MODELING WINTER SEVERITY AND HARVEST OF MOOSE: IMPACTS OF

NUTRITION AND PREDATION

A

THESIS

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ABSTRACT

Climate change is expected to have both positive and negative impacts on northern ungulate populations. Moose (*Alces alces*) will likely benefit from an increase in the growing season length and frequency of wildfire. However, increases in extreme weather events may result in moose population declines, particularly for nutritionally stressed moose populations. Management strategies to reduce the nutritional stress of populations may become increasingly important. We used stage-structured population models to examine the impact of deep-snow events on moose population trajectories and evaluated female harvest strategies designed to mitigate nutritional stress by decreasing intraspecific competition. Population trajectories were primarily influenced by young adult and prime adult survival. Populations held at low density by predation are likely buffered against the effects of severe weather events, whereas nutritionally stressed populations are vulnerable to population declines from the same environmental conditions. Harvest of cow-calf pairs may be an effective way to maximize harvestable yield and maintain population resilience when nutritional condition is poor. Moose population abundance over the long-term may become more variable due to the effects of climate change. Future modeling needs to incorporate alternative harvest and climate scenarios to help us better understand how we can promote moose population resilience.

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CHAPTER 1

GENERAL INTRODUCTION

Although climate change is predicted to decrease overall biodiversity, the responses

of individual species remain uncertain (Bellard *et al.* 2012). Amplified warming at

northern latitudes is likely to have particularly striking impacts on both northern

ecosystems and the species that inhabit them (Intergovernmental Panel on Climate

Change, IPCC 2007). Large ungulates often play important roles in community and

ecosystem ecology where they influence predator-prey dynamics, nutrient cycling, and

plant successional trajectories (Kielland *et al.* 2006, Pastor *et al.* 2006). Additionally,

large ungulates provide important social and economic resources. This is certainly true

in many northern regions where traditional subsistence cultures often depend on

resources provided by caribou, reindeer or moose (Krupnik and Jolly 2002, Nelson *et al.*

2008).

Northern ungulate species are likely to experience both positive and negative

impacts of climate change. For example, many northern ungulates may benefit from

increases in growing season length (Schwartz *et al.* 1988, Renecker and Schwartz 2007,

Parker *et al.* 2009) and fire frequency (Franzmann and Schwartz 1985, MacCracken and

Viereck 1990), both of which are expected to have a positive influence on forage quality

and availability. In addition, many northern ungulates are likely buffered from the

negative effects of climate change by their relatively high phenotypic plasticity (Morris *et

al.* 2008, Canale *et al.* 2012) and dispersal ability (Schloss *et al.* 2012). However,

increases in the frequency of extreme environmental events, (e.g. heavy precipitation, prolonged drought, large fires) are likely to have substantial negative impacts on populations of northern ungulates (Bishop and Rausch 1974, Hansen *et al.* 2011). A better understanding of the likely population responses of northern ungulates to climate change will aide in future management and conservation of these important species.

In the northern boreal forest, moose (*Alces alces*) contribute greatly to ecosystem function by influencing plant demography, plant succession, and nutrient cycling. For example, herbivory by moose exerts control over litter decomposition through fecal inputs high in microbial nitrogen, which influences soil nitrogen cycling and plant productivity (Kielland *et al.* 2006). However, sustained heavy browsing pressure on preferred deciduous species such as willow (*Salix spp.*), paper birch (*Betula papyrifera*), and aspen (*Populus tremuloides*) often leads to high mortality of these species and results in a transition to less productive and less palatable tree species (Kielland and Bryant 1998, Pastor *et al.* 2006, Butler and Kielland 2008). In addition to being important ecosystem engineers (Jones *et al.* 1994), moose are a key game species. For example, in Scandinavia, moose is by far the most important game species, and it accounts for more than 2% of the yearly meat consumption in Norway and Sweden (Olaussen and Skonhoft 2011). In Interior Alaska, moose have traditionally represented the primary terrestrial food resource for subsistence users (Nelson *et al.* 2008), allowing them to ameliorate the high cost of living as well as maintain a subsistence lifestyle (Krupnik and Jolly 2002, Nelson *et al.* 2008).

Northern populations of moose are expected to benefit from projected increases in spring and fall temperatures (Schwartz *et al.* 1988, Parker *et al.* 2009) by way of access to higher quality browse earlier in the spring and later in the fall (Myneni *et al.* 1997,

Keyser *et al.* 2000, Parmesan 2007). These are critical times of the year when moose are either recovering from or preparing for the winter. This is especially true for juvenile moose, which generally have higher maintenance costs and lower body reserves (Parker *et al.* 2009), and for parturient cows experiencing high costs associated with late gestation and lactation in the spring and early summer (Parker *et al.* 2009).

However, warmer summer temperatures are expected to result in increased heat stress for moose (Murray *et al.* 2006; Lenarz *et al.* 2009, 2010; van Beest *et al.* 2012). Despite such direct, negative implications of warmer summer temperatures, temperature increases will likely benefit moose overall through increases in browse availability. In addition, an increase in fire frequency (Flannigan *et al.* 2000, 2005; Kasischke *et al.* 2010), as a result of warmer temperatures (Flannigan *et al.* 2005, Westerling *et al.* 2006), is expected to have a positive impact on moose by increasing forage quality and availability (MacCracken and Viereck 1990). However, the positive implications of increased fire will depend on fire severity and the extent and uniformity of area burned. Fire severity and extent will greatly influence the type of vegetation regeneration, and burn uniformity will determine whether or not residual trees or islands are left to provide seedfall and cover from predators (Fisher and Wilkinson 2005).

Like many large ungulates that inhabit unpredictable environments, moose populations are quite resilient to extreme environmental conditions (Gaillard *et al.* 2000). An iteroparous life history allows moose to forgo reproductive costs under harsh environmental conditions and instead invest in adult survival and future reproductive events. Despite their precocity, juveniles of large ungulates are vulnerable to extreme environmental events because of their low body reserves and relatively high maintenance costs (Parker *et al.* 2009). However, because of the high resilience of

adults, extreme environmental conditions rarely result in substantial population declines

for large ungulates (Gaillard *et al.* 2000). In addition to their reproductive plasticity,

moose show great behavioral plasticity. Under heat stress moose will seek out

coniferous habitats for thermal cover (Dussault *et al.* 2004, van Beest *et al.* 2012) or

seek refuge in ponds and lakes, which also offer good forage in the form of aquatic

plants. If warmer summer temperatures lead to reduced forage quality, moose may

adjust their foraging range across elevational and latitudinal gradients to access higher-

quality vegetation (Leblond *et al.* 2010, van Beest *et al.* 2011). When snow depth begins

to impede movement, moose disperse into areas with shallower snow in an effort to

reduce energetic costs and find available forage (Hundertmark *et al.* 1990, Ballard *et al.*

1991, Peek 2007). These behaviors notwithstanding, it is clear that moose populations

vary substantially in nutritional condition, which will influence their capacity to respond to

environmental challenges.

Although moose are well adapted to cold temperatures, deep snow decreases forage

availability and increases the energetic costs of movement (Coady 1974). Even under

mild snow conditions, moose in good nutritional condition enter into a negative energy

balance during the winter (Renecker and Hudson 1985). Moose with poor nutrition are

vulnerable to substantial mortality during deep snow years (Bishop and Rausch 1974,

Peterson *et al.* 2003). Increased precipitation at high latitudes (IPCC 2007) leading to

deeper snow (Groisman and Easterling 1994, Zhang *et al.* 2000, Hyvarinen 2003, Kohler

et al. 2006) may result in nutritional stress of moose populations and subsequent

population declines.

Whereas many Interior Alaska moose populations are held at low density by

predation (Gasaway *et al.* 1992), other populations exist at high density due to relatively

low predator densities or a combination of low predator densities and relatively mild winters (Boertje *et al.* 2009). Managers also seek to maintain high population densities to provide maximum harvest opportunity (Boertje *et al.* 2009). However, high-density populations are more vulnerable to substantial declines from extreme environmental events (Boertje *et al.* 2009).

Overall, high-density populations that exhibit poor nutrition are likely to benefit from longer growing seasons and increased fire because increased nutrition, at least in the short term, will reduce vulnerability to the effects of environmental stress. However, unless harvest is managed to curb population growth, populations that experience low predation will likely increase until the available resources are depleted, at which point the population will once again become nutritionally-stressed and at increased risk of decline from severe weather events.

We used stage-structured models to examine the impact of deep snow events on moose population trajectories and evaluate harvest strategies to mitigate negative impacts of high population density. Models were parameterized from Interior Alaska moose populations varying in nutritional condition and predation pressure. Specifically, we compared: 1) population trajectories of different moose populations that exhibit variation in survival during a deep snow year as a result of their nutritional state and level of predation, and 2) two possible female harvest strategies aimed at increasing health of a nutritionally-stressed moose population.

CHAPTER 2

**POPULATION MODELS OF INTERIOR ALASKA MOOSE: IMPACTS OF
NUTRITIONAL CONDITION ON RESPONSES TO WINTER SEVERITY AND
POTENTIAL MANAGEMENT STRATEGIES[1]**

ABSTRACT

Nutritionally stressed moose populations are likely to be more vulnerable than
populations exhibiting good nutritional condition to both direct and indirect impacts of
changing climate. Populations exhibiting nutritional stress may benefit from increased
forage availability following fire but they are also more susceptible to negative impacts of
extreme weather events, both of which are expected to increase in frequency.
Management strategies to reduce the nutritional stress of populations may become
increasingly important. We constructed female-only stage-structured population models,
parameterized using data from Interior Alaska moose (*Alces alces gigas*) populations
varying in nutritional condition and predation pressure. We examined the impact of
deep-snow events on moose population trajectories and evaluated two female harvest
strategies designed to mitigate nutritional stress by decreasing intraspecific competition.
Harvest rates for both non-accompanied adult females (cows ≥ 1 year that are not
accompanied by calves) and cow-calf pairs were held constant (6% of female

population) in order to achieve the population objective by the end of the 5-year-period. Elasticity analysis predicted that population trajectories would be strongly influenced by prime adult female survival yet relatively insensitive to changes in recruitment and calf survival. Models of high-nutrition populations, where only calf survival was influenced by a deep-snow event, predicted population growth regardless of the frequency of a deep-snow event. The same was true for the low-nutrition population when deep snow was assumed to only influence calf survival; however, when survival of all age classes was influenced by deep snow the model predicted negative population growth. Populations held at low density by predation are likely buffered against the effects of severe weather events, whereas nutritionally stressed populations are vulnerable to population declines from the same environmental conditions. Both harvest strategies produced the desired decrease in population size within 5 years when harvesting 6% of female population each year, but 54% more moose (11% more biomass) could be harvested when calves were included in the harvest. Population models provide a useful management tool for both predicting population dynamics under varying conditions and exploring possible harvest strategies aimed at reducing populations when deemed necessary for sustained, long-term yield.

INTRODUCTION

Moose populations are sensitive to both direct and indirect effects of climate. Indirect effects of climate, acting through changes in forage quality and availability, are constantly exerting an influence on population growth, whereas direct effects of climate rarely have major impacts on population growth when acting alone. Both direct and indirect effects, acting together, however, can have substantial impacts on population dynamics of moose. Climate change across boreal ecosystems is predicted to involve

increases in growing season length (Myneni *et al.* 1997, Keyser *et al.* 2000, Schwartz *et al.* 2006, Parmesan 2007), frequency of wildfires (Kasischke and Turetsky 2006, Westerling *et al.* 2006, Kasischke *et al.* 2010), frequency of extreme environmental events (Intergovernmental Panel on Climate Change, IPCC 2007), and disease and parasite occurrence (Murray *et al.* 2006, Samuel 2007, Hoberg *et al.* 2008, Laaksonen *et al.* 2010). Moose forage quantity and quality are likely to increase with increases in growing-season length and fire frequency, resulting in improved body condition, as well as increases in fecundity and juvenile survival. In contrast, increases in extreme environmental events, such as increases in heavy snowfall or drought as well as increases in disease and parasite incidence are likely to negatively impact moose.

Warmer spring temperatures leading to earlier snowmelt (Groisman *et al.* 1994) and earlier leaf emergence (Myneni *et al.* 1997, Keyser *et al.* 2000, Parmesan 2007) will likely increase forage availability and quality for moose at a critical time when body reserves are low (Renecker and Schwartz 2007, Parker *et al.* 2009). Earlier access to these important resources will enable moose to achieve a higher nutritional state over the summer, likely increasing both conception rates in the fall (Cook *et al.* 2004) and survival through the following winter. Additionally, a longer snow-free period in the fall that prolongs access to higher quality forage may contribute to higher productivity and winter survival (Schwartz *et al.* 1988). Increases in forage quality and availability will likely have the greatest impact on winter survival of juveniles due to their low body reserves and high metabolic demands relative to adult moose (Parker *et al.* 2009).

In Interior Alaska, excluding cold, poorly drained sites, post-fire successional trajectories typically result in the return of more productive deciduous tree species (Chapin *et al.* 2006) that are preferred by moose. Thus, recent increases in northern

boreal forest fire frequency and severity (Kasischke *et al.* 2010) have positive
implications for moose nutrition. Increased availability of higher quality forage following
fire has been linked to an increase in body condition and moose fecundity (Franzmann
and Schwartz 1985) and is likely to increase winter survival of juveniles.

In general, climate change models predict an increase in the frequency of
heavy-precipitation events at high latitudes (IPCC 2007) with some forecasting increases
in heavy snowfall across the Unites States and Canada (Groisman and Easterling 1994,
Zhang *et al.* 2000). Moose survival can be negatively impacted by snow depth because
it increases energetic demands while simultaneously restricting movement and access
to forage (Coady 1974, Parker *et al.* 2009).

The effects of deep snow on moose populations can be exacerbated in populations
where nutritional condition is poor, making these populations more vulnerable to the
impacts of deep snow (Bowyer *et al.* 2000, Boertje *et al.* 2009). Moose with poor
nutrition are less likely to have the body reserves to buffer them against the impacts of
higher energetic requirements and lowered food intake during periods of deep snow. In
addition, due to over-browsing, the habitat of a nutritionally stressed population is likely
to contain forage of low quality and low availability. Starvation, resulting from a
combination of high population densities and severe winter conditions, is thought to be
responsible for precipitous declines in moose populations in various parts of their range
(Bishop and Rausch 1974, Peterson *et al.* 2003).

In Alaska, many moose populations are largely maintained at low densities by
predation (Gasaway *et al.* 1992, Van Ballenberghe and Ballard 1994), but some
populations experience relatively low predation pressure and reach high densities
resulting in nutritional stress (Boertje *et al.* 2007, 2009). Predator-limited and

nutritionally stressed populations will likely respond differently to climate change. Whereas predator-limited populations are expected to have little or no capacity to grow in response to increased forage availability caused by longer growing seasons and increased wildfire (Weixelman *et al.* 1998), their excellent body condition buffers against the negative effects of severe winter conditions (Bowyer *et al.* 1998). Thus, excepting effects mediated by predator-prey interactions, these populations may respond little to climate change. In contrast, we expect that nutritionally stressed moose populations will respond positively to longer growing seasons and increased fire frequency. However, nutritionally stressed moose populations are also at increased risk of decline from severe weather events such as deep snow.

Although nutritionally stressed moose populations are more susceptible to environmental stressors, the increased density provides higher surplus for harvest (Boertje *et al.* 2009). Management of moose populations at the upper end of their nutritional limitation requires a balance between population health and harvest opportunity. Female harvest strategies are often used to moderate population growth, improving population health and increasing harvest opportunity (Timmermann and Buss 2007, Young and Boertje 2011).

Stage-structured population models can be used as a valuable tool to compare and contrast the impacts of climate change on specific age classes in different population states. For example, studies employing stage-structured models have suggested that impacts of climate change may both increase vulnerability of resource-limited populations (Wilmers *et al.* 2007) and lead to substantial shifts in moose distribution (Murray *et al.* 2006, Lenarz *et al.* 2010). Moreover, stage-structured population models can be used to explore harvest strategies targeting different age classes to most

efficiently achieve management objectives (Saether *et al.* 2001, 2009; Nilsen *et al.* 2005; Xu and Boyce 2010).

We used stage-structured models to examine the impact of deep-snow events on moose population trajectories and evaluate harvest strategies to mitigate negative impacts of high population density. Models were parameterized from Interior Alaska moose populations varying in nutritional plane and predation pressure. Specifically, we compared: 1) trajectories of moose populations that exhibit variation in survival during a deep-snow year as a result of their nutritional condition and level of predation, and 2) two possible female harvest strategies aimed at increasing health of a nutritionally stressed moose population.

METHODS

Model Structure

To better understand moose population responses to an increase in the frequency of years with deep snow, we constructed female-only, post-reproductive, stage-structured population models (Caswell 2001). Nutritional state and predation level are likely to impact the response of moose populations to an increase in the frequency of years with deep snow. Therefore, we parameterized models for three different types of moose populations. Moose populations are commonly found to exist either as nutritionally stressed or nutritionally robust populations. Nutritional stress is often the result of low predation pressure, which can lead to rapid population growth and high intraspecific competition (low nutrition/low predation: LN/LP). Conversely, heavy predation pressure can greatly inhibit population growth, thereby reducing intraspecific competition and lead to a nutritionally robust population (high nutrition/high predation: HN/HP). In addition to nutritionally stressed and nutritionally robust populations we considered a population

with high nutrition and low predation (high nutrition/low predation: HN/LP), both as a point of comparison for the other models and to represent populations that have recently been released from nutritional stress or high predation, as could occur during colonization of new habitat or predator-control.

Based on similarities in survival and reproduction among ages, population models included 5 stages: calves, yearlings, young adults (2 to 4 years), prime adults (5 to 11 years), and old adults (12+ years). Age-specific survival and reproductive rates reported in the literature (Boertje *et al.* 2009, Keech *et al.* 2011) were weighted by within-stage stable age distributions (Caswell 2001) to calculate annual stage-specific survival and reproductive rates (Table 1).

Recruitment values make up the first row of the transition matrix, and survival values within each stage and survival to succeeding stages completed the matrix (Fig. 1). For stages lasting more than one year, we calculated the probability of a surviving individual growing to the next stage:

$$\gamma_x = \frac{\left(\dfrac{\sigma_x}{\lambda}\right)^{T_x} - \left(\dfrac{\sigma_x}{\lambda}\right)^{T_x - 1}}{\left(\dfrac{\sigma_x}{\lambda}\right)^{T_x} - 1} \tag{1}$$

Where x represents the stage, σ is the stage-specific survival rate, T is the stage duration, and λ is an initial estimate of the finite rate of increase (Caswell 2001). Therefore, survival and growth to the next stage (G_x) is the product of the stage-specific survival rate (σ_x) and the probability of a surviving individual growing to the next stage (γ_x). Survival within a stage (P_x) is the product of the stage-specific survival rate (σ_x) and the probability of an individual surviving and staying within the same stage-class (1-γ_x).

We calculated fecundity (average number of calves/female/yr) using the equation:

$$m_x = p_x(1 + tw_x) \tag{2}$$

Where p_x is the yearly probability of a female in stage x giving birth, and tw_x is the average twinning rate of females within stage x (Boertje *et al.* 2009).

Recruitment values (F_x) for our post-reproductive, female-only model assume sex ratio parity in calves (Schwartz and Hundertmark 1993, Harris *et al.* 2008, Boertje *et al.* 2009) and combine the probability of surviving over the year with fecundity at the end of the year.

$$F_x = 0.5 * [(P_x * m_x) + (G_x * m_{x+1})] \tag{3}$$

Model Parameterization

To parameterize the LN/LP model we used 12 years (1996-2007) of age-specific vital rates from a subpopulation of moose occupying the Tanana Flats and adjacent foothills of the Alaska Range just south of Fairbanks in central Interior Alaska (Table 1; Boertje *et al.* 2009). Several nutritional indices, including an assessment of browse utilization, indicated that this population was on a low nutritional plane (Boertje *et al.* 2007). Predation rates on moose occupying the Tanana Flats are low (19% of the post-calving population is killed by predators) compared to other moose populations in Interior Alaska (31-41% of the post-calving population is killed by predators; Boertje *et al.* 2009). Although predators account for the majority of calf mortality (92%), calf mortality is relatively low (50%) compared to other Interior Alaska populations (Boertje *et al.* 2009).

To parameterize the HN/HP model we used age-specific data collected near McGrath in western Interior Alaska where heavy predation limited population growth (Table 1; Keech *et al.* 2011). Because bears are responsible for most predator-induced mortality of calves whereas wolves are responsible for most predator-induced mortality of

yearlings and adults we chose to use calf survival rates from 2001 to 2002, prior to bear removal initiated in 2003, and yearling and adult survival rates from 2001 to 2003 prior to intensive wolf removal initiated in 2004 (Keech *et al.* 2011) to represent a population with high predation (Table 1). Nutritional indices indicated moose in this population were in good nutritional condition (Boertje *et al.* 2007, Keech *et al.* 2011). Predation rates on moose were identified as being high relative to other Interior Alaska moose populations (34% of the post-calving population is killed by predators; Boertje *et al.* 2009). Predators accounted for the majority of calf mortality (94%), which was high (70%) compared to the Tanana Flats population (Keech *et al.* 2011).

The HN/LP model was also parameterized using data from McGrath, Alaska, but subsequent to predator removal (Table 1; Keech *et al.* 2011). To represent a population with low predation, we used calf survival from 2003 to 2007 and yearling and adult survival from 2004 to 2007 because these time periods corresponded to periods following predator removal for each respective stage (*see above*). Parturition and twinning rates remained high for ≥ 2 years following the initiation of predator removal, and it was assumed this population occupied a high nutritional plane (Keech *et al.* 2011). Estimated predation rates following predator removal were low (16% of the post-calving population is killed by predators; M. A. Keech, Alaska Department of Fish and Game, *unpubl. data*). Although predation was still the proximate cause of calf mortality (65%) total calf mortality following predator removal was relatively low (54%; Keech *et al.* 2011).

Fifty years of data (1960-2010) from the Tanana Flats/Alaska Range foothills population, where the density ranged from 0.2 to 1.8 moose/km^2, were used to examine density-dependent effects on each vital rate. Blood (1973) reported that for moose a

time lag of two years best explained the relationship between recruitment values and population density. Therefore, we used linear regressions to examine relationships between vital rates and population density with time lags of up to two years (N_t, N_{t-1}, and N_{t-2}). All vital rates were natural log transformed for the analyses (Morris and Doak 2002). We found no evidence of density-dependent effects on survival or parturition of any age-class within the Tanana Flats/Alaska Range foothills population. However, in the same population, twinning rates significantly declined with population density with a time lag of 1 year ($P = 0.02$; Fig. 2) and 2 years ($P = 0.01$). The LN/LP population matrix model was parameterized both with and without density-dependence on twinning rates. Population projections with and without density-dependence were similar over the 30-year time frame of our projections, so we opted to use only density-independent models for our analyses. Based on the lack of strong density-dependent effects in the high-density Tanana Flats/Alaska Range foothills population, we assumed no density-dependent effects on survival or reproduction in low-density (0.3 to 0.6 moose/km^2) populations used to parameterize the high-nutrition population models.

Environmental stochasticity was not included in the models because we did not have access to data allowing the estimation of variance in vital rates. Large ungulates tend to exhibit low interannual variance in adult survival rates; however, calf survival rates and fecundity rates often exhibit high interannual variance (Gaillard *et al.* 2000).

Model Performance

Yearly estimates of total female population size generated by the LN/LP model were compared to female population abundance estimates of the Tanana Flats/Alaska Range foothills moose population from 1999 to 2009 (ADF&G 2010) to evaluate model performance. Estimates of female population abundance incorporated a geospatial

population estimate (GSPE; Ver Hoef 2008) for observed moose as well as a composite

sightability correction factor (SCF) to account for females not seen (Boertje *et al.* 2009).

Goodman's formula for estimating the exact variance of products (Goodman 1960) was

used to calculate 90% confidence intervals around the combined estimate and SCF (*see*

Keech *et al.* 2011). For a detailed explanation of how total population abundance

estimates were calculated for the Tanana Flats/Alaska Range foothills population *see*

Boertje *et al.* (2009). We restricted our comparison to these years because the GSPE

survey method (Ver Hoef 2008) provided a greater degree of confidence in the

population abundance estimates than earlier survey methods. The initial female

population size for the model was derived from the 1999 fall population estimate

(10,207/13,044 km^2), from which we calculated the female segment of the population

based on the estimated number of adult females and half of the proportion of yearlings

and calves (assuming equal sex parity for yearlings and calves). The adult age-structure

could not be determined from survey data. Therefore, we assumed the starting

population was at the stable stage distribution from preliminary density-independent

population projections (Table 2). It was likely the female population was at or near

stable stage distribution in 1999 because females were not being harvested in large

numbers and there were no large mortality events that would have resulted in a shift in

the proportion of females per stage-classes. In years when females accounted for a

proportion of the harvest we included harvest mortality in the model. The total number of

harvested females took into consideration reported harvest, unreported harvest, and

wounding loss (Boertje *et al.* 2009). Because hunter records did not distinguish yearling

and adult stages, we divided harvest mortality proportionally among stages following the

yearly stage distributions.

Yearly estimates of total female population size from both the HN/HP and HN/LP

models were compared to female population abundance estimates (*see* Boertje *et al.*

2009 for explanation of methods used to estimate abundance) from a population of

moose occupying a 2,896 km^2 study area near McGrath, Alaska from 2001 to 2007

(ADF&G 2010) to determine model performance. Unlike Boertje *et al.* (2009), sightability

correction factors (SCFs), were calculated annually for the moose population near

McGrath, Alaska (Keech *et al.* 2011). We restricted the comparison to these years

because the GSPE survey method (Ver Hoef 2008) provided a greater degree of

confidence in the population abundance estimates than earlier survey methods. The

initial female population density was set to that estimated for the study area during the

2001 fall survey (640/2,896km^2) following the same assumptions as the LN/LP model

(*see above*; Table 2). Because data used to parameterize the HN/HP model and HN/LP

models are from the same population of moose we projected total female population size

for the first two years (2002-2003) using vital rate data from the HN/HP model and the

remaining four years (2004-2007) using vital rate data from the HN/LP model.

Sensitivity of Population Growth Rate to Changes in Vital Rates

Elasticity values were calculated to determine the sensitivity of population growth

rates to proportional changes in stage-specific survival and reproduction. This was done

manually by subtracting 1% of the value of the original vital rate from the original vital

rate ($r_{original}$) to produce a new vital rate (r_{new}) and a new growth rate (λ_{new}) (Morris and

Doak 2002). These values were used to determine the proportional effect of each vital

rate on population growth.

$$E_r = \frac{\frac{\lambda_{new} - \lambda_{original}}{\lambda_{original}}}{\frac{r_{new} - r_{original}}{r_{original}}} = \frac{\frac{\Delta\lambda}{\lambda}}{\frac{\Delta r}{r}} \qquad (4)$$

Projected Increase in Deep Snow Years

The projected increase in frequency of heavy snowfall events that result in deep snow is expected to have a negative impact on moose populations, especially among populations that exhibit low nutritional status. Although some aspects of climate change are expected to have a positive influence on moose populations (e.g. increases in the length of growing season, increases in fire frequency), they are not explicitly represented in the model.

Snow Depth

Moose survival rates can be strongly influenced by snow depth, which can lower overwinter survival by restricting movement to the extent that energy requirements cannot be met (Coady 1974). Coady (1974) suggested deep snow depths that exceeded 70-cm would restrict movements of adult moose and that snow depths greater than 90-cm would likely result in an inability to maintain adequate food intake. We developed a dichotomous classification of snow depth, where average winter snow depth was calculated as the mean of the depths on 15 January, 15 February, and 15 March (Ballard *et al*. 1991, Keech *et al*. 2011). When the average snow depth was equal to or exceeded 90-cm it was classified as a deep snow year.

Historical snow depth data archived by the Alaska Climate Research Center (http://climate.gi.alaska.edu/) over the last 30 years (1982-2012) was used to establish the historical frequency of deep snow years. Data from two different areas in Interior Alaska that have experienced different levels of snow depth was used to represent a

minimum (Fairbanks, Alaska; 2 deep snow years in last 30 years) and maximum

frequency (McGrath, Alaska; 8 deep snow years in last 30 years) of deep snow years.

In addition, we used 4 deep snow years in a 30-year period to represent a moderate

frequency of deep snow. Although the frequency of deep snow years was set at 2, 4, or

8 during the time frame modeled, the sequence of normal and deep snow years was

random within each model run.

Population Responses to Deep Snow Events

We used the matrix population model to compare moose population responses to

varying frequencies of deep snow years over a 30-year-period. The model was

parameterized based on estimated changes in survival rates during deep snow years.

We used 30-year trajectories because longer trajectories become increasingly less

realistic when modeling wildlife populations and shorter trajectories might not capture

important population dynamics for a long-lived species such as moose. While deep-

snow conditions can impact survival of all age classes of moose, calf survival is

particularly vulnerable regardless of the nutritional state of the population. As the

nutritional state of a population decreases, older age groups may also become more

vulnerable to mortality from deep-snow years because of poor body condition, likely at

least partly as a result of reduced feeding efficiency due to tooth wear (Klein and Olson

1960, Skogland 1988, Hindelang and Peterson 1994).

Age-specific survival data during a deep snow year were unavailable for the Tanana

Flats or any other high-density Alaska moose population. Therefore, we based the

parameterization of the LN/LP population model on age-specific survival data from a

moose population in Isle Royale National Park, MI following a severe winter (Fig. 3b; J.

A. Vucetich, Michigan Tech., *unpubl. data*). Poor nutritional condition (Peterson 1995)

coupled with severe winter conditions in 1995-1996 resulted in substantial mortality of the Isle Royale moose population (Peterson *et al.* 2003). Observations on the Tanana Flats during the severe winter of 1965-1966, where average snow depths exceeded 90-cm, suggest that winter conditions and poor nutrition led to a similar precipitous decline in the moose population (Bishop and Rausch 1974). We considered two mortality scenarios: a "best case scenario" where deep snow only impacted calf survival (Fig. 3a), and a "worst case scenario" where deep snow influenced survival of all age classes (Fig. 3b). We were unable to obtain data on fecundity after a deep snow year for a nutritionally stressed moose population. Although several studies have shown an influence of deep snow on future fecundity of moose (Crete and Courtois 1997, Mech *et al.* 1987), population growth is largely insensitive to changes in fecundity (Gaillard *et al.* 2000). Therefore, changes in fecundity during a deep-snow year were not explored in the model scenarios.

Our estimates of the impact of deep snow on survival for populations that exhibit high nutritional condition were derived from McGrath, Alaska moose population subsequent to a predator removal study (Keech *et al.* 2011). Severe winter conditions were not experienced by this population prior to predator removal, however when a severe winter occurred subsequent to predator removal, calf survival was reduced while survival of other ages was unchanged (M. A. Keech, Alaska Department of Fish and Game, *unpubl. data*). Therefore, deep snow only influenced survival of calves for the high nutrition population models. Annual calf survival during a deep-snow year was estimated as the product of summer survival prior to predator removal (0.37) and winter survival from a year with deep snow subsequent to predator removal (0.42) for the HN/HP model (Fig. 3a; M. A. Keech ADF&G, *unpubl. data*). Calf survival for the HN/LP model during a deep

snow year was the product of summer survival (0.79) subsequent to predator removal and winter survival (0.49) from a year with deep snow subsequent to predator removal (Fig. 3a; M.A. Keech, ADF&G, *unpubl. data*).

Simulations of all populations started at stable stage distribution with 500 females to allow for comparison among the populations that differed greatly in density (0.38 moose/km^2 to 1.4 moose/km^2). We compared the average population abundance over the 30-year-period among the three different models. Except for the random occurrence of deep snow years, model simulations were deterministic. Therefore 1000 iterations were performed to detect general trends in moose population responses to an increase in the frequency of a deep snow year. Population projections were produced by matrix multiplication of the transition matrix and a population vector using the software MATLAB®2008bSV.

Population Responses to Female Harvest Scenarios

Nutritionally-stressed moose populations experiencing high levels of intraspecific competition are more vulnerable to conditions that can lead to sudden population declines from environmental stressors such as severe winters. We considered two possible female harvest strategies aimed at reducing population vulnerability while increasing harvest opportunity. Harvesting reproductively mature females is the fastest way to reduce population density and improve nutrition because these females are the population segment that most contributes to population growth. Therefore, we used the LN/LP population model to compare the effect of harvest of non-accompanied females (cows ≥ 1 year that are not accompanied by a calf) to harvest of cow-calf pairs. In each case, we modeled a 6% annual female harvest rate over a 5-year-period. This yearly harvest rate resulted in a reduction of the modeled population to a real ADF&G

population objective (10,000-12,000 total moose) at the end of the 5-year-period (ADF&G 2010).

For the harvest model we assumed a starting population of 10,000 females (14,500 total moose) at stable stage distribution (Table 2; ADF&G 2010). Survival and reproductive rates were assumed to be constant over the 5-year population projections. Because long-term empirical data from the LN/LP population (Tanana Flats/Alaska Range foothills) indicated that 2-year-olds rarely reproduce at high population densities, we constrained yearling recruitment to zero. We limited projections to 5 years to investigate the short-term response of populations to selective harvest. Because most hunters cannot readily distinguish between adult age-classes of moose and likely don't distinguish between yearlings and adults, yearlings and adult females are likely taken in relative proportion to their availability. Harvest of non-accompanied females was allotted across yearling and adult stages in proportion to availability and harvest of cow-calf pairs was similarly allotted across the three adult stages. For the cow-calf pair harvest strategy we assumed a 50% chance of harvesting a female versus a male calf based on sex parity in the calf cohort. Additionally, harvested cows were assumed to have only a single calf. Because we modeled a harvest level to achieve a constant rate of population decline (6% annual female harvest rate), a different number of animals were harvested each year.

Mortality is not constant throughout the year and mortality prior to hunting season influences which individuals are available for harvest. In particular, calf mortality prior to harvest influences the proportion of adult females in each stage with accompanying calves at the time of harvest, and thus impacts the allocation of harvest among stage classes. Therefore, we partitioned survival for all stage classes into 3 different periods:

survival from recruitment to harvest (first 3 months), harvest survival, and survival from post-harvest to recruitment the next year (remaining 9 months). The loss of a calf in the first 3 months was used to recalculate the proportion of females with and without accompanying calves at harvest time. Calf survival from recruitment to 3 months of age was 0.70 and from post-harvest to the following recruitment period was 0.71, yielding an annual survival rate of 0.50. Despite studies on caribou (Whitten *et al.* 1992), elk (Singer *et al.* 1997), and moose (Keech *et al.* 2000) that suggest calf survival likely varies with size of the mother, there is a lack of evidence in moose that female age alone has an influence on calf survival (Keech *et al.* 2000). Therefore, we made the simplifying assumption of equal calf survival across cow stage classes. Survival of yearlings and adult female stages were assumed to be constant across months and all harvested females were removed from the population and therefore did not contribute to recruitment the following year.

We estimated harvestable yield in two ways: as the total number of animals harvested and as total biomass harvested (based on minimum carcass weights for adult females, 155-kg, and calves, 66-kg; Sylven 1995). In addition, we evaluated the effect of each harvest strategy on the age-structure of the population. Harvest strategies of non-accompanied females and cow-calf pairs were modeled using Microsoft Excel® with annual harvest numbers estimated iteratively.

RESULTS

Model Performance

For years when observed population estimates are available from the Tanana Flats/Alaska Range foothills moose population, yearly model estimates were within 90% confidence intervals (CI) of the geospatial population estimate in all years except 2008

and 2010 (Fig. 4a). In 1 of the 3 years allowing a comparison, model estimates calculated using a combination of vital rates from the HN/HP model (2 years) and HN/LP model (4 years) were within 90% CI of the GSPE population estimates from McGrath, Alaska (Fig. 4b). Only 3 years were compared because we used the 2001 GSPE population estimate as the starting population estimate for the model.

Sensitivity of Population Growth to Changes in Vital Rates

Patterns of sensitivity of population growth rate to small proportional changes in vital rates were very similar across the three models (Fig. 5). Population growth rate was most sensitive to changes in survival of prime and young adults and least sensitive to fecundity for all stage-classes (Fig. 5).

Population Responses to Deep Snow Events

For climate scenarios where we limited deep snow effects to a reduction in calf survival, population trajectories for all models showed population increase regardless of the frequency of a deep-snow year (Fig. 6). Despite this deep snow did have an impact on population trajectories; as the frequency of deep snow years increased projected population sizes decreased (Fig. 6). For the LN/LP model in particular, a comparison of the population growth rate between a low and high frequency of deep snow showed an increase in the doubling time of the population from 15 years ($\lambda = 1.05$) to 24 years ($\lambda = 1.03$).

When only calf survival was reduced the HN/HP and LN/LP models had similar population growth rates at low to moderate frequencies of deep-snow years ($\lambda = 1.04$-1.05; Fig. 6). In these cases the higher survival of old adults and higher fecundity of all stages in the HN/HP model balances the normally higher calf and yearling survival of the LN/LP model. However, at a high frequency of deep-snow years, population growth of

the LN/LP population falls behind that of the HN/HP population (λ = 1.03 and λ = 1.04, respectively). In this case the high calf and yearling survival in the LN/LP population during normal years was not sufficient to offset the effects of deep snow years.

Under the scenario where survival of all stages was greatly reduced during a deep snow year the population trajectory for the LN/LP model was positive when the frequency of deep snow was low (λ = 1.01; Fig. 6). However, the population declined when the frequency of deep snow was either moderate or high, with near extirpation of the population within 20 years at a high frequency of deep snow (λ = 0.89; Fig. 6). In the LN/LP model scenario, steep population declines were largely due to increased mortality of prime adults. If prime adult survival was held constant while other stage classes incurred high mortality during a deep snow year, population growth was positive at both a low (λ = 1.03) and moderate (λ = 1.01) frequency of deep snow years.

Reduced calf survival following deep snow years had little effect on population growth for the HN/LP model (λ = 1.17-1.18; Fig. 6). The relatively small increases in calf mortality (Fig. 3) imposed by deep snow in this scenario resulted in a population highly resilient to winter severity. In fact, population growth rates differed very little from population growth rates when deep snow was not incorporated (Table 3).

Population Responses to Female Harvest Scenarios

To reach the management objective in 5 years, we modeled a harvest between 678 and 843 (6% of the female population) non-accompanied females for a total harvest of 3,836 individuals. The same population decline was achieved with a harvest of between 537 and 655 (6% of the female population) cow-calf pairs each year for a total harvest of 5,918 moose. This estimate includes a total of 1,479 male calves because male and female calves cannot be distinguished.

While targeted harvests of non-accompanied females or cow-calf pairs would both allow for desired population declines, harvest of cow-calf pairs resulted in a greater harvestable yield, with 54% more individuals and 11% more biomass harvested over the 5-year-period. In addition, fewer yearlings and adult females were harvested in the cow-calf pair harvest strategy, and the resulting age distribution at the end of the 5-year-period included a higher proportion of young adult and prime-adult females (0.60) than that for the non-accompanied females (0.57). A population with a greater proportion of reproductive females is more resilient because of the immediate ability of reproductive females to contribute to population growth following a perturbation event.

DISCUSSION

Population Responses to Deep Snow Events

The models suggested that survival of prime adults has the greatest potential to influence population growth. This was supported by elasticity analyses, which indicated that population growth rates were most sensitive to changes in young and prime adult survival. For example, when a nearly 50% reduction in prime adult survival was included, the nutritionally stressed population declined in response to moderate to high frequencies of deep snow years. In contrast, modeled populations continued to increase and displayed only slight declines in population growth rate when calf survival alone was reduced by as much as 72% in response to deep snow.

Adult female survival is unlikely to be strongly impacted by deep snow or other inclement weather conditions unless nutritional condition of the population is extremely poor and/or environmental stress is particularly great (Bishop and Rausch 1974, Peterson *et al.* 2003). Indeed, in long-lived vertebrates adult female survival is the vital rate least affected by density-dependence and environmental factors (Eberhardt 1977,

2002) and, predation aside, in large herbivores substantial reductions in adult female survival are mostly associated with extreme environmental events (Gaillard *et al.* 2000). Despite the general resilience of adult female moose to extreme environmental events like deep snow years, substantial population declines have been recorded when density-dependent (e.g. high population densities) and density-independent factors (e.g. deep snow) have combined to increase mortality of adult females (Bishop and Rausch 1974, Peterson *et al.* 2003).

In contrast, in the models, even striking reductions in calf survival following deep snow years failed to strongly impact population growth. In ungulates, calves generally have the most variable survival (16%-88%; Gaillard *et al.* 2000) and are the most vulnerable to disturbance (Gaillard *et al.* 2000). Yet, populations may experience low sensitivity to this variability (Gaillard *et al.* 1998, 2000; Eberhardt 2002; *but see* Raithel *et al.* 2007). Even under the highest disturbance frequency and lowest calf survival scenario, the low nutrition population model showed positive growth, and the population growth rate only declined 2% with the addition of disturbance events. Although this did result in fewer moose on the landscape over the time period modeled the population still increased in size. In the high-nutrition models population growth rates displayed even less response to the inclusion of deep snow years and increased calf mortality. Bowyer *et al.* (1998) argued that low calf survival due to heavy predation released adult females from the high costs of lactation, allowing them to enter the following winter in better body condition. If this is the case, it would further reduce the slight negative impacts of low calf survival predicted by the models because of the likely increase in future reproductive success of females in years following deep snow. However, as we have seen from the models, reductions in calf survival during deep snow years have an impact on population

abundance over time. An increase in the frequency of consecutive deep snow years could, therefore, result in consecutive years with low calf recruitment, introducing gaps in the age-structure of the population and likely resulting in less stable population dynamics. This coupled with high temporal variability generally associated with calf survival is likely to have an influence on longer-term population trends. Therefore, we suggest future models should, 1) include environmental stochasticity to better understand how variability in calf survival influences long-term population trends and 2) examine how consecutive years with deep snow influence both short- and long-term population trends.

   At least in the short term, nutritionally stressed moose populations are likely to benefit from longer growing seasons and more frequent wildfires because of the increase in forage availability brought on by these changes. Conversely, populations exhibiting good nutrition are unlikely to increase in response to the same environmental changes. If predator-mediated constraints on population growth remain stable, predator-limited populations will likely remain relatively stable at low densities even if forage availability increases with climate change.

    Unlike adult female survival, fecundity in moose can be strongly influenced by deep snow (Saether *et al.* 1996) especially when moose exist at high population densities (Post and Stenseth 1998). Deep snow can have negative effects on moose reproduction through reduced body condition of adult females (Mech *et al.* 1987, Crete and Courtois 1997, Post and Stenseth 1998). Elasticity analysis suggested however, that changes in fecundity were likely to have a minimal impact on population-level trends. Therefore the model results should be fairly robust without incorporating reductions in fecundity during a deep snow year.

Deterministic population models ignore the stochasticity found in natural systems (Morris and Doak 2002) and consequently can produce misleading population projections. However, deterministic models can be very useful when vital rate data are sparse and if model assumptions can be biologically justified (Morris and Doak 2002).

Our models assumed constant stage-specific vital rates across all but deep snow years and thereby ignored the impacts of all other environmental as well as demographic stochasticity, and any possible delayed effects of deep snow years. Previous studies of large ungulate population dynamics indicate that environmental stochasticity has the greatest influence on calf survival and young adult fecundity (Gaillard *et al.* 2000). However, large variability in calf survival and young adult fecundity would likely not have had major impacts on population trajectories due to low elasticity values associated with those vital rates. Demographic stochasticity was not incorporated into our model because we were not dealing with small populations.

Although delayed effects of deep snow were not considered in the models, deep snow years likely would have a variety of delayed effects on fecundity and survival. For instance, a substantial drop in population density caused by widespread mortality following a deep snow year would likely improve the nutritional plane for surviving individuals and result in increased reproduction and survival, albeit with a short time lag. Studies have shown that changes in recruitment rates for red deer lag 3 years behind changes in population density (Fryxell *et al.* 1991). Indeed, changes in moose twinning lag 1 to 2 years behind changes in population density (Blood 1973, *this paper*). Following the extreme conditions that resulted in the population crash of the Isle Royale moose population, there was a 1-year lag before the population showed growth (Peterson *et al.* 2003). Barring a major increase in predator:prey ratios, survival rates

would likely improve for all age-classes following a precipitous decline. However, low elasticity values for juvenile and old adult survival indicate changes to these parameters would have relatively less influence on population growth rate. Moreover, young adult and prime adult survival are often constrained by previous high survival rates.

Several other factors that could contribute to a delay in the population response include epigenetic effects due to being born at high density (Solberg *et al.* 1999, 2004; Bonenfant *et al.* 2009) and slow vegetation response to a reduction in herbivory as a result of chronic overbrowsing. In some cases, vegetation recovery following chronic overbrowsing may be quite prolonged and require a landscape disturbance such as fire. This is because chronic overbrowsing of preferred deciduous species often results in heavy mortality of those species, shifting the competitive advantage in favor of less palatable, late successional tree species (Kielland and Bryant 1998, Pastor *et al.* 2006, Butler and Kielland 2008) that do not support high densities of moose. Vegetation recovery may then depend on the fire return interval, which even with an increase in the frequency of fire on the landscape could take decades (Kasischke *et al.* 2010). Therefore, we do not expect these delayed changes in survival or reproduction to have large, immediate impacts on population growth. Overall, the ability of a nutritionally stressed moose population to rebound following a precipitous decline appears to be limited.

Population Responses to Female Harvest Scenarios

Harvesting cow-calf pairs rather than non-accompanied females achieved the desired population reduction while maximizing harvestable yield. Although the desired population reduction could be achieved with either harvest strategy, harvest of cow-calf pairs resulted in a greater number of individuals and total biomass harvested over the 5-

year-period. The greater number of individuals removed from the landscape with cow-calf pair harvest will reduce intraspecific competition and lead to a more immediate improvement in nutrition for the remaining population. In addition, harvest of cow-calf pairs resulted in a lower overall harvest of yearling and adult females compared to harvest of non-accompanied females, leaving the population far more resilient to disturbance. Harvesting cow-calf pairs is a more conservative management approach because population dynamics are highly sensitive to harvest of adult females (Sylven 2003).

The cow-calf pair harvest resulted in a greater harvestable yield because the calf stage contributes far less to population growth than either reproductive females or females nearer to reproductive age. Even for populations subject to low predation, calves have relatively low survival rates, and calf mortality from harvest may be largely compensatory in nutritionally stressed populations that exist near carrying capacity (McCullough 1979, Bartmann *et al.* 1992, Singer *et al.* 1997). Further evidence that juveniles were less valuable to the population than adult females was demonstrated when we experimentally excluded yearlings from the non-accompanied female harvest strategy. When yearlings were included the total harvestable yield was greater than if yearlings were excluded. This follows population dynamic theory, which suggests that a juvenile has relatively low value in terms of future population growth compared with a reproductive female that has given birth for the first time (Stearns 1992).

Although the cow/calf harvest strategy provided more harvest opportunity and a more robust age structure, this harvest strategy may not always be acceptable to hunters. In some areas, hunters are reluctant to harvest not only cows (Young *et al.* 2006) but also cows accompanied by calves (Young and Boertje 2004, Nilsen and Solberg 2006).

Nonetheless, it may be possible to achieve hunter acceptance of selective harvest strategies. In Scandinavia, prior to the 1970s, it was illegal to shoot juvenile moose (Milner *et al.* 2011), but a policy to maximize yield was implemented that called for heavy harvest of both juveniles and adult males (Solberg *et al.* 1999). This harvest strategy has resulted in an enormously productive population that supports high annual harvest rates (Nilsen and Solberg 2006) and provides substantial economic value (Olaussen and Skonhoft 2011). However, it has also led to variations in the sex- and age-structure of populations (Solberg *et al.* 2002, Milner *et al.* 2007) and overabundance issues that have resulted in considerable economic costs (Olaussen and Skonhoft 2011). Incorporating modeled harvest scenarios into public outreach and education could greatly improve the understanding and acceptance of female harvest strategies by the public.

Management Implications

Populations that exhibit low nutrition are likely to benefit from longer growing seasons and increased fire because increased nutrition, at least in the short term, is likely to reduce vulnerability to the effects of environmental stress. However, with little predation or harvest to influence population growth, these increases in nutrition will likely be short-lived as increasing density will lead to intraspecific competition and plant succession will reduce forage quantity and quality. When these populations return to a state of poor nutrition they will again be vulnerable to declines from severe weather events such as years with deep snow. On the other hand, predator-limited populations are unlikely to respond to the same environmental changes if predator-meditated constraints on population growth remain stable. The complexity of wildlife population dynamics coupled with the uncertainty of climate change predictions requires that

managers use population models to minimize risk of major population declines. Therefore, harvest strategies aimed at reducing vulnerability of moose are important to consider. We suggest the use of cow-calf pair harvests to reduce population density is a more favorable strategy to minimize population vulnerability and increase harvest opportunity. We acknowledge this harvest strategy may be difficult to implement without buy-in from local hunters, and therefore suggest educational outreach to attempt to explain honestly the biological benefits of cow-calf pair harvests. It is important that the effects of female harvest strategies be monitored by continuous collection of age-specific vital rate data and independent data reflecting nutritional condition (browse surveys). Continuous monitoring of population indices, such as proportional browse removal (Seaton *et al.* 2011) will allow managers to evaluate the effectiveness of the harvest strategy and reassess population health once the original population objective has been met.

ACKNOWLEDGMENTS

$$\begin{pmatrix} 0 & F_Y & F_{YA} & F_{PA} & F_{OA} \\ G_C & 0 & 0 & 0 & 0 \\ 0 & G_Y & P_{YA} & 0 & 0 \\ 0 & 0 & G_{YA} & P_{PA} & 0 \\ 0 & 0 & 0 & G_{PA} & P_{OA} \end{pmatrix}$$

Fig. 1. Stage-structured matrix model. Matrix parameters are the stage-specific recruitment values (**F$_x$**), stage-specific probabilities of surviving to the next stage (**G$_x$**) and stage-specific probabilities of surviving within a stage (**P$_x$**).
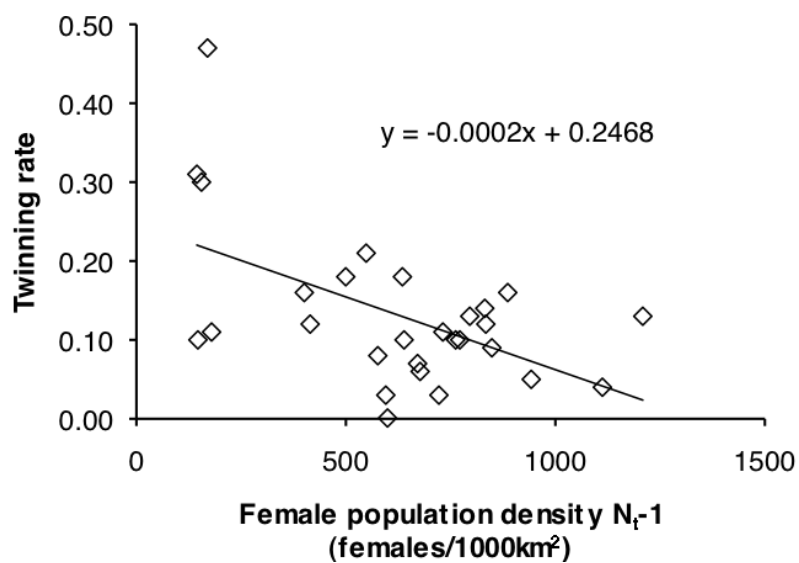
Fig. 2. Twinning rates in relation to population density. Data from Tanana Flats/Alaska

Range foothills moose population.
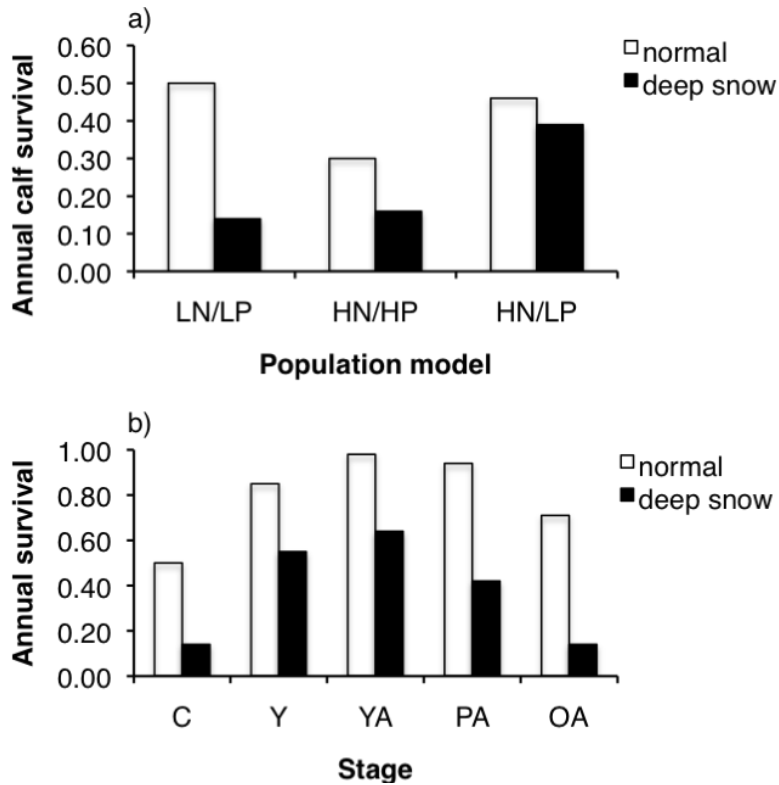
Fig. 3. Annual survival probabilities under normal and deep snow conditions: a) calf survival rates when only calf survival was reduced following a deep snow year and b) stage-specific survival rates of the low nutrition/low predation population matrix model for both normal and deep snow years where survival of all stages was reduced following a deep snow year. C, calf survival; Y, yearling survival; YA, young adult survival; PA, prime adult survival; OA, old adult survival.
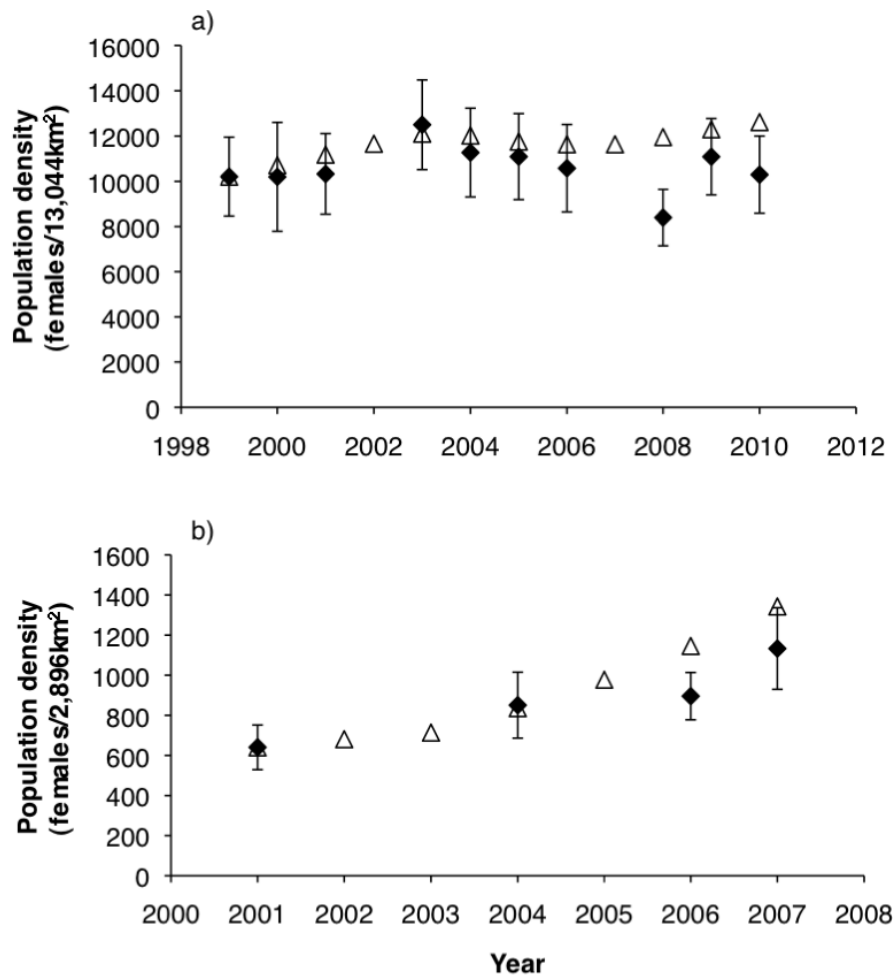
Fig. 4. Comparison of model and field population estimates. Deterministic model estimates (open triangles) and geospatial population estimates of female moose (closed diamonds) including 90% confidence intervals from a) a moose population occupying the Tanana Flats/Alaska Range foothills and b) a moose population occupying a 2,896km^2 study area near McGrath, Alaska.
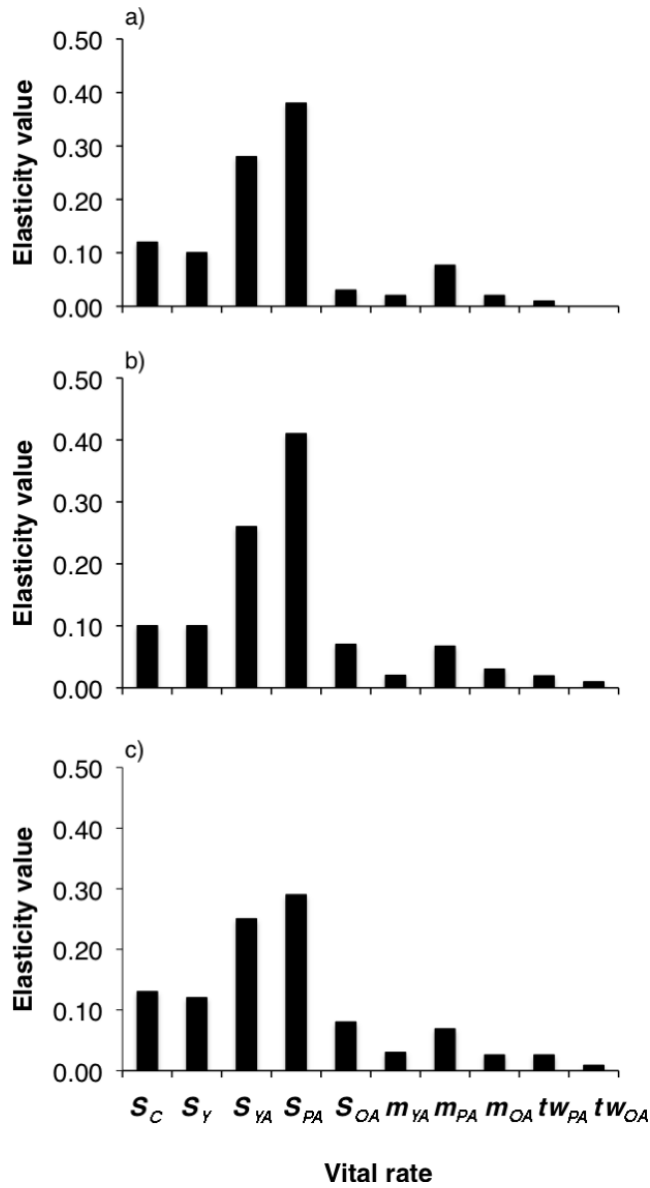
Fig. 5. Stage-structured model elasticity values. Values incorporate survival (S_x), parturition (m_x) and twinning (tw_x) for a) low nutrition/low predation, b) high nutrition/high predation, and c) high nutrition/low predation model. For stages lasting more than 1 year, S_X includes survival within a stage (P_x) and growth to the next stage (G_x).
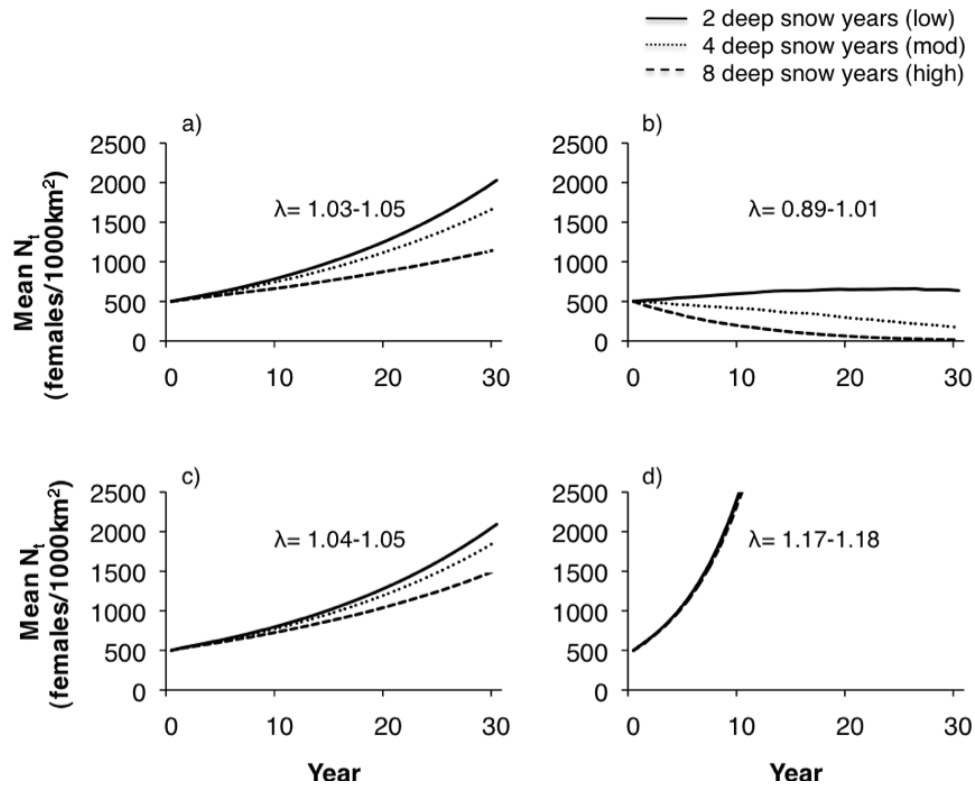
Fig. 6. Mean population trajectories for various frequencies of years with deep snow: a) low nutrition/low predation population model where calf survival is reduced from 0.50 to 0.14 and b) where survival of all stages for the low nutrition/low predation model are reduced, c) high nutrition/high predation population model where calf survival is reduced from 0.30 to 0.16, and d) high nutrition/low predation population model where calf survival is reduced from 0.46 to 0.39. Because of the large difference in scaling between population trajectories of the high nutrition/low predation model and the other models the figure does not follow the population trajectory of the high nutrition/low predation model past year ten to illustrate changes in the direction of the population trajectories for the other models.

Table 1. Stage-specific vital rates of matrix population models. Annual survival is partitioned between survival to the next stage (G_x) and survival within a stage (P_x). The parameter m_x is the proportion of females giving birth and tw_x is the twinning rate.

Stage	Vital rates											
	Low nutrition/Low predation model[1]				High nutrition/High predation model[2]				High nutrition/High predation model[3]			
	G_x	P_x	m_x	tw_x	G_x	P_x	m_x	tw_x	G_x	P_x	m_x	tw_x
Calf	0.50	0.00	0.00	0.00	0.30	0.00	0.00	0.00	0.46	0.00	0.00	0.00
Yearling	0.85	0.00	0.00	0.00	0.77	0.00	0.00	0.00	0.92	0.00	0.00	0.00
Young adult	0.31	0.67	0.34	0.00	0.31	0.67	0.57	0.13	0.28	0.72	0.58	0.14
Prime adult	0.10	0.84	0.77	0.10	0.10	0.84	0.90	0.53	0.08	0.91	0.90	0.53
Old adult	0.00	0.71	0.71	0.13	0.00	0.83	0.84	0.49	0.00	0.95	0.84	0.50

[1] Average annual survival and reproductive data from a moose population occupying the central Tanana Flats near Fairbanks, Alaska (Boertje *et al.* 2009, Boertje *unpubl*).

[2] Average annual survival and reproductive data from a moose population near McGrath, Alaska prior to predator removal (Keech *et al.* 2011).

[3] Average annual survival and reproductive data from a moose population near McGrath, Alaska following predator removal (Keech *et al.* 2011*)*.

Table 2. Stable stage distributions of matrix population models.

	Stable stage distribution		
Stage	Low nutrition/Low predation model	High nutrition/High predation model	High nutrition/Low predation model
Calf	0.22	0.31	0.29
Yearling	0.10	0.09	0.11
Young adult	0.23	0.19	0.24
Prime adult	0.35	0.28	0.26
Old adult	0.10	0.13	0.10

Table 3. Finite rates of population growth of matrix population models. Compared model scenarios without deep snow and scenarios with various frequencies of deep snow. Deep snow years of low, moderate, and high correspond to a frequency of 2, 4, and 8 deep snow years in a 30-year-period, respectively. In all cases except those indicated with *superscript* increased mortality following a deep snow year was limited to calves.

Model	No deep snow	Frequency of deep snow		
		Low	Moderate	High
Low nutrition/Low predation	1.05	1.05	1.04	1.03
		1.01[1]	0.96[1]	0.89[1]
High nutrition/High predation	1.05	1.05	1.05	1.04
High nutrition/Low predation	1.18	1.18	1.18	1.17

[1] Indicates high mortality of all stages for the LN/LP model following a deep snow year.

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CHAPTER 3

GENERAL CONCLUSIONS

Climate change is likely to have both positive and negative impacts on wildlife populations in Interior Alaska. An increase in the frequency of wildfire and length of the growing season will likely favor moose populations, whereas an increase the frequency of severe weather events will likely have a detrimental effect on moose. Under the scenarios examined in this study, our models suggested that over the short term Interior Alaska moose populations exhibiting good nutritional condition are resilient to an increase in the frequency of deep snow years. Nutritionally stressed moose populations, on the other hand, appeared to be vulnerable to population declines from deep snow conditions when there is substantial mortality among prime adult females. Although empirical studies have shown that substantial mortality among prime adult females rarely occurs and likely requires nutrition to be extremely poor or snow conditions to be severe (Gaillard *et al.* 2000) there is valid concern regarding the vulnerability of nutritionally stressed populations to a possible increase in severe weather conditions associated with climate change. Adaptive management strategies that are informed by population models should be pursued to ensure the long-term health and resilience of these important moose populations.

In nutritionally stressed populations, harvest of females, in addition to traditional bull harvests, has proven to be an effective way to quickly reduce population density (Young and Boertje 2011) and thereby relieve browsing pressure on vegetation (Boertje *et al.*

2007). Our harvest model indicated that a harvest approach focused on cow-calf pairs rather than on non-accompanied females (cows ≥1 year old that are not accompanied by a calf) resulted in a greater harvestable yield, while harvesting fewer females. The removal of more individual moose from the landscape will reduce competition for limited resources, and because population dynamics are highly sensitive to harvest of adult females with high reproductive value (Sylven 2003), the removal of fewer adult females leaves the population more resilient to environmental perturbations. Thus, such a management strategy could prove to be a win-win situation.

Although long-term projections of how moose will respond to climate change are difficult to make because of the many variables that influence moose population dynamics, thoughtful consideration of how moose populations will respond to climate change over the long term is important. The countervailing effects of climate change may result in greater fluctuations in the amplitude of moose population abundance over time, especially if a long string of years consisting of favorable conditions are interrupted by year(s) with unfavorable conditions (Wilmers *et al.* 2007). This is because many years of favorable conditions can facilitate rapid population growth to high densities, at which point the nutrition of the population is compromised, which may decrease the potential of all segments of the population to survive a severe winter. A string of severe winters could reduce moose population resilience of nutritionally stressed moose, even leading to local extirpation of moose.

Populations that are not limited by predation are likely to exhibit greater changes in population abundance than those limited by predation. For example, although nutritionally-stressed moose will likely benefit from the increase in forage availability resulting from longer growing seasons and increased fire frequency, without

commensurate increases in predation or harvest to curb population growth, these populations are likely to quickly return to a nutritionally-stressed state and once again become vulnerable to extreme environmental events. Likewise, dispersing moose populations without high predation or harvest to curtail growth will likely approach ecological carrying capacity and also become vulnerable to deep snow conditions. Both of these scenarios illustrate further challenges for wildlife managers.

For moose populations that reach a nutritionally stressed state due to a lack of top-down control, severe winter conditions can initiate substantial population declines that lead to a shift in predator:prey ratios. In multiple predator systems or systems dominated by wolves, high predator:prey ratios can exacerbate the precipitous decline of a previously food-limited population and result in a predator-limited population maintained at low density ("predator pit") (Gasaway *et al.* 1983). This type of scenario was observed for an Interior Alaska moose population that was likely near ecological carrying capacity at the time of several consecutive deep snow years (1965-1966, 1966-1967). Although no quantitative data exist, deep snow conditions resulted in substantial mortality, particularly for calves (Bishop and Rausch 1974). The decline in moose numbers resulted in an increase in predator:prey ratios, worsened by yet another severe winter and concurrent harvest of moose (Gasaway *et al.* 1983). Moose declined to very low levels following these events and only began to recover following wolf removal efforts initiated in 1976 (Gasaway *et al.* 1983).

Although our models did not incorporate changes in predator-prey dynamics, it is likely that predator-prey dynamics will be affected by climate change, and that they will have an impact on moose population abundance under certain circumstances. For example, an increase in the frequency of winter precipitation at northern latitudes, both

in terms of snow and rain (Groisman and Easterling 1994, Zhang *et al.* 2000, Kohler *et al.* 2006), could result in deeper, heavier snow (Zhang *et al.* 2000). These conditions could facilitate wolves gaining an advantage over moose because of their ability to travel on top of the snow while moose, because of their heavier foot load, would have to plow through the deep snow (Owen-Smith 2009). This scenario would be of particular concern for moose populations that exist in areas that have historically experienced a high frequency of winters characterized by deep snow, such as those in Western Interior Alaska and Southcentral Alaska. Higher kill rates have been observed for gray wolves (*Canis lupus*) on white-tailed deer (*Odocoileus virginianus*; Nelson and Mech 1986*)* and elk (*Cerphus elaphus;* Huggard 1993) as snow depth increased. Moreover, deep snow conditions have led to wolves altering their hunting behavior by increasing their pack size, which can increase hunting success (Post *et al.* 1999). In low-density, predator-limited populations these conditions could result in local extirpations of moose populations, similar to those documented for white-tailed deer (Nelson and Mech 2006).

Climate change could also impact predator-prey dynamics in ways that benefit moose. For instance, an increase in the frequency and areal extent of wildfire (Kasischke *et al.* 2010) that results in higher quality browse would influence moose productivity and possibly population abundance. Although heavy predation pressure acts as a constraint on the response of predator-limited populations to improved habitat, factors that could facilitate escape of these populations from low densities include access to calving refugia, predator saturation, change in prey preference, and inter-pack strife among wolves, all of which would lead to reduced predation rates and increased survival of moose (Gasaway *et al.* 1983). It therefore seems possible that under certain

circumstances interactions between climate change and predator-prey dynamics could lead to greater changes in population abundance of predator-limited populations.

We suggest that future population models investigate additional climate scenarios likely to influence moose population dynamics. In particular, the impacts of consecutive deep snow years should be examined. Due to the influence of large-scale climate indices (e.g. North Atlantic Oscillation, North Pacific Oscillation), years associated with deep snow can be temporally correlated (Hurrell 1995). It is possible the increase in environmental variability projected to occur with climate change (IPCC 2007) may result in more frequent and consecutive deep snow years in the future. Several consecutive years of deep snow will undoubtedly have the most influence on nutritionally stressed moose because of their low body reserves but could also result in local extirpation of low-density, predator-limited populations (Nelson and Mech 2006). In our models, when consecutive years with deep snow resulted in high mortality of all stages it had a substantial impact on moose population density. For example, two to three consecutive years of deep snow resulted in a moderate population decline for our LN/LP model (3% population decline when deep snow years are consecutive) when only calves incurred high mortality, however, these populations recovered to their pre-decline density within 2 years. The same number of consecutive deep snow years resulted in a major population decline for our LN/LP model (> 35% population decline when deep snow years are consecutive) when we subjected all age-classes to high mortality and the population did not recover to pre-decline density for ≥ 20 years.

Additional work needs to incorporate a vegetation component into the matrix model so we can examine how changes in browse availability as a result of climate change may more directly influence moose population trajectories. The model would be a

simple predator-prey model where effects of climate change, plant succession, and moose herbivory on vegetation could be modeled explicitly.

Further investigation of alternative harvest strategies using the stage-structured population model could be helpful for managers tasked with maintaining the long-term health and sustainability of important moose populations. We suggest that future population models incorporate the male component of the population to make modeling scenarios more realistic and informative, and to assess other management objectives, including management for trophies. Combining the knowledge that results from additional harvest scenarios with that from different climate scenarios will help us better understand how we can promote moose population resilience in the face of climate change.

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