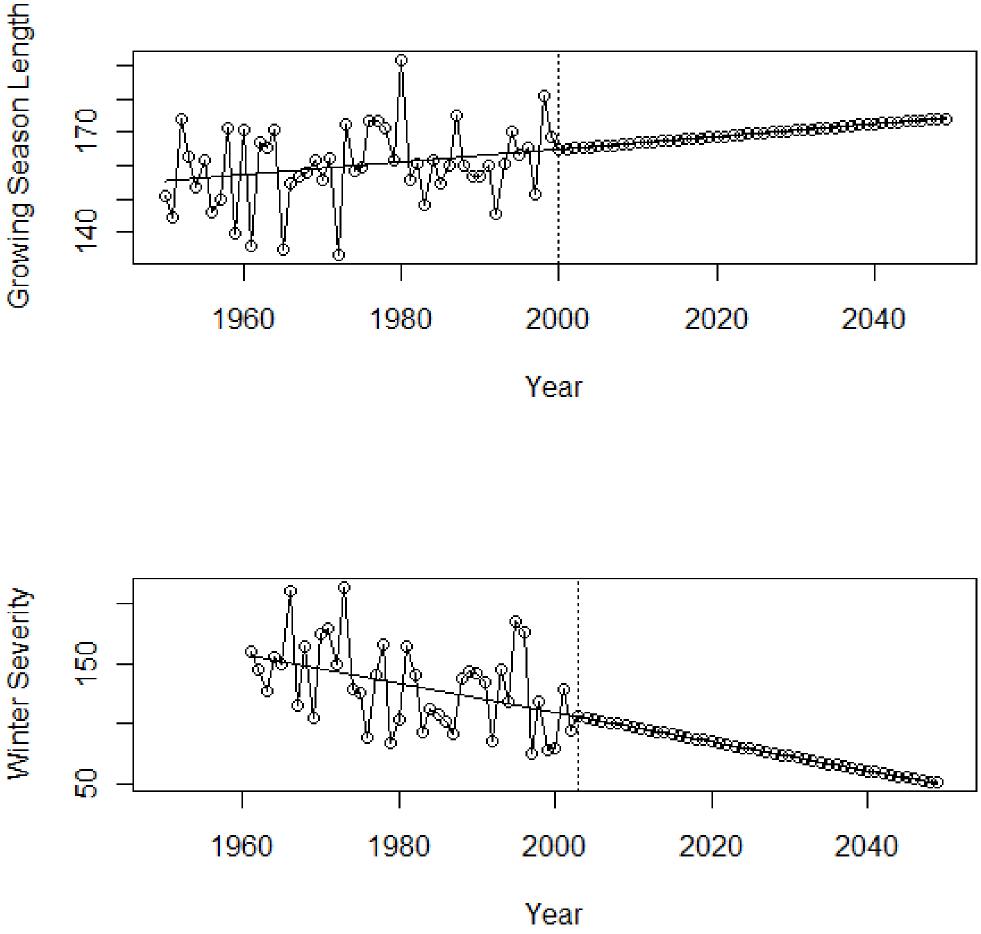


Figure 5.2: Change per year in winter severity (A) and growing season length (B) from 1961 – 2002 and 1950 -1999 respectively. Darker colors show greater change toward less severe winters and longer growing seasons.

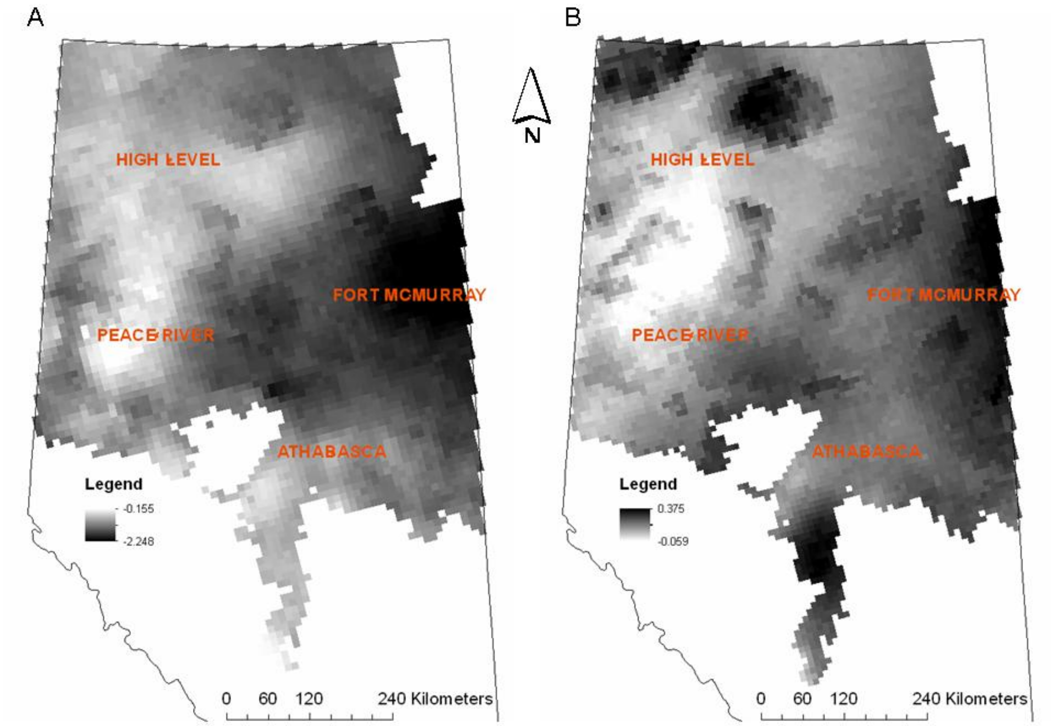
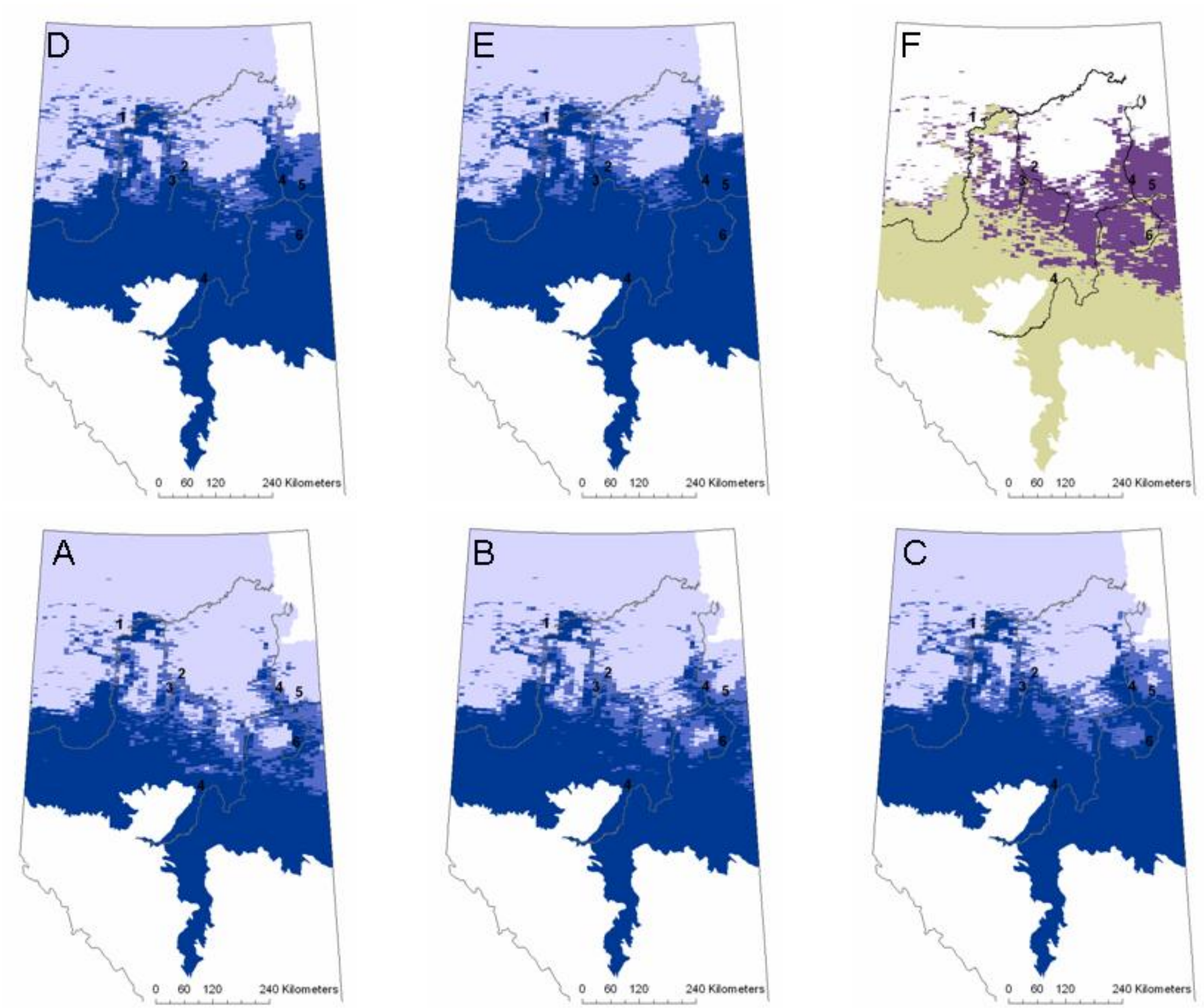


Table 5.1: Climate variable ranges used to predict white-tailed deer distributions. WSIswe is the winter severity measured in index units and growing season length was measured in number of days. Area is the size of the region where predicted probability is greater than 0.72.

	WSIswe		Growing season		Area
Decade	Range	Mean	Range	Mean	(km^2)
2000	14.82 – 216.36	133.12	129.00-178.21	160.3	138900
2010	13.37 - 211.57	126.47	130.75 - 178.97	161.31	157000
2020	11.96 - 207.16	120.37	132.44 - 179.80	162.28	175000
2030	10.54 - 202.75	114.27	134.12 - 180.78	163.24	190200
2040	9.22 - 198.35	108.18	135.81 - 181.83	164.21	205800
2050	8.19 - 193.94	102.14	137.50 - 183.49	165.17	219800

Figure 5.3: Predicted decadal distributions for 2010s (A), 2020s (B), 2030s (C), 2040s (D), and 2050s (E). Blue colors designate where predicted probability of white-tailed deer presence is greater than or equal to 0.73 (dark blue), between 0.37 and 0.72 (medium blue), or less than 0.37 (light blue). The numbers correspond to the Peace (1), Wabasca (2), Loon (3), Athabasca (4), Clearwater (5), and Christina (6) Rivers. The difference in area with a predicted probability of presence greater than or equal to 0.73 between 2050 (purple) and 2000 (beige) is shown in F.


D
E
F
A
B
C
1
2
3
4
5
6
0 60 120 240 Kilometers

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Chapter 6: White-tailed deer, *Odocoileus virginianus* range expansion and implications for woodland caribou, *Rangifer tanandus caribou*.

General discussion

Summary

In this dissertation I show that climate, winter severity in particular, has been the major factor driving range expansion of white-tailed deer in northern Alberta during the last half of the 20th century. To do this, it was necessary to develop a method for calculating winter severity at small spatial grain, large spatial extent, and for multiple years. This allowed me to use the differences in spatial and temporal change in climate and land use variables to discriminate the relative importance of each of these on white-tailed deer range expansion. The winter severity index calculated using snow water equivalent (WSIswe) provided a good measure of relative winter severity across space and time and showed a strong influence on white-tailed deer spatial distribution (chapters 2 and 3). The subsequent species distribution model developed using the WSIswe had good predictive accuracy and provided predictions of past distributions that made ecological sense and matched closely to changes noted in the past (Webb 1967) chapter 3). These model predictions suggest that as climate became more favorable, white-tailed deer likely expanded their distribution beyond the agricultural boundary in the south and into areas with more deciduous forest along the Peace, Loon, Wabasca, Athabasca and Christina rivers. In addition, the current distribution is predicted to include the western developed region of the province with low probability of presence beyond 58.55° north latitude.

Predicted changes in winter severity as well as growing season length suggest that further changes in white-tailed deer distribution can be expected in northern Alberta during the first half of the 21st century. Specifically, in the next few decades, white-tailed deer are predicted to continue expanding north along occupied river valleys and into the area east of Christina River to the border of Saskatchewan. By the end of 2050, most of the boreal region south of 56.71° north latitude is predicted to be occupied, as well as the area northeast of Fort McMurray and up to 100 km north of Fort McMurray along the Athabasca River. The predicted probability of white-tailed deer presence north of High Level should remain low throughout the first half of the 21st century.

White-tailed deer were absent from some locations where presence was predicted (chapter 4) highlighting that these predictions are conditioned on the ability of white-tailed deer to exploit newly available habitat. I argue that where presence of a species may have a negative effect on the native community, the consequences of over predicting the realized distribution are lower than the consequences of expecting the species to be absent when they are in fact present. The uncertainty must be considered when applying predictions made for future scenarios, however the value of predictions despite the uncertainty is that they can direct monitoring, and alert managers to potential impacts on native species and ecosystems.

Management implications

Changes in summer and winter climate are driving range expansion of white-tailed deer in northern Alberta, and further changes are expected. Although winter die offs in deer populations due to severe winters are common (Severinghaus 1947, Edwards 1956, Kelsall and Prescott 1971, Verme and Ozoga 1971, Roper and Lipscomb 1973, Sæther 1997, DelGiudice et al. 2002), the species distribution model developed in chapter 3 suggests that white-tailed deer may be present in highly developed landscapes even where average winter severity is high. This means that a series of severe winters will likely not change the fact that white-tailed deer occupy the northern Alberta boreal forest and suggests that wildlife managers in Alberta face big challenges now and into the future.

Of greatest concern in this province is caribou conservation. Figure 6.1 shows the location of woodland caribou herds in northern Alberta in relation to the distribution predicted for the 2000s and the 2050s. Currently, the seven caribou herds in the East side of the Athabasca (ESAR) range, and the West side of the Athabasca (WSAR), Cold Lake, Slave Lake, and Nipisi herds all have higher probability of white-tailed deer presence in or around their ranges (Figure 6.1A). Chinchaga and Red Earth also have areas of higher probability of white-tailed deer presence in the southern portions of their ranges (Figure 6.1A). By 2050, the southern part of the Red Earth, WSAR and Richardson ranges, as well as the complete ranges of herds in the southern boreal, have a high predicted presence of white-tailed deer and the predicted probability of presence is greater than zero for northern ranges (Figure 6.1B). White-tailed deer have already been implicated as drivers of increased predation on caribou in the WSAR range through apparent competition (Dale et al. 1994, Latham et al. 2011). Although these effects are already evident, the predicted probabilities of white-tailed deer occurrence inside that range are currently relatively low. Although increases were seen within the WSAR range, Latham et al (2011) suggested that increased presence and abundance of white-tailed deer in uplands surrounding caribou range also contributed to higher wolf numbers and increased predation on caribou populations. Future predictions from the model suggest that white-tailed deer presence will increase inside caribou range as well as in the uplands, because once climate is more favorable (low WSIswe and long growing season length), the probability of presence in peatland regions increases as well (chapter 3). This is not unreasonable. Latham and Boutin (2008) reported white-tailed deer in a fen complex in the WSAR caribou range and showed evidence of selection for arboreal lichen. Under these predictions and if wolves respond similarly across the region as in the WSAR range, all caribou herds in northern Alberta face increasing threats in the coming decades.

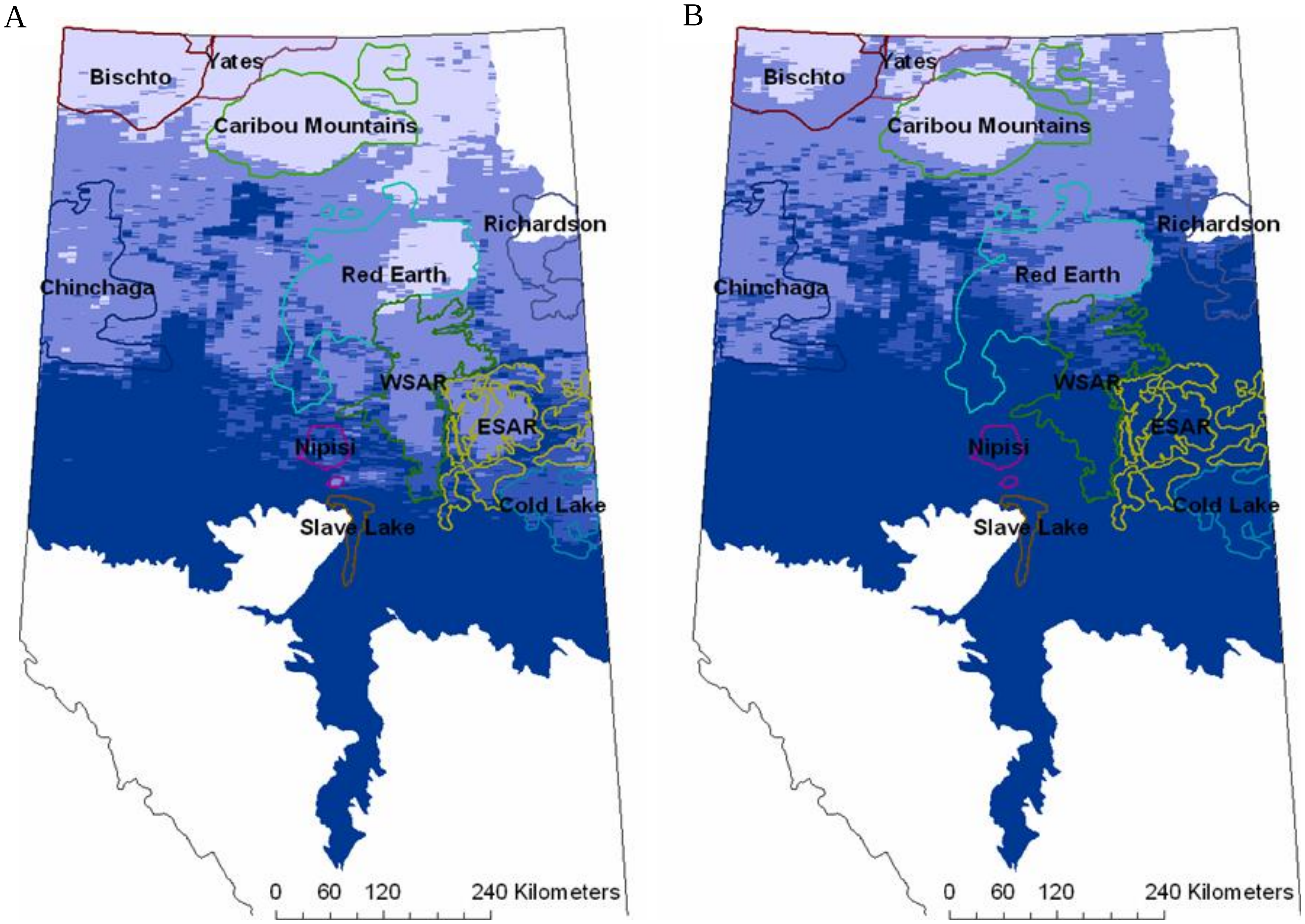
Changes in community composition under climate change will pose new challenges for decision making and multi-species management. The predictions here can help direct monitoring, while monitoring these locations will help verify the model predictions. Understanding the change is just a first step. Addressing the subsequent problems likely requires development of new tools for managers.

At the same time, caribou conservation is just one component of the potential consequences of white-tailed deer range expansion. The question remains of what other effects white-tailed deer may have on the boreal forest ecosystem and whether those effects will be positive, negative, or neutral. The answer is of both ecological and applied interest.

Research contribution

White-tailed deer are among a large suite of species expanding their geographic ranges (Hughes 2000, Peterson et al. 2001, Parmesan and Yohe 2003, Wardle et al. 2011). This work contributes to the growing effort to understand what is driving these changes and is among the few attempts to investigate multiple hypotheses to explain recent range expansion (see Melles et al. 2011, Rubidge et al. 2011 for other examples). This work is also among the first to show climate driven range expansion in a large mammal species (see Hersteinsson and Macdonald 1992 for another example). The WSIswe index developed here can be adapted for use with other ungulates in northern climates, and the method can be used to replace snow depth data in any climate index requiring snow depth, with the benefit of increased spatial and temporal coverage. Finally, the maps produced showing the predicted current distribution and future predicted changes in white-tailed deer distribution will be useful for managers in Alberta faced with managing a changing boreal forest ecosystem, under the impacts of land use and climate change.

Figure 6.1: Caribou range boundaries compared to predicted decadal distributions for 2000s (A), and 2050s (B). Blue colors designate where predicted probability of white-tailed deer presence is greater than or equal to 0.73 (dark blue), between 0.37 and 0.72 (medium blue), between 0.01 and 0.37 (light blue), or 0 (lightest blue). Caribou ranges are labeled with herds from each range outlines in the corresponding color.



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