Identifying large herbivore distribution mechanisms through application of fine-scale snow modeling
by Mathew Adam Messer

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Fish & Wildlife Management
Montana State University

Abstract:
Climatic variation can influence species responses to the environment by changing landscape conditions at fine spatial scales over short time periods. Snowpack has recently been modeled in a geographic information system at 30 m spatial resolution, detail sufficient to expanding the assessment of animal responses to dynamic landscape conditions during the winter season. I examined elk distributional responses to variable snowpack conditions by comparing landscape characteristics at observed locations of instrumented elk to randomly selected locations representing the landscape available to those elk in the upper Madison River drainage of Yellowstone National Park, Wyoming, USA. Snow mass was estimated for 3126 elk locations and associated random locations collected over 5 winter seasons. Using log odds ratios, I documented a higher likelihood of elk occurring at locations with relatively lower snow mass estimates. These likelihoods increased at low snow mass levels as landscape-scale snow severity increased. In addition, the likelihood of elk occurrence increased as snow heterogeneity (ie. the variability of snow mass) at a location increased. Conditional logistic regression and Akaike's Information Criterion model comparison techniques revealed that snow heterogeneity had a strong positive coefficient estimate when added to models containing static landscape covariates and greatly increased the explanatory power of such models. However, snow mass was not well supported using this approach, suggesting that the explanatory power of snow mass is provided by landscape covariates already in the model. This finding suggests incorporating additional mechanisms related to these static landscape covariates, such as herbaceous productivity, into future model comparisons. Results from these analyses support known distributional responses of large herbivores to snow, and also reveal additional complexity in those responses associated with landscape-scale snow conditions and local snow pattern. Advancement and application of current climatic modeling techniques will enable further assessment of species responses to variation in climate at increasingly detailed biological, temporal and spatial scales.

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APPROVAL

of a thesis submitted by

Mathew Adam Messer

This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citation, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

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ABSTRACT

Climatic variation can influence species responses to the environment by changing landscape conditions at fine spatial scales over short time periods. Snowpack has recently been modeled in a geographic information system at 30 m spatial resolution, detail sufficient to expanding the assessment of animal responses to dynamic landscape conditions during the winter season. I examined elk distributional responses to variable snowpack conditions by comparing landscape characteristics at observed locations of instrumented elk to randomly selected locations representing the landscape available to those elk in the upper Madison River drainage of Yellowstone National Park, Wyoming, USA. Snow mass was estimated for 3126 elk locations and associated random locations collected over 5 winter seasons. Using log odds ratios, I documented a higher likelihood of elk occurring at locations with relatively lower snow mass estimates. These likelihoods increased at low snow mass levels as landscape-scale snow severity increased. In addition, the likelihood of elk occurrence increased as snow heterogeneity (ie. the variability of snow mass) at a location increased. Conditional logistic regression and Akaike's Information Criterion model comparison techniques revealed that snow heterogeneity had a strong positive coefficient estimate when added to models containing static landscape covariates and greatly increased the explanatory power of such models. However, snow mass was not well supported using this approach, suggesting that the explanatory power of snow mass is provided by landscape covariates already in the model. This finding suggests incorporating additional mechanisms related to these static landscape covariates, such as herbaceous productivity, into future model comparisons. Results from these analyses support known distributional responses of large herbivores to snow, and also reveal additional complexity in those responses associated with landscape-scale snow conditions and local snow pattern. Advancement and application of current climatic modeling techniques will enable further assessment of species responses to variation in climate at increasingly detailed biological, temporal and spatial scales.

INTRODUCTION

Climatic variation is a stochastic component of the abiotic environment that influences the plant and animal species inhabiting most ecosystems (Andrewartha and Birch 1957, Fretwell 1972, Ackerly 2003). This variation can be influential to the biotic community at many spatial and temporal scales, including regional multi-annual precipitation trends to site-specific daily temperature fluctuations. For example, when waterfowl avoid drought-affected landscapes or reptiles orient their bodies to maximize solar exposure, they are responding to dynamic environmental conditions (Florides et al. 1999, Neimuth and Solberg 2003). Interpreting such behavior not only depends upon identifying influential environmental scales, but also carefully defining the biological scale of response (Levin 1992, Karl et al. 2000). While an animal's initial response to landscape characteristics is a reflection of physiological requirements, assessing immediate physiological economics is often difficult in the field (Dailey and Hobbs 1989, Harder and Kirkpatrick 1994). However, in meeting these physiological needs animals may distribute themselves upon the landscape in a manner that maximizes benefits while minimizing costs, and as such their resulting locations can provide an effective biological scale at which responses to the landscape can be examined (Fretwell and Lucas 1969). By comparing the characteristics of an animal's location to the characteristics of the landscape available across its normal range the extent to which different components of the landscape influence animal distributions can be assessed (Manly et al 1993). Such assessments typically use geographic information system (GIS) data layers to determine the characteristics of the landscape at a particular location, and are more reliable with increasingly accurate representations of the landscape. However, in environments that experience pronounced seasonal variation, spatially explicit climate data is rarely available at temporal and spatial detail sufficient to adequately model variation in animal location data.

In mid- to-high-latitude ecosystems, climate during the winter season can quickly change landscape conditions, causing animals to distribute themselves in a manner that minimizes energy expenditures and maximizes benefits (Fretwell 1972). Wind, freezing temperatures and snow during winter can cause the costs of movement, thermoregulation and food acquisition to vary across the landscape (Parker et al. 1984, Wickstrom et al. 1984, Root 1988,). While some populations can considerably minimize these costs through migratory behavior or hibernation, other populations cope by changing resource use within their local environment (Fancy et al. 1989, Berthold 2001, Humphries et al. 2003). Animals unwilling or unable to avoid the energetic costs associated with severe winter climate can experience pressures that may ultimately influence their vital rates and, hence, fitness. In particular, seasonal snow patterns can negatively affect juvenile survival and body mass, alter sex ratios and increase adult mortality (Loison and Langvatn 1998, Post and Stenseth 1999, Mysterud et al. 2000, Forchhammer et al. 2001, Garrott et al. 2003). Such demographic changes reflect consequences of climate at extensive spatial and temporal scales and encourage questions about the interactions between organisms and their environment at finer spatial and temporal scales. Advancements in tagging and radio marking animals continue to improve the ability to obtain detailed biological data, while the progression in computer technology and remote sensing has begun to provide increasingly detailed and accurate landscape data (White and Garrott 1990, Fred Watson personal communication). Using such data researchers can now begin to examine the influence of dynamic landscape components, including snowpack, upon animal movement and distribution patterns.

Various landscape components contribute to make snow accumulation and ablation highly variable across space and time, making it challenging to represent in a GIS for subsequent comparison to animal responses (Coughlan and Running 1997, Marsh 1999). Precipitation interacts with abiotic components of the environment, such as elevation, aspect, temperature, wind, and solar radiation, as well as biotic components including vegetation structure to result in snowpack variation (Hardy and Hansen-Bristow 1990, Coughlan and Running 1997, Greene et al. 1999, Marsh 1999). Unique combinations of these environmental components may create heterogeneous patterns of snowpack across the landscape. While many studies have looked at how seasonal climatic changes influence animal distributions upon the landscape (Craighead et al. 1973, Schmidt 1993, Nellemann 1998), few have attempted to utilize dynamic climatic conditions at finer temporal scales. Turner et al. (1994), used historical monthly weather measurements to estimate one ha snow metrics every three days for assessing the influence of landscape variation on ungulate distribution and survival. Based upon simulated ungulate movement and distribution patterns, they determined that winter severity had a significant effect on post-fire survival. Arthur et al. (1996), compared polar bear locations to several categories of sea ice concentration, calculated daily at a 625 km^2 spatial scale, to determine how seasonal changes in bear distribution were influenced by changing sea ice density. Recently, hydrological modeling efforts have provided daily estimates of snowpack at spatial scales of less than 900 m^2 (Fred Watson personal communication). While snowpack is commonly measured using depth, these models estimated snow water equivalent (SWE) as a more direct indicator of snowpack, because it reflects snow mass, the product of snow depth and density (Farnes et al. 1999). These data are novel in both spatial and temporal resolution, providing the opportunity to build upon previous research by examining the relationships between animal distributions and climate, such as site-specific SWE estimates and SWE variation, in even greater detail.

Responses of large herbivores to snow have been well researched, however, their distributions during winter have only been broadly correlated to changes in the spatial distribution of snowpack (Craighead et al. 1973, Houston 1982, Schmidt 1993, Nellemann 1998, Ball et al. 2001). In many ecosystems, including those in temperate to arctic regions, large herbivores have important effects on landscape processes such as nutrient cycling and plant community structures (McNaughton 1985, Hobbs 1986). Thus, identifying the mechanisms that influence large herbivore distributions upon the landscape is crucial to both ecological understanding and ecosystem management. The influence of snow accumulations on seasonal migration and localized movement has been documented, yet has often been based upon general observations and infrequent measurements of snow (Craighead et al. 1973, Sweeney and Sweeney 1984, Ball et al. 2001). Given these known responses in light of access to site-specific SWE estimates, the opportunity now exists to determine if snowpack estimates at relatively fine spatial and temporal scales can provide additional insight into the rôle of snowpack as a mechanism directing large herbivore distributions.

Rocky Mountain elk (*Cervus elaphus*) populations in Yellowstone National Park (YNP) inhabit a mid-latitude montane ecosystem, representing an ideal study system for examining the influence of snowpack on large herbivores. Elk herds in YNP have demonstrated distributional responses to changing seasonal snow conditions, including the non-migratory elk herd inhabiting the upper Madison drainage (Craighead et al. 1973, Houston 1982). My specific objective was to examine distributional responses of elk to snowpack dynamics by utilizing location information from the upper Madison elk herd and detailed SWE estimates. This examination compared SWE estimates at known elk locations to SWE estimates at locations selected at random from that area determined to be available to the population. I assessed the response of elk to changing SWE estimates under several landscape-scale snow conditions. I also compared the contributions of a suite of landscape components, including SWE, in explaining variation in elk distribution. To determine these contributions, I developed models to represent my biological hypotheses and compared the resulting suites of competing models using model selection techniques based on Akaike's Information Criterion (AIC) (Burnham and Anderson 1998).

STUDY AREA

The study area encompasses 31,400 hectares of the upper Madison River drainage in west central YNP, Wyoming (Figure 1). Ranging in elevation from 2050 to 2650 meters, the landscape is composed primarily of forested plateaus and river canyons, with meadow and riparian habitats along the Gibbon, Firehole and Madison rivers. Located on the western edge of the Yellowstone caldera, the landscape contains high concentrations of geothermal features. Seasons are characterized by long, cold winters and short cool summers with average annual temperatures ranging from -11.1 to 17.7° C, and a mean annual temperature of 3° C. Average annual precipitation ranges from 56 to 108 cm at low and high elevations, respectively. At low elevations snow accumulation usually begins during early November, with approximately 190 days of measurable snow cover and maximum SWE values of 58 cm. At higher elevations snow accumulation usually begins during mid-October, with approximately 235 days of measurable snow cover and maximum SWE values of 113 cm (Natural Resource Conservation Service SNOTEL data). Accumulation and ablation rates of snow are highly variable across all sites, with geothermal areas exhibiting accelerated ablation rates.

Elk utilize vegetation within forest and meadow habitats for cover and forage. In 1988, fires burned 48% of the area and the landscape now supports a mosaic of mature lodgepole pine (*Pinus contorta*) forests and various stages of regeneration, with small areas of Engelman spruce (*Picea englemannii*) and subalpine fir (*Abies lasiocarpa*) (Aune 1981, Despain et al. 1989). Meadow vegetation consists of grasses (*Agropyron* spp., *Deschampsia* spp.), sedges (*Carex* spp.) and marsh reedgrass (*Calamagrostis* spp.)

(Aune 1981). Big sagebrush (*Artemisia tridentata*) and Idaho fescue (*Festuca idahoensis*) occur on drier sites (Despain 1990). While winter vegetation is primarily senescent, providing minimal nutritional value to large herbivores (Hobbs et al. 1983), geothermal activity from numerous geyser basins support unique plant and algal communities that photosynthesize year round (Despain 1990).

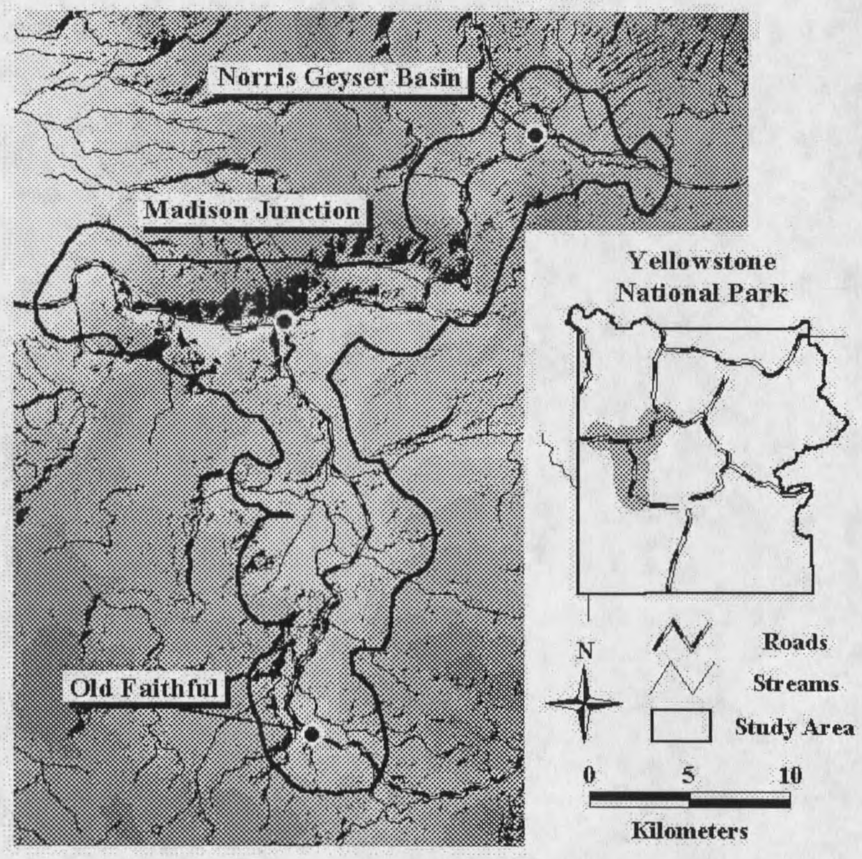

Figure 1. Upper Madison study area boundary, as defined by 3126 random telemetry locations of 76 instrumented cow elk collected during five winter seasons (15 November – 15 May), within Yellowstone National Park, Wyoming, USA.

The study population consists of 600-800 non-migratory elk occurring in relatively small herds across the landscape (Craighead et al. 1973, Eberhardt et al. 1998). This population exists in a protected natural landscape that is relatively uninfluenced by anthropogenic factors. Although an average of 133,000 people visit the study area each winter, human use is primarily confined to the 75 kilometers of roads that run adjacent to the three rivers (National Park Service 1999). Park protection and frequent human exposure facilitate data collection, because elk are acclimated to both park visitors and the presence of researchers (Hardy 2001). Elk in the upper Madison drainage share their winter range with YNP's central bison (*Bos bison*) herd, whose population ranges from approximately 300 to 1200 throughout the winter season (Bjornlie and Garrott 2001, Ferrari and Garrott 2002). Wolves (*Canis lupus*) were successfully restored to the study area in 1995 in the Firehole River valley, and the wolf population now provides a source of predatory pressure on the large herbivore populations (Mech et al. 2001)

METHODS

Elk Distribution

Adult female elk were captured, instrumented and monitored to collect distribution data. Elk were arbitrarily selected for capture, while attempting to maintain an even distribution of individuals throughout the study area. Animals were captured using ground-based delivery of immobilization drugs via dart rifle and fitted with collar-mounted radio-transmitters. The sample from this population varied from 25 to 40 individuals, dependent upon mortality and YNP permits. Animal locations were sampled during five winter seasons (1991-92, 1992-93, 1994-95, 2000-01 and 2001-02) from approximately 15 November until 15 May, following a restricted randomization sampling design (Garrott et al. 1996). I divided the study area into several geographically defined strata and randomly selected a stratum to be sampled. Instrumented elk inhabiting the selected stratum were located in a randomly determined order and all remaining strata were subsequently sampled before re-sampling. Locations were obtained diurnally using hand-held telemetry equipment and homing procedures (White and Garrott 1990). Upon sighting, the location of the animal was recorded in Universal Transverse Mercator coordinates using United States Geological Survey (USGS) quadrangle maps.

I defined a binary response variable using instrumented elk locations compared to randomly selected locations deemed available to the study population during winter. The spatial extent of available landscape was delineated with a kernel density estimator using the Home Range Extension program (Rodgers and Carr 1998) in ArcView Geographic

Information System (GIS) software (ESRI 1998). Performance of kernel density estimators is primarily dependent upon smoothing parameter selection (Worton 1989). While the program calculates a reference smoothing parameter, least squared cross validation (LSCV) is considered the most precise parameter estimation technique (Seaman and Powell 1996). However, fragmented boundaries are generated when kernelling with LSCV for linear home ranges (Blundell et al. 2001). Thus, I calculated a smoothing parameter that was 30% of the reference estimate, compared to the 10% suggested by LSCV. I generated a 99.5% boundary (Figure 1) around all independent elk locations using a fixed kernel at a grid resolution of 30 m, unit variance standardization and a smoothing factor of 0.077. To represent the landscape available to the study population, random locations were selected from within this boundary at a 20:1 ratio to instrumented elk locations. Random locations were assigned the same date as their corresponding elk location to ensure equal temporal distribution between elk and random locations.

Landscape Covariates

Landscape covariates were assigned to instrumented elk and random locations using GIS data layers (Table 1). Geographic information system data layers used to examine variation in large herbivore distributions usually represent temporally static landscape attributes (Cooper and Millspaugh 1999, Karl et al. 2000). Typical static attributes include slope, aspect, elevation and vegetation cover type. However, using a single static data layer is inadequate for representing snow, as it is highly variable over short time periods. Because of this, I used a frequently updated data layer to capture the temporal dynamic of snow. Both temporally static and dynamic covariates were obtained from data layers of 30 m resolution, or pixel size.

Table 1. Landscape and snow covariates used to examine variation in winter elk distribution. All continuous covariates were measured in meters, except solar radiation, which is unitless.

Variable	Definition
HBT	Categorical Habitat: geothermal, meadow, burned forest, unburned forest
SRI	Solar Radiation Index
ELV	Elevation
SWEA*	Local Snow Water Equivalent - mean of SWE for all pixels within 100 m radius of location
SWEL*	Landscape Snow Water Equivalent - mean of SWE for all pixels within the boundary of the study population
SNHA*	Local Snow Heterogeneity - standard deviation of SWE for all pixels within 100 m radius from point location
SNHL*	Landscape Snow Heterogeneity - standard deviation of SWE from within the boundary of the study population

* Snow covariates SWE and SNH are referred to as Landscape or Local in text.

A USGS digital elevation model was used to acquire estimates of slope, aspect and elevation. Aspect cannot be used directly in modeling efforts, as it is a continuous circular measure where 1° is similar to 359°. This problem is usually overcome by treating it as a categorical variable and designating up to eight parameters defined by the cardinal and sub-cardinal directions (Cooper and Millspaugh 1999). However, the biological importance of aspect can become more pronounced on greater slopes due to the solar exposure of a site. Solar exposure can influence thermoregulation of organisms, as well as vegetative productivity and snow dynamics on the landscape (Cook et al. 1998, Greene et al. 1999). I used a solar radiation index (SRI) as a parsimonious metric representing this slope-aspect relationship. A SRI is calculated using latitude, slope and aspect, and requires the estimation of only one parameter (Iqbal 1983). SRI values range from a minimum -0.72 for northerly aspects of 90° slope to a maximum of 1.0 for southerly aspects of 45° slope, with values of 0.69 on all areas with no slope.

Habitat categories were designated using vegetation cover type and geothermal data layers developed by The Watershed Institute (TWI), California State University Monterey Bay (Fred Watson personal communication). Classifications were conducted using MicroImages processing software (MIPS 2003), with 30 m resolution visual band and 60 m resolution thermal band input from Landsat 7 Enhanced Thematic Mapper satellite imagery acquired in spring 2001. Cover types classified were meadow, and burned and unburned forest. Geothermal areas were identified by estimating ground heat production and then assigned a heat index value ranging from 0 to 300. All pixels registering heat production >0 were categorized as geothermal regardless of the vegetation cover type of that pixel. By combining data from the vegetation cover type and geothermal data layers I obtained four habitat categories; burned forest, unburned forest, meadow and geothermal.

A mechanistic-based model (Langur, Fred Watson personal communication) was developed to estimate the spatial and temporal heterogeneity of the snowpack each winter. Langur generated daily estimates of SWE throughout the study area using temporally dynamic precipitation and temperature data, and spatially explicit slope, aspect, elevation, ground heat, vegetation cover type and mean annual precipitation data. Daily precipitation and minimum and maximum temperature data were collected from two automated snow telemetry weather stations (Natural Resource Conservation Service SNOTEL data), the Madison Plateau station west of the study area and the Canyon station to the northeast. Snow was modeled to accumulate when precipitation occurred at freezing temperatures, with ground accumulation limited by interception of snow in the forest canopy. Ablation occurred through vapor loss and snowmelt, depending upon changes in heat content of the snowpack due to air temperature, ground heat and solar radiation. Accuracy of Langur was validated using data from 1233 snow cores collected by TWI during the 2000 and 2001 winter seasons (Fred Watson personal communication). Using Langur output I characterized snowpack using two metrics, SWE and snow heterogeneity (SNH), with each metric calculated at a local and landscape scale. Snow water equivalent was calculated as the average of all pixels within the scale of interest and represented the mean water content of the snowpack. Snow heterogeneity was calculated as the standard deviation of all pixels within the scale of interest and represented the spatial variability of the snowpack. The local scale was considered all pixels within a 100 m radius of each elk and random location, as I assumed elk responses to snow would occur at a scale larger than that of a single 30 m pixel. The landscape scale was considered all pixels within the defined boundary of the study population, as I assumed all elk had the capability of moving throughout the study area during the course of each winter. Landscape and local snowpack estimates were obtained daily and local snowpack estimates were assigned to each elk location and its corresponding random locations on that day.

Model Development and Analyses

I used log odds ratios to determine the likelihood of an elk occurring at a particular location on the landscape depending on the local snowpack conditions at that location, as well as the characteristics of the snowpack at the landscape-scale (Agresti 1990). Elk locations, and their associated random locations, were first categorized by the landscape SWE estimate on their date of collection. Then, within each landscape SWE category, locations were categorized again by their local SWE estimate. The categories of landscape SWE (low 0.000-0.099, moderate 0.100-0.169, high 0.170-0.229 m) were designated so that all three categories had the same approximate number of elk locations. Local SWE levels were designated at every 0.05 m within each landscape SWE category and odds ratios were then calculated for each local SWE level. The odds of an elk location occurring in a particular local SWE level were calculated by taking the probability of an elk location occurring in that level divided by the probability of an elk location not occurring in that level. The odds of a random location occurring in that level were then calculated. An odds ratio was derived by dividing the odds of an elk location by the odds of a random location occurring in that level. Log odds ratios were obtained by taking the natural log of the odds ratio. Log odds ratios were calculated with 95% confidence intervals when the proportion of locations occurring in a particular local SWE level exceeded 0.01. Odds ratios have an asymmetrical distribution ranging from 0 to infinity with values >1 indicating increased odds of occurrence, values <1 indicating decreased odds and values of 1 indicating equal odds of occurrence. Log odds ratios are symmetrical about 0 and allow comparison of the strength of positive and negative relationships. Using the previous approach, I also calculated log odds ratios at 0.02 m levels of local SNH within the three landscape SWE categories, and for local SWE and local SNH across three levels of landscape SNH. Due to the energetic costs of movement and foraging in heavier snow, I predicted that the odds of elk occurrence would decrease with increasing local SWE, meaning elk would be less likely to occupy areas of high snow mass as opposed to low snow mass. The range of local SWE increases as local SNH increases and I predicted increasing odds of elk occurrence with increasing local SNH, as elk would have a greater range of local SWE to select from. Lastly, I predicted that as landscape SWE and landscape SNH increased the odds of elk occurrence across local SWE and local SNH levels would become more pronounced.

To assess the contribution of SWE in explaining variation in winter elk distribution, I compared *a priori* hypotheses representing the potential effects of static landscape and dynamic snowpack covariates. Hypotheses were expressed as a set of candidate models, and each model was placed in one of three suites, depending upon which covariates it contained (Table 2). The first suite, composed of 7 models, contained only static landscape covariates and represented traditional approaches to explaining winter distributions of large herbivores. Within this suite I hypothesized that lower elevations, higher SRI and geothermal habitats would be selected for due to lower energy requirements for foraging and movement, as all of these were thought to be correlated with lower SWE. In addition, I hypothesized that elk should select geothermal or meadow habitats, which exhibit higher vegetative production and greater potential forage biomass, over less productive habitats such as burned or unburned forests. While some geothermal habitats associated with active thermal features are devoid of vegetation, many provide higher quantities and/or quality of forage by supporting wet meadow areas

Table 2. Candidate a priori models for examining effects of static and temporally dynamic landscape covariates on variation in elk distribution.

Suite 1 - Static Landscape Effects	
1.1	HBT
1.2	SRI
1.3	ELV
1.4	HBT+SRI
1.5	HBT+ELV
1.6	SRI+ELV
1.7	HBT+SRI+ELV
Suite 2 - Dynamic Snow Effects	
2.1	SWEA
2.2	SNHA
2.3	SWEA+SNHA
2.4	SWEA+SNHA+(SWEA*SNHA)
Suite 3 - Static Landscape and Dynamic Snow Effects	
3.1	SWEA+HBT
3.2	SWEA+HBT+ELV+SRI
3.3	SWEA+SNHA+HBT
3.4	SWEA+SNHA+HBT+ELV+SRI
3.5	SWEA+HBT+(SWEA*HBT)
3.6	SWEA+HBT+(SNHL*HBT)
3.7	SWEA+SNHA+HBT+(SWEA*HBT)
3.8	SWEA+SNHA+HBT+(SNHA*HBT)
3.9	SWEA+SNHA+HBT+(SNHL*HBT)
3.10	SWEA+SNHA+HBT+(SWEA*SNHA)
3.11	SWEA+SNHA+HBT+(SWEA*SNHA)+(SWEA*HBT)
3.12	SWEA+SNHA+HBT+(SWEA*SNHA)+(SNHA*HBT)
3.13	SWEA+SNHA+HBT+(SWEA*SNHA)+(SNHL*HBT)

with high vegetative productivity or plants that photosynthesize year round (Despain 1990). A second suite of 4 models containing only temporally dynamic snowpack covariates was used to directly examine the influence of snowpack on elk distribution. I predicted decreased selection with increasing local SWE, increased selection with increasing local SNH, and stronger responses to local SWE with increasing local SNH. The third suite, containing 13 models, combined both static landscape covariates and dynamic snowpack covariates. Within this suite I developed several models using elevation, SRI and local SWE. However, I assumed that local SWE estimates were correlated with elevation and SRI and that by using only local SWE I could assess changes in elk distribution with more precision. Thus, elevation and SRI were only included in two simple additive models. The remaining models within this suite examined variation in elk distribution with combinations of snowpack covariates and habitat.

Models were fit and parameter coefficients estimated through conditional logistic regression analyses using PROC PHREG (SAS Institute Inc. 2000). Conditional logistic regression is a matched case-control analysis, where binary data are matched, or stratified, by a potential confounding variable. As a result of matching, the intercept term cancels out of the conditional logistic regression equation and a coefficient is not estimated for this parameter. I matched elk and random locations by date to ensure that comparisons were made between locations with identical landscape snowpack metrics. Because only one value is obtained for landscape SWE or landscape SNH for each date, there is no variation between matched data. Consequently, landscape snow covariates could not be used as additive terms in model building. Therefore, to assess the effect of changing snowpack characteristics at the landscape scale, interaction terms containing landscape snowpack metrics were used. This allowed me to examine if the relationship between elk distribution and local-scale covariates varied across the range of landscape snowpack metrics. However, due to the relatively high correlation between landscape SWE and landscape SNH (Pearson correlation = 0.58), I chose to use only landscape SNH in model building. I expected better explanatory power from landscape SNH, as the increasing variation indicated a wider range of SWE from which elk could select.

When using PROC PHREG, there are no formal goodness-of-fit or overdispersion estimates available. Thus, I assessed model fit through interpretation of deviance residuals. One potential source of lack of fit was variation between the early (1991-92 to 1993-94) and later (2000-01 to 2001-02) years of the study, due to wolf reintroductions in 1997 (Smith et al. 2003) and advancing forest regeneration following the 1988 fires (Turner et al. 2003). Shifts in elk distribution may have occurred if wolf presence elicited behavioral adaptations to predation pressure (Lima and Dill 1990, Lima 1998), or forest regeneration changed the biomass and structure of vegetation (Turner et al. 2003). To examine these potential confounding influences, models were fit and rankings compared for both time periods separately. Models were ranked and the best approximating models, supported by the data, were selected using AIC (Burnham and Anderson 1998).Due to the large sample size, comparisons did not need to be made using $\mathrm{AIC_c}$ values. Before fitting models I centered and scaled all continuous covariates by subtracting the midpoint and dividing by half the range. Resulting values fall between –1 and 1 with a mean of 0, allowing for comparison of coefficient strength between covariates.

After obtaining results from *a priori* model comparisons, I conducted post-hoc exploratory analyses to provide insight for future analyses. Exploratory analyses were conducted by systematically adding or eliminating covariates from the most parsimonious model from my *a priori* model suites, in an attempt to develop an even more parsimonious model based on AIC values. This method of model building allowed me to explore the role of parameters and interactions suggested from the interpretation of results from my original model suites.

RESULTS

In total, 4077 locations were collected from 76 instrumented elk over 5 winter seasons. Group sizes ranged from 1 to 80, with a mean of 6.8. When multiple instrumented elk were located simultaneously in a single group, only data from one individual were used for analyses. I retained 3126 locations (range 441-872 loc./season) after censoring dependent data, with 2064 and 1062 locations collected during the 1991-94 and 2000-02 time periods, respectively.

Snowfall during the five seasons was average to below average (Figure 2). Historic SWE accumulations are presented in cm days, the summation of daily SWE measurements throughout the season (Oct. 1 - Apr. 31) as measured from snow telemetry stations (Garrott et al. 2003). From 1968 to 2002, SWE measurements ranged from 2975 to 12400 cm days, with an average of 7139 cm days. Winter seasons during my studies had SWE measurements ranging from 3965 to 6715 cm days with a mean of 5675 cm days.

Langur output indicated that wintering elk encountered pronounced seasonal and annual variation in snowpack characteristics. Seasonal changes in snowpack for the narrowest (2000-01) and broadest (1992-93) ranges of snow conditions encountered during this study are presented in Figure 3. These graphs depict minimum, maximum, and average landscape SWE estimates, as well as landscape SNH throughout the winter season. Average and maximum landscape SWE estimates follow similar trends of increase throughout the winter season and then quickly decreasing at the beginning of spring melt, however, a small portion of the study area always remained snow free due to geothermal activity. Landscape SNH, represented by the range of SWE values with measurable accumulation, increased throughout the season, but did not decrease as quickly as average and maximum landscape SWE in the spring. These general seasonal trends were more pronounced during years of heavier snowfall (Fig. 3), with higher maximum and average landscape SWE estimates and greater landscape SNH.

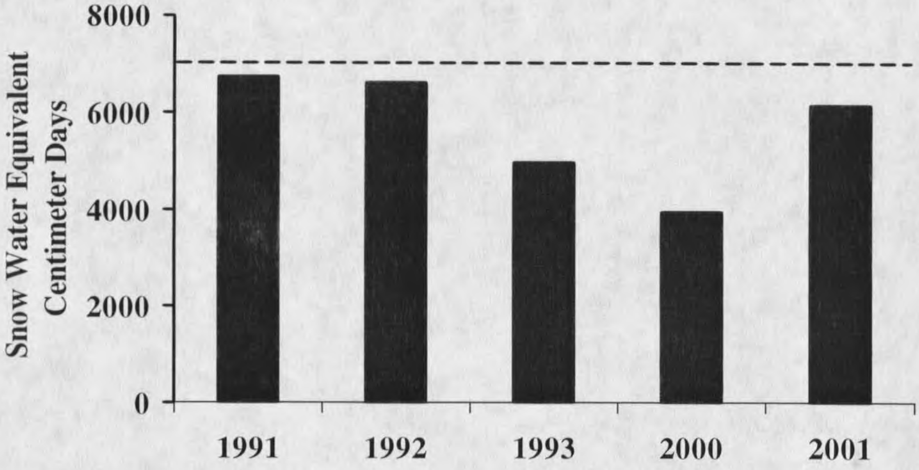

Figure 2. Yearly snow water equivalent accumulations across the five winter seasons of this study. Dashed line represent historic average at 7139 cm days.

As predicted, log odds ratios indicated that elk were less likely to occur in areas with higher local SWE and more likely to occur in areas with higher local SNH. These trends were similar across all categories of landscape SWE and landscape SNH. Because relationships were stronger using landscape SWE, log odds are only presented using landscape SWE (Fig. 4). When landscape SWE was relatively low (< 0.1 m), log odds for the three lowest levels of local SNH were -0.58 (SE = 0.08), 0.40 (SE = 0.09), 0.82 (SE = 0.15) respectively. This trend, similar to results within moderate and high

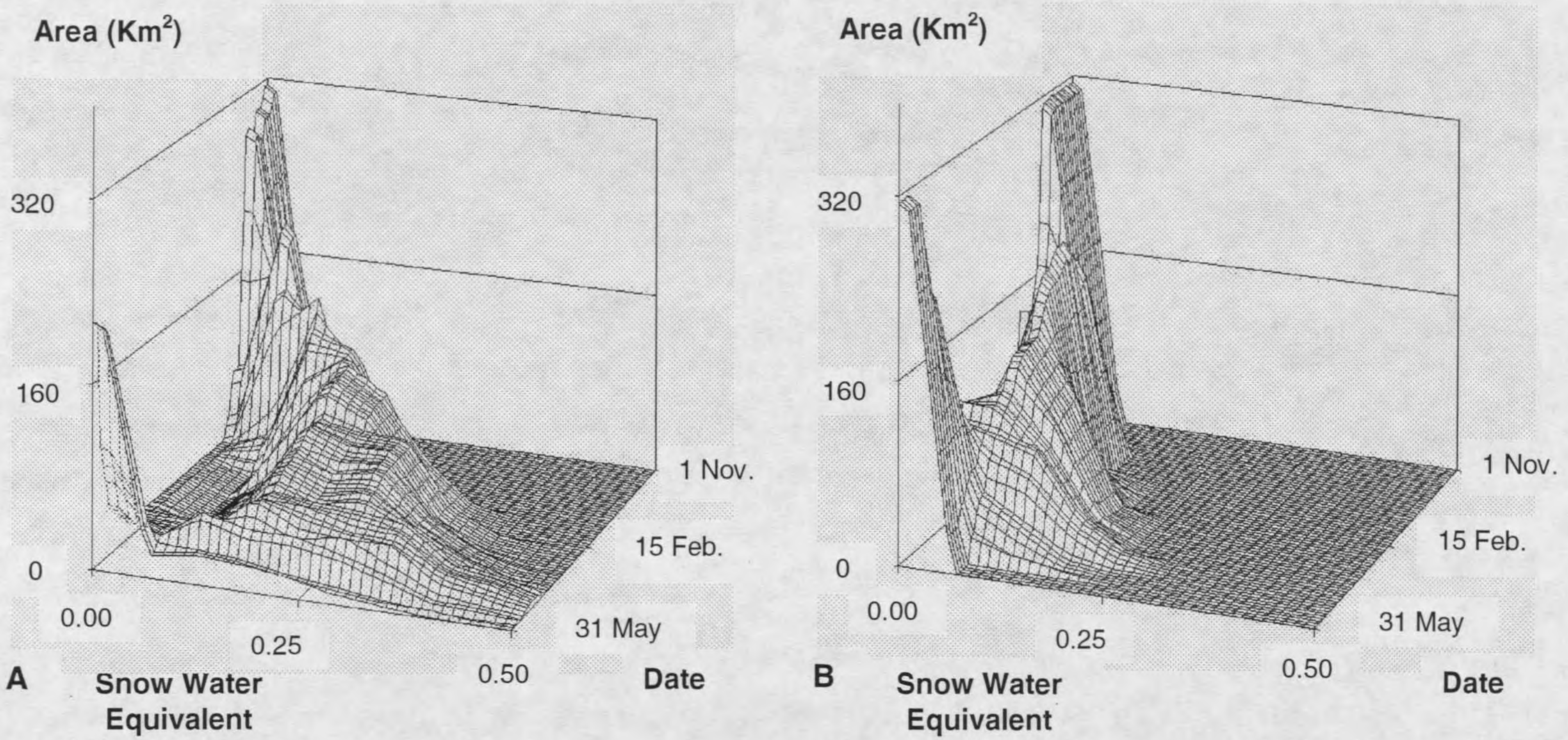

Figure 3. Temporal pattern of snow water equivalent estimates for the 314 km^2 study area during the broadest range of snowpack, 1992 (A) and the lightest range of snowpack, 2000 (B) experienced during the study.

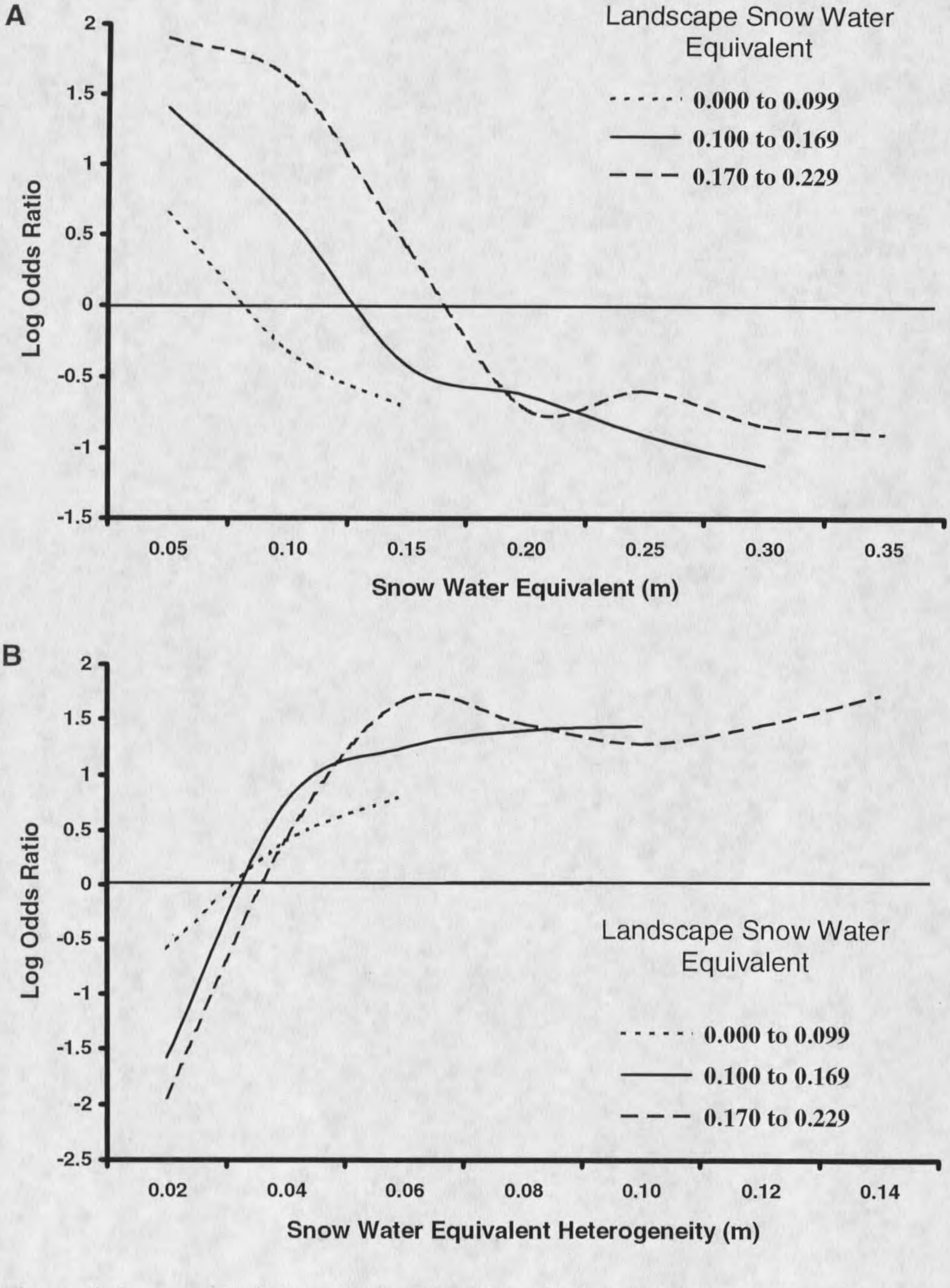

Figure 4. Log odds of elk selection (likelihood elk occurrence) across the range of snow water equivalent (A) and snow water equivalent heterogeneity (B) for three categories of average landscape snow water equivalent.

landscape SWE categories, illustrates a pronounced increase in the likelihood of an area being used by an elk as local SNH increased. An alternative assessment would be to interpret the odds ratio of 0.56 (CI = 0.48, 0.66) at the lowest local SNH level (< 0.02 m). This value indicates that the odds of an elk occurring in this level were approximately 44% lower than the odds of a random location occurring in this level. As landscape SWE increased from moderate to high, log odds within the lowest local SNH level decreased from -1.58 (SE = 0.06) to -1.97 (SE = 0.07), while values at the 0.04-0.06 m local SNH level increased from 1.24 (SE = 0.09) to 1.67 (SE = 0.09). Comparison of odds ratios between landscape SWE categories within a local SNH level, suggest that while the odds of an elk occurring within a local SNH level varied slightly as landscape SWE increased, they were not greatly influenced by this change. In general, elk locations became more likely than random locations at approximately 0.03 m local SNH across all categories of landscape SWE. Beyond the 0.04-0.06 m local SNH level, log odds were relatively stable at approximately 1.45, with confidence intervals overlapping for both moderate and high landscape SWE categories. Beyond this level, elk were equally likely to occur regardless of increasing variation in local SNH or changing landscape SWE. In contrast to local SNH, the likelihood of elk occurrence declined across increasing levels of local SWE. Within the low landscape SWE category, odds ratios for local SWE decreased from 0.65 (SE = 0.07) to –0.31 (SE = 0.07) to –0.72 (SE = 0.12). This decreasing trend was similar between all landscape SWE categories, however, changes in log odds ratios between landscape SWE categories were greater within local SWE levels than within local SNH levels. For example, within the lowest local SWE level (< 0.05 m), log odds increased from 0.65 (SE = 0.07) to 1.40 (SE = 0.08) to 1.90 (SE = 0.10), as landscape SWE categories increased. In addition, the local SWE value where the log odds of elk occurrence became negative increased from approximately 0.08 m to 0.13 m to 0.17 m across low, moderate and high categories of landscape SWE. These values indicate that changing snowpack conditions at the landscape scale greatly influence the likelihood of an elk occurring within a particular local SWE level. This landscape-scale influence was present within all local SWE levels <0.2 m. Above 0.2 m local SWE, log odds appeared to stabilize at approximately -0.80, with confidence intervals overlapping for all landscape SWE categories. Beyond this level, elk were equally likely to occur regardless of increasing local SWE levels or changing landscape SWE. These results suggest that elk are either choosing to occupy areas with more snow mass as landscape-scale snowpack increases, or simply have no choice but to occupy areas of greater snow mass. These results also suggest that changes in elk responses to local and landscape snowpack conditions were limited to those areas with <0.2 m local SWE

The influence of local SWE estimates on the likelihood of elk occurrence in an area, as demonstrated by interpretation of log odds, can be illustrated by examining a subset of elk location data. I selected a subset of locations from Old Faithful, a relatively high elevation area in the southern end of the study system, because this location typically exhibits a wide range of snowpack conditions. One hundred and four elk locations were selected from days when landscape SWE was less than 0.07 m and 102 locations selected from days when landscape SWE was greater than 0.2 m. The extent of elk spatial distributions diminished as landscape SWE estimates, and corresponding local

SWE estimates, increased (Figure 5). Estimated 90% kernel density boundaries generated using these locations decreased 62%, from 15.1 km^2 under low landscape SWE to 5.7 km^2 during high landscape SWE. I found that elk locations concentrated closer to geothermal areas as landscape SWE increased, with distance to geothermal areas decreasing from a mean of 251 m (SE = 27) under low landscape SWE to 83 m (SE = 14) under high landscape SWE. Corresponding local SWE estimates for elk increased from a mean of 0.056 m (SE = 0.001) to 0.209 m (SE = 0.009). This example supports my findings from log odds ratio interpretation, that the likelihood of elk occurrence is related to local and landscape SWE.

Results from model comparison techniques were not entirely consistent with results from interpreting log odds ratios, but did support some predictions regarding the ability of covariates to explain variation in elk distributions. Initial AIC values supported pooling data between time intervals, 1991-94 and 2000-02. During both time intervals the same models were selected as most parsimonious within each of the 3 model suites. The 3 most parsimonious models across all model suites were also the same between time intervals. While the second and third ranked models were reversed between early and later years, during both time intervals there was overwhelming support for one model as most parsimonious. Therefore, I concluded there were minimal differences between time intervals and present model comparison results for the pooled data (Table 3). The most parsimonious model in the first suite was an additive model containing all static landscape covariates: habitat, elevation and SRI. The most parsimonious model from the

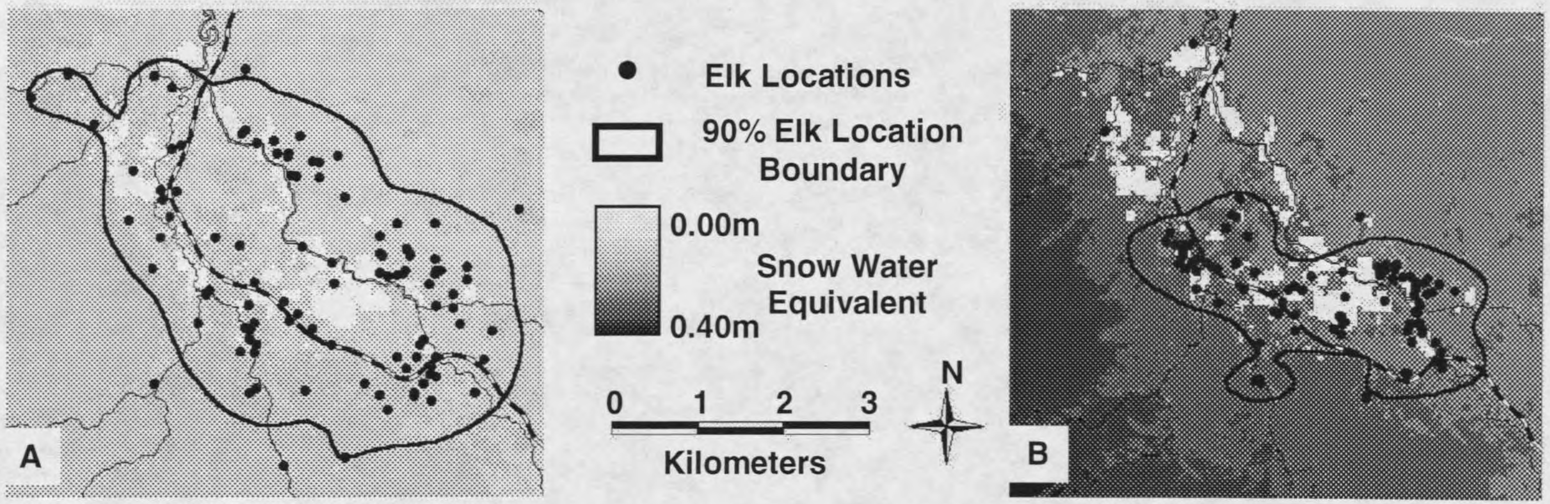

Figure 5. Elk locations from Old Faithful, Wyoming, USA, during light snowpack (*n* = 104 : A) and heavy snowpack (*n* = 102 : B). Area of elk distribution within a 90% kernel density boundary decreased from 15.1 km^2 when landscape snow water equivalent averaged less than 0.07 m, to 5.7 km^2 when landscape snow water equivalent averaged greater than 0.2 m. Background snow data layers were selected from 1 Dec. 1992 (A), and 15 Feb. 1993 (B). White areas, depicting 0 m snow water equivalent, represent the location of geothermal features.

Table 3. Model selection results for *a priori* hypothesized models examining the effects of static landscape and dynamic snow covariates on variation in winter elk distribution. The 5 best-supported models are presented.

Model	Description	K	Delta AIC	AIC weights
3.4 α	SWEA+SNHA+HBT+ELV+SRI	7	0.00	1.00
3.2	SWEA+HBT+ELV+SRI	6	826.83	0.00
1.7	HBT + SRI + ELV	5	827.31	0.00
3.12	SWEA+SNHA+HBT+(SWEA*SNHA)+(SNHA*HBT)	4	1034.17	0.00
3.8	SWEA+SNHA+HBT+(SNHA*HBT)	8	1121.62	0.00
2.4*	SWEA+SNHA+(SWEA*SNHA)	3	1387.57	0.00

α AIC value for model 3.4 is 19337.1

* Model 2.4 - the most parsimonious model from Suite 2 is ranked 13th across all model suites.

second model suite, using only dynamic snow covariates, included the additive effects of local SWE, local SNH and their interaction. The combination of static and dynamic covariates in the third suite resulted in the most parsimonious model across all suites, an additive model using all covariates: location SWE, location SNH, habitat, elevation and SRI. Each of these three models had an AIC weight of 1.0 within their particular model suite, suggesting none of the other competing models from within each suite were well supported. The most parsimonious model from the third suite also had an estimated AIC weight of 1.0 when compared across all competing models regardless of suite. This again suggests no support is evident for any other model when comparing across suites. Model fit was assessed for the most parsimonious model within each suite and as the deviance residuals from these models did not exceed a value of 3, I assumed that these models fit the data well. For a complete listing of AIC rankings for all models see the Appendix.

Coefficient estimates for the most parsimonious model in each of the three model suites supported predicted effects of covariates in explaining variation in the distribution of elk. Within the first model suite, topographical covariates provided the most explanatory power with SRI having a positive coefficient estimate (2.66, 95% CI = 2.37, 2.95) and elevation a negative estimate (-2.19, 95% CI = -2.31, -2.08). These results demonstrate the explanatory power of topography and suggest the value of elk distribution mechanisms related to topography. Possible mechanisms may include snowpack characteristics and vegetative productivity. Within this model habitat coefficients are interpreted relative to the geothermal class, which was used as the reference variable. The strength of habitat effects increased from meadow (-1.14, 95% CI = -1.26, -1.02) to burned forest (-1.46, 95% CI = -1.57, -1.35) and unburned forest (-1.81, 95% CI = -1.94, -1.69) classes, as expected. These coefficients correspond to perceived differences in ground herbaceous productivity among the three non-geothermal habitat classes. The second model suite supported the negative effect of local SWE (-3.53, 95% CI = -3.76, -3.30) and positive effect of local SNH (0.77, 95% CI = 0.49, 1.04) as predicted, and supported the results obtained from log odds ratio analyses. The interaction of these two covariates had a positive coefficient estimate (2.62, 95% CI = 2.19, 3.07), moderating the effect of SNH at low SWE estimate and increasing the positive effect of SNH at higher SWE estimates. Thus, local SNH provided stronger explanatory power as local SWE estimates increased. While the most parsimonious model from the third suite revealed similar coefficient estimates for all static landscape covariates as those from the first suite, dynamic snow covariate estimates were quite different than those calculated in the second suite. Habitat coefficient estimates decreased from meadow (-0.49, 95% CI = -0.64, -0.35) and burned forest (-0.58, 95% CI = -0.72, -0.44), to unburned forest (-0.83, 95% CI = -0.98, -0.68), but coefficient strength was less pronounced compared to the first suite. Predictions related to herbaceous productivity were still supported, although the confidence intervals overlapped for meadow and burned forest. Elevation had a negative coefficient estimate (-2.42, 95% CI = -2.57, -2.27) and SRI a positive estimate (2.76, 95% CI = 2.46, 3.01), with both demonstrating stronger effects than in the first suite. The effect of local SWE remained negative (-0.09, 95% CI = -0.33, 0.15), however, the confidence interval for this estimate encompassed zero. This result suggests that the power of local SWE to explain variation in elk distributions, as seen in the second suite, was accounted for by other covariates in this model. Local SNH showed a positive effect (2.31, 95% CI = 2.16, 2.46) nearly as strong as that of SRI and ELV, indicating that this dynamic covariate maintained explanatory power, even when combined with static covariates.

Exploratory analyses provided insight into some of the results suggested by analysis of original model suites (Table 4). As my original decision to restrict models with SRI and elevation from the third model suite was not supported, these explorations allowed me to assess more complex models with these topographical covariates. Building exploratory models in a systematic fashion, I first eliminated local SWE from the most parsimonious model in the third suite. The resulting AIC value indicated increased model performance, an expected result based upon the weak explanatory power of local SWE in the original model. The habitat and local SNH interaction, which was supported in the

Table 4. Model selection results for exploratory models examining the effects of static landscape and dynamic snow covariates on variation in winter elk distribution, using pooled data.

Model Description	K	Delta AIC	AIC weights
α SNHA+HBT+SRI+ELV+(SNHA*HBT)+(SNHL*ELV)	10	0.00	1.00
SNHA+HBT+SRI+ELV+(SNHA*HBT)	9	43.23	0.00
SNHA+HBT+SRI+ELV+(SNHL*ELV)	7	165.72	0.00
SNHA+HBT+SRI+ELV+(SRI*HBT)	9	174.01	0.00
SNHA+HBT+SRI+ELV+(SNHL*SRI)	7	188.86	0.00
SNHA+HBT+SRI+ELV	6	205.15	0.00
* SWEA+SNHA+HBT+ELV+SRI	7	206.56	0.00

α AIC value for the most parsimonious model is 19130.54
* Most parsimonious model from original model suites

third suite, also increased model performance. As landscape SNH was highly correlated with local SWE and local SNH, the interactions between landscape and local snowpack covariates could not be incorporated into the original model building approach. However, my original results suggested that elevation and SRI were providing explanatory power for snowpack metrics and other possible mechanisms. Given that elevation and SRI were not highly correlated with landscape SNH, I could examine if the explanatory power of these topographical covariates varied with landscape SNH. The most parsimonious model from exploratory analyses was comprised of local SNH, habitat, SRI, elevation, a local SNH and habitat interaction, and a landscape SNH and elevation interaction. The SRI coefficient was similar to that from SRI in the most parsimonious model from the third model suite. The strength of habitat covariates increased slightly, while local SNH and elevation both decreased, possibly due to their presence in the interaction terms. Local SNH coefficient strength was strongly influenced by habitat category, with coefficient estimates increasing from meadow (9.37, 95% CI = 6.28, 12.47) to burned forest (17.50, 95% CI = 14.34, 20.66) to unburned forest (22.37, 95% CI = 18.49, 26.26). This indicates that the power of local SNH was much greater in habitats that were assumed to have lower forage potential, suggesting that elk responded quite strongly to variation in snowpack when the perceived benefits of forage decreased. Explanatory power of elevation varied with changes in landscape SNH. The coefficient strength of the elevation and landscape SNH interaction (-8.07, 95% CI = -10.43, -5.07) indicates that the negative response of elk distribution to elevation becomes stronger with greater variation in landscape snow pattern. These results suggest that more complex relationships may exist between dynamic snowpack covariates and static landscape covariates.

DISCUSSION

Snowpack estimates at fine spatial and temporal scales can be important to consider when using landscape components to assessing the winter distribution of large herbivores in high latitude ecosystems. These results empirically support previous research documenting negative associations between large herbivore responses and increasing severity of snowpack characteristics, including depth (Rongstad and Tester 1969, Schmidt 1993, Loison and Langvatn 1998, Nelleman 1998, Ball et al. 2001). My results provide this support by utilizing spatial representations of SWE, and to my knowledge, only one other publication has utilized SWE to determine changes in large herbivore distributions (Turner et al. 1994). This suggests that the utilization of SWE, a more direct measure of snowpack than depth, can be a valuable tool in future efforts to expand upon historical research of the winter ecology of large herbivores. In addition, these results suggest that the response of elk to local snow conditions is dependent upon landscape-scale snow conditions, a conclusion not documented in the existing literature. I noted an increased likelihood of elk locations occurring at low SWE levels, as landscape SWE estimates increased. Also, the range of local SWE estimates where elk had a greater likelihood of occurring increased as landscape SWE estimates increased. This dynamic response was interpreted to indicate that the study population was constrained to areas with higher local SWE as landscape SWE increased. In essence, elk generally selected areas with the least amount of snow, but began to occupy areas of increased snow as less and less of the total area within the study system fell within low snow levels. While increasing landscape SWE estimates caused the likelihood of elk occurrence to change at low levels of local SWE, the likelihood at higher levels of local SWE remained consistent as landscape SWE estimates increased. This consistency in the likelihood of elk occurrence stabilized between 0.15 and 0.20 m of SWE, similar to the upper threshold of cow elk foraging (0.15 m) suggested by Turner et al. (1994). These results do not indicate any thresholds related to SWE, but suggest that in areas with high local SWE elk persist at low levels regardless of changing landscape SWE estimates. However, it is important to note that these results represent analyses conducted on data from years of average to below average snowfall. It is quite probable that expanding these analyses will allow future documentation of both foraging and occupancy thresholds.

The strong positive relationship documented between elk occurrence and increasing SNH was an assessment not possible prior to snow modeling efforts. Snow heterogeneity has not been widely documented as a mechanism influencing the distribution of large herbivores, possibly because assessing spatial variation in snowpack is difficult outside of a modeling environment and detailed snow models have not existed until recently (Schmidt 1993). However, the importance of heterogeneity in the landscape to explain variation in the distribution of organisms, and their utilization of resources, is well known and led to my predictions regarding the response of elk to heterogeneity in the snowpack (Weins 1989, Kotliar and Weins 1990, Pearson et al. 1994). I predicted an increased likelihood of elk occurrence in areas with greater local SNH. While both log odds ratios and model selection analyses supported this prediction, there was only a weak tendency for the likelihood of elk occurrence to increase as landscape SWE increased. This did not support my prediction that likelihoods within a particular SNH level would become more pronounced as landscape SWE increased. I concluded that given the range of climatic conditions examined, changing landscape SWE estimates did not influence the response of elk to SNH. In addition, I also noted the likelihood of elk occurring within a particular SNH level did not change above 0.06 m SNH. This demonstrated that elk exhibited a strong positive response to increasing SNH up to the 0.06 m level, after which the likelihood of elk occurrence was equally likely, regardless of SNH estimate.

Support for snow as a mechanism affecting the distribution of the study population, as provided by log odds ratio interpretation, was not clearly evident when interpreting model comparison results. While local SNH and local SWE coefficients supported predictions for these parameters in the most parsimonious model from the second suite, local SWE provided minimal explanatory power in the most parsimonious model when compared to other covariates, including local SNH. While these results were unexpected, they provide additional insight into the influence of snow on the spatial dynamics of elk distribution. Research has documented the importance of both snow and topographical features in affecting resource utilization and distribution of large herbivores during the winter season (Irwin and Peek 1983, Turner et al. 1994, Nellemann 1998, Ball et al. 2001). The influence of topographical features results in part from the correlation of snowpack characteristics to those features, such as slope, aspect and elevation, and is interpreted as such in most literature (Coughlan and Running 1997, Green et al. 1999). Given these findings, I anticipated that when including SWE models with either elevation and/or SRI that the SWE estimate would account for much of the explanatory power of these topographical covariates, by providing a direct estimate of snow. While the most parsimonious model from the second suite strongly supported the explanatory power of local SWE, this was not supported in the most parsimonious model overall. Several reasons may explain why the coefficient strength of local SWE was much less than that of elevation or SRI in the most parsimonious model. First, Langur may need to be improved to increase its' accuracy in estimating snow at fine spatial scales. Future development to increase the accuracy of both Langur and model input parameters will undoubtedly provide better assessments of the influence of landscape parameters. However, snow estimates appear adequate to assess distributional responses as the model was fairly accurate at estimating local SWE, based on ground measurements (Fred Watson personal communication), and analytical results support the majority of predictions. A second possible explanation is that elevation and SRI partially explain variation in elk distribution, due to similarities with several mechanisms including local SWE. Thus, the strength of these covariates comes in part from their correlation with local SWE estimates (Pearson correlation = ELV- 0.38; SRI- 0.08), as well as a correlation with some other mechanism such as temperature or forage productivity. If this interpretation is correct, these results not only demonstrate the importance of snow in explaining variation in the distribution of large herbivores, but also indicate that some other mechanism related to topography is influencing the distribution of the study population.

This research focused on identifying the mechanisms influencing species distributional response to the environment, not interpreting this relationship through examining surrogates of the true mechanism (Morrison 2001). The direct role of these landscape components was examined by utilizing snowpack estimates, and even SRI, yet other known mechanisms were unaccounted for in these analyses. For example, large herbivores are known to respond to the quality and quantity of herbaceous vegetation during the winter (Wallace et al. 1995), even though senescent plants provide poor quality forage and snow reduces accessibility to these plants (Hobbs et al. 1983, Parker et al. 1984). Few previous attempts to model large herbivore distributions have had direct measures of these attributes at meaningful spatial scales, and while unable to obtain detailed vegetation biomass estimates, these efforts demonstrate the utility of working toward spatially and temporally dynamic landscape characteristics which more accurately represent the animal's environment. Additional efforts are underway to determine the influence of wind in displacing snow in this study system, a possible step toward eventually determining the role of this dynamic landscape component on animal distributions (Fred Watson personal communication). Perhaps with greater spatial and temporal detail of snowpack, wind, temperature, vegetation structure and vegetation biomass, understanding biological responses in greater detail will be possible. For example, comparing landscape characteristics to individual energetic responses, such as those provided through urinary indices (Garrott et al. 1996).

These results represent an initial effort to incorporate dynamic components of the landscape into assessments of species-habitat relationships, and support expanding the scope of such assessments. This assessment of elk responses to variable snowpack should be extended to years of greater than average snowfall, as these results suggest that responses can change as landscape-scale snow conditions become more severe. In addition, the study system supports another large herbivore, the bison, whose winter ecology and responses to snow have important research and management implications (Bjornlie and Garrott 2001). Beyond the direct effects on elk distribution assessed here, the possibility exists to determine how snowpack might indirectly influence these species by altering the vegetative community upon which they forage. Andrewartha and Birch (1957) noted that climatic conditions could influence animal populations both directly and indirectly. The ability to assess both direct and indirect influences can be extended to include a multitude of other species, including individual and population responses to the environment at a variety of scales (Johnson 1980, Levin 1992). This research highlights a significant effort to incorporate a mechanism of climate into the understanding of species distribution. As climatic modeling increases in prevalence and accuracy, researchers will have a greater ability to apply data, novel in both its' spatial and temporal detail, to a wide array of ecological questions.

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APPENDIX

AKAIKE'S INFORMATION CRITERIA MODEL RANKINGS

		AIC			Within Suites - Delta AIC			Between Suites - Delta AIC		
Model	K	Early	Late	Pooled	Early	Late	Pooled	Early	Late	Pooled
1.1	3	14446.6	7501.0	21959.4	1237.9	569.0	1802.1	1913.8	719.8	2629.5
1.2	1	15195.2	7740.8	22939.6	1986.5	808.8	2782.4	2662.4	959.6	3609.7
1.3	1	14156.7	7201.1	21356.8	948.0	269.0	1199.6	1623.9	419.9	2026.9
1.4	4	14219.6	7434.4	21668.8	1010.9	502.4	1511.5	1686.8	653.2	2338.8
1.5	4	13477.9	7009.5	20499.0	269.2	77.4	341.8	945.1	228.3	1169.1
1.6	2	13860.9	7115.1	20979.4	652.1	183.1	822.2	1328.1	333.9	1649.5
1.7	5	13208.7	6932.0	20157.3	0.0	0.0	0.0	675.9	150.8	827.3
2.1	1	14513.4	7354.4	21870.7	980.0	177.4	1153.1	1980.6	573.2	2540.7
2.2	1	14261.3	7535.5	21799.7	727.9	358.5	1082.2	1728.5	754.3	2469.7
2.3	2	13653.6	7183.2	20847.2	120.2	6.2	129.6	1120.8	402.0	1517.2
2.4	3	13533.4	7177.0	20717.5	0.0	0.0	0.0	1000.6	395.8	1387.6
3.1	4	14001.7	7233.8	21249.8	1468.9	452.6	1919.9	1468.9	452.6	1919.9
3.2	6	13210.7	6925.9	20156.8	677.9	144.7	826.8	677.9	144.7	826.8
3.3	5	13488.6	7135.4	20635.2	955.8	354.2	1305.3	955.8	354.2	1305.3
3.4	7	12532.8	6781.2	19330.0	0.0	0.0	0.0	0.0	0.0	0.0
3.5	7	13867.6	7227.6	21109.8	1334.8	446.4	1779.8	1334.8	446.4	1779.8
3.6	7	14002.0	7236.0	21247.5	1469.2	454.8	1917.5	1469.2	454.8	1917.5
3.7	8	13449.1	7135.4	20601.8	916.3	354.2	1271.9	916.3	354.2	1271.9
3.8	8	13328.1	7107.6	20451.6	795.3	326.4	1121.6	795.3	326.4	1121.6
3.9	8	13490.9	7128.6	20637.7	958.1	347.4	1307.8	958.1	347.4	1307.8
3.10	6	13362.0	7126.2	20492.9	829.2	345.0	1163.0	829.2	345.0	1163.0
3.11	9	13343.8	7125.5	20479.9	811.0	344.3	1149.9	811.0	344.3	1149.9
3.12	9	13252.5	7103.7	20364.1	719.7	322.5	1034.2	719.7	322.5	1034.2
3.13	9	13365.3	7119.5	20497.9	832.5	338.3	1168.0	832.5	338.3	1168.0

Akaike's information criteria model rankings for early, late and pooled time periods. Both within and between suite Delta AIC values are presented.