SPATIO-TEMPORAL DYNAMICS OF THE CENTRAL BISON HERD IN YELLOWSTONE NATIONAL PARK

by

Jason Edward Bruggeman

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APPROVAL

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Jason Edward Bruggeman

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

Dr. Robert A. Garrott ______________________________ ___________
(Signature) Date

Approved for the Department of Ecology

Dr. Dave W. Roberts ______________________________ ___________
(Signature) Date

Approved for the College of Graduate Studies

Dr. Bruce. R. McLeod ______________________________ ___________
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ABSTRACT

The spatio-temporal dynamics of Yellowstone National Park bison (*Bison bison*) are complex and affected by multiple abiotic and biotic mechanisms. In the Madison-Firehole area, which provides winter range for the migratory central herd, this suite of effects is particularly intricate owing to geothermally influenced habitats, severe winter climate, and variability in resource distribution. Understanding factors influencing bison spatio-temporal dynamics is of importance to Yellowstone, which is faced with managing a growing bison population that is expanding its range. I gathered data from 1997-2005 using field methods and used statistical modeling and information theoretic techniques to examine spatial and temporal patterns in bison migration, road and off-road travel, and foraging behavior in relation to abiotic and biotic factors. Numbers of bison migrating were related to density and drought severity, while snow, drought, and density affected timing of migration. The probability of bison travel and spatial distribution of travel corridors were affected by topographic and habitat attributes including slope, landscape roughness, habitat, and distances to streams, foraging areas, and forested habitats. Streams were the most influential landscape feature affecting travel and results suggest the bison travel network is defined largely by the presence of streams. Probability of travel was higher in regions of variable topography (i.e., canyons). Pronounced travel corridors existed both in close association with roads and distant from any roads, and results indicate roads may facilitate bison travel in areas. Multiple effects influenced temporal bison travel patterns. Road travel was negatively correlated with road grooming and I found no evidence that bison preferentially used groomed roads during winter. Snowpack, density, and springtime melt were correlated with bison road and off-road travel. Bison foraging area residence times were affected by the ratio of local to landscape scale snowpack, previous foraging experiences, and local and landscape scale competition. Bison patch scale foraging behavior was predominantly affected by snowpack, with biomass and competition having minimal influence. My results indicate bison spatio-temporal dynamics are affected by multiple, interacting, scale-dependent mechanisms. Overall, factors influencing resource availability provide the primary impetus for variability in bison distribution, movements, and foraging behavior.

FOREWARD

Bison (*Bison bison*) and Yellowstone National Park—perhaps no combination of a species and location conjures up a sense of wilderness in both a historic and current context in the lower 48 United States. As they traveled west through the Dakotas in 1804, Lewis and Clark documented immense herds of bison roaming the hills and plains (DeVoto 1953). Even as recent as the mid-1800s bison grazed the Great Plains, and beyond, in magnificent numbers. However, this symbol of the American West was nearly extirpated by the early 20th century owing to unabashed slaughter by settlers and traders. One of the few small groups of bison remaining from the once spectacular plains herds was located in Yellowstone National Park (Meagher 1973).

Yellowstone is the last remaining intact ecosystem in the lower 48 States. Home to such wildlife as elk (*Cervus elaphus*), wolves (*Canis lupus*), grizzly bears (*Ursus horribilis*), and a variety of waterfowl and bird species, Yellowstone often is considered the “crown jewel” of the National Park system as much for its vast expanse of untouched wilderness as its stunning array of wildlife. In Yellowstone, certain species have recovered from near extirpation, while others thrive with populations bordering on overabundant status. Bison form an integral part of Yellowstone’s ecosystem as their grazing of the landscape influences processes across multiple spatio-temporal scales (Hobbs 1996). To present, bison have been minimally affected by predation and are mostly influenced by bottom-up processes affecting resource availability, such as climate variability and density related effects. However, the true relationships between abiotic and biotic effects and bison spatio-temporal dynamics have never been rigorously quantified or studied.

In the late 20th century through present, bison and Yellowstone have also been symbolic of controversy as the use and management of resources in Yellowstone has been under debate. In particular, the appropriateness of motorized winter recreation (snowmobiles and snowcoaches) in the park has resulted in numerous lawsuits and modifications of winter use planning over the past decade (National Park Service 2000*b*, National Park Service 2004*a*,*b*). Also, controversy has arisen because of bison leaving Yellowstone and grazing on nearby public lands because of the potential of brucellosis transmission to cattle (National Park Service 2000*a*). Grooming of the road system in winter, required to facilitate snowmobile and snowcoach travel, has been implicated in assisting bison travel out of the park and helping the bison population grow unabated (Meagher 1993). However, no study has rigorously addressed this topic to understand the actual relationship between roads and bison travel patterns. Overall, problems of both applied and fundamental nature are of interest regarding Yellowstone bison to managers and the scientific community.

Large herbivores make decisions across a hierarchy of spatial and temporal scales (Senft et al. 1987). At each scale, an assortment of abiotic and biotic effects may influence these decisions and the relative importance of each effect may vary with scale (Senft et al. 1987, Bailey et al. 1996). In this dissertation, I examine three aspects of bison ecology—distribution patterns, movements, and foraging behavior—across multiple spatial and temporal scales to understand the relative influences of density dependent and density independent factors on these processes. My research focuses on the central Yellowstone bison herd, which is the larger of the two herds in the park with the other being the northern herd. Since bison decisions are made across a hierarchy of scales, I have ordered chapters accordingly starting from the largest spatial and temporal scales that I consider (entire ranges and years), and ending with the smallest (foraging patches and minutes).

In Chapter 1, I examine effects of climate variability and population density on the annual seasonal migration of the central herd from its summer range in the Hayden and Pelican Valleys to its winter range in the Madison, Gibbon, and Firehole drainages. Chapters 2 and 3 delve into the temporal and spatial dynamics of bison movements and travel, respectively. In Chapter 2, I compare temporal trends in bison road and off-road travel during winter and early spring, and quantify the influences of snowpack, density, winter recreation, and road grooming affecting the amount of travel. I analyze the spatial component of bison travel patterns using Global Positioning System data from individual bison in Chapter 3 to examine how topography, habitats, and roads affect spatial variability in bison travel throughout the entire year. Chapters 4 and 5 provide a focus on bison foraging behavior in the Madison-Firehole area during winter. I present a novel method for analyzing large herbivore foraging behavior on large scales in Chapter 4 with definition of the foraging area residence time. Then, I evaluate how abiotic and biotic mechanisms acting across multiple scales, and previous foraging experiences, influence residence times for bison. Finally, in Chapter 5, I examine how bison patch scale foraging behavior is affected by snowpack, forage quantity, and competition.

CHAPTER 1:
MECHANISMS AFFECTING MIGRATION OF A LARGE HERBIVORE IN YELLOWSTONE NATIONAL PARK

Abstract

Understanding the mechanisms of density dependent feedbacks and environmental factors on migratory behavior is essential for developing strategies to manage species and conserve this ecological phenomenon. Many bison (*Bison bison*) from the central herd of Yellowstone National Park (YNP) in the western United States are migratory, spending winters in lower elevation, geothermally influenced drainages and summers in higher elevation valleys. Migratory bison that leave YNP boundaries are subject to management actions, including lethal removal. I conducted ground surveys twice monthly (n = 99) during nine winters (1997-2005) to quantify the number of bison occupying the primary winter range. I used multiple regression and information theoretic model comparison techniques to evaluate the relative influence of snowpack, drought, and population density on the timing and extent of migration. The number of bison migrating each winter was related to density and drought severity, while the timing of migration was influenced by snow accumulation on the summer range, drought, and an interaction between drought and density. My results suggest limitations in forage resources provided the major impetus for bison to migrate and support previous reports of positive relationships between snowpack, density, and migration. I also found the bison migration was influenced by the same density dependent and density independent factors

that affected population dynamics of the central herd during the late 20th century. This coupling of extrinsic and intrinsic factors offers insights into mechanisms limiting populations of both migratory and non-migratory ungulates. My research offers novel findings about Yellowstone bison migration patterns, presents direct implications for management, and highlights the importance of long-term data collection for migration research. Quantifying the influences of abiotic and biotic mechanisms on migration over long time periods affords better opportunities to develop effective management strategies, comprehend population processes, evaluate habitat requirements for sensitive species, and preserve migratory phenomenon.

Introduction

On large spatial scales, migration serves to reduce the environmental heterogeneity experienced by an organism and place it under favorable conditions for survival (Dingle 1996). Migratory movements by animals are often predicated on the need for resources, especially food, which may be affected by biotic and abiotic factors (e.g., Whitehead 1996, Knight et al. 1999). A density-related reduction in per capita resources may lead to the establishment of migratory behavior for a species or affect the timing and extent (i.e., number migrating) of migration (Mahoney and Schaefer 2002, Whalen and Watts 2002, Marra et al. 2005). The effects of season and climate on migratory patterns have been documented in various studies (Kaňuščák et al. 2004), including temperature on birds (Gordo et al. 2005) and precipitation on insects (Dingle et al. 2000). These factors, which may modify the availability and quality of suitable habitat and forage, can interact to influence an animal's choice of migratory destinations and the rate of movement during migration (Ahola et al. 2004, Hulbert et al. 2005). Thus, quantifying the effects of density dependent and density independent mechanisms on migratory behavior is essential for comprehending population processes, evaluating habitat requirements, and designing management strategies for migratory species.

Extrinsic and intrinsic processes affect ungulate population dynamics (Sæther 1997, Post and Stenseth 1999, Gaillard et al. 1998). For example, populations of Alpine ibex (*Capra ibex*), red deer (*Cervus elaphus*), moose (*Alces alces*), and white-tailed deer (*Odocoileus virginianus*) were limited by density dependence and climate (Langvatn et al. 1996, Forchhammer et al. 1998, Post and Stenseth 1998, Jacobson et al. 2004). Migrations in response to these same limiting factors have been documented for assorted ungulate populations (Bergerud 1988, Fryxell and Sinclair 1988, Pettorelli et al. 2005). While wildebeest (*Connochaetes taurinus*) migration in response to rainfall (Pennycuick 1975, Maddock 1979) is a classic example, many other large herbivores follow forage productivity gradients and migrate in response to climate variation (Leimgruber et al. 2001, Mysterud et al. 2001). Snow may directly influence an ungulate's choice of habitat during winter in temperate ecosystems. Mule deer (*Odocoileus hemionus*) migration between winter and summer ranges in response to snow has been detailed (Gilbert et al. 1970, D'Eon and Serrouya 2005). Further examples include sika deer (*Cervus nippon*) and elk (*Cervus elaphus*), which have been found to migrate to areas of lesser snowpack in winter (Igota et al. 2004, White and Garrott 2005). Thus, the combined influences of climate variability and density dependence must be evaluated when analyzing migratory movements for large herbivores to further understand their role in population dynamics, which may be affected by the same intrinsic and extrinsic effects. Managers may also need to account for annual variability in these factors, particularly if spatial and population dynamics of an ungulate species are sensitive to climate and density.

In the early 20th century the central Yellowstone bison (*Bison bison*) herd, which consisted of <100 animals after nearly being extirpated, was non-migratory and remained year-round in the Hayden and Pelican Valleys of east-central Yellowstone National Park (YNP), Wyoming, USA (Meagher 1973). In response to increasing density during the 1940s, however, the central herd expanded its range to lower elevation, geothermally influenced areas in west-central YNP (Meagher 1973). Today, seasonal migrations are the norm, with migration into the Madison, Gibbon, and Firehole (MGF) drainages from the higher elevation summer range in the Hayden and Pelican Valleys beginning in autumn and continuing through winter (Bjornlie and Garrott 2001, Bruggeman et al. *in press*) until bison return to the summer range in June after calving. Expansion of bison winter range beyond the MGF has been occurring more prominently since the early 1990s. This growth was particularly notable during the harsh winter of 1996-97 when >1100 bison left YNP in search of more accessible forage and were killed to prevent the possibility of brucellosis transmission to livestock (Baskin 1998, Cheville et al. 1998, National Park Service 2000*a*). Since 2000, YNP and the State of Montana have implemented a management plan for bison that leave YNP boundaries that involves hazing bison back into YNP, testing for brucellosis, and/or lethal removal (National Park

Service 2000*a*), which are controversial actions. The debate over appropriate management activities has continued to intensify since the YNP bison population grew unabated to >5000 animals by 2005 (Gates et al. 2005). Bison movements beyond park boundaries vary annually and are likely dependent upon density and climate stochasticity.

Previous work has documented that the autumn migration is influenced, in part, by snow accumulation on the summer range (Bjornlie and Garrott 2001, Bruggeman et al. *in press*). However, there undoubtedly are other factors driving these movements because some bison migrate before significant snow build-up. Density dependent and density independent effects have been found to affect population dynamics of the central herd (Fuller et al. *in review*). Further, the central herd is only partially migratory with some bison remaining on the summer range year-round. Variability in individual migratory behavior has been found in other ungulates (e.g., Talbot and Talbot 1963, Nelson et al. 2004) and we anticipated a suite of factors would influence bison migration just as they do for population processes. Understanding these effects is of direct importance to Yellowstone bison management.

My goal was to quantify the influence of biotic and abiotic mechanisms on the timing and extent of the central herd's annual migration to the winter range using a nine-year data set (1996-97 to 2004-05) spanning a wide range of climate conditions and population densities. I used an information theoretic approach to evaluate competing hypotheses regarding the relative influence of snowpack, drought, and population size on the timing and extent of migration. This study provides insights to factors affecting ungulate migrations and population processes, and reinforces the role of resource limitation on animal migratory behavior in general. It also offers novel findings about Yellowstone bison migration patterns, presents direct implications for management, and highlights the importance of long-term data collection for migration research.

Study Area

The study area encompassed the portion of the winter range of the central bison herd in the Madison, Gibbon, and Firehole (MGF) drainages in the west-central portion of in Yellowstone National Park (YNP), Wyoming, USA, their summer range in east-central YNP, and a migration corridor connecting these ranges along the Mary Mountain trail and Nez Perce Creek (Figure 1.1; Bjornlie and Garrott 2001, Hess 2002, Bruggeman et al. *in press*). Bison from the central herd increased from 200 to >3000 animals during 1960-2005 (Gates et al. 2005). Bison shared winter range habitat with the non-migratory Madison-Firehole elk (*Cervus elaphus*) herd, which numbered 400-800 during the study (Garrott et al. 2003).

Meadow complexes and geothermal areas provided foraging habitats for bison on both ranges, with major foraging areas often connected by corridors through canyons and/or along streams (Bruggeman et al. *in review, a*). High elevation plateaus and/or mountain ranges constrained bison to lower elevation valley bottoms during winter. There were four major geothermal areas in the MGF—the Upper, Midway, Lower, and Norris Geyser Basins—along with smaller pockets of geothermal activity that had

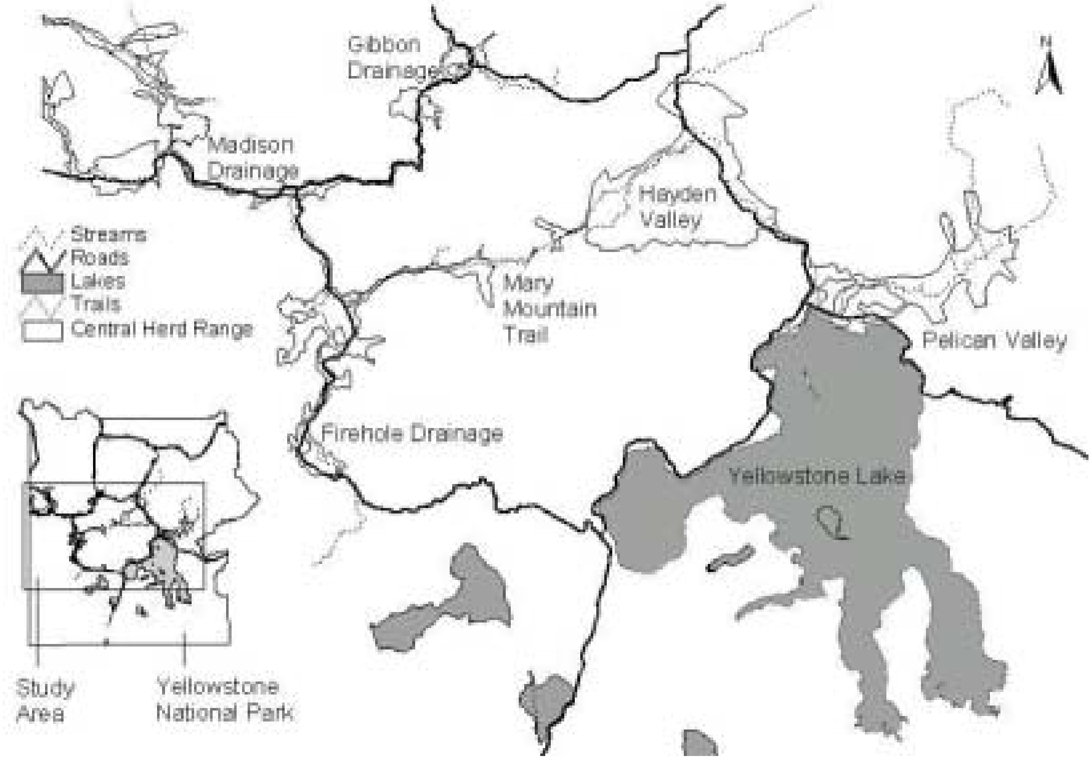


Figure 1.1. The study area in Yellowstone National Park, Wyoming and Montana, USA, in the Madison, Gibbon, and Firehole (MGF) drainages in west central Yellowstone, and the Hayden and Pelican Valleys in east central Yellowstone.

reduced snow accumulation and longer growing seasons compared to surrounding meadows. There were also a number of geothermally influenced areas along Nez Perce Creek, the Mary Mountain trail, and throughout the summer range. Sedges (*Carex* spp.) and grasses (*Calamagrostis* spp.) characterized wet meadows, while dry meadows were dominated by grasses (*Poa* spp., *Festuca idahoensis*) and sagebrush (*Artemesia* spp.). More than 50% of forested areas burned during summer 1988 (Despain 1990) and these areas were characterized by downed trees, snags, regenerating lodgepole pine, Ross' sedge (*Carex rosii*), elk sedge (*Carex geyeri*), and leafy aster (*Aster foliaceus*) during our study. Unburned forested areas were predominantly lodgepole pine (*Pinus contortus*) with understories of elk sedge, grouse whortleberry (*Vaccinium scoparium*), and pinegrass (*Calamagrostis rubescens*). The lowest elevation areas (2000 m) also included scattered Douglas fir (*Pseudotsuga mensiesii*), while Engelmann spruce (*Picea engelmanni*) and subalpine fir (*Abies lasiocarpa*) occurred at higher elevations (2500 m).

The winter range typically experiences severe winters with an annual average of 189 days of snow cover (Natural Resources Conservation Service National Water and Climate Center 2006). Mean annual peak snow water equivalent (SWE) was 30.8 cm at the West Yellowstone Natural Resources Conservation Service (NRCS) Snowpack Telemetry (SNOTEL) site (elevation 2042 m) during 1980-2005 and ranged from 15.0-48.5 cm (28.8 ± 3.4; mean ± SE) during our study (1996-97 to 2004-05). Snowpack began accumulating in late October in the valleys and continued to build until April, at which point ablation occurred. Winters on the summer range were more severe than the winter range with an annual average of 220 days of snow cover and mean annual peak SWE of 35.9 cm at the Canyon SNOTEL site (elevation 2466 m) during 1980-2005 (NRCS National Water and Climate Center 2006). Mean annual peak SWE at Canyon ranged between 24.6 and 60.2 cm (36.4 ± 3.7) during our study. Climate on the summer range was generally warm and dry as from May 1-August 31 mean summer precipitation (MSP) accumulation was 20.9 ± 1.0 cm and the mean maximum daily temperature (T_{max}) was 18.0 ± 0.3ºC at Canyon from 1989-2005. During our study, MSP ranged from 11.9-29.0 cm (20.1 ± 1.6) and T_{max} from 16.6-19.5ºC (18.2 ± 0.3) at Canyon (NRCS National Water and Climate Center 2006).

Methods

Response Variables

The number and distribution of bison wintering in the MGF area were determined by conducting ground surveys every 10-14 days during November-May, 1996-97 through 2004-05. Seventy-four sampling units were surveyed over two days using six distinct routes that afforded a nearly complete enumeration of bison in this area (Ferrari 1999, Bjornlie 2000). However, I was unable to survey winter range areas along the Mary Mountain trail and west park boundary, resulting in a portion of migratory bison being uncounted. Observers using snowmobiles, trucks, or snowshoes started each route simultaneously to minimize missing or double counting bison (Bjornlie and Garrott 2001). Observers recorded the location and age/sex composition of each observed group. I defined two-week time intervals, i ($1 \leq i \leq 14$), from November through May for each winter, j ($1 \leq j \leq 9$), centered on the bimonthly ground surveys that provided a census of migratory bison. To investigate the extent of migration I defined a response variable, ε_j, as the maximum number of bison in the MGF for each winter as enumerated during ground surveys. I also defined a response variable, τ_{ij}, to examine the timing of migration as the number of bison in the MGF for the ij^{th} period as determined from ground surveys.

Climate and Population Covariates

I used daily SWE measurements from the Canyon SNOTEL site (NRCS National Water and Climate Center 2006) to index snowpack on the summer range. I added these daily SWE values from October 1-April 30 to calculate a covariate, SWE_{acc}, and obtain a measure of annual snowpack severity (Garrott et al. 2003) for use in the extent of migration analysis. I also defined a covariate, SWES, as the average summer range SWE for each ij^{th} period between November through May for each year to be used in the timing of migration analysis. I used SWE, rather than snow depth, to characterize snowpack because SWE accounts for the amount of water in the snow and is more biologically relevant to bison (Bruggeman et al. *in press*).

Warm season climate variation—particularly with regard to precipitation, temperature, and the rate of evapotranspiration—influences plant growing conditions, which, in turn, influences the quantity and quality of grasses available as forage for bison (McNaughton 1985, Sala et al. 1988, Stephenson 1990). Rather than use each of these climate variables as separate covariates I used the Palmer Drought Severity Index (PDSI; Palmer 1965) as a single integrator of annual variability of warm season climate. The PDSI, a standard measure of drought severity in the United States (Heim 2002), is based on a water balance model and uses a suite of inputs for its calculation, most significantly precipitation, evapotranspiration, soil moisture, and temperature. Negative values of the PDSI indicate drought while positive values denote a wet period. I obtained monthly PDSI values for the Yellowstone region of Wyoming (region 1) from the National Climate Data Center (National Climate Data Center 2006). I defined a covariate, DROUGHT, as the average of monthly PDSI from May-August for each year to index drought conditions during the growing season before the migration began. My definition of the May-August growing season was based on the fact that the majority of plant growth occurs during the first 750 growing degree days (GDD; Walker et al. 1994; Farnes et al. 1999), a metric that indexes growth beginning at the time of break from dormancy after the snowpack has completely melted. On the summer range in most years, snowpack melted in May and 750 GDD were reached in August. Finally, aerial population estimates for the central herd were obtained each year prior to the migration during late July or August (Dobson and Meagher 1996, Hess 2002; R. Wallen, Yellowstone Center for Resources, unpublished data). I used these annual estimates to define a covariate, BISON, which provided a measure of the effect of bison density on the migration.

Model Development and Statistical Analyses

I developed and compared *a priori* hypotheses, expressed as multiple regression models, in two separate modeling exercises to estimate the relative contributions of snowpack, drought, precipitation, and density on variations in ε and τ. I calculated variance inflation factors (VIFs) while forming the model list to quantify multicollinearity between model predictors, including interactions. Models containing predictors having a VIF>6 were removed from the *a priori* list. Despite a correlation between BISON and DROUGHT ($R^2 = 0.50$, $P = 0.03$, $df = 7$), both predictors met the VIF criterion and were included simultaneously in the models. Hypotheses for the timing and extent analyses were each expressed as 11 regression equations in the form of additive main effects and interactions of covariates (Appendix 1A).

I predicted ε would be positively correlated with BISON because increasing population size would lead to a decrease in per capita resources on the summer range and result in more bison migrating to the MGF winter range to find forage. Second, I hypothesized that ε would be negatively correlated with DROUGHT since severe drought would decrease the quality and quantity of forage and bison would need to migrate to obtain food resources. Third, I predicted increasing SWE_{acc} would result in increased ε because greater snowpack severity on the summer range would provide more impetus for bison to migrate. Fourth, I anticipated the influence of density would vary with snowpack in the form of a $BISON*SWE_{acc}$ interaction effect because high population sizes at high SWE_{acc} would result in increased ε. Finally, I hypothesized that density would interact with drought (BISON*DROUGHT) because the influence of population size would be accentuated during years of severe drought, leading to increased ε.

I used similar rationale for the timing of migration analysis to hypothesize that τ would be positively correlated with BISON and negatively correlated with DROUGHT. I expected the rate of migration to be affected by annual indices of density and drought severity. Second, I predicted that τ would be positively correlated with SWES because increasing snowpack on the summer range would provide an impetus for more bison to migrate to the lower elevation, geothermally influenced winter range with easier access to forage. I anticipated the effect of population size would vary with climate in the form of BISON*SWES and BISON*DROUGHT interactions as I expected combinations of high population sizes and high snow levels, or high population and severe drought, would further increase τ.

I used regression techniques in R version 1.9.0 (R Development Core Team 2004) to fit models and estimate parameter coefficients for each modeling exercise. To allow comparisons of parameter coefficients on a similar scale, each continuous predictor was centered and scaled prior to analysis by subtracting the midpoint and dividing by half of the range resulting in values between –1 and 1. I calculated a corrected Akaike's Information Criterion (AIC_c) value for each model and then ranked and selected the best approximating models for the timing and extent analyses using ΔAIC_c values (Burnham and Anderson 2002). Finally, I calculated Akaike weights (w_k) to obtain a measure of model selection uncertainty and calculated predictor weights ($w_{+(i)}$) to estimate the relative importance of each covariate for each modeling exercise (Burnham and Anderson 2002).

Results

The number of bison observed in the MGF (τ) increased with time each winter, usually peaking in late March or early April (Figure 1.2*a*). During 99 ground distribution surveys, τ ranged from 205-1538 bison (770 ± 32; mean ± SE). The maximum number of bison counted in the MGF for each year (ε) varied between 888-1538 bison (1183 ± 71). The central herd population grew from 1473-3339 bison (2500 ± 231) during 1997-2004 after decreasing during 1996-1997 owing to management based removals at the park

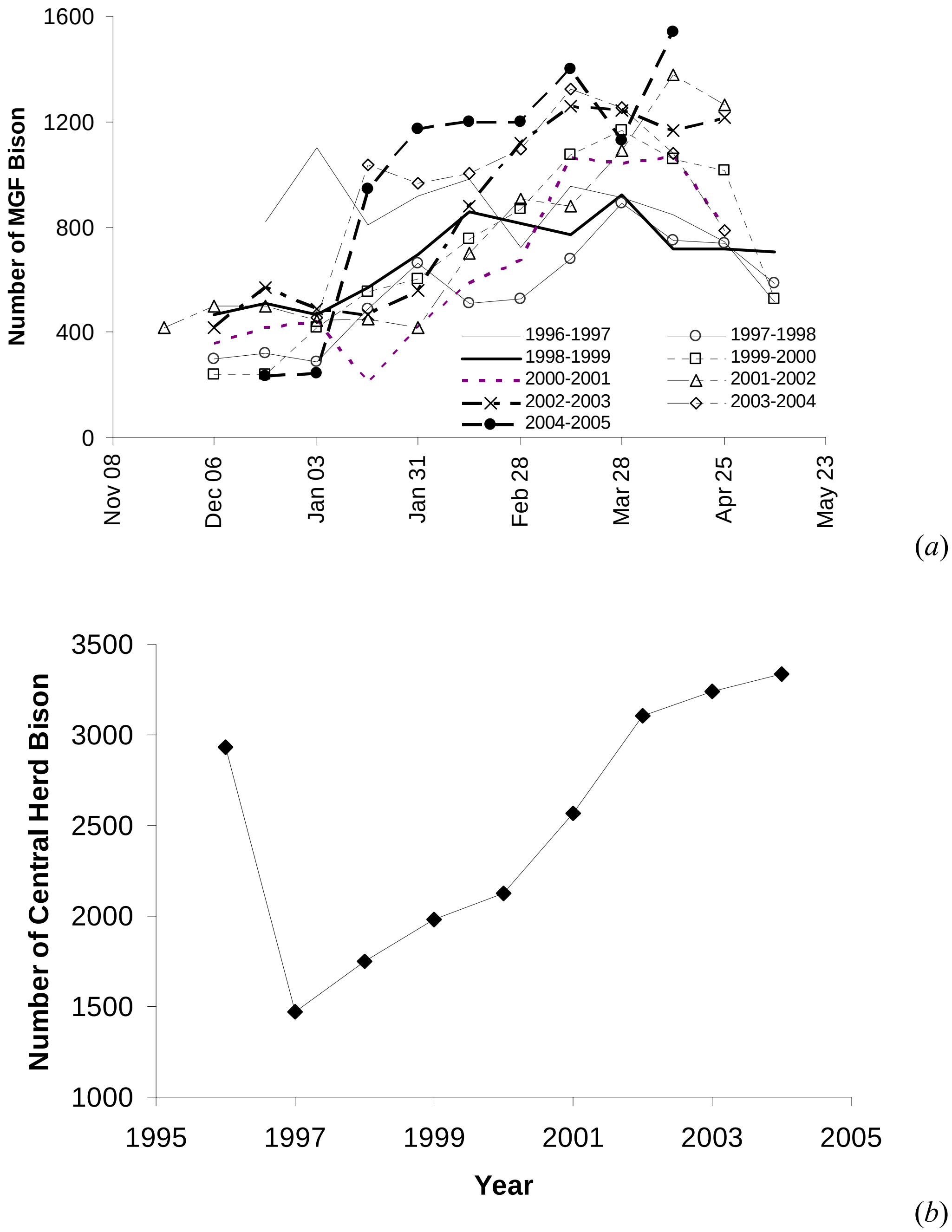


Figure 1.2. Temporal patterns in (*a*) the number of bison counted during ground distribution surveys in the Madison-Gibbon-Firehole area of Yellowstone National Park during winter, 1996-97 to 2004-05, and (*b*) annual central herd bison counts from summer flights, 1996-2004, for Yellowstone National Park.

boundary and mortality from a severe winter (Figure 1.2*b*). On the summer range, snowpack accumulation began in October and built throughout the winter before generally peaking in early April with SWES ranging from 0.1-59.6 cm (21.7 ± 1.2) (Figure 1.3*a*). Temporal trends in snowpack accumulation and ablation were similar on the winter range (Bruggeman et al. *in press*). The covariate SWE_{acc} varied between 2527-7279 cm days (3879 ± 488). The DROUGHT covariate ranged from -8.7 to 1.7 (-4.3 ± 1.2) and followed a generally decreasing trend with time as drought worsened in the Yellowstone region during the study (Figure 1.3*b*).

Two best approximating model structures were supported by the data and had $\Delta AIC_c<2$ in the extent of migration modeling efforts. The top model had $w_k = 0.45$ and a relative likelihood of 1.4 compared to the second best model, which differed by 0.60 AIC_c units (Table 1.1; Appendix 1B). The DROUGHT covariate was significant in both top models, with confidence intervals not spanning zero and the highest predictor weight of 0.87 (Table 1.2). The BISON covariate was contained in the second best model and had the second highest predictor weight of 0.49. As hypothesized, DROUGHT was negatively correlated with ε (Figure 1.4*a*) and BISON was positively correlated with ε, but—contrary to my predictions—neither SWE_{acc} nor interactions were included in the top approximating models.

One top approximating model was supported by the data in the timing of migration modeling exercise, with $w_k = 0.98$ and a relative likelihood of 68.0 compared to the second best model (Table 1.1; Appendix 1B). The covariates SWES, DROUGHT, and the BISON*DROUGHT interaction were significant effects in the top model, with

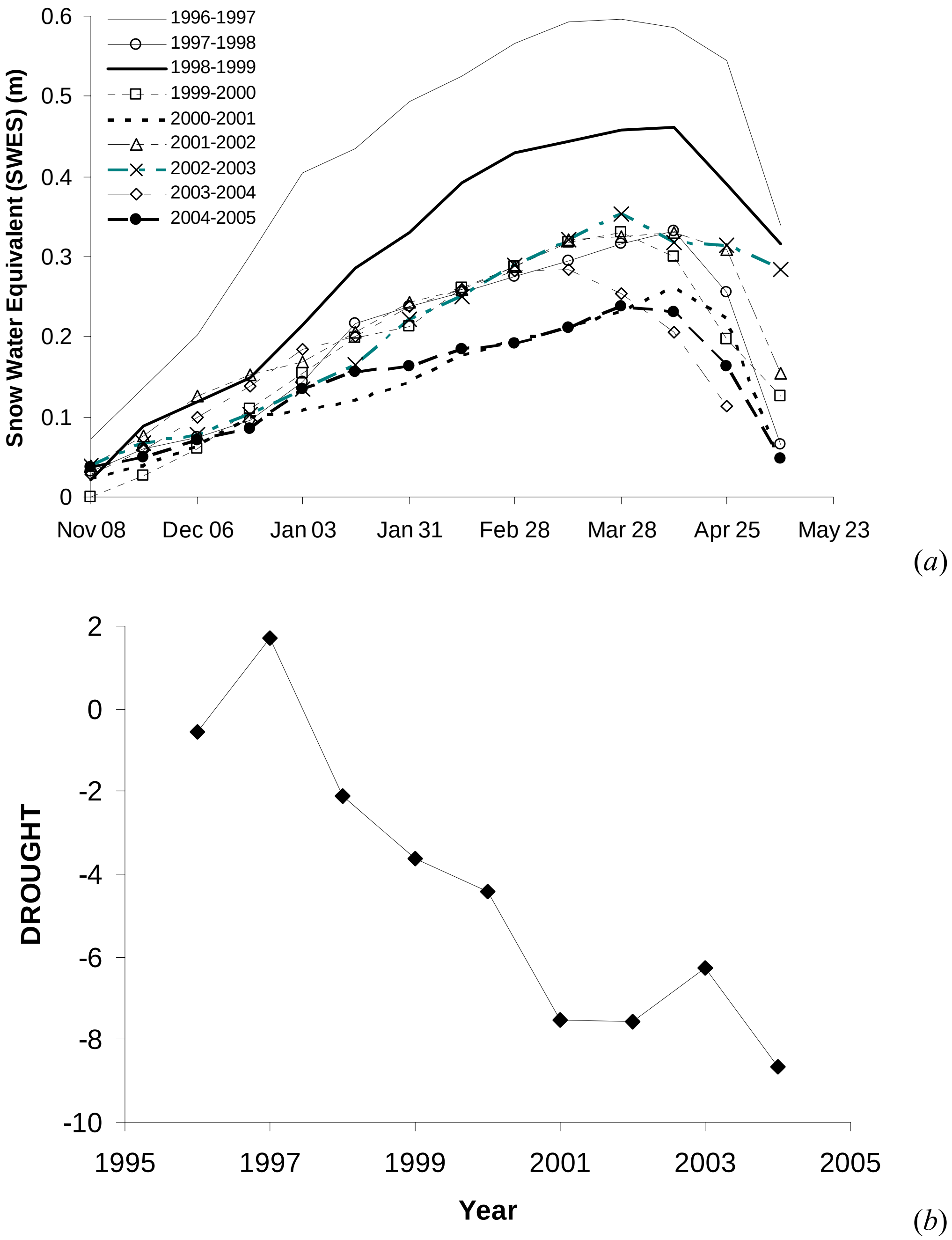


Figure 1.3. Temporal patterns in (*a*) the summer range snow water equivalent covariate (SWES) during winter, 1996-97 to 2004-05, and (*b*) the annual drought covariate (DROUGHT), 1996-2004, for Yellowstone National Park. Snow water equivalent values were measured at a SNOTEL site at Canyon, Wyoming, and averaged over two-week intervals. Values for DROUGHT were obtained from monthly averages of the Palmer Drought Severity Index during the growing season. Note that drought severity increases as values of DROUGHT become more negative.

Table 1.1. Model selection results for *a priori* hypothesized models examining the effects of central herd population size, drought, and annual summer range snowpack severity on the extent of bison migration (ε), and the effects of population size, drought, and summer range snowpack on the timing of bison migration (τ). The best approximating models for each modeling exercise are presented along with the number of parameters (K), the ΔAIC_c value, the Akaike weight (w_k), and R^2 value.

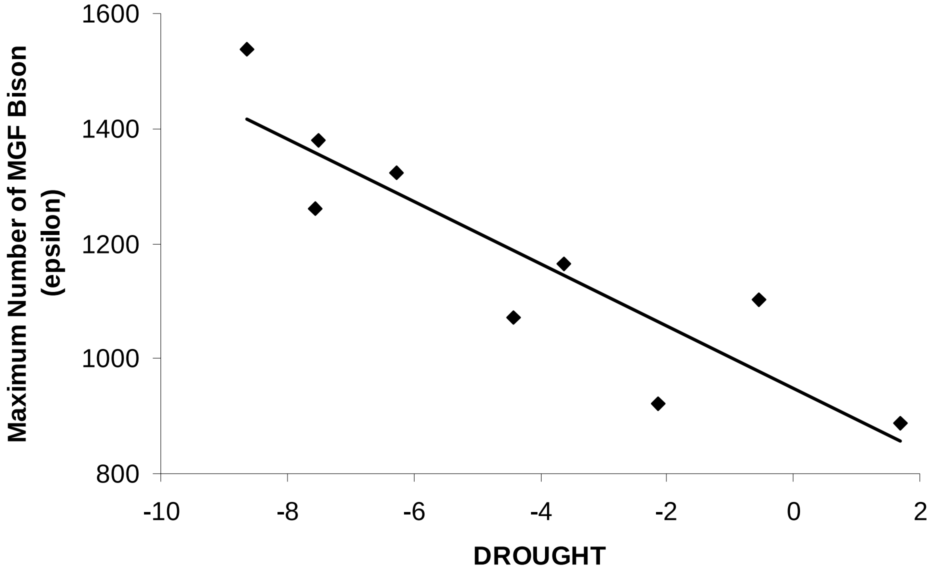
Model	**Structure**	**K**	**ΔAIC_c**	**w_k**	**R^2**
	Extent of Migration—Top Approximating Models				
E3‡	$\beta_0 + \beta_1$(DROUGHT)	2	0.000	0.453	0.79
E6	$\beta_0 + \beta_1$(BISON) + β_2(DROUGHT)	3	0.602	0.335	0.87
E1	$\beta_0 + \beta_1$(BISON)	2	3.718	0.071	0.68
	Timing of Migration—Top Approximating Models				
T11§	$\beta_0 + \beta_1$(BISON) + β_2(SWES) + β_3(DROUGHT) + β_4(BISON)*(SWES) + β_5(BISON)*(DROUGHT)	6	0.000	0.977	0.50
T6	$\beta_0 + \beta_1$(SWES) + β_2(DROUGHT)	3	8.438	0.014	0.42

‡ AIC_c value for model E3 is 115.000

§ AIC_c value for model T11 is 1366.737

Table 1.2. Coefficient values and lower (LCI) and upper (UCI) 95% confidence limits from the best approximating models identified through AIC model comparison techniques for the extent of bison migration modeling exercise. Bold notation denotes significant coefficients at α=0.05. Predictor weights ($w_{+(i)}$) are presented for the overall modeling exercise.

	Model	**E3**	**E5**
Covariate	**$w_{+(i)}$**	**β_i (LCI, UCI)**	**β_i (LCI, UCI)**
Intercept		**1136.63 (1055.06, 1218.20)**	**1139.86 (1069.96, 1209.76)**
DROUGHT‡	0.866	**-279.33 (-402.45, -156.21)**	**-191.46 (-340.37, -42.55)**
BISON§	0.491		113.8 (-22.53, 250.13)
SWE_{acc}	0.130		
BISON*DROUGHT	0.011		
BISON*SWE_{acc}	0.002		



(*a*)

(*b*)

Figure 1.4. Original data demonstrating the relationship between (*a*) the extent of migration (ε) (i.e., maximum number of bison in the Madison-Gibbon-Firehole (MGF)) and DROUGHT, and (*b*) the timing of migration (τ) (i.e., number of bison in the MGF) and summer range snow water equivalent (SWES).

Table 1.3. Coefficient values and lower (LCI) and upper (UCI) 95% confidence limits from the best approximating model identified through AIC model comparison techniques for the timing of bison migration modeling exercise. Bold notation denotes significant coefficients at α=0.05. Predictor weights ($w_{+(i)}$) are presented for the overall modeling exercise.

	Model	**T11**
Covariate	**$w_{+(i)}$**	**β_i (LCI, UCI)**
Intercept		**787.10 (724.62, 849.58)**
SWES	1.000	**504.32 (375.20, 633.44)**
DROUGHT	0.999	**-298.90 (-440.78, -157.02)**
BISON	0.986	12.74 (-93.13, 118.61)
BISON*SWES	0.980	152.54 (-41.95, 347.03)
BISON*DROUGHT	0.977	**-247.31 (-374.70, -119.92)**

confidence intervals not spanning zero and three of the five highest predictor weights (Table 1.3). As predicted, SWES (Figure 1.4*b*) and DROUGHT were positive and negative effects on τ, respectively. While there was no significant BISON main effect as expected, the BISON*DROUGHT interaction was negatively correlated with τ as hypothesized.

Discussion

The migration of central Yellowstone bison is influenced by multiple biotic and abiotic mechanisms. My results suggest that, across large spatial scales, bison migrate in response to variation in forage availability and quality, snow, and density-related feedbacks. While density dependence and drought affected the extent of migration, the timing of migration was influenced by snow build-up on the summer range, drought, and an interaction between drought and density. These factors all share the common attribute of influencing forage and resource availability for bison and, in general, ungulates. Migratory movements—related to tracking optimal resource availability—that are affected by snow, forage quality, or population density have been studied for various ungulates (McNaughton 1985, Garrott et al. 1987, Wilmshurst et al. 1999). Migrations in response to forage limitations are also well documented for insect (Knight et al. 1999), marine (Fiedler et al. 1998), and bird species (Newton and Dale 1996).

Drought had a significant effect on the extent of migration and was negatively correlated with ε—a result owing to how PDSI is defined since it decreases as drought conditions worsen. By itself, drought explained 79% of variability in the data in the top approximating model. Further, drought was influential on the timing of migration, being negatively correlated with τ as both a main effect and interaction. These results indicate that during years of severe drought, both the rate and extent of bison migration are accentuated. Drought can affect both the quantity and quality of forage by reducing plant productivity and diminishing the duration of nutritious forage throughout the growing season (Frank and McNaughton 1992). In addition, drought impacts may last more than one growing season because plants injured during one year of drought can be limited in potential productivity the following year (Frank and McNaughton 1992). My findings suggest these drought-induced limitations in forage resources on the summer range provide an additional stimulus for bison to migrate, a result documented with other species (Polovina et al. 2001, Burtenshaw et al. 2004, Varpe et al. 2005). Further, because bison graze the summer range at high intensity, the relative availability of forage on the winter range likely provides an impetus for migration. In summer, bison presence in the MGF is minimal and elk often choose habitat on high elevation plateaus, resulting in the majority of vegetation in meadows remaining ungrazed and thereby providing a "forage reservoir" (McNaughton 1985) for bison come winter.

The strength of evidence in the data supports the hypothesized role of density dependence on migration by central herd bison. Population size was a significant effect on the timing of migration, appearing in the top model as a negative interaction effect with drought. The extent of migration was also influenced by density as the second best approximating model contained a positive BISON effect. These findings further support the importance of resource limitations on migration since an increasing population leads to a decrease in per capita resources. The coupling of drought and density in a negative interaction effect indicates that more bison migrate during years of high density and severe drought—conditions encountered during the study. During these periods when forage biomass and quality are reduced, per capita resource availability is further constrained as intraspecific competition increases. As a result, more bison migrate to access foraging areas on the winter range and reduce competition. Density-related movement responses have been documented for bison in other regions (Gates and Larter 1990) and other ungulates (Heard and Calef 1986, Reynolds 1998, Mahoney and Schaefer 2002). Also, food limitations during periods of drought are known to affect population dynamics (Sinclair et al. 1985, Mduma et al. 1999), potentially making ungulates more sensitive to these conditions and necessitating long distance movements in search of forage.

Snow accumulation on the summer range had a positive effect on the timing of migration with more bison moving to the lower elevation MGF drainages as winter progressed and snowpack deepened. Ungulate migrations, movements, and habitat use are affected by snow in many ecosystems, often owing to the need for easier access to forage (Sweeney and Sweeney 1984, Sabine et al. 2002, Doerr et al. 2005, Messer et al. *in review*). On small scales, limitations on access to forage by deep or wet snow is the major factor influencing bison foraging behavior in the MGF (Bruggeman et al. *in review, c*) and migration to lower elevations is likely one manifestation of this small-scale preference. Further, bison spend the majority of their time foraging, and displacing snow to access forage is a prominent energetic cost to bison (Bjornlie and Garrott 2001, Bruggeman et al. *in press*). The MGF area also affords easier access to vegetation in winter because of geothermal basins that minimize or reduce snowpack accumulation in areas, providing a refuge for bison from nearby areas of deep snow. Additionally, while forage in these areas may be of poor quality owing to chemical compounds released by geothermal features (Garrott et al. 2002), some of this vegetation does not senesce during winter.

The suite of factors affecting the timing of bison migration offers insights into variability in individual migratory behavior. Early migrants that leave the summer range before snow significantly accumulates may be responding to bison density and reduced forage biomass and early plant senescence owing to drought. Later migrants likely leave in response to deep snow that limits access to forage. However, this variability in timing may also be due to inherent individual behavioral differences that are not captured by climate or population covariates. Behavioral variability in individual migratory behavior, such as variation in the timing of movement or site fidelity to one range (i.e., partial migration in a population), have been documented for a variety of species (Dingle 1996, Whalen and Watts 2002, Hulbert et al. 2005). This intra-population variation may have a strong genetic component (Dingle 1996) and could be related to a combination of demographic tradeoffs associated with migration and annual climate stochasticity (e.g., Nicholson et al. 1997). Animals choose a migration strategy to maximize their survival and reproductive success (Fretwell 1972). While a resident strategy may result in better bison survival and recruitment during mild winters, this same approach can lead to decreased survival in severe winters when the energetic costs of foraging increase and food availability is limited. An early migrant strategy may be most beneficial during years with severe drought, high animal density, or a harsh winter because it would allow bison to access winter range forage with minimal competition before snow significantly accumulated. The accrual of fat reserves during summer and fall is essential for ungulate survival and reproductive success in severe winter climates (Frank 1998). A late migrant strategy likely represents a tradeoff between a resident and early migrant approach and may lead to increased survival during mild winters or when summer growing conditions are favorable. Overall, animals that adopt an adaptive strategy in response to annual climate and population variability will likely have the highest lifetime reproductive success.

My results indicate that bison migration is influenced by the same density dependent and density independent factors that affected population dynamics of the central Yellowstone herd. Fuller et al. (*in review*) concluded that drought and annual snowpack severity on the summer range, in addition to density dependent limitations, affected bison population growth in the late 20th century. In other research, density and climate has affected temporal variation in ungulate survival and recruitment (e.g., Clutton-Brock et al. 1985, Post and Stenseth 1998, Coulson et al. 2000). This coupling of density dependent and density independent factors offers insights into mechanisms limiting populations of both migratory and non-migratory ungulates.

My results have direct relevance to issues confronting managers regarding bison control actions and removals. I found: 1) density effects on migration (and subsequent movements beyond YNP boundaries) will be exacerbated during droughts; 2) substantial migration (and movements beyond YNP boundaries) could occur during severe droughts even at relatively low bison densities, 3) drought and/or a severe winter could result in earlier migration to a constrained winter range with limited resources and earlier or greater movements beyond YNP boundaries. Given this information, an adaptive management approach could be implemented in planning for removals by considering annual variability in population and climate conditions, and adjusting removals accordingly. An annual population estimate obtained in the fall could be used to anticipate the number of bison migrating and provide a relative index of expected bison leaving the park each winter. This estimate could also be used to determine the appropriate number of removals for each winter. Managers could then account for potential additional climate effects on these movements to adjust their planning of devoting personnel and resources to control actions. For example, in years of high density, drought, and/or a harsh winter, control actions may need to begin much earlier in the winter than in a year of lower density, no drought, and a mild winter.

The relevance of my findings is not limited solely to large herbivore migration and population dynamics. Climate and density has been found to influence insect populations and migrations between ephemeral habitats that offer unpredictable resources throughout space and time (Woiwod and Hanski 1992, Dingle et al. 2000). The timing of long-distance bird migrations is often correlated with forage productivity and climate conditions (Kaňuščák et al. 2004, Saino et al. 2004), and bird populations can be limited by intrinsic and extrinsic factors (Greenwood and Ballie 1991). Further, density (Carlson and Baremore 2003) and variation in spatio-temporal alterations in prey quality and density as well as intraspecific competition (Hulbert et al. 2005) affects shark population dynamics and migration patterns. Management of endangered, sensitive, overabundant, and economically important migratory species can be improved by evaluating potential coupling of intrinsic and extrinsic factors on population processes (e.g, Yako et al. 2002).

This research illustrates that long-term studies are necessary for evaluating mechanisms affecting migration. The interacting influences of annual variation in climate, as well as long-term population and climate trends, on migratory behavior cannot be accurately quantified without continuous data collection spanning a variety of conditions. The value of such long-term work is present in research on migratory behavior of animals such as Serengeti wildebeest (Sinclair 1975, McNaughton 1985), Nearctic-Neotropical birds (Marra et al. 2005), Pied Flycatchers (*Ficedula hypoleuca*; Both and Visser 2001, Ahola et al. 2004), and blue whales (*Balaenoptera musculus*; Burtenshaw et al. 2004). Understanding the influences of abiotic and biotic mechanisms on migration across long time periods will afford opportunities to better develop effective management strategies, comprehend population processes, evaluate habitat requirements for sensitive species, and preserve migratory phenomenon.

CHAPTER 2:
MECHANISMS AFFECTING SPATIAL VARIABILITY IN LARGE HERBIVORE TRAVEL BEHAVIOR IN YELLOWSTONE NATIONAL PARK

Abstract

Understanding mechanisms influencing the movement paths of animals is essential for comprehending behavior and accurately predicting use of travel corridors. In Yellowstone National Park, the effects of roads and winter road grooming on bison (*Bison bison*) travel routes and spatial dynamics have been debated for more than a decade. However, no rigorous studies have been conducted on bison spatial movement patterns. I collected 121380 locations from 14 female bison with GPS collars in central Yellowstone to examine how topography, habitat, roads, and elevation affected the probability of bison travel and selection of travel corridors. I also conducted daily winter bison road use surveys during 2003-2005 to quantify how topography and habitat influenced spatial variability in the amount of bison road travel. Using model comparison techniques, I found that the probability of bison travel and spatial distribution of travel corridors were affected by multiple topographic and habitat attributes including slope, landscape roughness, habitat, and distances to streams, foraging areas, and forested habitats. Streams were the most influential landscape feature affecting bison travel and corridor use, and my results suggest that the bison travel network throughout central Yellowstone is spatially defined largely by the presence of streams that connect foraging areas. Also, the probability of bison travel and corridor use was higher in regions of

variable topography that constrain movements, such as in canyons. Pronounced travel corridors existed both in close association with roads and distant from any roads, and results indicate that roads may facilitate bison travel in certain areas. However, my findings suggest that many road segments used as travel corridors serve as natural travel pathways since road segments receiving high amounts of bison travel had similar landscape features as natural travel corridors. Landscape attributes were ineffective at predicting some known high use corridors, suggesting that bison develop some travel routes using learned experiences from exploratory movements. I suggest that most spatial patterns in bison road travel are a manifestation of general spatial travel trends. My research offers novel insights into bison spatial dynamics and provides conceptual and analytical frameworks for examining movement patterns of other species.

Introduction

Patterns in animal travel are a critical aspect of ecology affecting population level processes. Migration, dispersal, and small-scale redistribution—movements often predicated upon the need for resources—all influence population dynamics through either direct or indirect causes (Taylor and Taylor 1977, Dobson and Jones 1985, Fryxell and Sinclair 1988, Dingle 1996, Turchin 1998). It is important to understand how an animal arrived at a given location to relate resource selection to population processes in a spatially heterogeneous environment. Predators, climate, and anthropogenic influences affect survival and can influence an animal's choice of habitat use and travel routes (Baur and Baur 1990, Fraser et al. 1995, Poole et al. 2000, Mahoney and Virgl 2003, Ferguson and Elkie 2004, Cimprich et al. 2005). Additionally, topography and habitat characteristics have been shown to affect the movements of insects (Turchin 1991), birds (Williams et al. 2001), fish (Meyer and Holland 2005), and mammals (Nams and Bourgeois 2004). Topographic constraints, elevation gradients, and habitat heterogeneity may guide animals to travel along paths of least resistance that form natural travel corridors. Repeated use of these routes, forming a travel network in the process, has been documented for both migratory and small-scale movements (Haddad 1999, Cronin 2003, Deutsch et al. 2003, Petrie and Wilcox 2003, Flamm et al. 2005). Overall, understanding mechanisms influencing the movement paths of animals is essential for comprehending behavior and accurately predicting use of travel corridors.

Human impacts on wildlife travel routes range from facilitation of movement for some species through the development of recreational trails (Buskirk et al. 2000) to hindrance by habitat degradation and fragmentation (Bruns 1977, Hilty and Merenlender 2004). Roads are particularly controversial because some species use them as major pathways while others avoid them owing to traffic or human presence (Banfield 1974, Brody and Pelton 1989, Dyer et al. 2002, Brock and Kelt 2004, Whittington et al. 2005). Interactions between wildlife, roads, and outdoor recreation are high profile issues, as the negative aspects on animals—such as habitat degradation, disturbance, stress, and lowered survival—become the focus (Trombulak and Frissell 2000, Taylor and Knight 2003). The impact of winter recreation on large mammals (Dorrance et al. 1975, Freddy et al. 1986, Goodrich and Berger 1994, Borkowski et al. *in press*) is particularly debatable owing to added physiological stresses of deep snow, restricted forage, and cold temperatures (Moen 1976, Anderson 1995, Gabrielsen and Smith 1995).

The influence of winter recreation on bison (*Bison bison*) in Yellowstone National Park (YNP) has been a subject of intense debate since park staff began grooming (i.e., packing) snow on interior park roads in 1971 to facilitate the safe passage of visitors on over-snow vehicles (OSV) such as snowmobiles and coaches. Over the decades that followed, motorized winter recreation increased substantially from 2000 to >100000 riders per winter during the mid-1990s (Gates et al. 2005) and, concurrently, counts of central Yellowstone bison increased from <500 to >3000 animals (National Park Service 2000*a*). As the population grew, bison expanded their range into the Madison, Gibbon, and Firehole (MGF) drainages and beyond YNP boundaries. Meagher (1993) attributed this expansion to groomed roads providing routes of energy-efficient travel for bison as an alternative to traveling through deep snow. The purported energy savings, which allowed bison to better survive winters and produce healthy calves in the spring, resulted in an unnatural population increase and alteration of bison spatial dynamics (Meagher 1993).

Conversely, Bjornlie and Garrott (2001) and Bruggeman et al. (*in press*) suggested that groomed roads in the MGF were not the cause of the likely density-dependent range expansion by YNP bison (Fuller et al. *in review*). They found no evidence that bison preferentially used groomed roads in winter and that bison road travel actually decreased during the road grooming period. These authors suggested temporal patterns in bison road travel were probably a manifestation of general travel behavior and any energy savings resulting from groomed road use were likely small since bison spent only 11% of their time traveling and developed an off-road trail network to minimize energy expenditures while traveling in winter (Bruggeman et al. *in press*).

This debate culminated in a series of court cases challenging the park's management of winter recreation (National Park Service 2000*b*, United States District Court for the District of Columbia 2003, National Park Service 2004*b*). These cases resulted in conflicting legal decisions from different courts—primarily owing to a lack of rigorous empirical studies to evaluate the merits of opposing claims. Previous attempts to address the effects of road grooming on travel by bison have been criticized for making strong inferences in the absence of rigorous experimental designs (e.g., controls, replicates). Such studies are problematic in YNP because shutting down sections of roads in winter reduces public access to enjoy the park and affects contracts with concessionaires and economic concerns by gateway communities. Also, potential annual variability in external abiotic and biotic factors, including winter severity and population size, may confound any grooming effect. No data were collected on bison distribution and travel before road grooming began and, therefore, no true experimental control case of bison road travel exists before bison gained knowledge of foraging areas in the MGF. As a result, it is impossible to conclusively determine through retrospective analyses why the use of groomed roads by bison began or if groomed roads facilitated range expansion.

Given these constraints, I explored an alternate approach to quantify the influence of landscape and habitat attributes on bison spatial use of travel routes in central YNP and to gain insight into how roads may currently affect bison travel. I evaluated competing hypotheses using an information theoretic approach in two modeling exercises to quantify the relative contributions of topography and habitat in influencing the odds of bison travel and bison selection of travel corridors. I used each of the top approximating models to predict the probability of bison travel and identify possible high use travel corridors throughout central YNP. In exploratory analyses, I examined potential effects of roads and elevation on bison travel corridors. I also quantified how topography and habitat affect spatial variability in the amount of bison road travel in the MGF. Finally, I developed maps to display both predicted and actual bison travel patterns to enhance my understanding of bison spatial ecology in YNP. My study offers novel insights into bison spatial dynamics in central Yellowstone and provides conceptual and analytical frameworks for examining movement patterns of other species.

Study Area

The study area in Yellowstone National Park (YNP), Wyoming, USA, encompassed the winter range of the central Yellowstone bison herd in the Madison, Gibbon, and Firehole (MGF) drainages in west-central YNP (Figure 2.1*a*) and their summer range in the Hayden and Pelican Valleys in east-central YNP (Figure 2.1*b*) as delineated by Hess (2002). Elevations varied between 2000-2500 m. Bison from the central herd, which increased from 200 to >3000 animals during 1960-2005 (Gates et al. 2005), began migrating to the MGF in late October along the Mary Mountain trail and

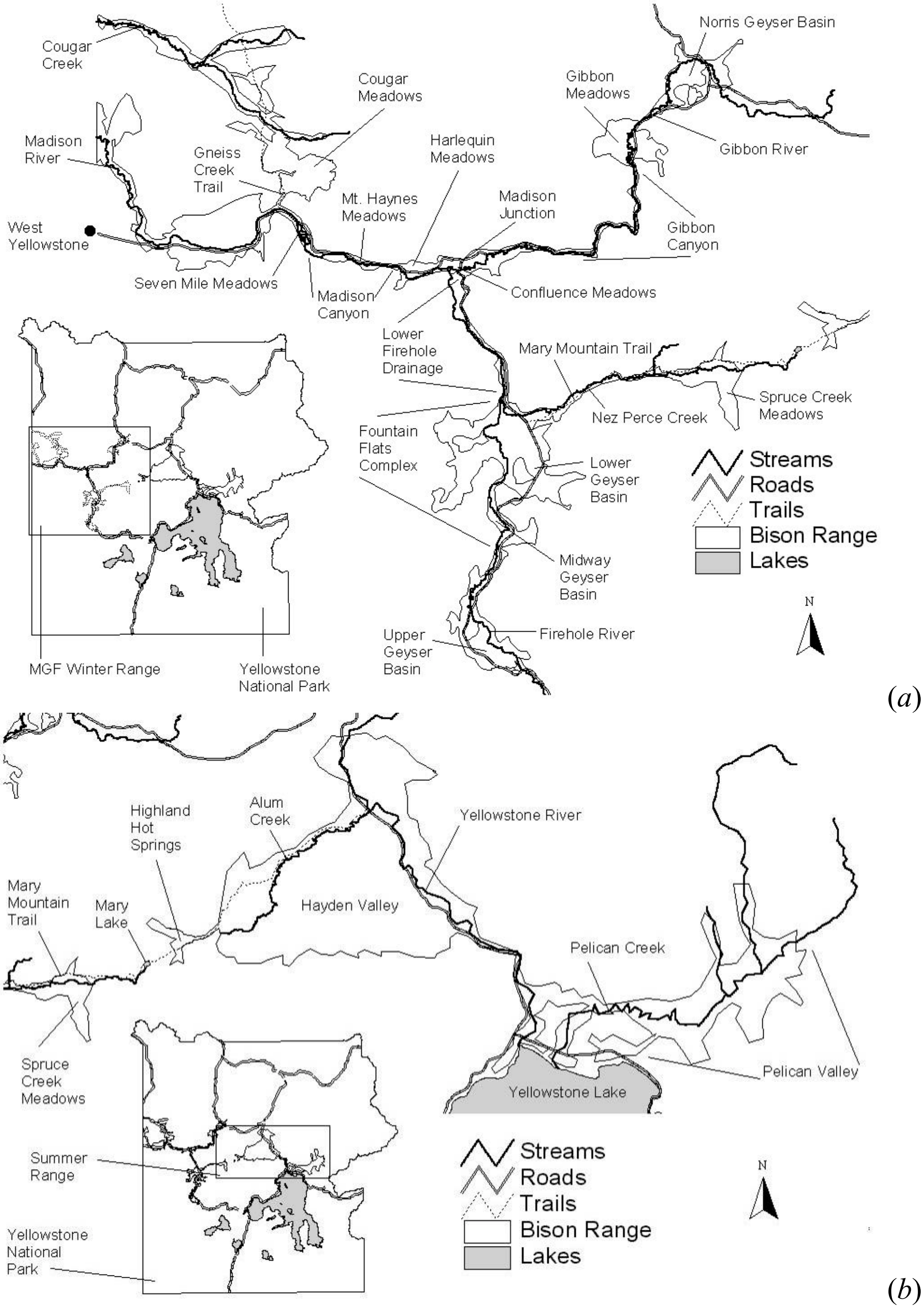


Figure 2.1. The study area in Yellowstone National Park, Wyoming and Montana in (*a*) the Madison, Gibbon, and Firehole (MGF) drainages in west central Yellowstone, and (*b*) the Hayden and Pelican Valleys in east central Yellowstone.

returned to the summer range in June (Bruggeman et al. *in press*). Meadow complexes and geothermal areas provided foraging habitats for bison on both ranges with major foraging areas often connected by corridors either through canyons and/or along streams (Figure 2.1). There were four major geothermal areas in the MGF—the Upper, Midway, Lower, and Norris Geyser Basins—along with smaller pockets of geothermal activity (Watson et al. 2002) that had reduced snow accumulation and longer growing seasons compared to surrounding meadows. There were also a number of geothermally influenced areas along Nez Perce Creek and the Mary Mountain trail, as well as throughout the summer range.

Sedges (*Carex* spp.) and grasses (e.g., *Calamagrostis* spp.) characterized wet meadows while dry meadows were dominated by grasses (*Poa* spp., *Festuca idahoensis*) and sagebrush (*Artemesia* spp.) in lower elevations. During the summer of 1988, >50% of forested areas burned (Despain 1990) and these areas were characterized by downed trees, snags, regenerating lodgepole pine, Ross' sedge (*Carex rosii*), elk sedge (*Carex geyeri*), and leafy aster (*Aster foliaceus*) during my study. Unburned forested areas were predominantly lodgepole pine (*Pinus contortus*) with understories consisting of elk sedge, grouse whortleberry (*Vaccinium scoparium*), and pinegrass (*Calamagrostis rubescens*). Lower elevations consisted of scattered Douglas fir (*Pseudotsuga mensiesii*) and lodgepole pine while Engelmann spruce (*Picea engelmanni*) and subalpine fir (*Abies lasiocarpa*) were found at higher elevations.

A network of paved, two-lane roads paralleled the Madison, Gibbon, Firehole, and Yellowstone Rivers through the study area (Figure 2.1) as described in Bruggeman et al. (*in press*). Roads were open to visitor travel in wheeled vehicles from mid-April until early November, at which point they were closed to visitors to allow snow accumulation for the motorized winter recreation season. Roads were groomed daily for snowmobile and snowcoach travel by visitors during mid-December until early March, at which point the roads were plowed and then opened in late April for the summer visitation season.

The MGF area typically experiences severe winters with an annual average of 189 days of snow cover (Natural Resources Conservation Service National Water and Climate Center Public Communication 2005). Mean annual peak snow water equivalent (SWE) was 34.1 cm at the West Yellowstone Natural Resources Conservation Service (NRCS) Snowpack Telemetry (SNOTEL) site (elevation 2042 m) during 1966-2005. During my study, annual peak SWE at the West Yellowstone SNOTEL site ranged from 21.1-30.7 cm. Winters in the Hayden Valley are more severe with an annual average of 220 days of snow cover (NRCS National Water and Climate Center Public Communication 2005) and mean annual peak SWE of 35.9 cm at the Canyon SNOTEL site (elevation 2466 m) during 1980-2005. Annual peak SWE at Canyon ranged from 24.6-36.3 cm during my study. Snowpack began accumulating in late October in the valleys and continued to build until April, at which point ablation occurred.

Methods

Data Collection

Fifteen GPS/VHF collars (Model TGW 3700, Telonics, Mesa, Arizona) were deployed on adult female bison beginning in November 2003. Collars were distributed on bison in the Hayden and Pelican Valleys and on early migrants to the MGF winter range using ground darting with Carfentanil. During winter, locations were recorded every 30 minutes from 0700 to 1900 with fixes also taken at 2300 and 0300. From mid-March through October, locations were recorded every 30 minutes from 0600 to 2300 with fixes also at 0100 and 0300. On occasion, fixes were missed owing to poor satellite reception.

Bison spatial use of roads in the MGF was recorded using daily bison road use surveys from November-April during three seasons (2002-03 through 2004-05) by four observers traveling independently using snowmobiles or trucks (Bruggeman et al. *in press*). The main 72.6 km road network in the MGF was divided into 52 segments based upon topographical similarities and common travel destinations. Observers mapped all bison groups encountered traveling on the road for at least 50 m and recorded survey effort per segment (km road traveled) while only collecting data from a single traverse of each road segment during a 30 minute period.

Model Development and Statistical Analysis Using GPS Data

I conducted two modeling exercises using GPS data to examine different aspects of bison travel. The first was designed to investigate spatial patterns in the probability of general bison travel (i.e., movements of all distances) while the second examined only long distance movements indicative of corridor travel. To obtain the most powerful predictive capabilities from my models, I censored the GPS data through a series of steps designed to retain important traveling vectors while minimizing vectors associated with foraging and resting activities. First, I removed all consecutive locations that were obtained more than 32 minutes apart to procure the most accurate travel paths possible consisting of at least one segment, defined as two consecutive points. Second, I calculated Euclidean distances (d) between consecutive points and turning angles (α; $0° \leq \alpha \leq 180°$) between segments, enabling me to define threshold values of ≥ 800 m and $\leq 90°$, respectively, to indicate a significant movement (Appendix 2A). All consecutive segments with $d < 800$ m and $\alpha > 90°$ were removed from the data set. My criterion of 800 m was determined from a plot of d against α as locations with $d < 800$ m exhibited nearly uniform scatter for all α. A positive correlation between d and α, anticipated for a significant movement, was present for $d \geq 800$ m (Appendix 2A). Based on field observations I also rationalized that bison moving at least 800 m in 30 min would spend the majority of time sustaining travel rather than foraging. My second criterion of 90° was chosen based on field observations of foraging and traveling bison. I decided that bison engaged in sustained travel (i.e., significant movement) would have a forward directional component (i.e., $\alpha < 90°$), similar to that with a correlated random walk (Turchin 1998), and that any movement with $\alpha < 90°$ would be more representative of a foraging or searching trajectory since it involves abrupt turns. After censoring, I identified each remaining individual travel vector, consisting of one or more significant movements, along with total vector distance and number of segments (i.e., significant movements) per vector. These vectors were used for the general bison travel analysis. For the corridor travel analysis I considered the subset of identified travel vectors with a length ≥3200 m, since longer distance movements by bison would be indicative of sustained travel in corridors and potentially important travel corridors that connected foraging areas were at least 3 km long.

I mapped each vector into a Geographic Information System (GIS) layer, created nodes at 400 m intervals along each vector, and systematically sampled for covariates at each node. Additionally, I created random movement data by taking each original vector and assigning 20 random relocations and orientations of the vector within my available traveling universe, YNP, with every random vector restricted to be contained entirely within the park boundary. Each random vector was then sampled for covariates at nodes separated by 400 m intervals. Nodes were assigned coded binary response variables and analyzed as use (1) versus availability (0) data using logistic regression techniques (Manly et al. 2002).

Landscape Covariates. I calculated ten covariates to characterize topography and habitat attributes for each node location using GIS data layers (Table 2.1). A United States Geological Survey Digital Elevation Model was used to calculate topography covariates while habitat covariates were determined using vegetation cover type and geothermal data layers developed by The Watershed Institute, California State University Monterey Bay. Topography covariates were calculated based upon averages of pixel values within a circle of 200 m radius from the node location as I assumed bison would choose travel paths based on topography at a scale larger than one 28.5 m x 28.5 m pixel. Average slope (SL), slope heterogeneity (SLHG), and average slope tangent (TAN) provided measures of landscape roughness. Habitat covariates were calculated based upon the habitat at the node point location. I classified each location into one of five habitat (HBT) categories as meadow (MD), burned forest (BF), unburned forest (UF), geothermal (TH), or other (OT; i.e., talus or aquatic). Additionally, I calculated the nearest distances to stream (DST), burned forest (DBF), unburned forest (DUF), and foraging area (PROX) from the point location with foraging areas defined as meadows of at least 25 ha. Streams were defined from the National Hydrographic Dataset (NHD) including streams of NHD Levels 3, 4, or 5 and excluding streams of NHD Level 6 or smaller. Finally, for each point location I determined the elevation (ELEV) and calculated the nearest distance to road (DRD) for use in an exploratory modeling exercise.

Model Development. I developed and compared *a priori* hypotheses, expressed as multiple logistic regression models, to estimate the relative contributions of topography and habitat attributes in influencing the odds of bison travel and selection of travel corridors. While forming my model list, I calculated variance inflation factors (VIFs) to quantify multicollinearity between model predictors, including interactions. I

Table 2.1. Topography and habitat covariates used in modeling exercises.

Covariate	Definition
SL	Average slope: calculated by averaging the slope of all pixels within a circle of 200 m radius about the point location.
SLHG	Slope heterogeneity: the standard deviation of average slope for all pixels within a circle of 200 m radius about the point location. Related to landscape roughness.
TAN	Average tangent of slope: the average tangent of the slope about the point location within a circle of 200 m radius. Calculated by taking the average of the tangent of eight slopes (in cardinal and sub-cardinal directions) between the point location and the edge of the 200 m circle. Related to vertical relief and landscape roughness.
HBT	Categorical habitat: meadow (MD), geothermal (TH), burned forest (BF), unburned forest (UF), or other (OT) classification assigned to the point location.
DST	Distance to stream: the nearest Euclidean distance to a stream from the point location.
DBF	Distance to burned forest: the nearest Euclidean distance to burned forest habitat from the point location.
DUF	Distance to unburned forest: the nearest Euclidean distance to an unburned forest habitat from the point location.
DRD	Distance to road: the nearest Euclidean distance to a road from the point location.
PROX	Proximity to foraging area: the Euclidean distance to the nearest defined foraging area (≥25 ha) from the point location.
ELEV	Elevation: the elevation of the point location.

removed models containing predictors having a VIF>6 from my *a priori* list. As a result of multicollinearity, I was unable to include covariate interactions in any of my *a priori* models. Hypotheses for each modeling exercise were expressed as 255 candidate models (Appendix 2B).

I formulated an *a priori* hypothesis for each covariate regarding the direction of its effect on the log odds response. First, I hypothesized that the odds of bison travel would be negatively correlated with SL because bison often avoid traveling on steep slopes. Second, I predicted that SLHG and TAN would positively affect the odds of travel since areas of variable topography would be more likely to influence bison choice of travel routes and restrict travel to a corridor. Third, I hypothesized that the odds of travel would be positively correlated with MD and TH habitats as my field observations indicated that bison establish travel networks through these habitats. Similarly, I expected that the odds of travel would be negatively correlated with BF, UF, and OT habitats since bison often avoid traveling in burned areas containing downed trees, heavily forested regions lacking suitable forage, and rocky talus areas. Fourth, I predicted that DST, DBF, and DUF would be negative effects on the odds of travel since bison would develop travel networks along stream corridors and near the edges of burned and unburned forest habitats. Fifth, I hypothesized that PROX would negatively affect the odds of travel because bison travel routes would be less likely farther from foraging areas. For my exploratory modeling exercise, I predicted that DRD would be negatively correlated with the odds of travel since bison are known to use some road corridors as travel routes. However, I hypothesized that DST would be a better predictor of the odds of travel than DRD. I also expected the odds of travel to be negatively correlated with ELEV because higher elevation areas receive more snowfall in winter and are farther from major waterways.

Model Calibration. I used a generalized estimating equation (GEE) approach (Liang and Zeger 1986, Hardin and Hilbe 2003) to examine bison travel and selection of travel corridors. Generalized estimating equations are an extension of generalized linear models used to analyze correlated data and provide efficient coefficient estimates, robust standard error estimates, and account for covariate covariance structure. Generalized estimating equations applied because my locations were independent among bison, but possibly correlated for each animal. One benefit of this method is that it allows use of all locations and finer scale sampling as opposed to sampling points at wider, uncorrelated intervals and losing information and predictive capability in the process.

For each analysis, I fit models and estimated parameter coefficients using logistic regression GEEs with PROC GENMOD in SAS version 9.1 (Allison 1999, Hosmer and Lemeshow 2000, SAS Institute Inc. 2003). All continuous covariates were centered and scaled prior to analysis by subtracting the midpoint and dividing by half of the range resulting in values between –1 and 1. Model fitting (i.e., calibration) was completed using 75% of the original and random vector data. The remaining data was saved for use in model validation per a data partitioning heuristic given by Fielding and Bell (1997). For each model, I calculated the quasilikelihood under the independence model information criterion value (QIC; Pan 2001), which is applicable for GEEs and based upon Akaike's Information Criterion (AIC). I then ranked and selected the best approximating models for each analysis using ΔQIC values (Burnham and Anderson 2002). I calculated Akaike weights (w_k) to obtain a measure of model selection uncertainty and predictor weights ($w_{+(i)}$) to estimate the relative importance of each covariate (Burnham and Anderson 2002). I used the top approximating models from each exercise to develop probability maps of bison travel in YNP by evaluating each covariate at a pixel scale using GIS layers.

Model Validation. I evaluated the predictive capability of the top approximating model from each analysis using independent data that consisted of the 25% of the original and random vector data not used to develop the model. Using the Receiver Operating Characteristic (ROC) technique, I generated a ROC curve by plotting model sensitivity vs. the false positive fraction for cutpoint values between zero and one (Fielding and Bell 1997, Hosmer and Lemeshow 2000, Pearce and Ferrier 2000). I then calculated the area under the ROC curve (AUC) to assess the predictive capability of each model (Hosmer and Lemeshow 2000).

Exploratory Analyses. I conducted two exploratory analyses using the ten most highly supported models from my *a priori* bison corridor travel modeling efforts. First, I added DRD and removed DST from each model to evaluate if the distance to road covariate provided a better predicting model for the odds of bison corridor travel than distance to stream. Second, I added ELEV and DRD to each of the top ten *a priori* models to see if these covariates resulted in an improved best approximating model. I then used the top model from this second exploratory analysis to develop a probability map of bison travel throughout YNP.

Model Development and Statistical Analysis Using Bison Road Use Survey Data

I used data from my bison road use surveys to define a response variable, η_{ij}, that quantified the amount of bison travel in each of the 52 defined road segments (*i*) for each of the three years (*j*). I calculated η_{ij}, with units of bison groups observed per segment/100 km surveyed per segment, as the total number of bison groups observed traveling in the i^{th} segment divided by the survey effort for the i^{th} segment (total km traveled by observers in the segment). I used a GIS road layer to define nodes at 400 m intervals along the 72.3 km primary road network in the MGF and assigned a segment code to each node corresponding to my 52 defined road segments. I calculated the following covariates at each node: SL, SLHG, TAN, DBF, DUF, DST, and PROX, with covariates defined above. For each of the 52 segments, I averaged the node values of each covariate across the segment to obtain one value of each covariate per segment. I did not assign a HBT code to each segment because of difficulty in defining an "average" habitat surrounding the road that would be meaningful in the final analysis. Finally, I used indicator variables to define a covariate for the year (YEAR).

I developed and compared *a priori* hypotheses, expressed as multiple regression models, to estimate the effects of topography and habitat on η_{ij}. While forming my model list, I calculated VIFs and removed models containing predictors having a VIF>6 from my *a priori* list. I was unable to include covariate interactions in any of my *a priori* models due to multicollinearity. Hypotheses were expressed as 190 candidate models (Appendix 2B) in the form of regression equations consisting of covariate main effects. I developed an *a priori* hypothesis about the effect of each covariate on η_{ij}. Using the same rationale as with my hypotheses for the GPS data analysis, I predicted that SLHG and TAN would be positively correlated with η_{ij} and that SL, DST, DBF, DUF, and PROX would be negatively correlated with η_{ij}. Also, I anticipated YEAR to be a positive effect on η_{ij} since the bison population increased during the study and the number of bison in the MGF has been documented to be positively correlated with the amount of bison road travel (Bruggeman et al. *in press*).

I fit models and estimated parameter coefficients using R version 1.9.0 (R Development Core Team 2004) using centered and scaled continuous covariates. Residual and normal probability plots demonstrated non-constant error variance and departures from normality in the error terms, so I applied a square-root transform on η_{ij} to stabilize the variance and normalize the errors to remedy these departures from regression assumptions. I calculated a corrected Akaike's Information Criterion (AIC_c) value for each model and then ranked and selected the best approximating models using ΔAIC_c values (Burnham and Anderson 2002). I also calculated w_k to measure model selection uncertainty and $w_{+(i)}$ to estimate the relative importance of each covariate (Burnham and Anderson 2002).

Results

Modeling and Predicting Spatial Variation in Bison Travel

A total of 121380 locations, spanning late November 2003 through early November 2004, were recorded from 14 collars with one collar failing to gather any data.

After censoring the data using the time, angle, and distance criteria for the general travel analysis I had 3200 locations comprising 1192 vectors with an average length of 2025 ± 51 m (SE) and an average of 1.68 ± 0.04 segments. I created 6753 node locations at 400 m intervals along the 1192 vectors and then generated a random vector data set consisting of 23840 vectors and 135060 node locations. After censoring outlying covariate data points, there were a total of 141791 observations that I then divided into vector data sets for model calibration (*n* = 106301 observations) and validation (*n* = 35490) for the general travel analysis. For the corridor travel analysis, adding the vector distance criterion left me with 918 locations, 187 vectors (average length of 5373 ± 144 m; average of 3.91 ± 0.11 segments), 2630 node locations at 400 m intervals, and a random vector data set consisting of 3740 vectors and 52600 node locations. I then divided the 55230 observations for the corridor travel analysis into vector data sets for model calibration (*n* = 40848) and validation (*n* = 14382).

General Bison Travel. General travel vectors were primarily located throughout the central herd's range, though some bison moved north to the northern range (Figure 2.2*a*). Vectors were concentrated in major meadow complexes, canyons in the MGF, the lower Firehole drainage, and along the Mary Mountain trail. Of all GPS locations obtained:

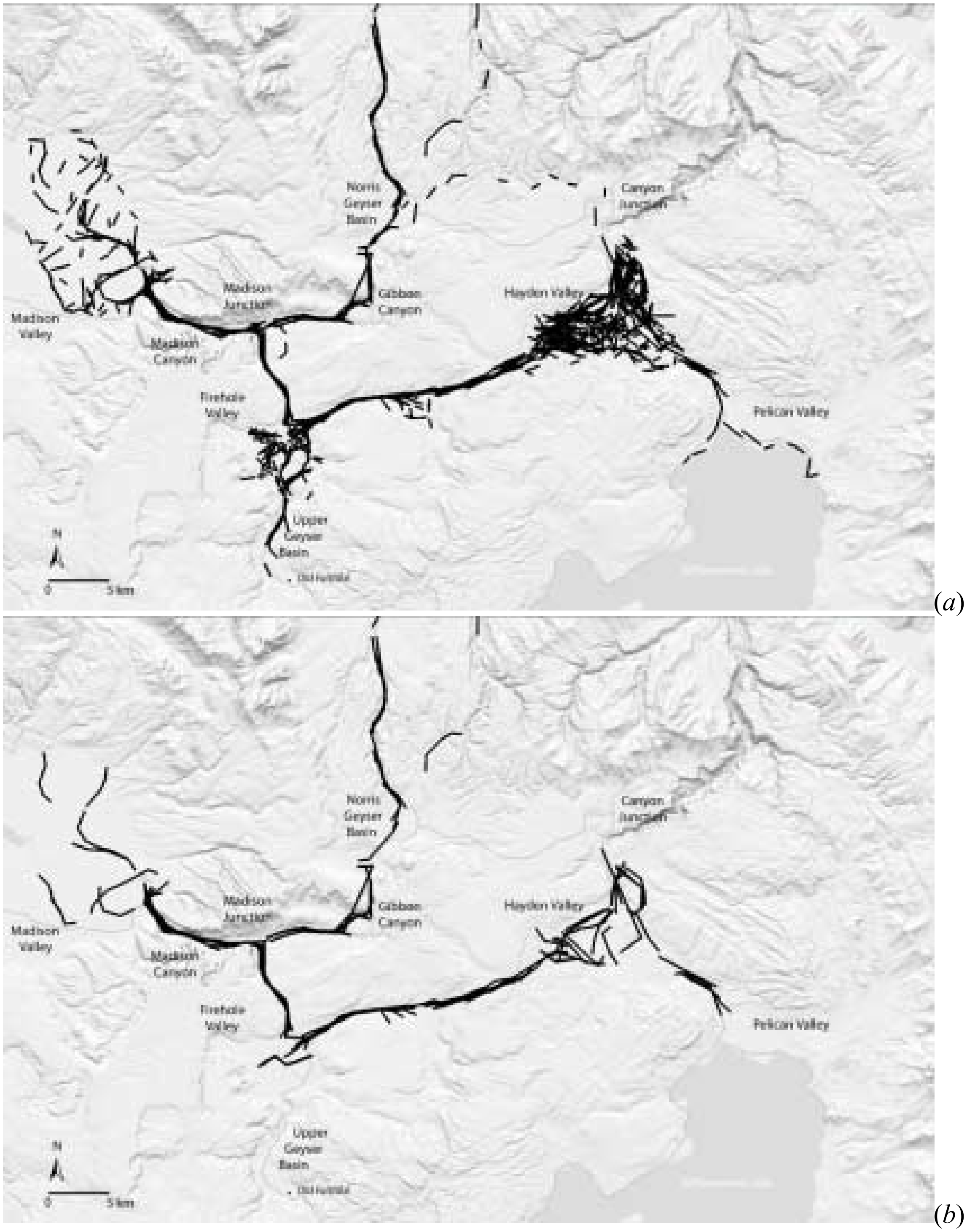


Figure 2.2. Maps of the spatial distribution of vectors from GPS collared bison for (*a*) general bison travel, and (*b*) bison corridor travel throughout central Yellowstone National Park. Black lines denote vectors and dark gray lines depict the road system.

1-5% were travel locations in major meadow complexes; 63-88% were travel locations in canyons, and 39% were travel locations along the central Mary Mountain trail.

One model was supported in the general travel modeling efforts. This model had an Akaike weight of 1.0 and was 191 QIC units better than the second best model (Table 2.2; Appendix 2C). Seven of the covariates contained in the best approximating model were significant effects with confidence intervals not spanning zero (Table 2.3). Additionally, all of the habitat categories, except BF, were significant effects. Since the use of scaled covariates facilitated comparisons between coefficient estimates, DST was the most influential effect in the model with SLHG and SL having comparable magnitudes of effect on the odds of bison travel. As hypothesized, SL, PROX, DST, and OT habitats were negative effects on the odds of bison travel while SLHG, TAN, and MD and TH habitats were positive effects. Contrary to my predictions DBF and DUF were positive effects on the odds of travel and BF habitat had no significant effect. The

Table 2.2. Model selection results for *a priori* hypothesized models examining the effects of habitat and topography covariates on spatial variation in the odds of general bison travel. The two best approximating models are presented along with the number of parameters (K), the ΔQIC value, and the Akaike weight (w_k).

Model	**Structure**	**K**	**ΔQIC**	**w_k**
HT217‡	$\beta_0 + \beta_1(\text{HBT}) + \beta_2(\text{DST}) + \beta_3(\text{DBF}) + \beta_4(\text{DUF}) + \beta_5(\text{PROX}) + \beta_6(\text{SL}) + \beta_7(\text{SLHG}) + \beta_8(\text{TAN})$	12	0.00	1.00
HT213	$\beta_0 + \beta_1(\text{HBT}) + \beta_2(\text{DST}) + \beta_3(\text{DBF}) + \beta_4(\text{PROX}) + \beta_5(\text{SL}) + \beta_6(\text{SLHG}) + \beta_7(\text{TAN})$	11	191.02	0.00

‡ QIC value for model HT217 is 29762.58

Table 2.3. Coefficient values and lower (LCI) and upper (UCI) 95% confidence limits from the best approximating models for the general bison travel analysis (model HT217) and the bison corridor travel analysis (model CHT213). Both top models were identified through QIC model comparison techniques examining spatial variability in the odds of general bison travel and bison selection of travel corridors. Bold notation denotes significant coefficients at α=0.05. Predictor weights ($w_{+(i)}$) are presented for each of the modeling exercises.

		General Bison Travel		**Bison Corridor Travel**
		MODEL HT217		**MODEL CHT213**
Covariate	$\mathbf{w_{+(i)}}$	$\boldsymbol{\beta_i}$ **(LCI, UCI)**	$\mathbf{w_{+(i)}}$	$\boldsymbol{\beta_i}$ **(LCI, UCI)**
Intercept (HBT=UF)		**-10.410 (-11.731, -9.090)**		**-13.472 (-15.182, -11.762)**
HBT=BF	1.000	-0.028 (-0.163, 0.107)	1.000	0.151 (-0.084, 0.385)
HBT=MD	1.000	**0.607 (0.500, 0.715)**	1.000	**0.518 (0.328, 0.708)**
HBT=OT	1.000	**-0.841 (-1.261, -0.421)**	1.000	**-0.403 (-0.751, -0.054)**
HBT=TH	1.000	**2.062 (1.026, 3.098)**	1.000	**2.859 (1.587, 4.131)**
DST	1.000	**-6.240 (-7.328, -5.151)**	1.000	**-8.607 (-10.131, -7.083)**
DBF	1.000	**0.980 (0.643, 1.316)**	1.000	**0.868 (0.497, 1.239)**
DUF	1.000	**1.494 (1.051, 1.937)**	0.004	
PROX	1.000	**-4.553 (-5.722, -3.384)**	1.000	**-2.828 (-4.168, -1.488)**
SL	1.000	**-5.761 (-7.345, -4.178)**	1.000	**-4.829 (-6.255, -3.402)**
SLHG	1.000	**5.956 (5.196, 6.716)**	1.000	**4.319 (3.707, 4.930)**
TAN	1.000	**2.555 (2.055, 3.055)**	1.000	**3.052 (2.530, 3.575)**

top approximating model had an AUC value of 0.882 and, therefore, provided "excellent discrimination" capabilities for predicting the probability of bison travel (Hosmer and Lemeshow 2000). I was unable to further measure model goodness-of-fit (GOF), however, because traditional logistic regression GOF techniques do not apply to GEEs. As expected, the top model predicted bison travel in the Madison Canyon and along the west portion of the Mary Mountain trail that parallels Nez Perce Creek (Figure 2.3*a*; Appendix 2E). Travel was predicted to be most likely along streams, with the Madison River and Cougar Creek along the west park boundary being of particular note. The model failed to predict substantial travel in three areas known to be frequently used by bison for travel: Gibbon Canyon, lower Firehole drainage, and the central Mary Mountain trail (Figure 2.3*a*; Appendix 2E). The model predicted frequent travel in several major meadow complexes and also incorrectly predicted bison travel in high elevation meadows on plateaus that are covered by deep snowpack during winter and beyond the central herd's range.

<u>Corridor Travel.</u> Corridor travel vectors were concentrated in the Madison Canyon, Gibbon Canyon, lower Firehole drainage, and along two segments of the Mary Mountain trail (Figure 2.2*b*). Of all GPS traveling locations: 9-18% were part of long distance corridor vectors in meadow complexes; 58-77% were part of corridor vectors in canyons, and 44-57% were part of corridor vectors along the Mary Mountain trail. Corridor

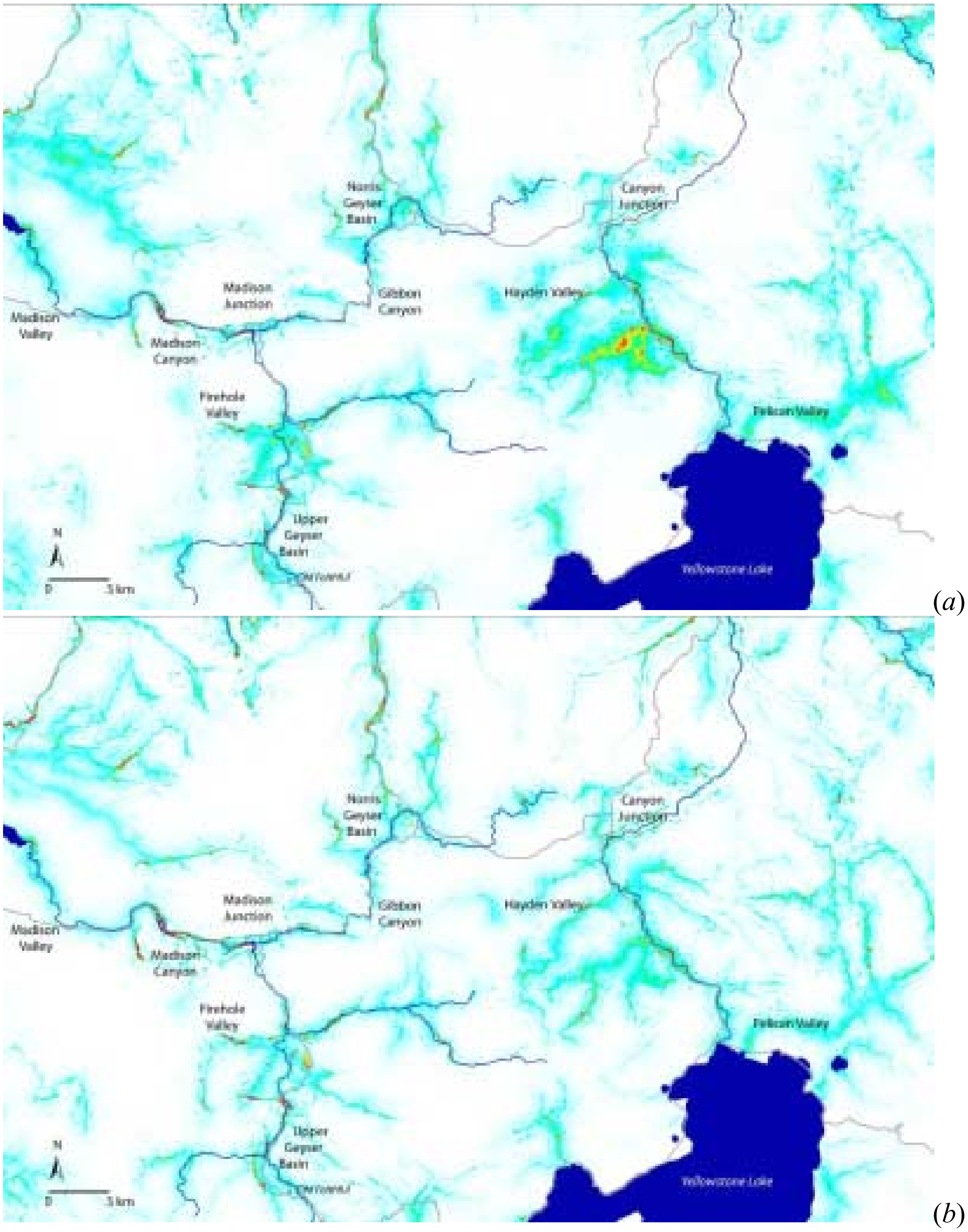


Figure 2.3. Probability maps developed from the best approximating *a priori* models examining the effects of topography and habitat attributes on (*a*) general bison travel, and (*b*) bison corridor travel throughout central Yellowstone National Park. White areas represent a travel probability of zero and travel probability increases as colors darken from green to red to dark blue, with dark blue corresponding to a probability of one. Roads are depicted in grayish shading and streams in blue.

vectors overlapped with 27% of roads in central Yellowstone (i.e., 27% of the roads were used for corridor travel; where a section of road was defined to have been used if it occurred between two consecutive corridor travel locations that were both within 50 m of a road).

I found one top approximating model in the corridor travel modeling exercise that had an Akaike weight of 0.995 and was 10.8 QIC units better than the second best model (Table 2.4; Appendix 2C). Six covariates, plus all habitats except BF, contained in the top model were significant effects with DST being the most influential effect (Table 2.3). As I predicted, SL, PROX, DST, and OT habitats were negatively correlated with the odds of bison selecting travel corridors while SLHG, TAN, and MD and TH habitats were positively correlated. Contrary to my hypotheses, DBF was a positive effect on the odds of selecting corridors and DUF and BF habitat were not significant in my best model. The top model had an AUC value of 0.876.

Table 2.4. Model selection results for *a priori* hypothesized models examining the effects of habitat and topography covariates on spatial variation in the odds of bison selection of travel corridors. The two best approximating models are presented along with the number of parameters (K), the ΔQIC value, and the Akaike weight (w_k).

Model	**Structure**	**K**	**ΔQIC**	**w_k**
CHT213‡	$\beta_0 + \beta_1(\mathrm{HBT}) + \beta_2(\mathrm{DST}) + \beta_3(\mathrm{DBF}) + \beta_4(\mathrm{PROX}) + \beta_5(\mathrm{SL}) + \beta_6(\mathrm{SLHG}) + \beta_7(\mathrm{TAN})$	11	0.00	0.995
CHT217	$\beta_0 + \beta_1(\mathrm{HBT}) + \beta_2(\mathrm{DST}) + \beta_3(\mathrm{DBF}) + \beta_4(\mathrm{DUF}) + \beta_5(\mathrm{PROX}) + \beta_6(\mathrm{SL}) + \beta_7(\mathrm{SLHG}) + \beta_8(\mathrm{TAN})$	12	10.76	0.005

‡ QIC value for model CHT213 is 11334.35.

The best approximating corridor travel model predicted long distance travel along streams and offered improved prediction along actual bison corridor travel routes, such as in the Gibbon Canyon, compared to the top general travel model (Figure 2.3*b*; Appendix 2E). Higher probability corridor travel was predicted in the Madison Canyon, the west Mary Mountain trail, and along portions of the Firehole River. Minimal corridor travel was predicted in meadow complexes, except along streams. The model failed to predict corridor travel along high use routes in the lower Firehole drainage and central Mary Mountain trail. Some travel was also incorrectly predicted in high elevation meadows and along streams on plateaus.

Both exploratory modeling efforts resulted in improved models compared to the top ten *a priori* corridor travel models. Contrary to my prediction, adding DRD and removing DST provided significant improvements in the QIC values (Appendix 2D, Table 2D.1) and a top model containing seven significant covariates with DRD negatively correlated with the odds of bison travel (Appendix 2D, Table 2D.2). Adding ELEV and DRD lowered the QIC values of the top ten *a priori* models (Appendix 2D, Table 2D.3) and provided a new overall best approximating model containing eight significant covariates with both ELEV and DRD negatively correlated with the odds of bison travel (Appendix 2D, Table 2D.4). The most influential covariate in the top model was still DST. Probability predictions with the new best approximating model addressed limitations that were present with predictions from the top *a priori* model (Figure 2.4; Appendix 2E). Models including ELEV predicted more bison travel in corridors along

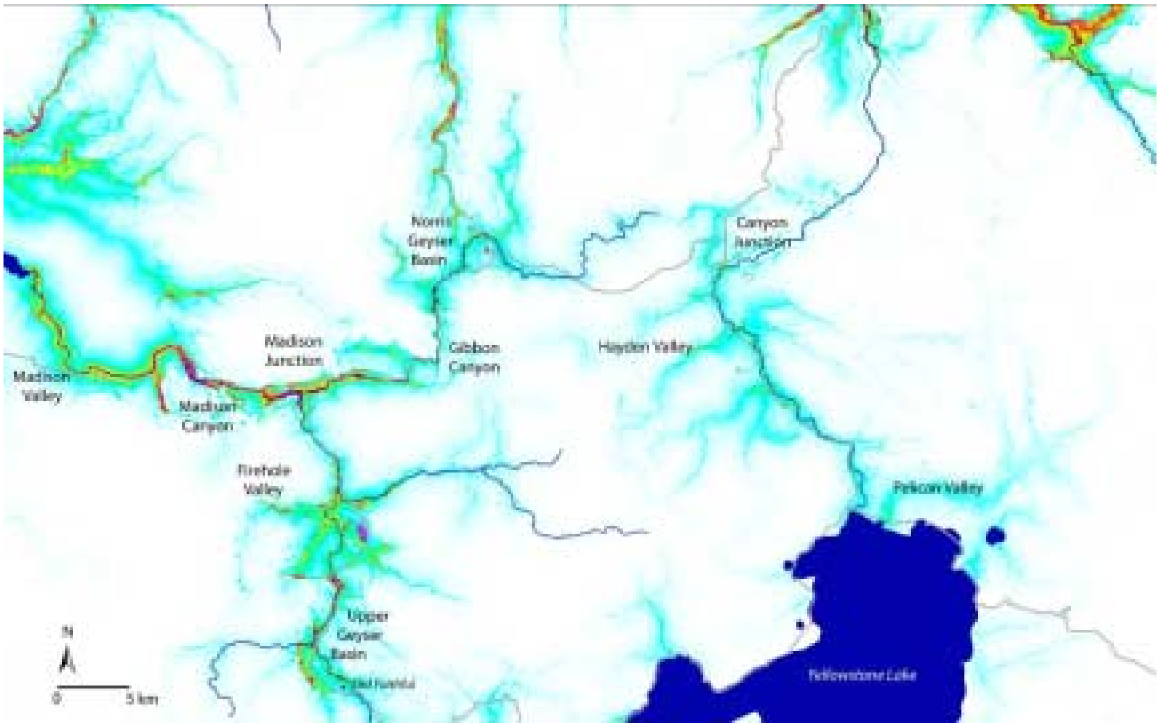


Figure 2.4. Probability map developed from the top exploratory model examining distance to road and elevation effects, along with habitat and topography attributes, on bison corridor travel throughout central Yellowstone National Park. White areas represent a travel probability of zero and travel probability increases as colors darken from green to red to dark blue, with dark blue corresponding to a probability of one. Roads are depicted in grayish shading and streams in blue.

lower elevation valley bottoms in the MGF, particularly in the Madison Valley along the west park boundary, and minimal travel on high elevation plateaus. Models including DRD improved prediction of travel corridors along roads in the lower Firehole and Gibbon drainages, but also predicted more corridor travel in meadows near roads (Figure 2.4; Appendix 2E).

Modeling Spatial Variation in Bison Road Travel

A total of 1444 bison groups were observed traveling on the MGF road system during daily bison road use surveys in 2002-2005, ranging from a minimum of 285 groups in 2002-03 to a maximum of 656 groups in 2003-04 (mean = 481 ± 108). The total number of individual bison documented in these traveling groups ranged from 4109 in 2002-03 to 8538 in 2003-04 (mean 6763 ± 1352). Survey effort varied between 25031 km in 2002-03 and 34464 km in 2004-05 (mean 29307 ± 2758). Bison spatial use of the road system varied greatly (Figure 2.5) with the average three year amount of bison travel per segment ranging between 0.0-11.7 bison groups observed in segment/100 km traveled in segment (mean 3.2 ± 0.4). Road segments receiving high amounts of bison travel were located in the lower Firehole drainage, Madison Canyon, and Gibbon Canyon (Figure 2.5).

One model received the most support in my road travel modeling exercise with an Akaike weight of 0.274 and a relative likelihood of 3.7 compared to the second best model, which differed by 2.6 AIC_c units (Table 2.5; Appendix 2C). Six of the covariates contained in the best approximating model were significant effects with confidence intervals not spanning zero with YEAR, DUF, and DST having the highest predictor weights (Table 2.6). In addition, the dichotomous YEAR effect was significant for the

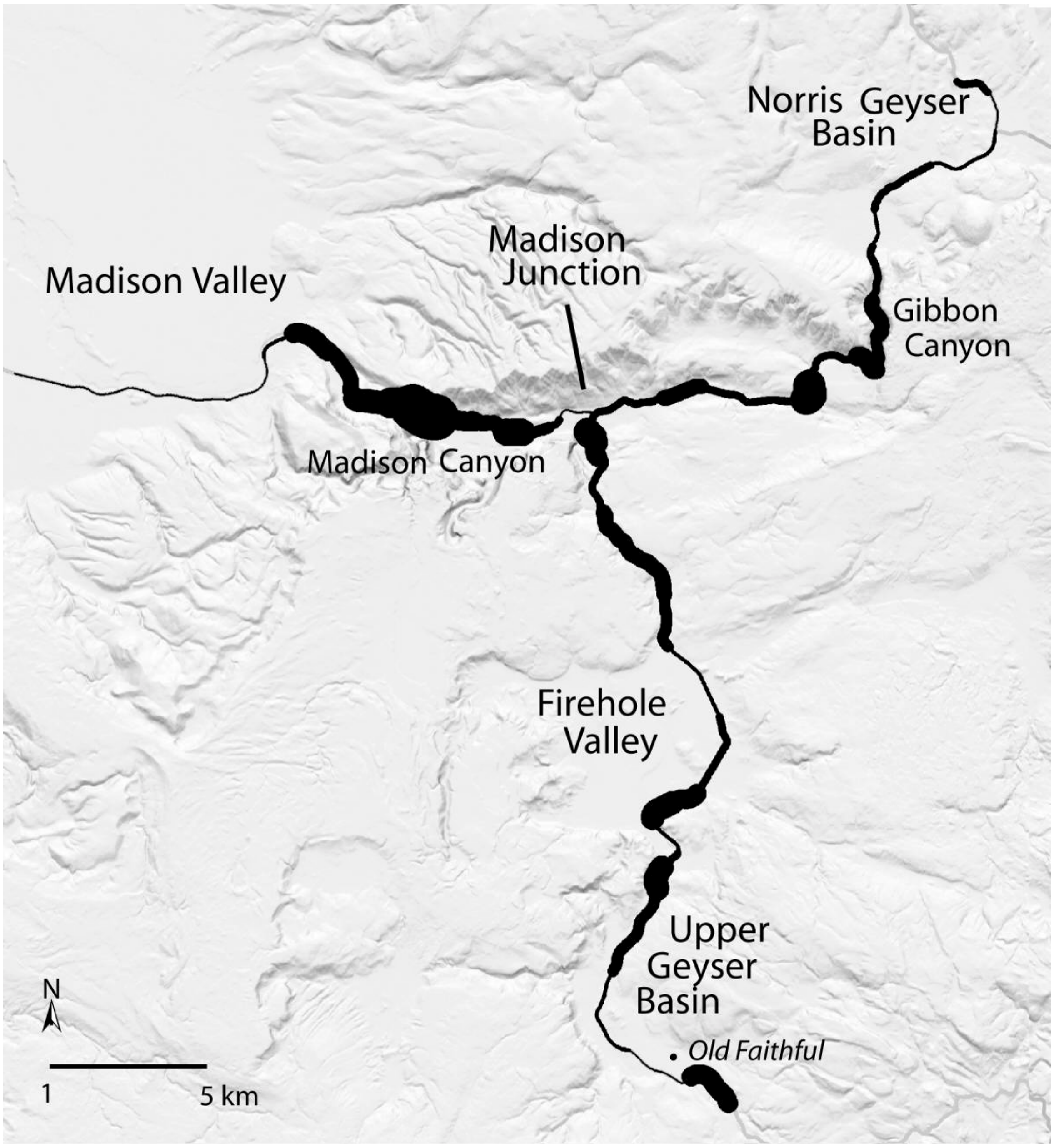


Figure 2.5. Map depicting spatial variability in the amount of bison road travel for the Firehole, Gibbon, and Madison drainages in west central Yellowstone National Park. The width of the black lines represents the magnitude in average bison road travel for each road segment for 2002-03 to 2004-05 with values ranging between 0.0-11.7 bison groups observed in segment/100 km traveled in segment. Roads are depicted in dark gray. Data on bison road use were obtained during winter bison road use surveys conducted from 2002-03 to 2004-05 in the Madison, Gibbon, and Firehole drainages.

Table 2.5. Model selection results for *a priori* hypothesized models examining the effects of habitat, topography, and year covariates on spatial variation in the amount of bison road travel. The four best approximating models are presented along with the number of parameters (K), the ΔAIC_c value, and the Akaike weight (w_k).

Model	**Structure**	**K**	**ΔAIC_c**	**w_k**
RHT150‡	$\beta_0 + \beta_1(DST) + \beta_2(DBF) + \beta_3(DUF) + \beta_4(PROX) + \beta_5(SLHG) + \beta_6(TAN) + \beta_7(YEAR)$	9	0.00	0.274
RHT148	$\beta_0 + \beta_1(DST) + \beta_2(DUF) + \beta_3(PROX) + \beta_4(SLHG) + \beta_5(TAN) + \beta_6(YEAR)$	8	2.64	0.073
RH30	$\beta_0 + \beta_1(DST) + \beta_2(DBF) + \beta_3(DUF) + \beta_4(PROX) + \beta_5(YEAR)$	7	2.83	0.067
RHT135	$\beta_0 + \beta_1(DST) + \beta_2(DBF) + \beta_3(DUF) + \beta_4(PROX) + \beta_5(SL) + \beta_6(SLHG) + \beta_7(YEAR)$	9	2.90	0.064

‡ AIC_c value for model RHT150 is 327.73.

2002-03 and 2003-04 seasons. As predicted, SLHG and YEAR (for two years) were positive effects and DST and DUF were negative effects on η. Contrary to my hypotheses, PROX and DBF were positively correlated with η, TAN was negatively correlated with η, and SL was not included in my top model.

Discussion

The spatial distribution of bison travel corridors and the probability of bison travel throughout central Yellowstone are both affected by multiple topographic and habitat attributes including slope, landscape roughness, elevation, habitat, proximity to foraging

Table 2.6. Coefficient values and lower (LCI) and upper (UCI) 95% confidence limits from the best approximating model (model RHT150) identified through AIC model comparison techniques examining spatial variability in the amount of bison road travel. Bold notation denotes significant coefficients at $\alpha=0.05$. Predictor weights ($w_{+(i)}$) are presented for the overall modeling exercise.

Covariate	$w_{+(i)}$	β_i **(LCI, UCI)**
Intercept		**0.936 (0.501, 1.371)**
DST	0.997	**-0.540 (-0.811, -0.268)**
DBF	0.635	**0.285 (0.027, 0.542)**
DUF	0.999	**-0.665 (-0.927, -0.404)**
PROX	0.727	**0.339 (0.071, 0.607)**
SLHG	0.632	**0.535 (0.086, 0.984)**
TAN	0.523	**-0.730 (-1.278, -0.182)**
YEAR (2003-04)	0.999	**0.599 (0.343, 0.855)**
YEAR (2004-05)	0.999	0.030 (-0.226, 0.286)

areas, and distances to streams, burned forest, and unburned forest. Roads, in some topographically constrained portions of the landscape, also apparently influence the distribution of travel corridors. While similar landscape characteristics influence both short and long distance bison travel, certain features have different magnitudes of effect on corridor movements suggesting specific areas have a higher probability of bison corridor travel throughout central Yellowstone. Indeed, the best approximating corridor travel model predicted bison travel corridors along rivers and creeks as well as in canyons that connect major foraging areas. My findings agree with those of other studies that found habitat and topography to affect the movements of mammals (Whittington et al.

2004, Dickson et al. 2005) and large herbivores to use corridors to connect feeding areas (Douglas-Hamilton et al. 2005).

My results suggest that the bison travel network throughout central Yellowstone is spatially defined largely by the presence of streams that connect foraging areas. Streams were the most influential landscape feature affecting both corridor and general bison travel locations. Streams are natural landscape elements that guide animal movement (Noss 1991) and bison regularly establish and use travel routes along them. Areas receiving the most bison corridor travel often paralleled major streams: along portions of the Madison, Firehole, and Gibbon Rivers, and Nez Perce Creek. Predicted corridors included these streams as well as along Pelican Creek and the Yellowstone River that guide bison movements throughout portions of the summer range. Another predicted corridor was along Cougar Creek, which facilitates bison travel towards the west park boundary. In addition to the natural pathways that streams provide year round, many streams in Yellowstone remain unfrozen during winter—a result of effluent from geothermal features entering waterways. The "heated," open streams reduce the snowpack along riverbanks and afford bison easier travel routes than nearby areas of deep snow.

Topography affects the probability of bison travel and use of corridors since the odds of travel were negatively correlated with SL and positively correlated with SLHG and TAN. Further, the odds of corridor travel were negatively correlated with ELEV in the top exploratory model. The negative effect of slope indicates that bison travel along gentle elevation gradients and avoid traversing steep slopes when other routes exist.

Correspondingly, the probability of travel and corridor use was higher in areas of variable topography that constrain movements, such as in canyons, which agrees with bison travel corridors that exist in the Madison, Gibbon, and Firehole Canyons. In these canyons, river corridors—that mostly parallel roads—assist in naturally guiding bison movements. The negative effect of elevation suggests, in part, that greater snowpack accumulation at higher elevations (and earlier meltout in lower regions) may hinder bison travel in some regions during winter and that some high elevation regions lack suitable foraging areas. Topography has been documented to influence the travel routes of species in a variety of environments. Whittington et al. (2004) discovered that areas of rugged topography affected the tortuosity of wolf (*Canis lupus*) movements. Dickson et al. (2005) documented that cougars (*Puma concolor*) preferred to traverse gentle slopes. Even in marine ecosystems, the movements of fish, sharks, and macrocrustacea have been found to be associated with topography (Klimley et al. 2002, Burrows et al. 2003, Meyer and Holland 2005).

Bison travel locations and corridors were more likely in close proximity to foraging areas—a result that suggests bison connect foraging areas using the most direct routes. Additionally, the probability of bison travel and corridors increased in meadow and thermal habitats, indicating bison develop some travel routes through interconnected foraging areas. This is how bison utilize the western part of the Mary Mountain trail that consists of a series of meadows along Nez Perce Creek. Thermal areas may also have increased importance as corridors since the magnitude of effect of thermal habitats was greater for corridor travel than general travel. In winter, thermal habitats—which also provide some forage—facilitate bison travel because of minimal snowpack accumulation in these areas. A comparison between maps of general and corridor travel vectors reveals that movements in large meadow complexes are generally of short distance and likely related to travel between patches of suitable forage. In contrast, bison travel behavior is different in habitats lacking adequate foraging areas (i.e., corridors) with travel consisting of long distance sustained movements. My findings agree qualitatively with other studies that document associations between animal movement behavior and habitat, many of which found travel speed or habitat preferences to be influenced by the availability of forage or prey (Ferguson and Elkie 2004, Laidre et al. 2004, Dickson et al. 2005).

Actual bison travel corridors coincided with 27% of the road network throughout central Yellowstone and distance to road was a significant, negative effect in the exploratory models. Road sections that passed through canyons, were closest to streams and unburned forest, and were farther from foraging areas received the most bison travel, suggesting bison primarily use roads when they are part of a natural travel corridor. However, I cannot discount the possibility that roads initially enabled or facilitated travel in some areas. Measured high use corridors overlapped with roads in the Madison Canyon, Gibbon Canyon, and the lower Firehole drainage, and portions of these road segments also received the highest amount of bison travel during my road use surveys. The top road travel model contained significant effects for some of the same landscape covariates that influenced bison corridor selection, most notably DST and SLHG. Indeed, road segments that passed through meadow complexes without topographic restrictions or that circumvented important foraging areas received below average bison travel.

Pronounced bison travel corridors existed both in close association with roads in parts of the MGF and distant from any roads along the Mary Mountain trail. While portions of corridors through the Madison and Gibbon Canyons were predicted from the top *a priori* corridor travel model using only landscape attributes, three important bison travel corridors were not well predicted: 1) along the central Mary Mountain trail that is not influenced by roads; 2) the segment of the Gneiss Creek trail connecting Cougar Meadows to the Madison drainage, and 3) portions of the lower Firehole drainage, which includes a road segment frequently used by bison. Landscape attributes were ineffective at predicting bison travel in these areas that do not completely parallel streams or that lack severe topographical constraints. However, the travel route along the road through the lower Firehole drainage was predicted after including DRD in exploratory models, indicating road influence on bison travel in this area. These results suggest bison develop and maintain some travel routes based on learning and experience and that landscape attributes alone cannot account for nuances in bison behavior. The corridors along the central Mary Mountain trail and lower Firehole drainage offer gentle elevation gradients compared to the surrounding landscape and both provide the most direct routes to nearby foraging areas. Historically, bison dispersing from the Hayden Valley in search of new foraging areas may have discovered the natural elevation gradient down Mary Mountain to access meadows along Nez Perce Creek and the Firehole drainage. This trail was identified as a significant elk migration route during the early 1900s (Skinner 1925). A similar circumstance may have led bison to discover the route in the lower Firehole drainage that connects major foraging areas. Repeated use of these routes may have ingrained behavior that was passed along through generations. Use of spatial memory to revisit foraging areas has been documented for several ungulate species (Bailey 1989, Gillingham and Bunnell 1989, Hewitson et al. 2005) and is likely used by bison given their well-defined travel corridors.

My findings suggest bison develop travel corridors using learned experiences from exploratory movements to acquire knowledge of the most direct routes between foraging areas. The corridor along the Mary Mountain trail between the Hayden Valley and Firehole drainage developed as early as the mid-1940s without the influence of modern roads or road grooming (McHugh 1958). Once bison expanded their range into the Firehole drainage, they had access to both streams and roads to facilitate movement. However, the important travel corridor along the Gneiss Creek trail likely developed out of necessity for forage resources rather than from the convenience of roads. The dearth of foraging areas along the road to the west of the Gneiss Creek trail, combined with the abundant resources throughout the Cougar Meadows area, probably led bison to learn and reuse this corridor that now provides access to meadows and travel routes beyond the western park boundary. I have no historic data to address how the lower Firehole corridor developed, but model results indicate that roads may facilitate travel in this area. Bison have been documented to travel between foraging habitats in corridors that incorporate roads and linear features (Gates et al. 2001) and roads may facilitate movements for other species (Buskirk et al. 2000, Trombulak and Frissell 2000, Dickson et al. 2005).

My results suggest bison use of certain road segments as travel corridors would persist whether or not roads were groomed during winter owing to repeated use of learned travel routes year round and the necessity of density related movements to access foraging areas. Bison use the Mary Mountain trail the entire winter for migration and to facilitate movements between foraging areas despite deep snow. Repeated use of the trail by bison traveling in single file lines maintains it in a “self-groomed” state—an adaptation for saving energy while traveling in snow (Telfer and Kelsall 1984). There are two alternative routes along groomed roads that would allow bison to migrate into the MGF and neither received bison travel possibly owing to a lack of foraging areas, nor were they predicted travel corridors. Given the population size of the central bison herd, access to foraging areas beyond the Firehole drainage is likely imperative for survival. Corridors along roads in the Madison and Gibbon Canyons—both predicted by the top *a priori* corridor travel model—offer the most direct travel routes along rivers to reach large meadows. Alternative paths are not likely because of topography and habitat constraints (i.e., plateaus or burned forest). My results agree with conclusions by Bjornlie and Garrott (2001) and reaffirmed by Gates et al. (2005) that Yellowstone bison use roads when convenient and when they align with natural travel pathways.

Although my study cannot fully resolve the debate over effects of winter road grooming on bison travel and range expansion in central Yellowstone, it offers novel insights into bison spatial dynamics. Completely separating the effect of roads on bison travel is impossible because bison do use travel corridors along portions of roads and there are areas where roads may have initially facilitated movements. A related study by Bruggeman et al. (*in press*) documented that temporal patterns in the amount of bison road travel were negatively correlated with the road grooming period and found no evidence that bison preferentially used groomed roads during winter. Temporal trends in bison road travel were influenced by similar abiotic and biotic factors as trends in off-road travel (Bruggeman et al. *in press*). I suggest that, like temporal trends in bison road travel, most spatial patterns in road use are likely a manifestation of general spatial travel trends throughout the landscape as topography and habitat attributes alone predicted the majority of bison travel corridors throughout central Yellowstone. Beyond investigating bison travel in Yellowstone, my study provides conceptual and analytical frameworks for examining animal movement patterns. Given the increasing use of GPS and GIS technology in wildlife research, I anticipate the methodology presented here will be applicable to investigating behaviorally influenced resource selection for a variety of species.

CHAPTER 3:
TEMPORAL VARIABILITY IN WINTER TRAVEL PATTERNS OF YELLOWSTONE BISON: THE EFFECTS OF ROAD GROOMING

Abstract

The influence of winter recreation on wildlife in Yellowstone National Park (YNP) is a controversial issue. In particular, the effects of road grooming, done to facilitate snowmobile and snowcoach travel, on bison (*Bison bison*) ecology are under debate. I collected data during winter, 1997-2005, on bison road use, off-road travel, and activity budgets to quantify temporal trends in the amount of bison road and off-road travel and identify the ecological factors affecting bison movements and use of the groomed road system in the Madison-Gibbon-Firehole (MGF) area of YNP. Using model comparison techniques I found bison travel patterns to be influenced by multiple, interacting effects. Road travel was negatively correlated with road grooming and I found no evidence that bison preferentially used groomed roads during winter. Snow water equivalent, bison density, and the springtime melt period were positively correlated with both bison road and off-road travel. From behavioral scans on 68791 bison, I found that travel is only a small percentage (11%) of all bison activity with foraging comprising 67% of observations. Also, only 7% of traveling bison and 30% of foraging bison were displacing snow and I suggest foraging, rather than traveling, is likely the major energetic cost to bison in winter. Bison utilize their own trail network, connecting foraging areas using stream corridors, geothermal pathways, and self-groomed travel routes. My results

indicate that temporal patterns in bison road travel are a manifestation of general travel behavior and that groomed roads in the MGF do not appear to be a major factor influencing bison ecology and spatial redistribution. I suggest that the changes in bison spatial dynamics during the past three decades have likely been the result of the natural phenomenon of density-dependent range expansion rather than caused by the anthropogenic influence of road grooming.

Introduction

Nonconsumptive outdoor recreation—including such activities as hiking, biking, boating, and snowmobiling—has increased in popularity during the past several decades (Cordell and Super 2000). Since much of the recreation occurs in habitats suitable for a variety of wildlife species there has been increasing concern regarding the impacts of these human activities on wildlife behavior, mortality, and population dynamics by both wildlife managers (Knight and Cole 1995, Cole and Landres 1996) and conservation groups (Flather and Cordell 1995). Boyle and Samson (1985) summarized research on the effects of outdoor recreation on wildlife and documented predominantly negative impacts such as disturbance (Stalmaster and Kaiser 1999, Taylor and Knight 2003, Whittington et al. 2005), habitat alteration (Ferguson and Keith 1982, Nellemann et al. 2003), and mortality (O'Shea 1995). The influence of winter recreation on wildlife (Dorrance et al. 1975, Freddy et al. 1986) is particularly important since disturbances in combination with cold temperatures, deep snow, and limited forage could lead to added physiological stress in animals (Anderson 1995, Gabrielsen and Smith 1995). As a result, natural resource managers must consider the potential impacts of recreation when devising management plans for wildlife on public lands (Garber and Burger 1995, Vaske et al. 1995, Steidl and Anthony 1996).

Perhaps nowhere is the winter recreation debate more prominent than in Yellowstone National Park (YNP). Habitat to wildlife such as bison (*Bison bison*), elk (*Cervus elaphus*), wolves (*Canis lupus*), and a wide array of waterfowl and raptors, Yellowstone has seen a dramatic increase in both annual and winter visitation over the past few decades (National Park Service 2000*a*). Since 1971, when YNP began grooming interior park roads to restrict winter travel to the road system and afford better access for visitors arriving in over-snow vehicles (OSV; snowmobile, snowcoach), winter recreation increased from approximately 20000 users annually to more than 140000 by the mid-1990s (Gates et al. 2005). Yellowstone managers now face the increasing challenge of balancing public demand for recreation while simultaneously preserving wildlife and habitat. Behavioral responses of wildlife to winter recreation vary from habituation in high areas of OSV traffic (Aune 1981, Hardy 2001) to flight in wildlife-skier interactions (Cassirer et al. 1992, Hardy 2001). Borkowski et al. (*in press*) quantified the behavioral responses of wildlife to OSVs from 1999-2004 and their results suggested some degree of habituation because <10% of interactions elicited active responses (e.g., travel, defense, flight) and responses decreased as cumulative OSV use increased within winters having the largest visitation.

Bison in YNP are at the center of the winter recreation debate because the population has grown from 500 in 1970 to over 4000 in 2005 (National Park Service 2000*a*, Gates et al. 2005), an increase purported by Meagher (1993) to be caused by road grooming. Meagher (1993) concluded that road grooming was the major influence in both dramatic increases in the bison population and range expansion both within and beyond YNP boundaries. The reported rationale for this argument is that the roads provide a means of energy-efficient travel between foraging areas as bison seek out the groomed roads as an alternative to traveling through deep snow. The overall energy savings result in reduced bison winter mortality and improved calf survival (Meagher 1993). Recommendations from Meagher (1993) included either fully or partially closing interior YNP roads to winter travel—an action that would reduce options for visitors to experience and enjoy Yellowstone in the winter and negatively impact the economies of gateway communities (National Park Service 2000*b*). Her interpretations, however, were restricted to qualitative assessments of incidental observations collected over several decades, during which many interacting ecological processes were undoubtedly influencing bison spatial and population dynamics (Meagher 1993).

The road grooming debate intensified after the harsh winter of 1996-97 when approximately 1100 bison left YNP in search of more accessible forage and were killed to prevent the possibility of brucellosis transmission to livestock (Baskin 1998, Cheville et al. 1998, NPS 2000*a*). These culls led to litigation by environmental groups and a settlement in which the NPS committed to preparing Environmental Impact Statements to provide YNP with both bison management and winter use plans (NPS 2000*a*, NPS

2000*b*). As part of these efforts, Bjornlie and Garrott (2001) conducted a two-year study on the distribution, movements, and activities of YNP's migratory central bison herd, which is at the center of the controversy because this herd winters in the area of the most intensive OSV traffic in the park. Bjornlie and Garrott (2001) concluded that bison on the Madison-Firehole winter range neither sought out nor avoided groomed roads, with the lowest magnitude of bison road travel occurring during the road grooming period. Locations where the roads received the most bison use were in areas of topographic constriction or high bison concentration. In addition, the majority (81%) of travel occurred off roads as bison, to avoid the unnecessary energy expenditure of displacing snow, established a network of trails that incorporated geothermal features as well as stream corridors (Bjornlie and Garrott 2001). This work was criticized for being conducted over a short time period, during mild winters, in a small study area, and using irrelevant data (Gates et al. 2005). At present the debate and litigation over winter recreation in YNP continues (United States District Court for the District of Columbia 2003, NPS 2004*a*, NPS 2004*b*).

The primary goal of this study was to evaluate the influence of road grooming on bison spatial dynamics in the Madison-Firehole winter range by extending Bjornlie and Garrott's (2001) work for an additional six years while addressing limitations and recommendations from their initial study. My research provides insights into mechanisms influencing bison travel in multiple ways. First, I assessed influences on temporal variation in bison travel, both on-and off-road, by evaluating competing hypotheses to determine the relative contributions of snowpack, road grooming, OSV traffic, bison density, and forage accessibility on the amount of travel. Second, I examined bison activity patterns to ascertain the extent of energy expended while traveling relative to other activities. Finally, I considered variability in bison travel on two major off-road bison trails to determine the extent of nocturnal travel and to further understand the role of the road system in bison ecology in the Madison-Firehole area. The analyses were conducted using three distinct data sets to assess and quantify bison movements throughout the entire winter range, not just on roads. Overall, I analyzed eight years of bison travel data—spanning a variety of winter severities—to quantify temporal travel trends and identify ecological factors affecting bison movements and use of the groomed road system.

Study Area

The study area in west central Yellowstone encompassed the drainages of the Firehole River upstream from Madison Junction to Old Faithful; the upper Madison River east from the Park boundary at West Yellowstone to Madison Junction, and the Gibbon River upstream to Norris Geyser Basin (Figure 3.1). It also included portions of the Mary Mountain trail extending from the Firehole drainage east to Mary Lake and meadows along Cougar Creek near the western boundary of the Park. Elevations within this 8000 ha area ranged from 2000-2250 m.

Meadow complexes and geothermal areas provided winter range for migratory bison in the Madison-Gibbon-Firehole (MGF) area. The central bison herd, which summers in the Hayden and Pelican Valleys, increased from 200 to >3000 animals during 1960-2005 (Meagher 1973, Bjornlie and Garrott 2001, Hess 2002, Gates et al. 2005). Sedges (*Carex* spp.) and grasses (*Calamagrostis* spp.) characterized wet meadows while dry meadows were dominated by grasses (*Poa* spp., *Festuca idahoensis*) and, in lower elevations in the Madison River valley, sagebrush (*Artemesia* spp.). During the summer of 1988 more than 50% of forested areas burned (Despain 1990) and these areas were characterized by downed trees, snags, regenerating lodgepole pine, Ross' sedge (*Carex rosii*), elk sedge (*Carex geyeri*), and leafy aster (*Aster foliaceus*) during my study. Unburned forested areas were predominantly lodgepole pine (*Pinus contortus*) with understories consisting of elk sedge, grouse whortleberry (*Vaccinium scoparium*), and pinegrass (*Calamagrostis rubescens*). Lower elevations consisted of scattered Douglas fir (*Pseudotsuga mensiesii*) and lodgepole pine while Engelmann spruce (*Picea engelmanni*) and subalpine fir (*Abies lasiocarpa*) were found at higher elevations.

There were four major geothermal areas in the study area—the Upper, Midway, Lower, and Norris Geyser Basins—along with smaller pockets of geothermal activity (Watson et al. 2002, Watson et al. *in review*). There were also a number of geothermally influenced locations along Nez Perce Creek and the Mary Mountain trail. These geothermal areas had reduced snow accumulation and longer growing seasons compared to surrounding areas. Also, the Firehole, Gibbon, and Madison Rivers remained ice-free throughout the winter owing to geothermal heat flux and run-off from thermal features.

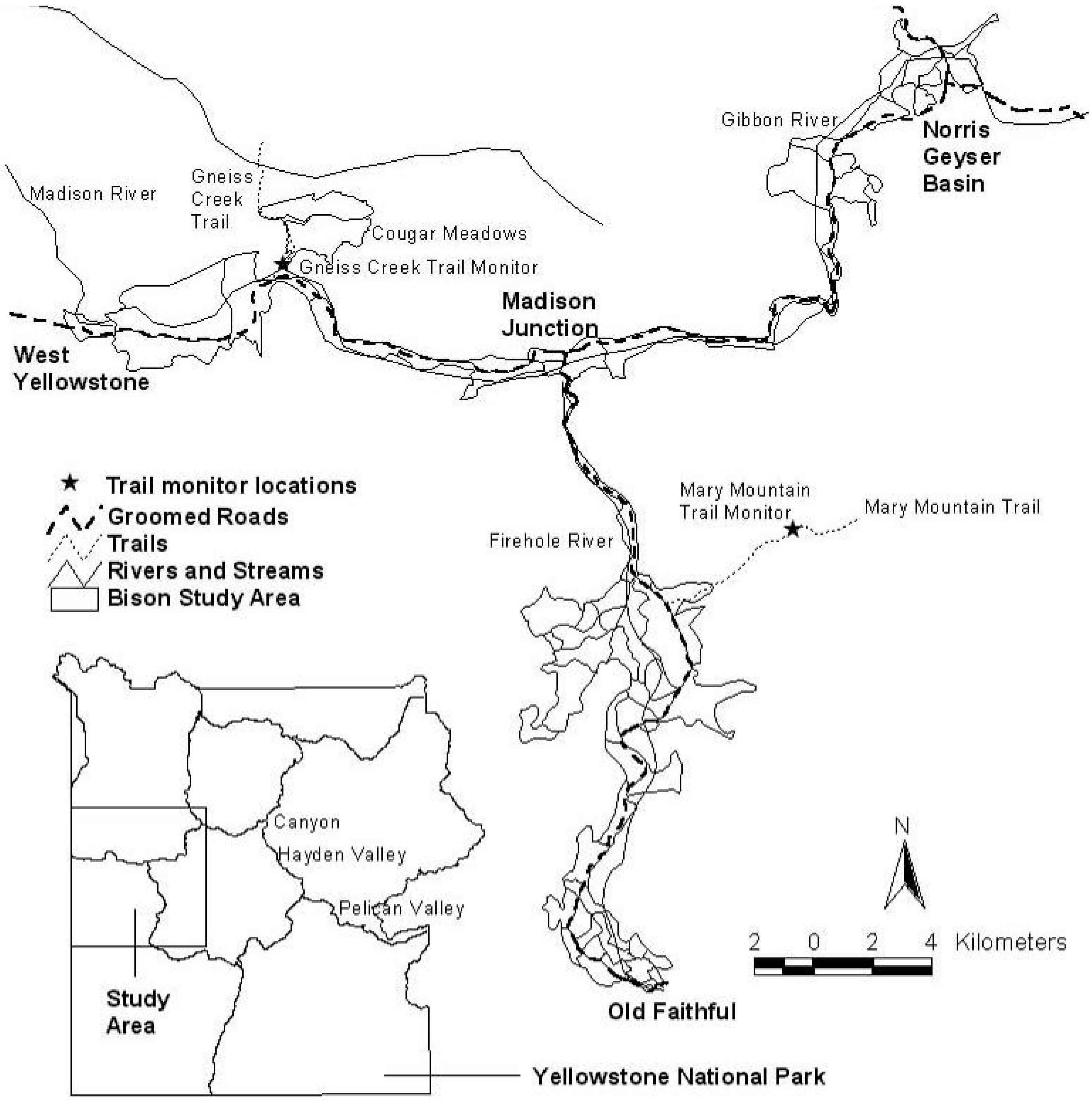


Figure 3.1. The Madison-Gibbon-Firehole study area in Yellowstone National Park, Wyoming and Montana.

The MGF area typically experiences severe winters with an annual average of 189 days of snow cover (Natural Resources Conservation Service National Water and Climate Center Public Communication 2004). Mean annual peak snow water equivalent (SWE) was 34.3 cm at the West Yellowstone Natural Resources Conservation Service

(NRCS) Snowpack Telemetry (SNOTEL) site (elevation 2042 m) during 1966-2004. Snowpack began accumulating in late October in the valleys and continued to build until April, at which point ablation occurred. At higher elevations, such as that represented by the Madison Plateau SNOTEL site (elevation 2362 m), snow began accumulating in mid-October and remained until the end of May. At this elevation mean annual peak SWE was 68.1 cm with an annual average of 236 days of snow cover during 1968-2004 (NRCS National Water and Climate Center Public Communication 2004).

A network of paved, two-lane roads paralleled the Madison, Gibbon, and Firehole Rivers through the study area. The 21.4 km section of road from West Yellowstone to Madison Junction passed through forest, along major meadow complexes, and through the Madison Canyon. The 25 km road section from Madison Junction to Norris Junction and north to Nymph Lake went through the Gibbon Canyon and large meadow complexes in Gibbon Meadows and Elk Park, and along a portion of the perimeter of the Norris geothermal basin. The Firehole River valley road system consisted of the 28.8 km segment extending from Madison Junction south to Kepler Cascades that passed through Firehole Canyon, large meadow complexes, and major geothermal areas. These roads were open to visitor travel in wheeled vehicles (WV) from mid-April until early November, at which point they were closed to visitors to allow snow accumulation for the motorized winter recreation season. Roads were groomed daily for snowmobile and snowcoach travel by visitors during mid-December until early March, at which point the roads were plowed daily (given new snowfall) and then opened in late April for the summer visitation season. Roads were open to administrative traffic (WV, OSV) by park staff and concessionaires throughout the year.

Methods

Bison Ground Distribution Surveys

The distribution and activities of bison wintering in the MGF area were recorded during eight winter seasons (1997-98 through 2004-05) by conducting comprehensive ground-based surveys every 10-14 days from late autumn until late spring. Seventy-four sampling units were surveyed over two days using six distinct routes that afforded a nearly complete enumeration of bison in this area (Ferrari 1999, Bjornlie 2000). Observers using snowmobiles or trucks and/or snowshoes started each route simultaneously to minimize missing or double counting bison (Bjornlie and Garrott 2001).

Observers recorded a Universal Transverse Mercator (UTM) location along with the age and sex composition for each observed group. Groups were defined as clusters of bison that were spatially segregated (>400 m) from any other surrounding bison. Within each group the activity of each bison was classified as foraging, resting, or traveling using instantaneous scan sampling (Altmann 1974). Foraging bison were considered to be an animal that was actively feeding or searching for forage. Resting bison were defined as those either bedded or standing and not involved in foraging or traveling.

Traveling bison were those engaged in sustained, purposeful travel and not moving in search of forage. Since an observer had to map and classify the bison group age and sex composition during surveys, he/she was present long enough to determine if bison in the group were sustaining traveling behavior. “Sustained and purposeful travel” refers to bison continuously walking with their head up. In contrast, bison can walk while foraging and in search of forage with their head lowered near the ground—behavior that was classified as foraging. For any traveling bison in each group observers recorded whether the animals were traveling off-road/off-trail, off-road/on-trail or on a road. Within both the foraging and traveling activities the number of bison displacing or not displacing snow were quantified (Bjornlie and Garrott 2001). For foraging bison, displacing snow behavior was classified by head sweeping or pawing motions to remove snow to access forage while traveling displacing snow behavior was considered as bison pushing snow with their legs while walking.

Bison Road Use Surveys

Bison use of roads was recorded daily during eight winter seasons (1997-98 through 2004-05) by four observers traveling independently using snowmobiles or trucks. The 87.3 km road network was divided into 61 segments based primarily upon topographical similarities and common travel destinations. Observers recorded survey effort (km road traveled) and only used data from a single traverse of each road segment during a 30 minute period. Group age and sex composition was recorded for all bison groups encountered traveling on the road (Bjornlie and Garrott 2001). Road use observations consisted of bison groups traveling on the road for at least 50 m. Observers also traveled road segments in early morning, before the daily influx of visitors, and recorded bison tracks on the freshly groomed roads to evaluate the magnitude of nocturnal bison road travel. Since roads were generally groomed each evening, tracks on the road in the early morning were made during the previous night.

Monitoring Bison Travel on Major Trails

I remotely monitored bison use of major migratory and travel routes by placing Trailmaster 1500 infrared trail monitors connected to 35 mm cameras along the Mary Mountain and Gneiss Creek trails (Figure 3.1) during the 1997-98, 1998-99, 2002-03, 2003-04, and 2004-05 seasons. The Mary Mountain trail is the primary bison migratory route between the Hayden Valley summer range and the MGF winter range (Meagher 1973, 1993; Bjornlie and Garrott 2001) while the Gneiss Creek trail provides an important connection between the Madison River Valley and Cougar Meadows area (Bjornlie and Garrott 2001). I placed monitors where terrain and habitat constraints forced bison to travel primarily single file in front of the monitor. As animals passed through the infrared beam the date, time, and event number were recorded and a photograph was taken to identify species and travel direction for the lead animal in the group. If the lead animal was a bison, then events clustered shortly thereafter informed me of how many bison were in the group. Several mechanical failures with the monitor resulted in short periods of missing data during all years the monitors were deployed.

Snowpack Dynamics and Covariates

The West Yellowstone SNOTEL site indexed SWE and climate trends for the lower-elevation valley bottoms in the MGF that were of particular importance to bison in the spring. I used daily data from this station from November through May for each winter to calculate three covariates related to snowpack and forage availability: 1) SWE; 2) maximum daily temperature (TEMP), and 3) springtime melt period (MELT). Snow water equivalent was used to characterize the snowpack because it represents the mean water content of the snow and affects bison energetics and forage availability more than snow depth alone, which fails to account for the density of the snowpack (Farnes et al. 1999). For instance, snow with a depth of 30 cm could consist of light powdery snow, heavy wet snow, or multiple crusted layers—all of which affect bison energetics differently. A SWE of 30 cm, however, unequivocally denotes that the snow contains the equivalent of 30 cm of water. Therefore, higher values of SWE represent greater energetic costs to bison traveling or foraging in snow. MELT was an indicator variable set to zero while snowpack accumulated, and set to one when snowpack had passed its annual peak SWE value and was declining. Both the TEMP and MELT covariates provided an index of forage availability as patches of vegetation in non-geothermal areas begin to emerge during the springtime ablation that leads to the subsequent green-up of nutrient-rich vegetation. I also obtained data from the Canyon SNOTEL site (elevation 2466 m) to examine large-scale trends in snowpack for the summer range in the Hayden Valley as one possible impetus for the bison migration (Bjornlie and Garrott 2001).

Model Development and Statistical Analyses

I defined two-week time intervals, i ($1 \leq i \leq 14$), from November through May for each winter, j ($1 \leq j \leq 8$), centered on the biweekly ground surveys that provided a census of the MGF bison population. To quantify the amount of bison road travel for each ij^{th} period I defined a road travel response variable as ρ_{ij} with units of bison groups observed per 100 km of road surveyed. Using data from my road use surveys I calculated the response as $\rho_{ij} = \beta_{ij}\sigma_{ij}$. The β_{ij} was calculated by summing the number of bison groups observed traveling on roads for the ij^{th} period and dividing by the total distance of road surveyed for that period. Dividing by survey effort was essential because of varying degrees of potential effort among periods (i.e., crew member availability) that could greatly affect the number of bison groups observed. The unitless σ_{ij}, defined as the road use weighting factor for each period, accounted for the temporally dynamic sizes of bison groups throughout the season. I calculated σ_{ij} as the total number of individual bison in road traveling groups for the ij^{th} period divided by the total number of individual bison documented in road traveling groups for the entire season. Use of a weighting factor was necessary because using β_{ij} alone would treat all bison groups equivalently, whether the group consisted of two or 100 bison, and not provide an accurate quantification of road travel.

Similarly, using data from my ground distribution surveys, I quantified the amount of bison off-road travel for each period by defining an off-road travel response variable as τ_{ij}, having units of bison groups observed traveling off-road per survey. I defined the off-road response as $\tau_{ij} = \alpha_{ij}\gamma_{ij}$, where α_{ij} is the total number of bison groups observed traveling off-road per ground distribution survey for the ij^{th} period, calculated as the sum of off-road/off-trail and off-road/on-trail traveling groups. I defined γ_{ij} as a unitless off-road travel weighting factor calculated as the number of bison observed traveling off-road during ground distribution surveys during the ij^{th} period divided by the total number of bison observed traveling off-road for the entire season during ground distribution surveys. I provide further insights into both of my response variables along with supporting figures in Appendix 3C.

Snowpack and temperature covariates were averaged across each time interval in the final analyses. In addition, I defined a covariate (GROOM) to denote if roads were groomed (0 = ungroomed; 1 = groomed) and another covariate (TRAFFIC) to provide a measure of the average numbers of OSVs entering the park's West Yellowstone entrance for each time interval. The West Yellowstone entrance receives the highest OSV visitation of any of the park's entrances with the majority of visitors traveling directly to the Old Faithful area, passing through the core bison MGF winter range in the process. Finally, I defined a covariate, BISON, using the total number of bison counted during ground surveys to obtain a measure of the influence of bison density in the entire MGF on travel.

I developed and compared *a priori* hypotheses to estimate the relative contributions of snowpack, bison numbers, the springtime melt, and—for the road travel analysis—road grooming and OSV traffic to the temporal variations in bison travel. Hypotheses were expressed as candidate models (37 models for off-road analysis; 121 for road (Appendix 3A)) in the form of regression equations consisting of covariate main effects and interactions, prudently developed to account for the complexity of the MGF ecosystem. Fitting all possible combinations of main effects and interactions (>1000 models for road analysis) would have lacked biological insight and failed to account for multicollinearity among predictors. I predicted that the same ecological factors would influence the total amounts of bison road and off-road travel and, as a result, road travel patterns would be similar to off-road travel patterns. Specifically, I hypothesized that travel would increase as a function of BISON. An increasing population density leads to more intraspecific competition for foraging areas and, as a result, increased redistribution of bison assuming dispersal by an ideal free distribution mechanism (Fretwell and Lucas 1969). Second, I predicted that road travel would increase and off-road travel would decrease with increasing SWE based on conclusions by Meagher (1993) that bison seek out energy efficient traveling opportunities (e.g., groomed roads) and accumulating snowpack deters bison travel in off-road areas. Third, I hypothesized that the effects of snowpack would depend upon bison density in a SWE*BISON interaction effect. Specifically, I expected that high SWE levels in a severe winter would further attenuate bison off-road travel and encourage road travel during periods with high bison numbers. Fourth, I predicted that travel would increase with TEMP as higher maximum temperatures in the spring would result in more snowmelt leading to increased and directed bison travel to newly melted out patches of vegetation—many of which are located in lower-elevation areas in the vicinity of the park boundary. Similarly, I predicted that travel would increase during MELT periods. Fifth, I hypothesized that bison density effects on travel would be greater at higher maximum temperatures (a positive BISON*TEMP effect) and during the springtime melt period (a positive BISON*MELT effect). Sixth, I predicted that road travel would decrease with increasing TRAFFIC because bison would attempt to minimize negative interactions with vehicles to reduce stress. I expected positive interaction effects between traffic and snowpack (TRAFFIC*SWE) and traffic and bison (TRAFFIC*BISON) because abiotic and biotic effects on travel would be accentuated during periods of high OSV traffic. Finally, I predicted that road travel would increase during GROOM periods per Meagher (1993) and that the positive effect of road grooming on travel would be greater in magnitude when either BISON or SWE was larger. That is, I expected positive estimates for GROOM*BISON and GROOM*SWE.

Because of uncertainty in the true functional relationship between bison travel and each covariate, I hypothesized *a priori* four functional structures for each continuous covariate: linear, pseudothreshold, exponential, and moderated. The linear form predicts a fixed rate of increase or decrease per unit increase in the covariate with the form of the model effect written as $\beta_i x_i$, where x_i is the centered and scaled i^{th} covariate and β_i the corresponding coefficient. The pseudothreshold form approximates an approach to an asymptotic value of the response variable with increasing covariate effects (Franklin et al. 2000) with the form of the model expressed as $\beta_i \ln(x_i+1.001)$. The exponential form allows for unbounded growth in the response variable with increasing covariate levels with a form of $\beta_i \exp(x_i)$. The moderated form (i.e., square root), expressed as $\beta_i(x_i+1)^{1/2}$, allows for faster increases in the response with x_i than the pseudothreshold function, but is attenuated at larger covariate levels unlike the linear form.

I used regression techniques in R version 1.9.0 (R Development Core Team 2004) to fit models and estimate parameter coefficients. I censored three road and one off-road outlying data points that represented either unusual periods of bison travel or low road survey effort, leaving 81 and 86 observations for road and off-road analyses, respectively. Residual and normal probability plots for both road and off-road models also demonstrated non-constant error variance and departures from normality in the error terms. I applied a square-root transform on both response variables that stabilized the variance and normalized the errors to remedy these departures from regression assumptions. I also calculated variance inflation factors (VIFs) to assess potential multicollinearity between model predictors, including interactions (Neter et al. 1996). Any model containing a predictor that had a VIF>6, given the other covariates in a model, was removed from the *a priori* model list. To allow comparisons of parameter coefficients on a similar scale, each continuous predictor was centered and scaled prior to analyses by subtracting the midpoint and dividing by half of the range resulting in values between –1 and 1.

I used a sequential model fitting technique that incorporated my *a priori* candidate model list and four hypothesized covariate functional forms. The sequential approach I implemented forced me to develop thoughtful and biologically plausible hypotheses for my models and covariate forms, the importance of which could be lost had I conducted exploratory analyses with all possible combinations of main effects, interactions, and covariate forms. I began by separately fitting all candidate models (Appendix 3A) containing only linear forms for the covariates. I calculated a corrected Akaike's Information Criterion (AIC_c) value for each model and then ranked and selected the best approximating models using ΔAIC_c (Δ) values (Burnham and Anderson 2002). Then, I selected those models whose Δ value was ≤ 10, leaving 23 and 17 models to be further evaluated for the off-road and road analyses, respectively. I chose a Δ of 10 as a criterion because models with $\Delta > 10$ have essentially no support and fail to explain variability in the data (Burnham and Anderson 2002). Next, I replaced the linear form of one covariate with its pseudothreshold form in each model (*k*) while preserving the model structure. I refit the models, calculated new AIC_c values ($AIC_{c,new,k}$), and compared $AIC_{c,new,k}$ to the previous value ($AIC_{c,min,k}$) for each model, which also represented the current minimum AIC_c available for each model structure. Then, I recalculated VIFs for the new model form with the transformed covariate. If $AIC_{c,new,k} < AIC_{c,min,k}$ and all VIFs were less than six, I then accepted the new form of the covariate for model *k*. Otherwise, the previous form was retained. This sequential procedure was repeated for each form of each covariate in each model structure. Upon completion of the sequential process I had the most appropriate covariate forms with respect to the data and model structure for each of the 23 off-road and 17 road models. As a measure of model selection uncertainty I calculated Akaike weights (w_k) based on these final models combined with the originally discarded linear models for the off-road and road analyses (full model results in Appendix 3B). To estimate the relative importance of each predictor variable, x_i, I summed Akaike weights for all models containing the predictor (in any form) to calculate the predictor weight, $w_{+(i)}$ (Burnham and Anderson 2002).

Results

Snowpack Dynamics

Snowpack accumulation began in late October to early November and built throughout the winter before peaking in late March of most years (Figure 3.2). Following the peak, ablation occurred rapidly—beginning in the lower elevation meadows in the Cougar Meadows and Madison drainage areas and ending in the high elevation meadows in the upper Firehole and Gibbon drainages. Yearly SWE accumulation (SWE_{ACC}), the sum of daily SWE measurements from October 1-April 30 (Garrott et al. 2003) at the West Yellowstone SNOTEL station, historically ranged from 908-6248 cm days from 1966-2005 with an average of 3405 cm days. Snowpack was average to below average during my study with a minimum SWE_{ACC} of 1380 cm days in 2000-01 and a maximum of 4155 cm days in 1998-99 (mean = 2487 cm days).

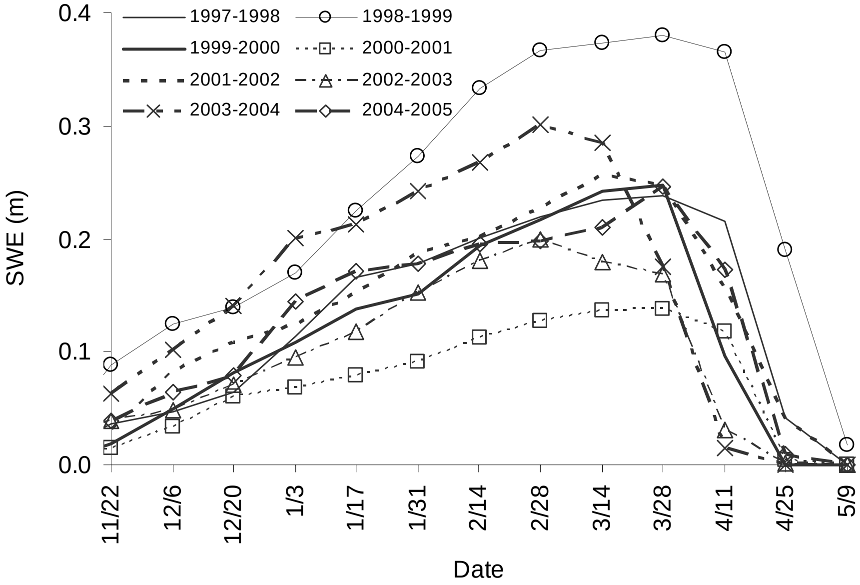


Figure 3.2. Temporal patterns in snow water equivalent in the Madison-Gibbon-Firehole area of Yellowstone National Park during winter, 1997-98 to 2004-05. Snow water equivalent (SWE) values were measured at a SNOTEL site near West Yellowstone, Montana, and averaged over two-week intervals.

Bison Migration onto MGF Winter Range

Numbers of bison in the MGF generally increased with time each winter and peaked in late March or early April (Figure 3.3). During 94 ground distribution surveys, observers counted a low of 205 bison in January 2001 and a peak of 1538 bison in late April 2005. Migration from the Hayden Valley summer range into the MGF generally started in late October and the average winter increase in bison numbers for the eight seasons was 853 ± 89 (SE). The number of bison in the MGF was positively correlated with SWE at the Canyon SNOTEL site that provided an approximation of SWE in the Hayden Valley. From regression results for individual years, R^2 ranged between a

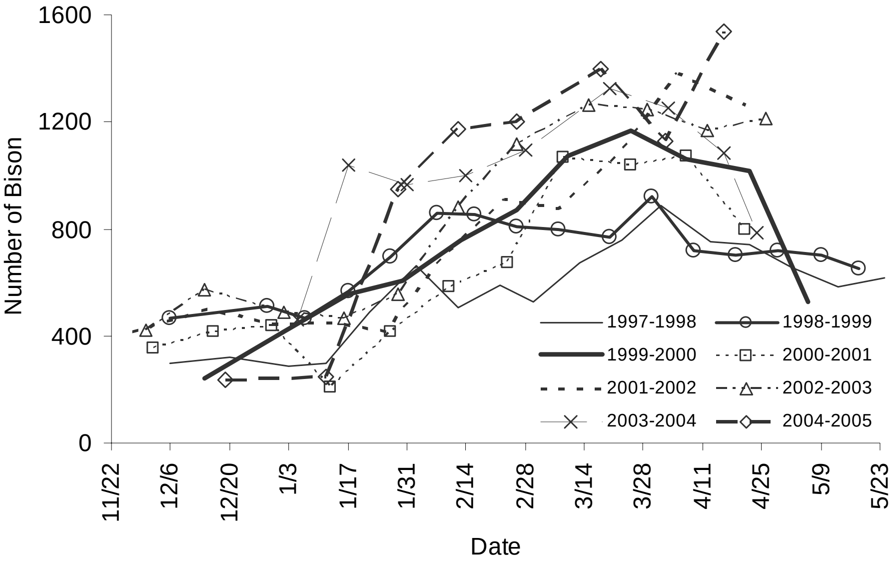


Figure 3.3. Temporal patterns in numbers of bison counted during ground distribution surveys in the Madison-Gibbon-Firehole area of Yellowstone National Park during winter, 1997-98 to 2004-05.

minimum of 0.52 (2003-04, *P* = 0.028, *n* = 9) to a maximum of 0.96 (1999-2000, *P* <0.001, *n* = 11), corroborating Bjornlie and Garrott's (2001) research suggesting snowpack in the Hayden Valley influenced bison migration to the MGF winter range.

Temporal Patterns in Bison Travel

The seasonal patterns in bison road travel documented during my road use surveys were similar across the eight years (Figure 3.4) with decreased travel throughout the middle of winter during the OSV season followed by a pronounced peak in the spring. From 1997-2005 a total of 3,156 bison groups were observed traveling on the road system during daily road use surveys, ranging from a minimum of 221 groups in 2000-01 to a maximum of 656 in 2003-04 (mean 394 ± 57). The total number of individual bison documented in these traveling groups varied from 3479 in 1999-2000 to 8538 in 2003-04 (mean 5093 ± 694) while survey effort ranged from 15067 km in 1999-2000 to 34464 km in 2004-05 (mean 23095 ± 2182). In addition to the 3156 groups observed, 256 sets of bison tracks on the road were recorded with 46% of these determined to be from nocturnal travel bouts, 43% diurnal, and 11% of unknown time of travel. From all 3412 observations only 7% represented periods of known nocturnal bison travel.

From 1997-2005, 768 bison groups were observed traveling off-road (sum of off-road/off-trail and off-road/on-trail groups) during my 94 ground distribution surveys

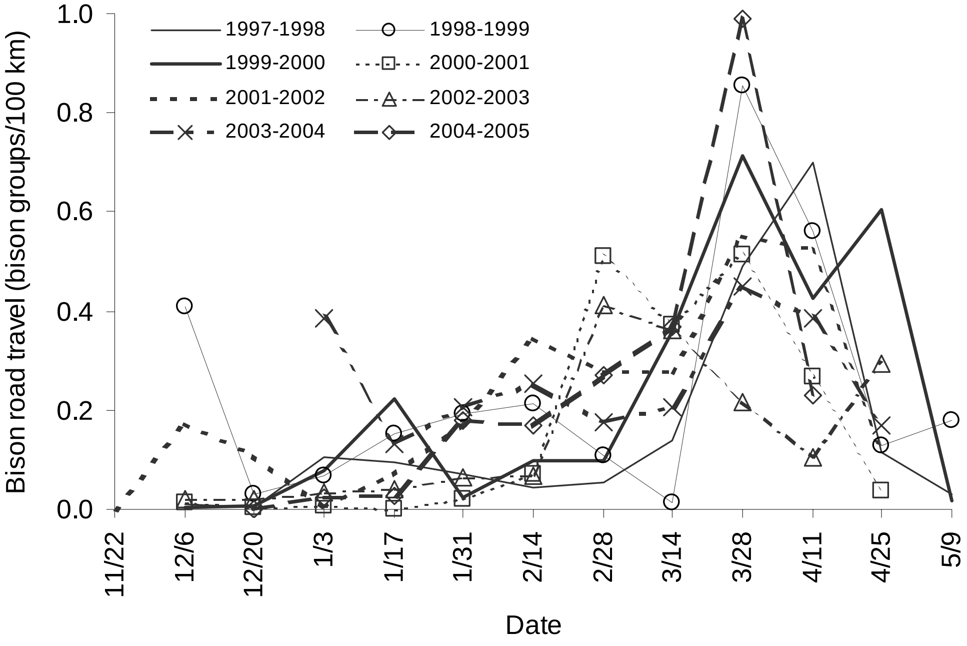


Figure 3.4. Temporal variability in bison road travel in the Madison-Gibbon-Firehole area of Yellowstone National Park during winter, 1997-98 to 2004-05. Bison groups per 100 km of road surveyed (ρ_{ij}), calculated from my road use surveys, are presented for each time interval (*i*) and year (*j*).

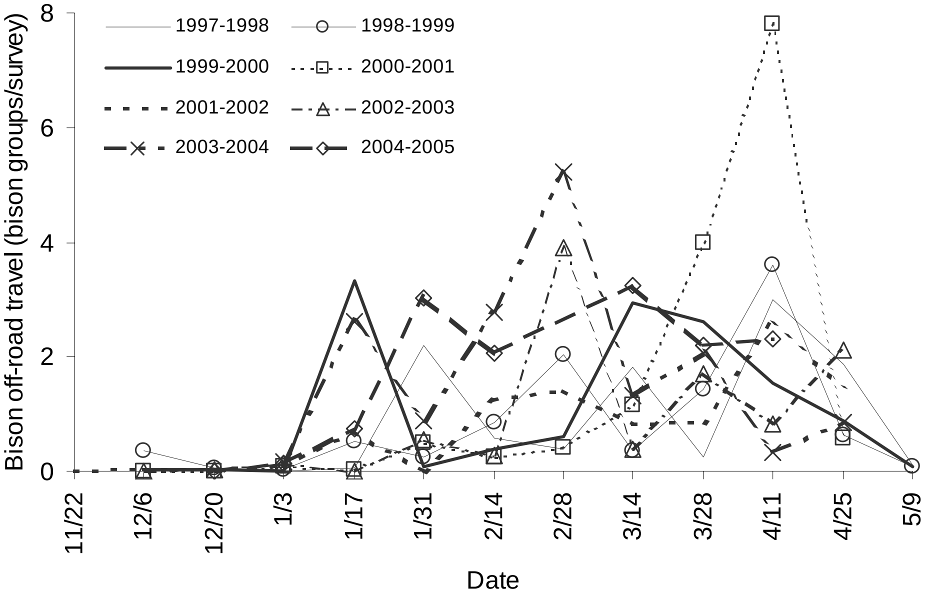


Figure 3.5. Temporal variability in bison off-road travel in the Madison-Gibbon-Firehole area of Yellowstone National Park during winter, 1997-98 to 2004-05. Bison groups traveling off-road per survey (τ_{ij}), calculated from my ground distribution surveys, are presented for each time interval (*i*) and year (*j*).

ranging from a minimum of 68 groups in 2002-03 to a maximum of 125 in 2003-04 (mean 97 ± 8). The number of individual bison in off-road traveling groups varied from a minimum of 462 in 2001-02 to a maximum of 962 in 2003-04 (mean 679 ± 63) while survey effort varied between eight surveys in 2004-05 and 17 surveys in 1997-98 (mean 12 ± 1). Seasonal patterns in off-road travel observed during ground distribution surveys (Figure 3.5) were similar to those observed for road travel during road use surveys.

Bison Activity Patterns

The behavior of 68791 bison was recorded during ground distribution surveys conducted from November to early May each year, 1997-2005, with 66.5% of bison classified as foraging, 10.5% traveling, and 23.0% resting. Thirty percent of foraging bison were displacing snow compared to only 7.0% of all traveling bison. Overall, 965 traveling bison groups were observed during my ground distribution surveys with the number of bison groups traveling on roads (n=197 groups), off-roads/off-trails (n=602), and off-roads/on-trails (n=166) differing significantly (ANOVA; $P<0.001$; Figure 3.6). The majority of bison travel observed during ground distribution surveys occurred off-road/off-trail (mean number of groups per survey, $\bar{x} = 6.2$; $P<0.001$) compared with road ($\bar{x} = 1.8$; $P<0.001$) and trail ($\bar{x} = 1.5$) usage.

Bison Travel on Major Trails

The trail monitor on the Mary Mountain trail recorded a total of 18321 bison events with the majority (75.4%) of travel having occurred diurnally. Across winters, the number of events ranged from 2473 in 1997-98 to 4644 in 2003-04 (mean 3664 ± 383). Temporal patterns in bison travel on the Mary Mountain trail varied between winters as the monitor indexed both variability in the migration into the MGF and travel between meadow complexes along Nez Perce Creek (Figure 3.7).

The Gneiss Creek trail monitor recorded a total of 18773 bison events with 82.9% of travel having occurred diurnally. Across winters, the number of events ranged from 3158 in 2004-05 to 4226 in 2003-04 (mean 3754 ± 243). Temporal trends in bison use of the Gneiss Creek trail were similar among winters as the trail received use in the late fall by early migrants into the MGF, but minimal travel during the middle of winter as snowpack accumulated (Figure 3.8). Bison travel on the Gneiss Creek trail peaked in spring when the lower elevation meadows in Cougar Meadows and the Madison Valley began to melt out and bison preferentially moved to these areas to take advantage of better foraging opportunities.

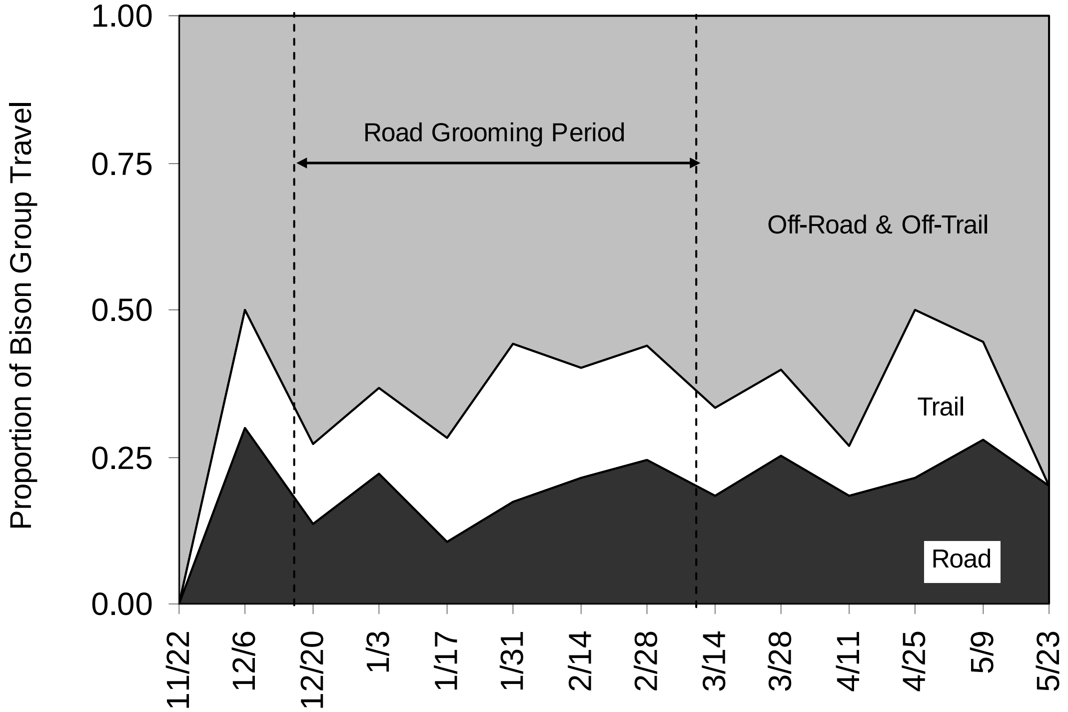


Figure 3.6. The proportion of bison groups traveling on roads, off-roads/on-trails, and off-roads/off-trails during ground distribution surveys in the Madison-Gibbon-Firehole area of Yellowstone National Park, 1997-98 to 2004-05. The winter road grooming season is delineated by dashed lines.

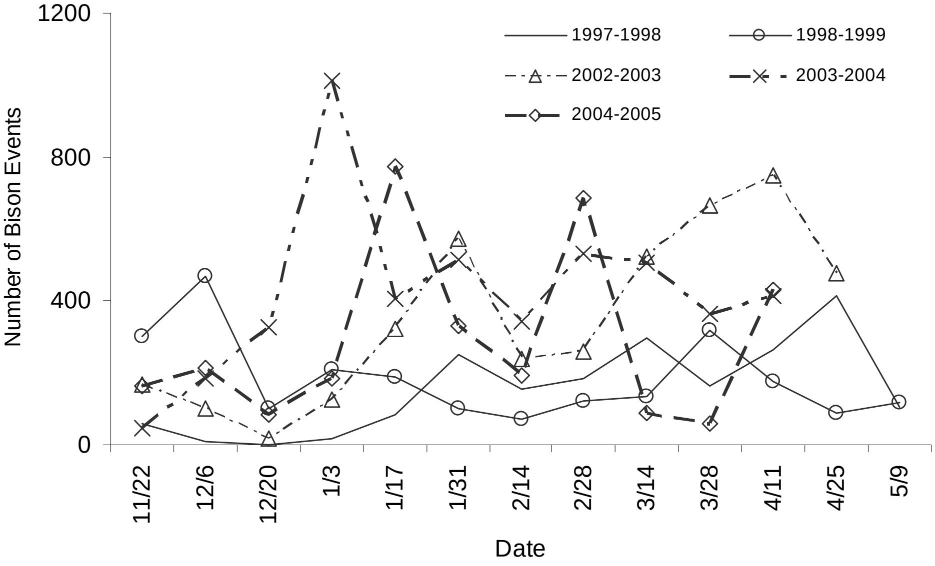


Figure 3.7. Number of bison movement events recorded by a trail monitor on the Mary Mountain trail between the Firehole and Hayden Valleys in Yellowstone National Park. Data were collected during the 1997-1999 and 2002-2005 seasons.

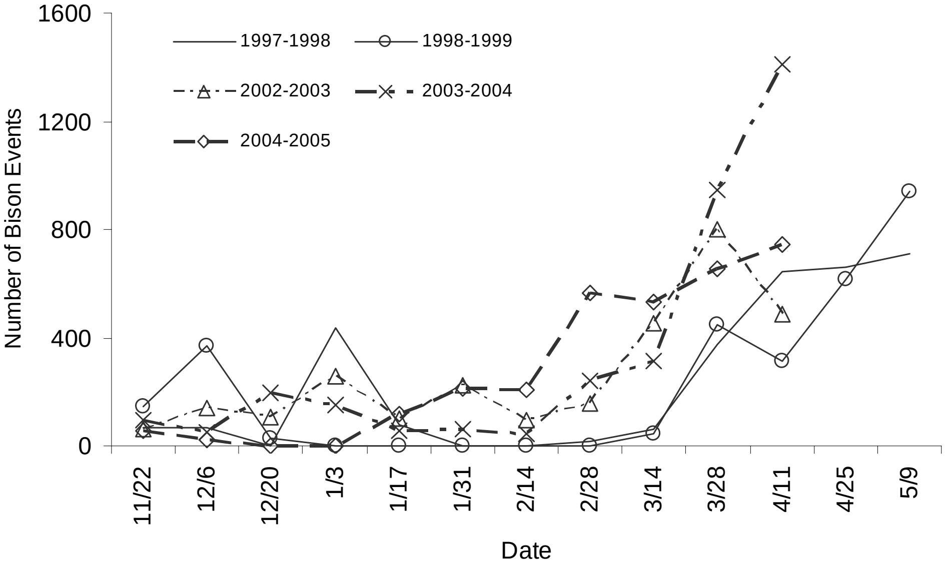


Figure 3.8. Number of bison movement events recorded by a trail monitor on the Gneiss Creek trail between the Madison River Valley and Cougar Meadows area in Yellowstone National Park. Data were collected during the 1997-1999 and 2002-2005 seasons.

Modeling Temporal Variation in Bison Travel Behaviors

Road Travel. Four models, each having Δ≤2, received the greatest support in my road travel analysis (Table 3.1) with model r2.8 considered the best approximating model with an Akaike weight (w_k) of 0.220. Model r2.10, differed from r2.8 by 0.85 AIC_c units and had a w_k of 0.144, resulting in a relative likelihood of 1.53 between the top two models and suggesting two nearly equivalent best approximating model structures. Models r2.14 and r2.66 had weights of 0.088 and 0.081, respectively, indicating r2.8 had nearly three times as much support in the data. The covariates SWE, BISON, and GROOM, and the SWE*BISON interaction were included in each of the four most parsimonious models and had the four highest predictor weights (Table 3.2). The covariate MELT was contained only in model r2.14, while TEMP was not included in any of the four top models (Table 3.1). Model r2.66, which contained the same

Table 3.1. Model selection results for *a priori* hypothesized models examining the effects of biotic, abiotic, and anthropogenic covariates on variation in bison road travel. The four best approximating models are presented along with the number of parameters (K), the ΔAIC_c value, and the Akaike weight (w_k).

Model	**Structure**	**K**	**ΔAIC_c**	**w_k**
r2.8‡	$\beta_0 + \beta_1(SWE) + \beta_2(BISON) + \beta_3(GROOM) + \beta_4(SWE)(BISON)$	5	0.000	0.220
r2.10	$\beta_0 + \beta_1(SWE) + \beta_2(BISON) + \beta_3(GROOM) + \beta_4(SWE)(BISON) + \beta_5(GROOM)(BISON) + \beta_6(GROOM)(SWE)$	7	0.851	0.144
r2.14	$\beta_0 + \beta_1(SWE+1)^{1/2} + \beta_2(BISON) + \beta_3(GROOM) + \beta_4(MELT) + \beta_5(BISON)(SWE+1)^{1/2}$	6	1.841	0.088
r2.66	$\beta_0 + \beta_1(SWE) + \beta_2(BISON) + \beta_3(GROOM) + \beta_4\ln(TRAFFIC+1.001) + \beta_5(SWE)(BISON)$	6	2.000	0.081

‡ AIC_c value for model r2.8 is –90.485

Table 3.2. Coefficient values and lower (LCI) and upper (UCI) 95% confidence limits from the four best approximating models (models r2.8, r2.10, r2.14, r2.66) identified through AIC model comparison techniques examining temporal variability in bison road travel. Bold notation denotes significant coefficients at $\alpha = 0.05$. Predictor weights ($w_{+(i)}$) are presented for the overall modeling exercise with interactions having $w_{+(i)}<0.005$ omitted for clarity.

	Model	**r2.8**	**r2.10**	**r2.14**	**r2.66**
Covariate	$w_{+(i)}$	β_i	β_i	β_i	β_i
SWE	1.000	**0.194 (0.123, 0.265)**	**0.230 (0.150, 0.309)**	**0.306 (0.194, 0.419)**	**0.197 (0.125, 0.269)**
BISON	1.000	0.083 (-0.001, 0.166)	0.067 (-0.042, 0.176)	**0.422 (0.223, 0.621)**	0.079 (-0.006, 0.164)
GROOM	0.996	**-0.187 (-0.254, -0.119)**	**-0.193 (-0.264, -0.121)**	**-0.179 (-0.255, -0.104)**	**-0.154 (-0.286, -0.022)**
SWE*BISON	0.853	**-0.265 (-0.426, -0.104)**	**-0.301 (-0.476, -0.127)**	**-0.354 (-0.584, -0.125)**	**-0.251 (-0.420, -0.082)**
GROOM*BISON	0.363		0.048 (-0.108, 0.204)		
GROOM*SWE	0.240		-0.160 (-0.332, 0.012)		
TRAFFIC	0.231				-0.006 (-0.026, 0.014)
MELT	0.202			0.063 (-0.026, 0.153)	
TEMP	0.144				

covariates as r2.8 plus TRAFFIC, had a Δ=2.0 indicating TRAFFIC added no explanatory power to the top model. The covariate SWE was of linear form in three of the models, but of moderated form in model in r2.14. The functional form of BISON was consistent in all four models with a linear effect. As hypothesized, SWE and BISON had positive effects on bison road travel. Contrary to my predictions, road grooming (GROOM) and the SWE*BISON interaction had negative influences.

Off-Road Travel. The off-road travel modeling efforts resulted in two models receiving the greatest support with model o1.19 considered the best approximating model with w_k=0.267 (Table 3.3). Model o1.23 differed by a Δ of 1.04 and had a weight of 0.158 indicating that model o1.19 was nearly twice as supported by the data than o1.23. The covariates SWE, BISON, MELT, and the BISON*MELT interaction had the highest predictor weights and were the only covariates to appear in each of the top two models. Both the SWE*MELT and SWE*BISON interactions were only included in model o1.23 (Table 3.4). SWE was of moderated form in model o1.19 and had a linear effect in model o1.23 while all other covariates were of linear forms in both models. As predicted, BISON and MELT had positive effects on bison off-road travel. Contrary to my predictions, however, the SWE influence was positive and the BISON*MELT effect was negative.

Table 3.3. Model selection results for *a priori* hypothesized models examining the effects of biotic and abiotic covariates on variation in bison off-road travel. The two best approximating models are presented along with the number of parameters (K), the ΔAIC_c value, and the Akaike weight (w_k).

Model	**Structure**	**K**	**ΔAIC_c**	**w_k**
o1.19‡	$\beta_0 + \beta_1(SWE+1)^{1/2} + \beta_2(BISON) + \beta_3(MELT)$ $+ \beta_4(BISON)(MELT)$	5	0.000	0.267
o1.23	$\beta_0 + \beta_1(SWE) + \beta_2(BISON) + \beta_3(MELT)$ $+ \beta_4(SWE)(BISON) + \beta_5(BISON)(MELT)$ $+ \beta_6(SWE)(MELT)$	7	1.041	0.158

‡ AIC_c value for model o1.19 is 81.052

Table 3.4. Coefficient values and lower (LCI) and upper (UCI) 95% confidence limits from the two best approximating models (models o1.19 and o1.23) identified through AIC model comparison techniques examining temporal variability in bison off-road travel. Bold notation denotes significant coefficients at $\alpha = 0.05$. Predictor weights ($w_{+(i)}$) are presented for the overall modeling exercise.

	Model	**o1.19**	**o1.23**
Covariate	**$w_{+(i)}$**	**β_i**	**β_i**
BISON	1.000	**0.927 (0.679, 1.176)**	**0.949 (0.653, 1.244)**
SWE	0.991	**0.506 (0.229, 0.783)**	0.042 (-0.272, 0.356)
MELT	0.780	0.160 (-0.075, 0.396)	0.151 (-0.075, 0.378)
BISON*MELT	0.603	**-0.583 (-1.009, -0.158)**	**-0.692 (-1.166, -0.218)**
SWE*BISON	0.353		-0.374 (-0.873, 0.124)
TEMP	0.298		
SWE*MELT	0.188		**0.447 (0.026, 0.868)**
TEMP*BISON	0.097		
TEMP*MELT	0.025		

Discussion

Temporal trends in bison travel in the MGF are influenced by multiple, interacting effects as the best approximating models found snowpack, bison density, and road grooming all to be influential factors affecting variability in the amount of bison road travel. Likewise, the most parsimonious off-road travel models found snowpack, bison density, and springtime snowmelt to be significant in accounting for temporal variation in the amount of bison off-road travel. My results suggest that temporal road travel patterns are likely a manifestation of general bison travel trends since both are affected by similar abiotic and biotic factors. Indeed, an examination of the tendencies of road and off-road travel (Figures 3.4 and 3.5) reveals a peak in travel in the spring and decreased travel during the winter, the road grooming period. Temporal variability in the movements and distribution of large mammals have been shown to be influenced by animal density (Ferguson et al. 1998, Reynolds 1998), snow (Messer 2003, Doerr et al. 2005), availability and quality of forage resources (Wallace et al. 1995, Pettorelli et al. 2003), and human disturbance (Klein 1991, Etter et al. 2002). While many studies have focused on the behavioral responses of wildlife to only one of these factors, my research used a combination of these elements to understand bison travel patterns in a temporally dynamic landscape.

Bison road travel was negatively correlated with road grooming, a result counter to Meagher's (1993) contentions that bison seek out groomed roads to avoid traveling through deep snow. I found no evidence that bison preferentially used groomed roads during winter because the amount of road travel was actually reduced during the grooming period. My conclusions, drawn from eight years of bison road travel data, extend and corroborate those reported by Bjornlie and Garrott (2001). Further, my findings indicate that this decrease in road travel during winter is likely a manifestation of natural bison travel behavior during winter rather than an avoidance response of bison to OSVs. The effect of anthropogenic influences on animal behavior and movements remains controversial (Kuck et al. 1985, Lott and McCoy 1995, Morrison et al. 1995), but my results suggest bison have learned to coexist with OSVs to some level because the TRAFFIC covariate did not appear as a significant effect in any of my best approximating models and had a low predictor weight. This is in accordance with Borkowski et al. (*in press*) who found that bison and elk had habituated to OSVs to some degree in the MGF.

Snow water equivalent had a positive influence on both bison road and off-road travel in the MGF and, on a larger scale, my results suggest that the bison migration to the MGF is driven, in part, by snow accumulation in their summer range in the Hayden and Pelican Valleys. My findings coincide with other studies that found snowpack dynamics to be a major impetus influencing ungulate movements in various ecosystems (Pruitt 1959, Sweeney and Sweeney 1984, Ball et al. 2001). The best approximating road travel models contained both significant linear and moderated SWE effects while the top off-road model had a moderated SWE form with a coefficient not spanning zero. As predicted, I found SWE to have a positive influence on road travel for both winter and spring, but also found off-road travel to be positively correlated with snowpack—contrary to my hypothesis. Since my results indicate that road travel is a manifestation of general bison travel behavior, this positive SWE influence may actually be the result of a combination of confounding factors. First, the peak in SWE in the spring (Figure 3.2) coincides with the beginning of the melt out of lower elevation meadows, which also corresponds with a large increase in bison travel compared to winter (Figures 3.4 and 3.5). As a result, the positive correlation of travel with snowpack is likely more an artifact of high SWE values at this time period when bison are actually responding to energy efficient foraging opportunities with increased travel to redistribute themselves to meadows that have partially melted out. Second, the West Yellowstone SNOTEL site does not afford estimation of small-scale, spatially explicit trends of snowpack. This is of particular importance during the springtime melt period when the heterogeneous landscape is comprised of small patches of snow-free vegetation amidst remnant snow. My future work will incorporate a spatially explicit snowpack model to better address the annual variability and complexities of snowpack influence on bison travel during the springtime melt.

In accounting for the importance of the springtime melt period one of my best approximating off-road travel models contained a significant and positive SWE*MELT effect resulting in increased travel during the spring (Table 3.4). This is further evidence that bison travel in response to snowmelt begins while SWE levels are still high. Additionally, my most parsimonious road travel models contain the covariate GROOM, which had a high predictor weight (Table 3.2). The negative influence of GROOM, which can also be thought of as a surrogate covariate for winter (i.e., MELT=0), resulted in a reduced amount of road travel in winter when roads were groomed relative to spring. This influence of snowpack on bison travel provides further evidence that road travel is an extension of general travel behavior because bison reduced both off-road and road travel during winter. To conserve energy bison reduce movements as snowpack accumulates because foraging areas, with the exception of geothermal meadows, are all covered with deep snow and contain senescent vegetation. My results agree with other studies that document forage availability and quality as primary factors influencing large herbivore distribution and movement in all seasons (Campbell and Hinkes 1983, Larter and Gates 1991, Wilmshurst et al. 1999).

Bison road and off-road travel were both positively correlated with the number of bison in the MGF. Increasing animal abundance and density have been shown to trigger movements, whether in the form of dispersal (Einum and Nislow 2005), migration (Mahoney and Schaefer 2002), or in search of forage (Ramp and Coulson 2002). My results support these findings and were anticipated because redistribution should eventually occur as more bison enter an area of limited space—be it a small meadow or a large drainage—and some threshold limit of occupancy is reached. As this threshold is approached, competition for food becomes pronounced and foraging is no longer optimal owing to poor forage quality, increased searching time, displacement by cospecifics, proximity to other suitable foraging areas, or some combination of these factors. Bison redistribution manifests itself in a travel bout, either of short distance to a nearby meadow or perhaps a longer movement along a travel corridor to a more distant foraging area. As the number of bison in the MGF increases throughout the winter, the frequency of redistribution should increase as foraging areas reach their occupancy limits. It is likely that the same type of density-dependent response led to the central herd's range expansion into the MGF and beyond as bison sought out new foraging areas as a result of increased resource competition.

As anticipated, given the complexity of the underlying ecological processes, significant interactions were present in my best approximating road and off-road models. Opposite of my hypothesis, road travel was negatively correlated with SWE*BISON, which was significant in all four top models with a predictor weight of 0.853 (Table 3.2). At high levels of either SWE or BISON this interaction attenuates the positive main effects of snowpack and bison density that, by themselves, may overestimate the amount of road travel. In the top off-road travel models I found a significant BISON*MELT interaction that was negatively correlated with travel. Similar to the SWE*BISON effect, I interpret this negative interaction as limiting the positive main effect of bison density on the magnitude of travel at high bison levels during spring.

My results have demonstrated bison travel in response to abiotic and biotic stimuli, but I have yet to consider possible behavioral changes owing to anthropogenic factors. Bison may have responded to increased interactions with OSVs over the years by traveling the road systems at night when traffic was minimal. Though I found no significant traffic effect in my models, I have limited data to address this hypothesis as monitoring of bison road use occurred primarily during daylight hours. However, data from the trail monitors that continuously recorded bison movements on the Mary

Mountain and Gneiss Creek trails suggested that 75% and 83%, respectively, of bison travel on these trails occurred during daylight hours. In addition, only 7% of observations during road use surveys represented nocturnal bison road travel bouts. This is in agreement with Meagher (1986), who stated that bison are primarily active during diurnal hours, and logs kept by nighttime road groomer operators who observed only nine and 22 bison groups traveling nocturnally during the 1997-98 and 1998-99 seasons, respectively (Bjornlie and Garrott 2001). These data, though limited, do not indicate bison switch to nocturnal road travel to avoid ephemeral interactions with OSVs. Indeed, Fortin and Andruskiw (2003) found that although bison responded to human disturbance, they altered their distribution and resource use only in relation to environmental factors and not negative interactions with people. Ongoing telemetry studies with Global Positioning System (GPS) collars on adult female bison from the central herd will lend additional insights to this question.

A further contention on the effect of road grooming is that bison seek out roads to avoid energy expenditures from having to displace snow while traveling. No accurate or validated models exist for predicting bison energy expenditures in snow (Gates et al. 2005). Studies on other ungulates have documented energy expenditure for locomotion to increase with snow density and sinking depth (Parker et al. 1984, Dailey and Hobbs 1989) and it is likely these general relationships apply to bison. However, I found that travel is only a small percentage (11%) of all bison activity with foraging comprising 67% of observations. Also, only 7% of traveling bison and 30% of foraging bison were displacing snow. Given that only 0.7% of all activity consisted of traveling bison displacing snow, I suggest foraging, rather than traveling, is likely the major energetic cost to bison in winter. I also documented that bison utilize their own trail network, connecting foraging areas using stream corridors, geothermal pathways, and self-groomed travel routes. In fact, one of the most heavily used travel corridors during winter is the Mary Mountain trail (Figure 3.7) that is not located near any roads. This trail was kept in a hard packed and "groomed" state by bison each winter owing to migrations to the MGF and movements between foraging areas along Nez Perce Creek.

No data was collected on bison distribution and travel before road grooming began and, therefore, no true experimental control case of bison road travel exists. Controlling external abiotic and biotic factors, such as winter severity and the number of bison in the MGF, is not possible and these variables may confound any grooming effect in a designed experiment anyway. While my study does not afford sufficient conditions to infer causation because of its observational design, my research is the first to address the issues of bison travel and road grooming in Yellowstone with long term data collected with systematic rigor. Overall, my results indicate that temporal patterns in bison road travel are an extension of general travel behavior. Grooming of roads in the MGF does not appear to be a major factor influencing bison ecology and spatial redistribution as proposed by Meagher (1993). In particular, my results suggest bison travel less during winter both on and off-road and that bison density, snowpack, and springtime melt are the primary factors influencing travel. Groomed roads are likely not significantly more energy efficient for travel than their own network of trails, which bison use extensively to connect foraging areas and for migration. In fact, bison interactions with OSVs at close proximity may actually result in occasional behavioral responses that would lead to increased energetic costs (Borkowski et al. *in press*). Bison leaving the park along the western boundary, which is one of the most controversial topics in bison management, does not appear to be facilitated by road grooming because these movements to lower elevations occur primarily in the springtime after road grooming has ceased. Additionally, the route that bison use to leave the park is not a road, but rather a series of trails along streams that begin with the Gneiss Creek trail. Range expansion and density-dependent dispersal by ungulates is a well-known response to increasing population size (Heard and Calef 1986, Messier et al. 1988, Gates and Larter 1990). I suggest that the changes in bison spatial dynamics during the past three decades have likely been the result of the natural phenomenon of density-dependent range expansion rather than caused by the anthropogenic influence of road grooming. I am currently analyzing bison GPS data to understand the role of topography and habitat in influencing spatial patterns in bison travel to further address this issue.

CHAPTER 4:
MECHANISMS AFFECTING FORAGING AREA RESIDENCE TIMES OF YELLOWSTONE BISON: APPLICATIONS FOR LARGE HERBIVORE MANAGEMENT

Abstract

One challenge in managing large herbivores and understanding their foraging dynamics is integration of information across several spatio-temporal scales. I present a method for analyzing large herbivore foraging behavior in dynamic landscapes across multiple scales using the foraging area residence time (τ), which can be expressed as a function of local and landscape level factors, including suites of abiotic and biotic effects and previous foraging experiences. I apply the method to bison (*Bison bison*) in the Madison-Gibbon-Firehole (MGF) area of Yellowstone National Park (YNP), Wyoming, USA. I used telemetry homing techniques to obtain 130 foraging area locations on 20 bison equipped with GPS collars during winter 2004 and 2005 and subsequently calculated τ from GPS data. In each area, I recorded group size and sampled snowpack snow water equivalent (SWE) and forage biomass. I conducted surveys twice monthly ($n = 13$) to enumerate the number of bison in the MGF and collected landscape scale SWE data. I used mixed effects multiple regression and information theoretic techniques to evaluate the relative influence of snowpack, competition, forage biomass, and previous foraging experiences on τ. Residence times were affected by the ratio of local to landscape scale snowpack SWE, previous foraging experiences, and both local and

landscape scale intraspecific competition. These results indicate the amount of time bison spend in one foraging area is dependent on a suite of abiotic and biotic factors that affect resource availability, and the perceived value of the area relative to other recently visited areas. The results reinforce the idea that foraging by large herbivores may be simultaneously affected by mechanisms operating across multiple spatial and temporal scales. My findings are of relevance to Yellowstone managers since knowledge of influential abiotic and biotic mechanisms affecting τ provides a means for quantifying habitat importance across space and time. This is essential for comprehending population processes for a bison population that is currently growing and expanding its range. Collectively, this work provides new insights into large herbivore foraging dynamics using a novel approach applicable to the management of numerous species.

Introduction

Comprehending the density dependent and density independent mechanisms affecting animal spatio-temporal dynamics, which may be related to foraging behavior, is of paramount importance to wildlife managers. Climate, predation, and density-related effects—which can affect resource availability and population level processes—may influence where animals forage, optimal foraging area residence time, and general foraging behavior (Willis 1966, Grubb 1975, Inouye 1978, Roubik 1980, Hanley 1984, Fleming and Heithaus 1986, Kohler and McPeek 1989, Mitchell et al. 1990, Wachob

1996, Kie 1999). Variability in climate affects food availability, predatory pressure may limit access to areas of abundant resources, and density-related feedbacks may be manifested in a limitation of per capita resources and variation in competition over space and time. As a result, an animal's perception and estimation of the value of a foraging area, based on the quality or abundance of resources, may change with space and time since abiotic and biotic effects are dynamic (Bailey et al. 1996). Therefore, the resulting spatio-temporal changes in foraging area use and residence times may be indicative of this variation in resource quality and abundance with time and across space.

Previous foraging experiences may also affect how animals perceive and estimate foraging area value (Valone and Brown 1989, Valone 1991). Birds have been found to use prior information about patches to assess quality (Valone and Giraldeau 1993) and Boivin et al. (2004) documented that some insects estimated patch quality based on the first patch encountered rather than a fixed estimate. Cattle, after feeding in a site of low quality forage, avoided the site for three weeks, instead preferring locations with higher quality forage (Bailey 1995). Spatial memory, needed for animals to apply previous information to evaluate foraging area quality, has been documented in assorted species, including large herbivores (Bailey 1989, Gillingham and Bunnell 1989, Hewitson et al. 2005). Further, in a dynamic landscape, an animal's perceptions and expectations of foraging area value based upon previous foraging experiences may vary spatially and temporally, and depend upon scale, as abiotic and biotic influences change.

Large herbivore foraging decisions are not independent of either spatial or temporal scale and may be affected by biotic or abiotic factors (Senft et al. 1987, Ward and Saltz 1994, Bailey et al. 1996, Fortin et al. 2002). The possibility exists that knowledge of mechanisms influencing foraging dynamics at one scale can be used to infer behavior at another in a hierarchical approach (Senft et al. 1987). Factors affecting foraging decisions at small patch scales, however, may not necessarily be considered in the absence of larger scale effects to predict behavior at landscape scales, especially in complex and dynamic environments (Wallace et al. 1995, Bailey et al. 1996, Fortin et al. 2003). The impacts of extrinsic and intrinsic processes, which affect large herbivore population dynamics (Sæther 1997, Post and Stenseth 1999, Gaillard et al. 1998), on resource availability and foraging behavior must be evaluated on both local and landscape scales. Climate effects, such as winter severity or drought, may affect where herbivores choose locations on broad scales, which may subsequently influence small-scale foraging decisions (Terry et al. 2000). The presence of predators, including wolves (*Canis lupus*), lions (*Panthera leo*), and spotted hyenas (*Crocuta crocuta*), may offer large herbivores with a continuum of choices—ranging from foraging in an area with good protection from predators but poor food supplies, to choosing an area of good food quality and abundance but high predation risk (Sinclair and Arcese 1995). Additionally, grazers often must make foraging decisions while competing with cospecifics in heterogeneous environments of patchy forage resources. Therefore, a challenge in managing large herbivores and understanding their foraging dynamics is the integration of information across multiple scales (Hobbs 1996, Gordon et al. 2004).

I present a method for analyzing large herbivore foraging behavior on large spatial and temporal scales in heterogeneous and dynamic landscapes that can be evaluated using metrics obtainable from observational field studies, which are often necessary with large mammals. My approach melds concepts from traditional foraging theory with a framework that focuses on behavioral processes (Senft et al. 1987) while integrating information on abiotic and biotic factors, as well as previous experiences of individual animals, across multiple scales. Essential to the method is the concept of optimal residence time and I define the foraging area residence time (τ_i) for area i as the total time an animal spends in one foraging area. Rather than using theory based on expected energy gains across an aggregation of patches as in foraging theory (Charnov 1976, Stephens and Krebs 1986), I define τ_i as the optimal residence time as dictated by animal behavior, which can be expressed as a function of local and landscape level factors at any point in time, i.e., $\tau_i = f(a,b,e)$, where a and b are suites of potentially influential abiotic and biotic effects, respectively, and e is an index of previous foraging area experiences. I also define τ_i as a measure of the perceived value of a foraging area by assuming that the longer an animal spends in one foraging area, the greater the energy gains (i.e., value) from abundant or high quality forage, minimal competition, low predation risk, and minimal interference from climate effects (e.g., deep snow covering vegetation). My definition of the spatial and temporal scales of a foraging area corresponds roughly to those from Bailey et al. (1996) that considers an herbivore to be in a “feeding site” for 1-4 hours. However, Bailey et al. (1996) does not define the temporal scales between a feeding site and a “camp.” Therefore, I define a foraging area as an area used by an animal for feeding and resting between foraging bouts that extends between 30 min and several days.

In observational field studies of large herbivores, measures of τ_i can be obtained through the use of individual animals equipped with Global Positioning System (GPS) collars. From the GPS data, subtracting the animal's arrival date/time into the foraging area from the departure date/time from the area affords estimation of τ_i. Potential explanatory covariates for a and b can be acquired through data collection on foraging area attributes by ground telemetry tracking individual animals to foraging areas. Landscape level covariates may be obtained from surveys for animal abundance and remote climate stations to approximate landscape conditions. The index of previous foraging area experiences (e) may be acquired by detailed examination of the GPS data.

I present an application of our method using bison (*Bison bison*) from Yellowstone National Park (YNP), Wyoming, USA, which encounter a complex array of biotic and abiotic factors that may influence foraging decisions on multiple scales. In the Madison, Gibbon, and Firehole drainages—which provide winter range for the migratory central Yellowstone bison herd—this suite of effects is particularly intricate owing to the geothermally influenced habitats, severe winter climate, and variability in resource distribution. Understanding what influences the spatio-temporal foraging dynamics of bison is of direct importance to YNP, which is faced with managing a growing bison population that is expanding its range beyond park boundaries. This expansion has resulted in controversy, in part, because of the possibility of brucellosis transmission from bison to livestock on public lands outside of the park (Baskin 1998, Cheville et al. 1998, National Park Service 2000*a*). The debate over appropriate management activities continues at present (Bruggeman et al. *in press*). Here I use an information theoretic approach to evaluate factors influencing winter foraging area residence times of bison and understand spatial and temporal variability in foraging area use in the context of management. Collectively, this work provides new insights into large herbivore foraging dynamics using a novel approach applicable to numerous species.

Study Area

The study area in west central Yellowstone National Park, Wyoming, USA, encompassed the drainages of the Firehole River upstream from Madison Junction to Old Faithful; the upper Madison River east from the Park boundary at West Yellowstone to Madison Junction, and the Gibbon River upstream to Norris Geyser Basin (Figure 4.1). The area also included portions of the Mary Mountain trail extending from the Firehole drainage east to Mary Lake and meadows along Cougar Creek near the western boundary of the Park. Elevations within this 8000 ha area ranged from 2000-2250 m.

The migratory central Yellowstone bison herd numbered >3000 animals (Gates et al. 2005) during this study (2003-2005). Meadow complexes and geothermal areas on the Madison-Gibbon-Firehole (MGF) winter range provided foraging habitats for migratory bison, with major foraging areas often connected by corridors through canyons and/or along streams (Bruggeman *et al. in review, a*). High elevation plateaus and/or mountain ranges constrained bison to lower elevation valley bottoms during winter.

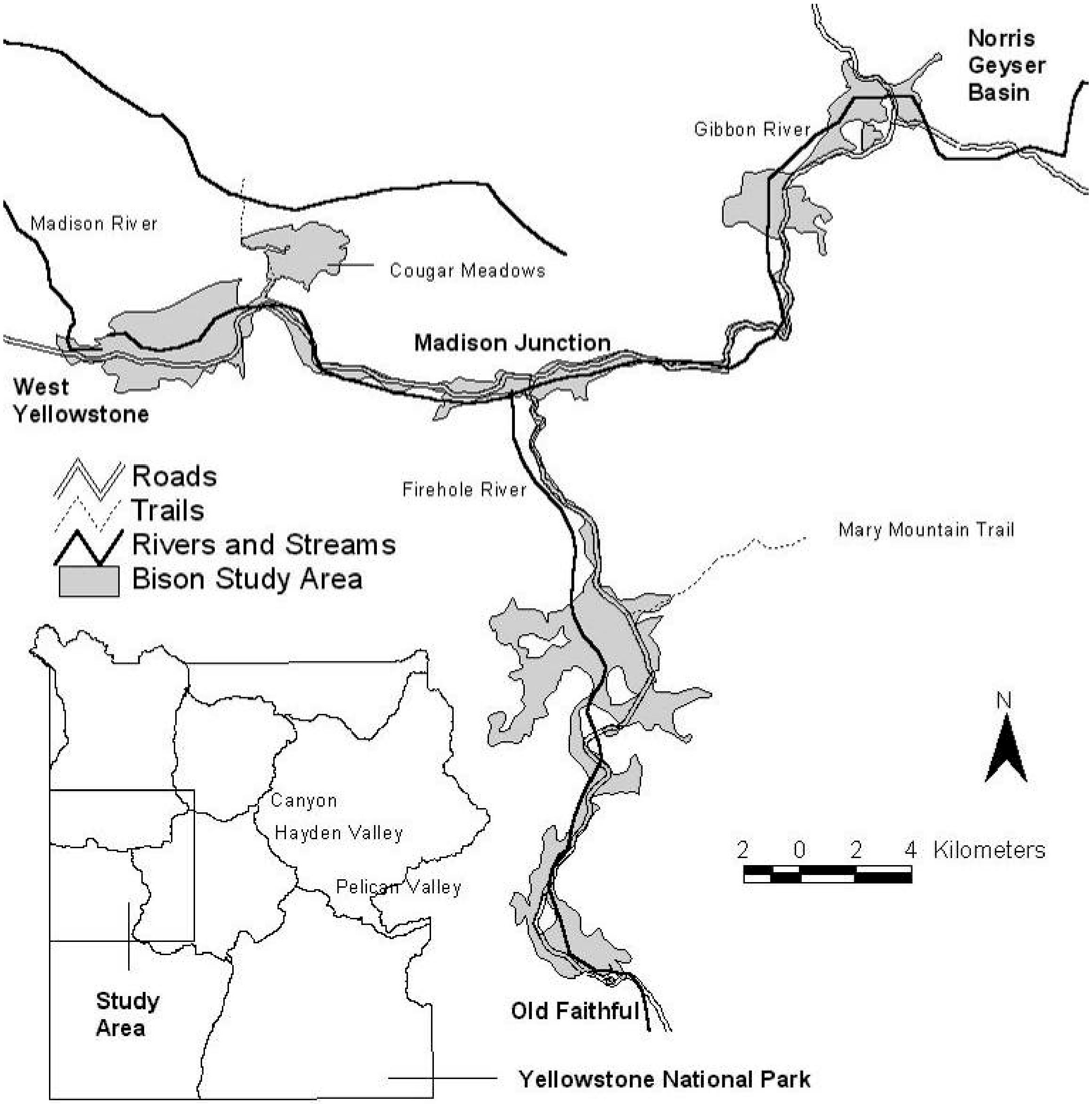


Figure 4.1. The Madison-Gibbon-Firehole study area in Yellowstone National Park, Wyoming and Montana, USA.

There were four major geothermal areas in the MGF along with smaller pockets of geothermal activity that had reduced snow accumulation and longer growing seasons compared to surrounding meadows. Sedges (*Carex* spp.) and grasses (*Calamagrostis* spp.) characterized wet meadows, while dry meadows were dominated by grasses (*Poa* spp., *Festuca idahoensis*) and sagebrush (*Artemesia* spp.). More than 50% of forested areas burned during summer 1988 (Despain 1990) and these areas were characterized by downed trees, snags, regenerating lodgepole pine, Ross' sedge (*Carex rosii*), elk sedge (*Carex geyeri*), and leafy aster (*Aster foliaceus*) during our study. Unburned forested areas were predominantly lodgepole pine (*Pinus contortus*) with understories of elk sedge, grouse whortleberry (*Vaccinium scoparium*), and pinegrass (*Calamagrostis rubescens*). The lowest elevation areas also included scattered Douglas fir (*Pseudotsuga mensiesii*), while Engelmann spruce (*Picea engelmanni*) and subalpine fir (*Abies lasiocarpa*) occurred at higher elevations.

The MGF area typically experiences severe winters with an annual average of 189 days of snow cover (Natural Resources Conservation Service (NRCS) National Water and Climate Center Public Communication 2006). Mean annual peak snow water equivalent (SWE) was 34.1 cm at the West Yellowstone NRCS Snowpack Telemetry (SNOTEL) site (elevation 2042 m) during 1966-2005. During our study, winters were relatively mild with a peak SWE of 30.7 cm in 2003-04 and 25.7 cm in 2004-05. Snowpack began accumulating in late October in the valleys and continued to build until April, at which point ablation occurred.

Methods

Foraging Area Residence Time

Fifteen GPS/VHF collars (Model TGW 3700, Telonics, Mesa, AZ) were deployed on adult female bison beginning in November 2003 and then redeployed on different adult female bison beginning in November 2004. Collars were distributed on bison in the Hayden and Pelican Valley summer range and on early migrants to the MGF winter range using ground darting with Carfentanil. From January to mid-March 2004, locations were recorded every 30 minutes from 0700 to 1900 with fixes also taken at 2300 and 0300. From mid-March onward, locations were recorded every 30 minutes from 0600 to 2300 with fixes also recorded at 0100 and 0300. In 2005, locations were recorded every 48 minutes during both day and night.

I visually located collared bison within a group of bison (≥1 animal) that were foraging using telemetry homing techniques (White and Garrott 1990) from January-March during 2004 and 2005 in the MGF area. I recorded the collar number, time, and foraging area location upon finding the animal. The frequencies of bison to be tracked were determined on a daily basis using a random sampling scheme without replacement to assure a representative sample of bison. Since the availability of collars in the MGF varied throughout the season as bison migrated from the summer range, I scanned for all frequencies on a weekly basis to determine collar availability for sampling.

I matched each of the telemetry locations to their corresponding GPS locations and identified the arrival and departure dates and times for the bison in that foraging area. I then defined a response variable for each collared bison in each foraging area (*i*) as the foraging area residence time, τ_i (hours), calculated by subtracting the arrival date/time from the departure date/time. The extent of a foraging area was determined by identifying a concentration of consecutive GPS locations in an area around the telemetry location with arrival to or departure from the area defined as one significant movement (>200 m) away from the concentration of locations. I used 200 m as a criterion based on a combination of my knowledge of MGF foraging areas and a detailed examination of the GPS data in GIS software. The MGF area is spatially heterogeneous with extremely variable snowpack, forage distribution, topography, habitats, and geothermal influences that reduce snow in areas. Therefore, I could not *a priori* define the spatial extent of available foraging areas throughout the MGF. Since GPS locations were not obtained at 30 min intervals during night in 2004, I identified any bison that arrived or departed a foraging area during this time and then removed these locations from the analysis to obtain the most accurate approximation of τ as possible (to the nearest 30 min).

Abiotic, Biotic, and Experience Effects

In each foraging area I recorded the age and sex composition of the bison group associated with the collared bison. A group was defined as the cluster of bison that contained the collared bison and was spatially segregated >400 m from any other surrounding bison. I sampled forage biomass and snowpack SWE at three locations in the foraging area. When bison foraging craters were distinctly defined in the snow, I sampled snow and forage immediately next to the craters in areas of undisturbed snow. I clipped forage within 0.25 m^2 quadrats at each of the three locations and vegetation samples were later dried for 60 h at 65°C and weighed to the nearest 0.1 g. At each of the three locations I made three measurements for SWE, each located one-meter apart in an equilateral triangular design. Snow water equivalent was measured by inserting an aluminum corer vertically through the entire snow column, removing the corer, and weighting it using a spring balance calibrated to record SWE in inches. I chose SWE as an indicator of snow rather than depth since SWE reflects snow mass and the amount of water contained in the snowpack (Bruggeman et al. *in press*).

The number and distribution of bison wintering in the MGF area were recorded from November-May during 2003-04 and 2004-05 by conducting comprehensive ground-based surveys every 14 days. Seventy-four sampling units were surveyed over two days using six distinct routes that afforded a nearly complete enumeration of bison in the MGF area (Ferrari 1999, Bjornlie 2000, Bjornlie and Garrott 2001, Bruggeman et al. *in press*). Surveyors recorded the location and age/sex composition of each observed group. I also used daily measurements from the West Yellowstone SNOTEL site (NRCS National Water and Climate Center 2006) to index landscape scale trends of SWE in the MGF area as these measurements provided an approximation of SWE in valley bottoms throughout the MGF.

To provide a measure of previous foraging experiences using the GPS data, I tracked each bison's movements and foraging area visits for seven days prior to her arriving in our ground telemetry located foraging area. Bailey et al. (1996) documented that cattle retained knowledge of previous foraging experiences for four to 20 days.

Using the same criterion that I applied to calculate τ_i, I recorded the number of foraging areas visited throughout these seven days (n_i) as well as the residence time in each (τ_j).

I calculated covariates for abiotic, biotic, and experience effects. For local foraging area scale factors I defined a covariate (SWE) as the average of the nine individual snow water equivalence measurements in m, and a covariate for forage quantity (BIO) as the average of the three biomass measurements in g/m^2. I characterized foraging area competition as the total number of bison in the group (BISON). For landscape scale factors I defined a covariate (SWERATIO) as the ratio of the covariate SWE to the snow water equivalence measurement from the West Yellowstone SNOTEL site for the corresponding date that the foraging area was sampled. I indexed landscape scale competition by defining a covariate (BISONMGF) as the number of bison in the MGF as determined from our biweekly ground surveys. To index previous foraging area experiences I calculated a covariate (τ_{ref}) as the average residence time of the n_i previous foraging areas visited (i.e., $\tau_{ref} = \left(\sum_{j=1}^{n_i} \tau_j \right) \Big/ n_i$). Finally, using indicator variables, I defined a covariate (ID) corresponding to the identity of the collared bison in the foraging area.

Model Development and Statistical Analysis

I developed *a priori* hypotheses expressed as 70 candidate models (Appendix 4A) to evaluate the influence of abiotic, biotic, and experience effects on τ. Hypotheses were in the form of mixed-effects regression models (MRM) consisting of additive main effects and interactions of the following covariates: SWE, SWERATIO, BIO, BISON, BISONMGF, τ_{ref}, and ID. All covariates were considered as fixed effects except ID, which was designated as a random effect on the intercept to account for variability in the repeated measurements of residence time on the individual collared bison. For each main effect and interaction, I formulated an *a priori* hypothesis about its effect on τ (Table 4.1).

I predicted that τ would decrease with increasing SWE since deep or wet snow would be more energetically costly to foraging and bison would depart the area quicker. Second, I hypothesized that τ would be positively correlated with BIO as more biomass in an area would offer higher quantities of forage and bison would remain in the area longer. Third, I anticipated that τ would be negatively correlated with BISON since increased local competition would lead to resource limitations and bison departing an area sooner. Fourth, since bison often prefer to forage in areas of lesser snowpack, I predicted that τ would decrease with increasing SWERATIO because bison would prefer to remain in a foraging area longer if local SWE was less than landscape SWE. Fifth, I hypothesized that τ would be negatively correlated with BISONMGF because an increase in landscape scale competition would result in increased frequency of redistribution of bison, and decreased τ, in accordance with an ideal free distribution. Sixth, I predicted that τ would be positively correlated with τ_{ref} since, as expectations of foraging area value increase, a bison would be more likely to choose subsequent areas of higher quality and

Table 4.1. The *a priori* hypothesized effects for each covariate main effect and interaction.

Covariate	**Hypothesized Effect**
SWE	$\beta_i < 0$
BIO	$\beta_i > 0$
BISON	$\beta_i < 0$
SWERATIO	$\beta_i < 0$
BISONMGF	$\beta_i < 0$
τ_{ref}	$\beta_i > 0$
SWE*BIO	$\beta_i < 0$
SWE*BISON	$\beta_i < 0$
SWE* τ_{ref}	$\beta_i < 0$
SWERATIO*BIO	$\beta_i < 0$
SWERATIO*BISON	$\beta_i < 0$
SWERATIO* τ_{ref}	$\beta_i < 0$
BIO*BISON	$\beta_i < 0$
BIO*BISONMGF	$\beta_i < 0$
BISONMGF*BISON	$\beta_i < 0$
BISON* τ_{ref}	$\beta_i < 0$

remain in that area longer.

For interaction effects I made the following hypotheses. First, I anticipated that the negative effect of SWE would be more influential than areas of high biomass such that a SWE*BIO interaction would be negatively correlated with τ. Similarly, I expected that a SWERATIO*BIO interaction would be negatively correlated with τ since local SWE effects would be more influential than high biomass and bison would still select areas with lesser snowpack relative to landscape SWE. Second, I hypothesized that the negative SWE effect would further accentuate the effect of BISON and a SWE*BISON interaction would be negatively correlated with τ. I also expected the negative effect of SWERATIO would be accentuated in areas of higher BISON such that the

SWERATIO*BISON interaction would be negatively correlated with τ. Third, I predicted that SWE*τ_{ref} and SWERATIO*τ_{ref} interactions would be negatively correlated with τ because the negative effect of deep or wet snow on a local scale would be more important in affecting residence time than previous experience. Fourth, I hypothesized that a BIO*BISON interaction would be negatively correlated with τ because high levels of competition would reduce the value of high biomass in an area and bison would depart quicker. Similarly, I expected that at high landscape level numbers of bison (i.e., high BISONMGF), overall competition would be greater for areas of high biomass and result in reduced residence time. Fifth, I expected that the negative effect of local competition would be accentuated during periods of high numbers of bison in the study area, such that a BISON*BISONMGF interaction would be negatively correlated with τ. Finally, I predicted that a BISON*τ_{ref} interaction would be negatively correlated with τ since the negative influence of local competition would reduce the effect of previous experience.

Because of uncertainty in the true functional relationship between τ and each covariate, I hypothesized *a priori* linear and quadratic functional structures for each covariate. The linear form predicts a fixed rate of increase or decrease per unit increase in the covariate with the form of the model effect written as $\beta_i x_i$, where x_i is the centered and scaled i^{th} covariate and β_i the corresponding coefficient. The quadratic form, expressed as $\beta_{1i} x_i + \beta_{2i} x_i^2$, predicts a maximum or minimum in τ at one value of the covariate.

I used mixed-effects regression techniques in R version 1.9.0 using package nlme (Pinheiro and Bates 2000, R Development Core Team 2004). Residual and normal probability plots demonstrated non-constant error variance and departures from normality in the error terms. I applied a square-root transform on the response variable that stabilized the variance and normalized the errors to remedy these departures from regression assumptions. I calculated variance inflation factors (VIFs) to assess potential multicollinearity between model predictors, including interactions. Any model containing a predictor that had a VIF>6, given the other covariates in a model, was removed from the *a priori* model list. Owing to multicollinearity, SWE and SWERATIO were not included together in any model. To allow comparisons of parameter coefficients on a similar scale, each continuous covariate was centered and scaled prior to analyses by subtracting the midpoint and dividing by half of the range resulting in values between –1 and 1.

I used a sequential model fitting technique that incorporated the *a priori* candidate model list and hypothesized covariate functional forms as detailed in Bruggeman et al. (*in press*). I began by separately fitting all candidate models containing only linear forms for covariates. I calculated a corrected Akaike's Information Criterion (AIC_c) value and ΔAIC_c values for each model (Burnham and Anderson 2002), and selected the top 15 models to further evaluate. Next, I sequentially replaced the linear form of one covariate with its quadratic form in each model (*k*) while preserving the model structure. I refit the models, calculated new AIC_c values ($AIC_{c,n,k}$), and compared them to the previous value ($AIC_{c,m,k}$) for each model. If $AIC_{c,n,k} < AIC_{c,m,k}$ and all VIF<6, I accepted the new form of the covariate for model k; otherwise, the previous form was retained. Upon completion I had the most appropriate covariate forms with respect to the data and model structure for each of the top 15 models. As a measure of model selection uncertainty I calculated Akaike weights (w_k) based on these final models combined with the originally discarded linear models. To estimate the relative importance of each predictor variable, x_i, I summed Akaike weights for all models containing the predictor (in any form) to calculate the predictor weight, $w_{+(i)}$ (Burnham and Anderson 2002).

Results

Foraging area residence times ranged from 0.5-72.0 hours (14.6 ± 1.3; mean ± SE, $n = 130$) and did not differ between years ($F_{1,128} = 0.99$, $P = 0.32$). Telemetry locations (i.e., foraging area locations) collected on 20 individual bison were distributed widely throughout the MGF (Figure 4.2). I collected snowpack SWE data at a total of 1170 points and clipped forage biomass samples at 390 sites in foraging areas. The covariate SWE ranged from 0.000-0.107 m (0.014 ± 0.002, $n = 130$), BIO ranged from 2.8-347.3 g/m^2 (79.6 ± 5.7, $n = 130$), and BISON ranged from 1-171 bison (37 ± 3, $n = 130$). Landscape scale trends in SWE, determined from measurements at the West Yellowstone SNOTEL site, varied temporally each year with snowpack accumulating throughout the winter and peaking in mid-March (Figure 4.3). The covariate SWERATIO ranged from 0.00-0.53 (0.07 ± 0.01, $n = 130$). The number of bison in the MGF, as determined from

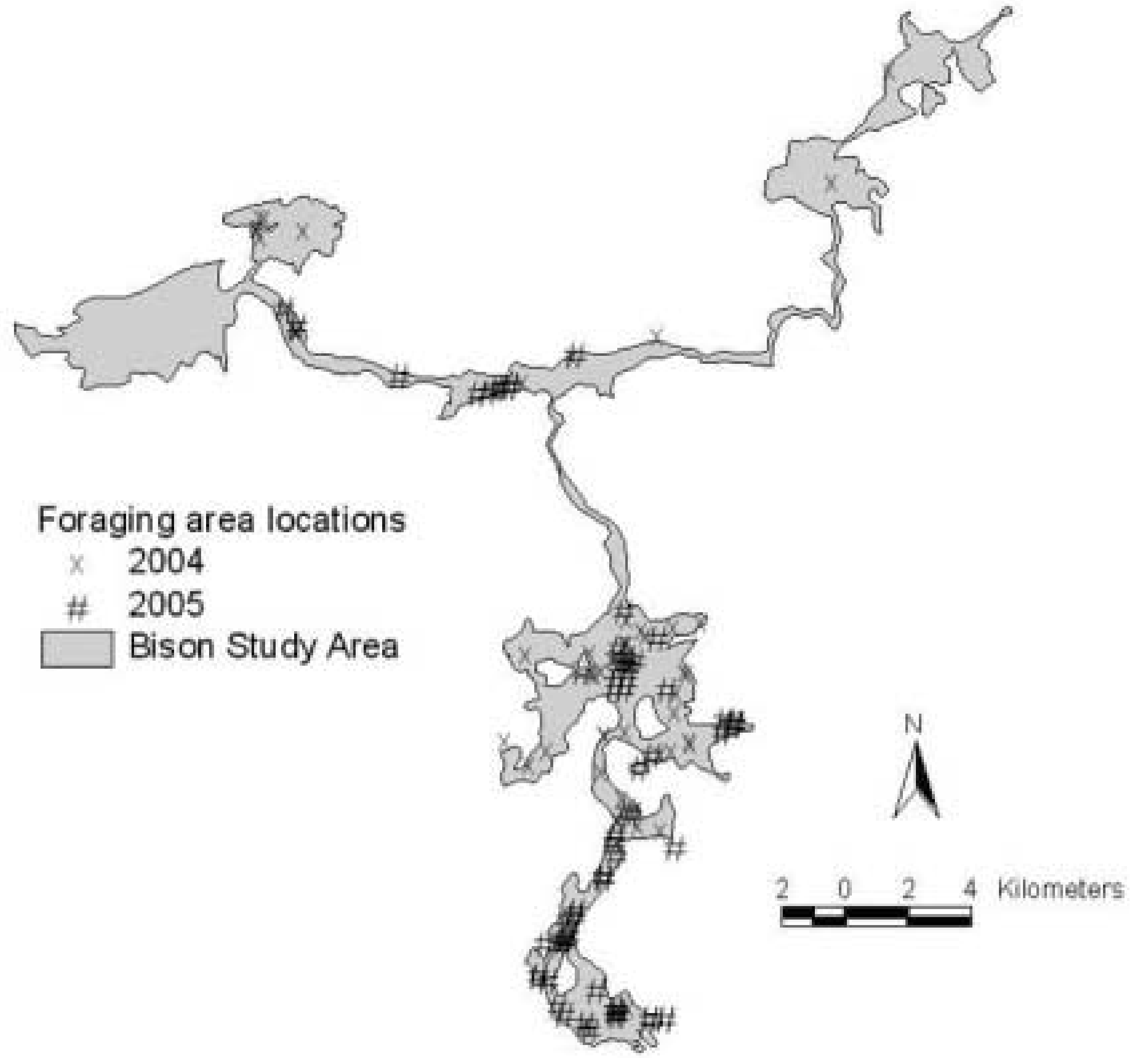


Figure 4.2. The distribution of the 130 foraging areas throughout the Madison-Gibbon-Firehole study area in Yellowstone National Park obtained from January-March during 2004 and 2005.

ground surveys, increased with time each winter as bison migrated into the MGF and peaked around mid-March (Figure 4.4). The covariate BISONMGF varied from 246-1400 bison (1017 ± 91, $n = 13$ surveys). The covariate τ_{ref} varied from 4.4-26.0 hours (8.9 ± 0.3, $n = 130$) as bison visited between 7-29 foraging areas (18.1 ± 0.4, $n = 130$)

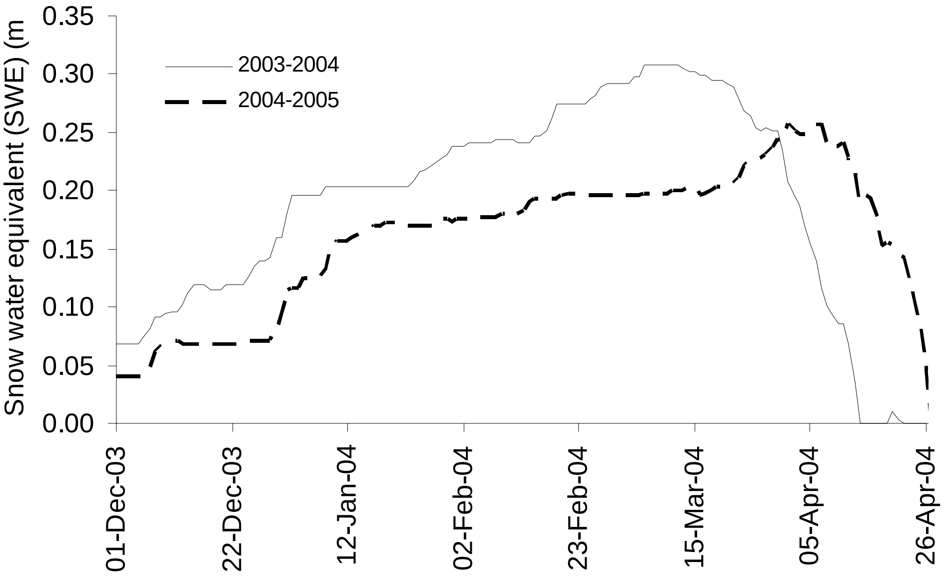


Figure 4.3. Temporal trends in snowpack snow water equivalent (SWE) as determined from daily measurements at the West Yellowstone SNOTEL site from December-April for 2003-04 and 2004-05.

in the week prior to arriving in the ground telemetry located foraging area.

Four best approximating model structures were supported by the data with $\Delta AIC_c<2$. The top model had a relative likelihood of 1.3 compared to the second best model, which differed by 0.48 AIC_c units (Table 4.2; Appendix 4B). The third and fourth best models had ΔAIC_c values of 1.04 and 1.49, respectively. The quadratic form of SWERATIO was significant in all four top models, with confidence intervals for both the linear and quadratic parameters not spanning zero and having the highest predictor weights of 0.48 and 0.46, respectively (Table 4.3; Figure 4.5). The covariate τ_{ref} was contained in three of four top models and had the third highest predictor weight of 0.36. The covariate BISONMGF appeared in two of the top models with a predictor weight of

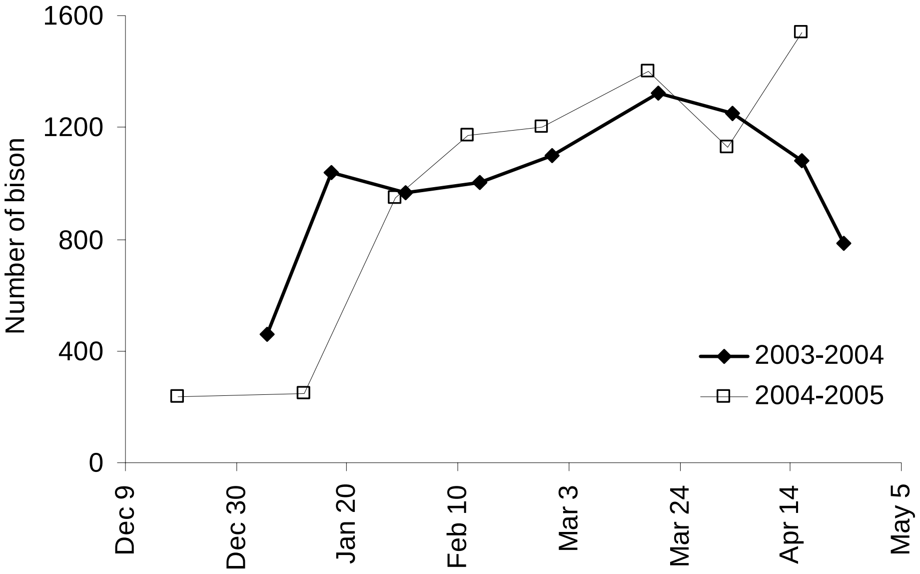


Figure 4.4. Temporal trends in the number of bison in the Madison-Gibbon-Firehole area of Yellowstone National Park as determined from ground surveys conducted every 14 days during December-April 2003-04 and 2004-05. The data were used to determine the BISONMGF covariate.

Table 4.2. Model selection results for *a priori* hypothesized models examining the effects of snowpack characteristics, forage biomass, intraspecific competition, previous foraging area experiences, and individual bison identity on τ. Coefficients for fixed covariate effects are denoted with β_i and those for random effects with b_i. The four best approximating models are presented with the number of parameters (K), the ΔAIC_c value, and the Akaike weight (w_k).

Model	**Structure**	**K**	**ΔAIC_c**	**w_k**
M32‡	$\beta_0 + \beta_1(\text{SWERATIO}) + \beta_2(\text{SWERATIO})^2 + \beta_3(\text{BISON}) + \beta_4(\tau_{ref}) + \beta_5(\text{BISON})*(\tau_{ref}) + b_6(\text{ID})$	7	0.000	0.093
M23	$\beta_0 + \beta_1(\text{SWERATIO}) + \beta_2(\text{SWERATIO})^2 + \beta_3(\text{BISONMGF}) + \beta_4(\tau_{ref}) + \beta_5(\tau_{ref})^2 + b_6(\text{ID})$	7	0.481	0.073
M7	$\beta_0 + \beta_1(\text{SWERATIO}) + \beta_2(\text{SWERATIO})^2 + \beta_3(\text{BISONMGF}) + b_4(\text{ID})$	5	1.042	0.055
M9	$\beta_0 + \beta_1(\text{SWERATIO}) + \beta_2(\text{SWERATIO})^2 + \beta_3(\tau_{ref}) + b_4(\text{ID})$	5	1.487	0.044
M1	$\beta_0 + \beta_1(\text{SWERATIO}) + \beta_2(\text{SWERATIO})^2 + b_3(\text{ID})$	4	2.017	0.034

‡ AIC_c value for model M32 is 523.36

Table 4.3. Coefficient values and lower and upper 90% confidence limits from the four best approximating models (models M32, M23, M7, M9) identified through AIC model comparison techniques examining variability in τ. Estimates of the between bison variance (σ^2_b) and error variance (σ^2) are provided. Bold notation denotes significant coefficients at $\alpha = 0.10$. Predictor weights ($w_{+(i)}$) are presented for the overall modeling exercise; predictors with $w_{+(i)} < 0.07$ are omitted for clarity.

Covariate	**$w_{+(i)}$**	**M32**	**M23**	**M7**	**M9**
Intercept		**4.418 (3.524, 5.313)**	**3.926 (3.206, 4.647)**	**3.892 (3.268, 4.516)**	**4.164 (3.468, 4.860)**
SWERATIO	0.483	**2.271 (1.317, 3.226)**	**2.126 (1.179, 3.072)**	**2.218 (1.281, 3.155)**	**2.201 (1.252, 3.151)**
SWERATIO^2	0.459	**1.784 (0.513, 3.055)**	**1.855 (0.565, 3.145)**	**1.845 (0.551, 3.138)**	**1.573 (0.313, 2.834)**
τ_{ref}	0.357	**1.710 (0.513, 2.908)**	1.043 (-0.064, 2.150)		0.777 (-0.107, 1.660)
BISONMGF	0.216		**-0.750 (-1.476, -0.023)**	**-0.713 (-1.379, -0.048)**	
BISON	0.185	0.987 (-0.316, 2.290)			
τ_{ref}^2	0.146		1.168 (-0.235, 2.571)		
BIO	0.143				
BISON*τ_{ref}	0.137	**2.132 (0.253, 4.012)**			
σ^2_b		0.0795	0.0003	0.0003	0.0066
σ^2		3.037	3.102	3.122	3.141

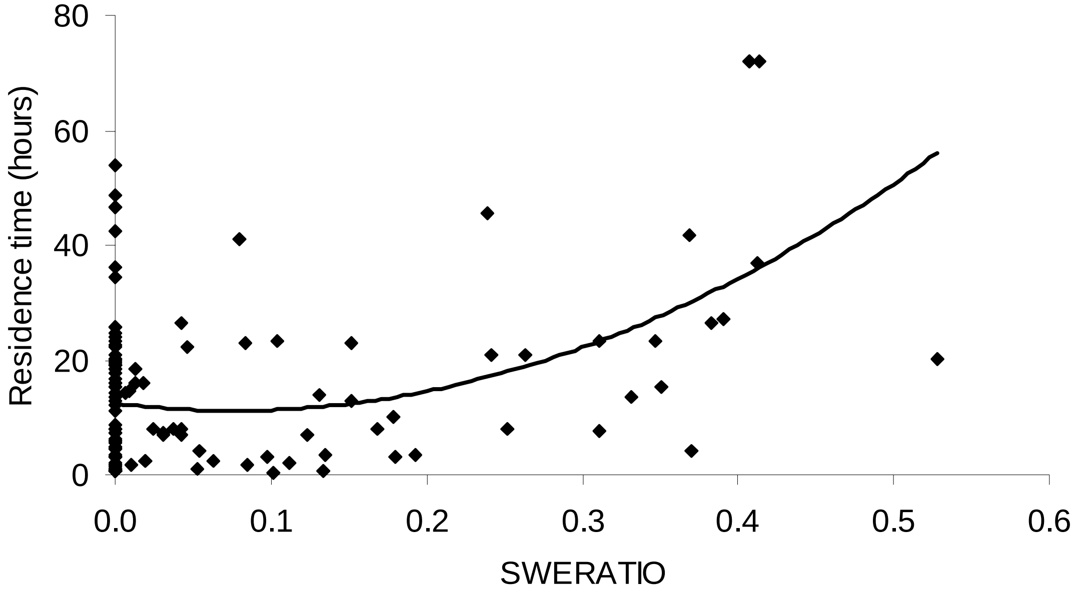


Figure 4.5. Plots of data points for foraging area residence time (τ) versus the SWERATIO covariate. Data are from bison foraging area locations in the Madison-Gibbon-Firehole area of Yellowstone National Park obtained from January-March during 2004 and 2005.

0.22. As hypothesized, τ_{ref} was positively correlated with τ (Figure 4.6) and BISONMGF was negatively correlated with τ. Contrary to my predictions, SWERATIO and the BISON* τ_{ref} interaction were positively correlated with τ, and no other effects or interactions were significant effects in the top approximating models.

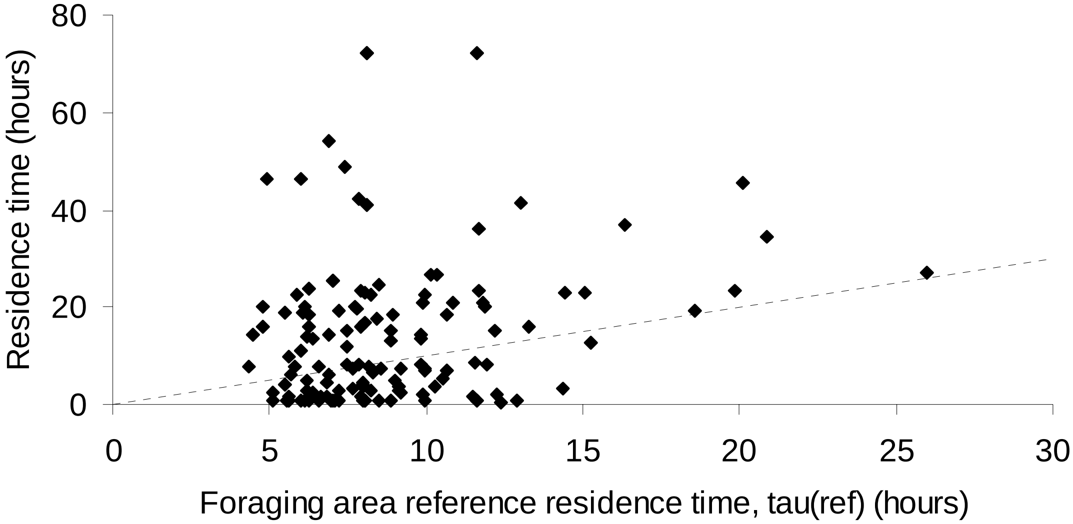


Figure 4.6. Plots of data points for foraging area residence time (τ) versus the reference foraging area residence time (τ_{ref}) with the line $\tau = \tau_{ref}$ denoted. Data are from bison foraging area locations in the Madison-Gibbon-Firehole area of Yellowstone National Park obtained from January-March during 2004 and 2005.

Discussion

Bison foraging area residence times in winter were affected by the ratio of local to landscape scale snowpack SWE, previous foraging experiences, and both local and landscape scale intraspecific competition. These results indicate that the amount of time bison spend in one foraging area is dependent on a suite of abiotic and biotic factors that affect resource availability, and the perceived value of the area relative to other recently visited areas. My findings support other work suggesting large herbivore foraging decisions are dependent upon scale and may be influenced by resource availability across multiple spatial and temporal scales simultaneously (Senft et al. 1985, Ward and Saltz

1994, Wallace et al. 1995, Dumont et al. 2002). Senft et al. (1987) developed a framework for understanding large herbivore foraging behavior using hierarchy theory to integrate decisions across several scales. Bailey et al. (1996) furthered this work by presenting a conceptual model incorporating biotic, abiotic, and animal memory effects to explain distribution patterns of grazers. Using τ, I extended these ideas to quantify and understand influential factors affecting bison foraging behavior and distribution.

Residence times were positively correlated with SWERATIO, appearing in the top approximating models as a quadratic effect. This suggests bison foraging decisions were made in response to snowpack at local, foraging area scales and to snow conditions in the surrounding landscape. The quadratic form, supported in all top models, predicts bison will spend more time foraging in areas of no, or minimal, snow, and in areas where foraging area SWE is similar to landscape SWE. Field observations indicate bison do have a preference for foraging areas containing minimal snowpack. In the MGF, geothermal influence in some foraging areas keeps them snow-free the entire winter, thereby affording bison energy efficient access to forage relative to that in snow covered, surrounding regions. These geothermal areas also often provide green vegetation throughout winter compared to senescent forage found elsewhere. However, this growing vegetation is often of low biomass, which may explain why I found no significant role of biomass in explaining variability in τ. At the other extreme, when local and landscape SWE are comparable, bison have little rationale to expend energy to move to a new foraging area since snow conditions are not more favorable. Therefore, bison accept the necessary energetic costs of displacing snow to forage and remain in the area longer, but save on energetic travel costs. In between these snowpack extremes, bison make decisions based on a continuum of local and landscape scale snow conditions, and the relative availability of resources in the foraging area.

Snowpack has also been found to affect Yellowstone bison travel patterns, distribution, and small-scale foraging behavior (Bjornlie and Garrott 2001, Bruggeman *et al. in press*, Bruggeman *et al. in review, b*, Bruggeman *et al. in review, c*). Further, large herbivore distribution, diet selection, and foraging behavior may be affected by snow (Larter and Gates 1991, Fortin et al. 2003, Messer 2003, Doerr et al. 2005). For example, muskoxen (*Ovibos moschatus*) preferred patches with low snow cover and adjusted their time spent in patches depending upon energetic costs of travel through snow to reach other patches (Schaefer and Messier 1995*a*,*b*). This importance of snowpack in affecting large herbivore foraging relates directly to forage resource limitations and increased energetic costs needed to displace snow (Parker et al. 1984), both of which may affect large scale population processes (e.g., Jacobson et al. 2004). Managers of large herbivore populations in high latitude ecosystems with severe winters must be able to quantify the influence of snowpack on animal distribution and foraging behavior. An example is provided from Yellowstone when, during the harsh winter of 1996-97, hundreds of bison left the park in search of forage at lower elevations and were consequently subjected to control actions (National Park Service 2000*a*). This study further documents the importance of snowpack on large herbivore foraging behavior and distribution using the concept of residence time.

As hypothesized, experiences in previous foraging areas on a landscape scale affected bison foraging behavior and τ in future areas. Reference memory has been shown to affect foraging behavior by grazers (Bailey et al. 1989). By definition, τ is a measure of the perceived value of a foraging area and, therefore, τ_{ref} can be thought of as the reference value to which bison compare current foraging experiences with the relative perceived value of the area defined as τ/τ_{ref}. My results indicate as expectations of value increase from previous experiences, a bison is more likely to select subsequent areas of higher quality and remain in those areas longer. This agrees with model predictions of Bailey et al. (1996) that suggest previous experience may influence expectations in a feeding site for grazers. In Figure 4.6, note that all data points below the $\tau = \tau_{ref}$ line denote foraging areas with a relative perceived value < 1 in which the bison's expectations were not met. This occurred in 60 locations (46%) during my study, indicating that bison chose foraging areas that exceeded their value expectations slightly more often than they did not. For further illustration, Figures 4.7 and 4.8 offer a histogram of τ/τ_{ref} and a plot of τ versus relative perceived value that indicates bison must have remained in foraging areas for >10 hours to exceed value expectations developed during the previous week.

These results suggest bison do not avoid low quality foraging areas, but minimize time spent in these locations while sampling areas throughout the landscape. The mean τ was greater and had more variability than average τ_{ref}, indicating bison will occasionally select a high quality area and remain there for multiple days. Indeed, Figure 4.6 depicts that average weekly residence times (τ_{ref}) were often between 4-13 hours while τ for the individual foraging areas ranged up to 72 hours. Why, then, would bison remain in a low quality area for any period of time? It is uncertain whether or not grazers can perceive differences in resource quality on large spatial scales (Bailey et al. 1996). Large herbivores can discriminate between plant swards, plants, and feeding stations, but these differences are perceived only on small scales (Espatch et al. 1993, Laca et al. 1993). Therefore, bison foraging behavior on larger spatio-temporal scales is likely affected by decisions on small scales, at least until an animal can evaluate area quality using an accumulation of small-scale foraging experiences. Likewise, constraints on the small-

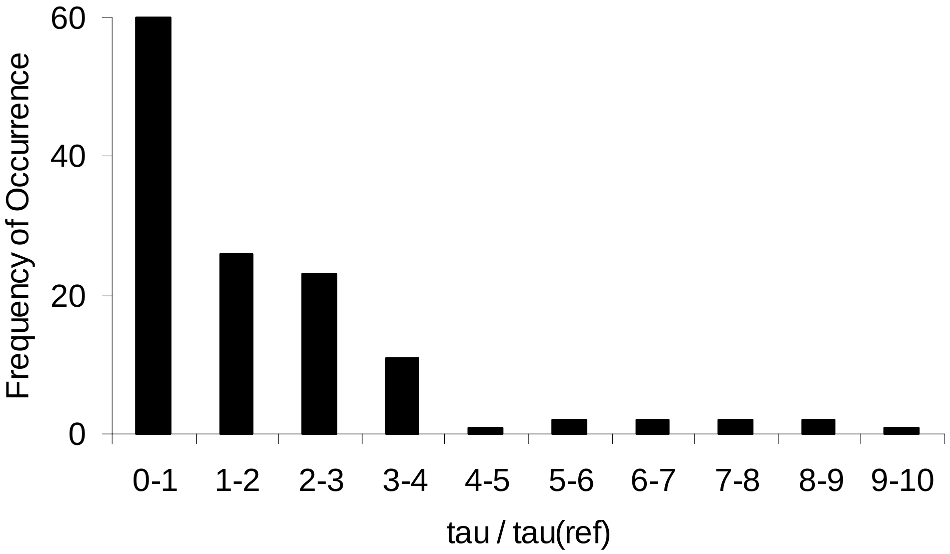


Figure 4.7. Histogram showing distribution of τ/τ_{ref} for 130 bison foraging areas in the Madison-Gibbon-Firehole area of Yellowstone National Park during January-March 2004 and 2005.

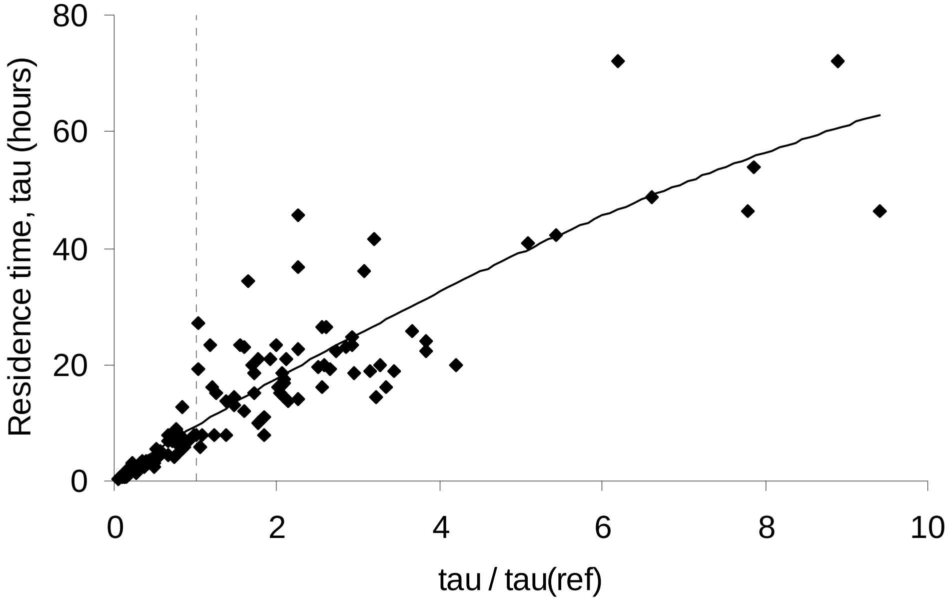


Figure 4.8. Plot of τ versus τ/τ_{ref} for bison foraging areas in the Madison-Gibbon-Firehole area of Yellowstone National Park during January-March 2004 and 2005. Data points to the left of the dashed line denoting $\tau/\tau_{ref} = 1$ indicate areas of negative perceived value; points to the right of the line denote areas of positive perceived value.

scale diet choice and quality are imposed by selection of a foraging area on broad spatial and temporal scales (Senft et al. 1987; Bailey et al. 1996).

The number of bison in the MGF was negatively correlated with τ as predicted, suggesting that competition on a landscape scale can affect foraging behavior. As the number of bison in the MGF increases throughout the winter as migration progresses, competition will increase in higher quality foraging areas. In theory, the frequency of bison redistribution should increase as density increases (Fretwell and Lucas 1969) resulting in decreased residence time, which agrees with my results. On a local scale, however, I found a positive correlation between τ and a BISON*τ_{ref} interaction, suggesting as both group size and foraging area value expectations increase, bison will remain in an area longer. This was contrary to my hypothesis since I expected increased local competition would lead to resource limitations and bison departing an area sooner. It is possible that many of the bison groups we observed were not large enough for competition to affect residence time. Group size could also provide an indicator of area quality such that larger aggregations of bison would denote an area of higher value. This may interact with value expectations developed on a landscape scale to positively influence τ. Overall, the significance of local and landscape scale density related effects on τ reinforces the idea that foraging by large herbivores may be simultaneously affected by mechanisms operating across multiple spatial and temporal scales.

My results are of direct relevance to Yellowstone managers, who are applying research findings to better understand bison ecology and adjust management actions accordingly. Knowledge of the influential density dependent and density independent effects, and their respective magnitudes, on τ provides a means for quantifying habitat importance across space and time, which is of relevance to comprehending population processes for a bison population that is currently growing and expanding its range. Because I found snowpack and density to be the most important abiotic and biotic factors affecting τ, managers can develop maps to predict how the value of winter foraging areas change with time using inputs of local and landscape scale SWE, bison population levels, and bison distribution and group size data. Further, since these factors also affect previous foraging experiences and τ_{ref}, sequential patterns of bison foraging area use and residence times may be predicted.

Using existing GPS data, managers can quantify τ/τ_{ref} to better understand how relative perceived value changes across time and space. Identifying areas that have positive relative perceived value (i.e., $\tau/\tau_{ref} > 1$) compared to negative (i.e., $\tau/\tau_{ref} < 1$) allows identification of specific areas of the landscape that may be particularly important to bison throughout the winter. In Appendix 4C, I present maps from this study to display foraging areas with positive and negative relative perceived value on a monthly basis. Ongoing GPS studies of Yellowstone bison offer the opportunity to expand this work to include a wider range of winter severities and population levels to develop improved predicting models. Further, more detailed investigations of sequential patterns in bison foraging area use, and the effect of spatial memory with bison revisiting the same foraging areas over time on τ, are possible.

The concepts and approach presented here may be applied to the management of numerous other large herbivore species. Quantifying the characteristics of high and low valued foraging areas can assist managers in identifying critical habitats for preservation, particularly for endangered or sensitive species. This, in turn, may help managers of national parks and public lands that receive high amounts of visitation to develop guidelines for recreation to minimize human impacts to these important areas (Boyle and Samson 1985). For species that are in conflict with people, understanding the factors affecting desirable habitat for herbivores may allow manipulation of habitat elsewhere to attract them away from important areas of human development (e.g., Rea 2003). This approach could also be applied to large herbivores in conflict with livestock on grazing lands. Overall, large herbivore foraging dynamics are complex and affected by abiotic,

biotic, and behavioral mechanisms that operate across several spatio-temporal scales. Here I have presented a novel method for analyzing large herbivore foraging behavior and understanding distribution changes in dynamic landscapes across multiple scales using the concept of foraging area residence time.

CHAPTER 5:
ABIOTIC AND BIOTIC EFFECTS INFLUENCING BISON PATCH SCALE FORAGING BEHAVIOR IN YELLOWSTONE NATIONAL PARK

Abstract

The foraging behavior of large herbivores is affected by heterogeneity acting across a hierarchy of spatial and temporal scales. I defined a new metric, the foraging ratio (ϕ), for quantifying small-scale foraging behavior of large herbivores and evaluated the influence of abiotic and biotic mechanisms on bison (*Bison bison*) patch scale winter foraging behavior in Yellowstone National Park, Wyoming, USA. During two winters, 2004-2005, I collected data on individual bison foraging behavior, group size, herd activity, and snowpack and forage attributes in foraging patches. Using information theoretic model comparison techniques I found that bison patch scale foraging behavior in winter was predominantly affected by snowpack, with forage biomass and intraspecific competition having minimal influence. This suggests snow is the primary factor reducing foraging efficiency and patch quality for bison, supporting other studies that found snow to influence the use of foraging areas, foraging behavior, and diet selection by large herbivores. My findings demonstrate scale dependence for factors influencing bison winter foraging decisions and reinforce the role of heterogeneity in affecting large herbivore behavior. Snowpack distribution in Yellowstone is highly variable and this heterogeneity is influential in affecting bison foraging behavior on multiple scales, which has implications on large-scale movements and distribution patterns. My research

provides an example of how ϕ can be used to examine large herbivore foraging behavior in heterogeneous and dynamic environments, and presents novel findings on the relative influence of abiotic and biotic mechanisms affecting Yellowstone bison patch scale foraging behavior in winter.

Introduction

Understanding animal responses to spatial heterogeneity in dynamic environments can enhance comprehension of ecological processes across multiple scales (Wiens 1976). Heterogeneity, in the form of biological or physical complexity, can affect animal distribution patterns (Andrew 1993, Kie et al. 2002, Fisher et al. 2005) and movements (Plowright and Galen 1985, McIntyre and Wiens 1999, Friar et al. 2005, Morales et al. 2005) that may subsequently influence processes on other spatio-temporal scales. Small-scale heterogeneity in resource availability, which may be affected by spatially and temporally variable abiotic and biotic mechanisms, influences where an animal forages (e.g., Thompson et al. 2001). On large scales, distribution patterns impact population dynamics (Johnson et al. 1992) because survival and recruitment are linked to density, climate, and predation risk (Denno et al. 2003, Garrott et al. 2003, Jacobson et al. 2004, Fisken et al. 2005, Viljugrein et al. 2005). Therefore, density dependent and density independent factors acting simultaneously across several scales can affect both individual and population level processes. However, the extent of influence of each factor may be scale dependent and knowledge of these relative effects on multiple scales is necessary to fully understand mechanisms affecting processes in ecological systems (Wiens 1989, Orians and Wittenberger 1991, Naugle et al. 1999, Cushman and McGarigal 2002, Thompson and McGarigal 2002).

The foraging behavior of large herbivores is affected by heterogeneity acting across a hierarchy of spatial and temporal scales (Senft et al. 1987, Pearson et al. 1995, Bailey et al. 1996). On the smallest scales, variation in plant sward characteristics can influence intake rates and functional responses (Bergman et al. 2000, Hobbs et al. 2003). Aggregations of plants, which form feeding stations, can affect diet composition owing to a herbivore's preference for certain species, some of which may be more palatable or nutritious (Senft et al. 1987). Herbivore selection of a patch, comprised of multiple feeding stations, may be affected by vegetation-related factors such as forage biomass and quality, and biotic and abiotic effects that influence small-scale forage availability (Bailey et al. 1996). On larger scales, herbivores may select foraging areas throughout a landscape based on a combination of broad scale heterogeneity in forage quantity (Wallace et al. 1995) and quality (McNaughton 1988), predation risk (Sinclair and Arcese 1995), competition, and climate effects on resource availability (Senft et al. 1987). However, herbivore foraging decisions at one scale are constrained by choices made at another (Hobbs 2003) and the effects of extrinsic and intrinsic processes, which affect population dynamics (Sæther 1997, Gaillard et al. 1998, Post and Stenseth 1999), on resource availability and foraging behavior must be evaluated on multiple scales.

Bison (*Bison bison*) in Yellowstone National Park make foraging decisions in a dynamic, spatially heterogeneous environment. These choices are complicated by severe winters, resulting in snowpack that limits access to forage and affects resource availability. The migratory central Yellowstone bison herd winters in the Madison, Gibbon, and Firehole drainages, an area characterized by deep snowpack, geothermal influence that minimizes snow accumulation in some areas, and meadow complexes connected by narrow canyons and situated amidst a mosaic of burned and unburned forest. This heterogeneous landscape affects bison distribution patterns and movements across several spatio-temporal scales (Bjornlie and Garrott 2001, Bruggeman et al. *in press*, Bruggeman et al. *in review, a*, Bruggeman et al. *in review, b*). Previous work on the central herd documented large-scale bison foraging behavior in winter to be influenced by several abiotic and biotic factors acting across multiple scales (Bruggeman et al. *in review, d*). Bison foraging area residence times were correlated with the ratio of local to landscape scale snowpack, previous landscape scale foraging experiences, and local and landscape scale competition (Bruggeman et al. *in review, d*). The influences of small-scale abiotic and biotic effects on bison patch scale foraging behavior, however, have yet to be elucidated.

The goal of this study was to determine the relative influences of abiotic and biotic mechanisms on bison patch scale winter foraging behavior in Yellowstone. I developed a new metric, the foraging ratio (ϕ), to quantify large herbivore foraging behavior in heterogeneous environments on small spatial and temporal scales. I defined ϕ as the proportion of time an animal spends finding forage relative to the proportion of time it forages such that ϕ provides an index of patch quality and foraging efficiency. Bison perceptions of patch quality may change with variation in biomass, snowpack conditions, and intraspecific competition. Therefore, I evaluated the relative effects of these factors on ϕ using an information theoretic approach. Overall, my work provides insights into bison patch scale foraging behavior and offers a novel approach to large herbivore foraging studies on small scales in complex and dynamic environments.

Study Area

The study area in west central Yellowstone National Park, Wyoming, USA, encompassed the drainages of the Firehole River upstream from Madison Junction to Old Faithful; the upper Madison River east from the Park boundary at West Yellowstone to Madison Junction, and the Gibbon River upstream to Norris Geyser Basin (Figure 5.1). It also included portions of the Mary Mountain trail extending from the Firehole drainage east to Mary Lake and meadows along Cougar Creek near the western boundary of the park. Elevations within this 8000 ha area ranged from 2000-2250 m.

The migratory central Yellowstone bison herd numbered >3000 animals (Gates et al. 2005) during this study (2003-2005). Meadow complexes and geothermal areas on the Madison-Gibbon-Firehole (MGF) winter range provided foraging habitats for migratory bison, with major foraging areas often connected by corridors through canyons and/or along streams (Bruggeman et al. *in review, a*). High elevation plateaus and/or

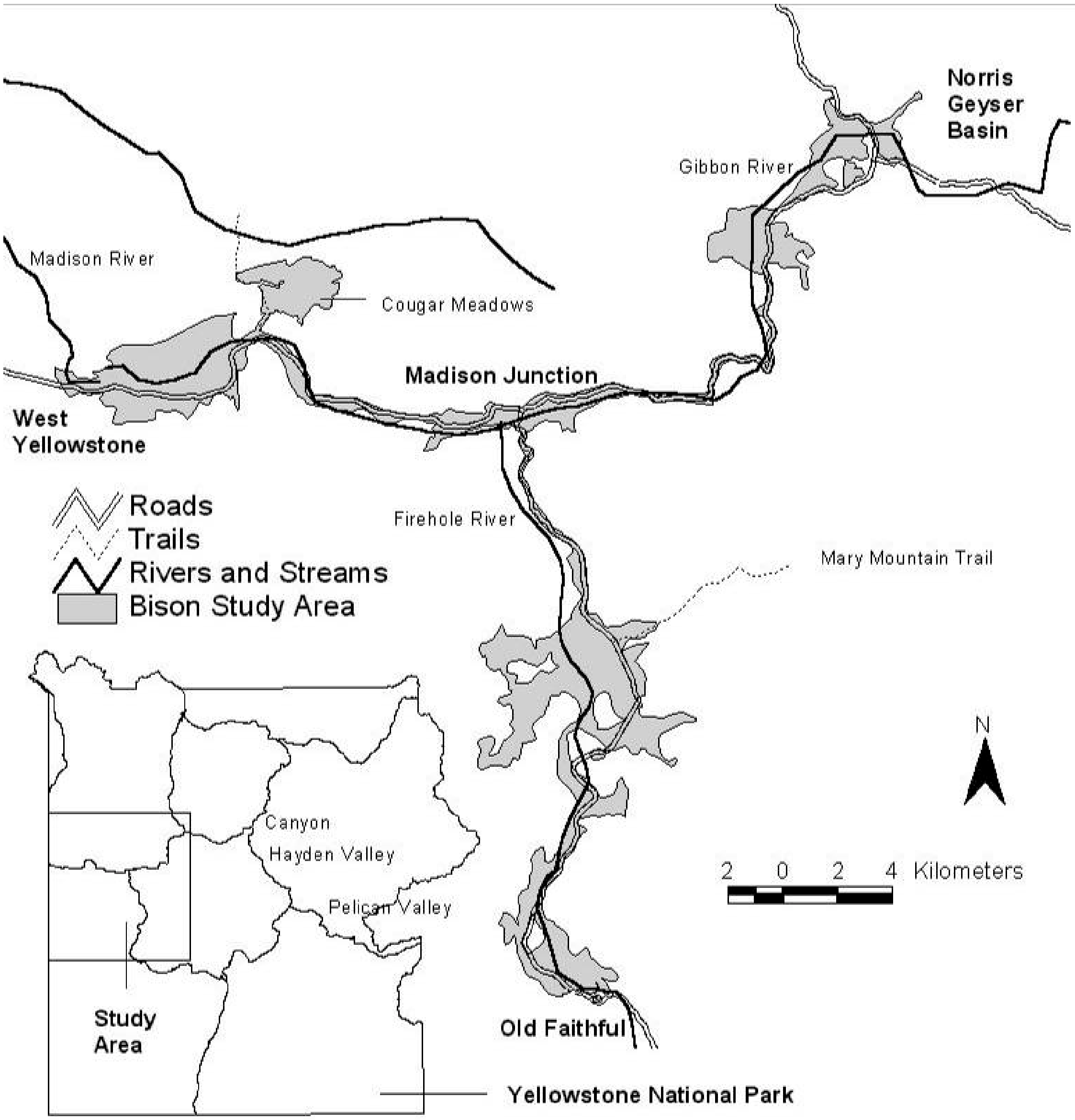


Figure 5.1. The Madison-Gibbon-Firehole study area in Yellowstone National Park, Wyoming and Montana, USA.

mountain ranges constrained bison to lower elevation valley bottoms during winter. There were four major geothermal areas in the MGF along with smaller pockets of geothermal activity that had reduced snow accumulation and longer growing seasons compared to surrounding meadows. Sedges (*Carex* spp.) and grasses (*Calamagrostis* spp.) characterized wet meadows, while dry meadows were dominated by grasses (*Poa* spp., *Festuca idahoensis*) and sagebrush (*Artemesia* spp.). More than 50% of forested areas burned during summer 1988 (Despain 1990) and these areas were characterized by downed trees, snags, regenerating lodgepole pine, Ross' sedge (*Carex rosii*), elk sedge (*Carex geyeri*), and leafy aster (*Aster foliaceus*) during our study. Unburned forested areas were predominantly lodgepole pine (*Pinus contortus*) with understories of elk sedge, grouse whortleberry (*Vaccinium scoparium*), and pinegrass (*Calamagrostis rubescens*). The lowest elevation areas also included scattered Douglas fir (*Pseudotsuga mensiesii*), while Engelmann spruce (*Picea engelmanni*) and subalpine fir (*Abies lasiocarpa*) occurred at higher elevations.

The MGF area typically experiences severe winters with an annual average of 189 days of snow cover (Natural Resources Conservation Service (NRCS) National Water and Climate Center 2006). Mean annual peak snow water equivalent (SWE) was 34.1 cm at the West Yellowstone NRCS Snowpack Telemetry (SNOTEL) site (elevation 2042 m) during 1966-2005. During our study, winters were relatively mild with a peak SWE of 30.7 cm in 2003-04 and 25.7 cm in 2004-05. Snowpack began accumulating in late October in the valleys and continued to build until April, at which point ablation occurred.

Methods

Bison Distribution and Behavioral Observations

Fifteen GPS/VHF collars (Model TGW 3700, Telonics, Mesa, AZ) were deployed on adult female bison beginning in November 2003 and then redeployed on different adult female bison beginning in November 2004. Collars were distributed on bison in the Hayden and Pelican Valley summer range and on early migrants to the MGF winter range using ground darting with Carfentanil (R. Wallen, Yellowstone Center for Resources, unpublished data).

I visually located collared bison using telemetry homing techniques (White and Garrott 1990) from December-March during 2003-04 and 2004-05 in the MGF area. The identities of bison to be tracked were determined on a daily basis using a random sampling scheme without replacement to assure a representative sample of bison. Since the availability of collars in the MGF varied throughout the season as bison migrated from the summer range, I scanned for all radio frequencies on a weekly basis to determine collar availability for sampling. I recorded the age and sex composition of the group ($\geq$1 animal) associated with the collared bison. A group was defined as the cluster of bison that contained the collared bison and was spatially segregated >400 m from any other surrounding bison.

I conducted five consecutive five-minute behavioral observations on randomly selected foraging adult female bison within the group using focal animal sampling

(Altmann 1974) and recorded behavior into a tape recorder using six categories: foraging (e.g., biting, chewing), searching for forage (e.g., walking with head lowered in between biting or chewing actions), displacing snow (e.g., pawing, head sweeping), walking, and resting (bedded or standing). Observations were not conducted on bison that were behaving unusually owing to the observer, vehicles, or other animals. Data were later transcribed while using a stopwatch to record the time between each change in behavior. At the start of each five-minute observation, I classified the behavior of each bison within the group as foraging, resting, or walking, resulting in six scans throughout the 25 minute period (Altmann 1974). I defined the spatial extent of each patch in which each focal bison was foraging using heuristics provided by Bailey et al. (1996). A patch was defined as an aggregation of feeding stations, of which each was defined as an aggregation of bites (Bailey et al. 1996).

Patch Attribute Sampling and Covariates

Following an observation session I sampled forage biomass, SWE, and snowpack hardness within three patches, each situated as close as possible to where the focal bison were observed foraging. When bison foraging craters were distinctly defined in the snow, I sampled snow and forage immediately next to the craters in areas of undisturbed snow. I clipped forage within 0.25 m^2 quadrats at each of the three patches and vegetation samples were later dried for 60 h at 65ºC and weighed to the nearest 0.1 g. At each of the three patches I made three measurements for SWE and hardness, each located one-meter apart in an equilateral triangular design. Snow water equivalent was measured by inserting an aluminum corer vertically through the entire snow column, removing the corer, and weighting it using a spring balance calibrated to record SWE in inches. I chose SWE as an indicator of snow rather than depth since SWE reflects snow mass and the amount of water contained in the snowpack (Farnes et al. 1999; Bruggeman et al. *in press*). Snowpack hardness was measured using a stainless steel ram penetrometer with a 45° cone tip. The penetrometer tip was placed on the snow surface and allowed to settle to a depth, which we recorded. If the tip had not yet reached the bottom of the snow column, I then dropped additional weight down a slide tube until the tip reached the ground. With each drop I recorded the weight dropped, drop height, and depth to which the tip entered the snow. I then calculated the total snowpack hardness in Newtons (N).

I defined covariates for snowpack attributes for each telemetry location using averages of the nine individual patch measurements for SWE, in m, and hardness (HD), in N. I defined a covariate for forage quantity (BIO) as the average of the three biomass measurements in g/m^2. Competition was characterized as the total number of bison in the group (BISON) and the proportion of foraging bison (HF). I calculated HF as the number of foraging bison observed during all six herd scans divided by the number of bison observed during the six scans.

Model Development and Statistical Analyses

To investigate bison patch scale foraging behavior, I defined a response variable from my individual bison observations for each telemetry location (*i*) as the foraging ratio $\phi_i = (t_{s,i} + t_{ds,i})/t_{f,i}$, where $t_{s,i}$ is the total proportion of time spent searching by individual bison in location *i*, $t_{ds,i}$ is the total proportion of time spent displacing snow, and $t_{f,i}$ is the total proportion of time spent foraging. The foraging ratio can be interpreted as the proportion of time spent finding forage relative to the proportion of time foraging and offers an index of patch quality and foraging efficiency using animal behavior. At $\phi = 0$, a herbivore is constantly foraging within a patch, is able to maximize its forage intake rate, and perceives patch quality to be high. As ϕ increases, however, foraging time and intake rates are reduced because of other factors, such as snow, competition for patches, or increased search time for quality or abundant forage.

I developed and compared *a priori* hypotheses, expressed as multiple regression models, to estimate the relative contributions of snowpack, forage biomass, and intraspecific competition to variation in ϕ. In addition to considering linear covariate functional forms, I chose an *a priori* nonlinear form for each covariate since bison foraging responses to these effects were unlikely to be completely linear. While forming the model list I calculated variance inflation factors (VIFs) to quantify multicollinearity between model predictors, including interactions, with models containing predictors having a VIF>6 being removed from our *a priori* list. As a result of multicollinearity I could not include interactions in the models. Hypotheses were expressed as 62 candidate models (Appendix 5A) in the form of regression equations consisting of additive main effects of covariates.

I predicted ϕ would be positively correlated with SWE and HD as bison would require more time to displace snow to reach forage if the snow was deep, wet, or had a crust, resulting in decreased foraging time. Second, I hypothesized ϕ would be negatively correlated with BIO since increasing biomass would result in bison spending more time foraging in one crater and less time searching or displacing snow. Finally, I predicted that increasing BISON and HF would lead to increased ϕ since more intraspecific competition for forage would result in bison spending more time searching for forage and being displaced from patches by cospecifics. For nonlinear covariate forms I anticipated that the rate of change in ϕ would decrease as SWE and HD increased since bison may stop foraging or leave patches at high levels of SWE or HD. As a result, I predicted that SWE and HD would have moderated (square root) forms as $(\mathrm{SWE}+1)^{1/2}$ and $(\mathrm{HD}+1)^{1/2}$, respectively. Similarly, I expected a moderated form for BISON since the rate of change of ϕ would decrease with increased competition. I predicted a negative exponential form for BIO ($e^{-\mathrm{BIO}}$) since bison would spend more time foraging, and less searching, with increasing biomass. Finally, I expected a positive exponential form for HF (e^{HF}) because ϕ would increase rapidly as more bison in the herd foraged.

I used regression techniques in R version 1.9.0 (R Development Core Team 2004) to fit models and estimate parameter coefficients. To allow comparisons of parameter coefficients on a similar scale, each continuous predictor was centered and scaled prior to analysis by subtracting the midpoint and dividing by half of the range resulting in values between –1 and 1. I calculated a corrected Akaike's Information Criterion (AIC_c) value for each model and then ranked and selected the best approximating models using $\Delta\mathrm{AIC}_c$

values (Burnham and Anderson 2002). Finally, I calculated Akaike weights (w_k) to obtain a measure of model selection uncertainty and calculated predictor weights ($w_{+(i)}$) to estimate the relative importance of each covariate (Burnham and Anderson 2002).

Results

I obtained 147 telemetry locations throughout the MGF from December-March in 2003-04 and 2004-05 (Figure 5.2). In total, we recorded the foraging behavior of 735 individual bison for five minutes each and 882 herd scans. The foraging ratio followed a decreasing trend throughout each season and ranged from 0.00-0.59 (0.15 ± 0.01, mean ± SE; Figure 5.3*a*). Group size varied between 1-171 bison (37.4 ± 2.5) and the HF covariate ranged from 0.12-1.00 (0.74 ± 0.02). I collected snowpack SWE and hardness data at a total of 1323 points and clipped forage biomass samples at 441 sites in patches. The average SWE for each location ranged from 0.000-0.164 m (0.022 ± 0.003; Figure 5.3*b*), average HD varied between 0.0-996.6 N (77.3 ± 14.5), and average BIO ranged from 2.8-347.3 g/m^2 (82.2 ± 5.4).

Three models had $\Delta\text{AIC}_c<2$ and received the most support with the best approximating model having $w_k = 0.218$ (Table 5.1; Appendix 5B). The top model had a relative likelihood of 1.4 compared to the second best model, which differed by 0.61 AIC$_c$ units, suggesting two best approximating model structures supported by the data.

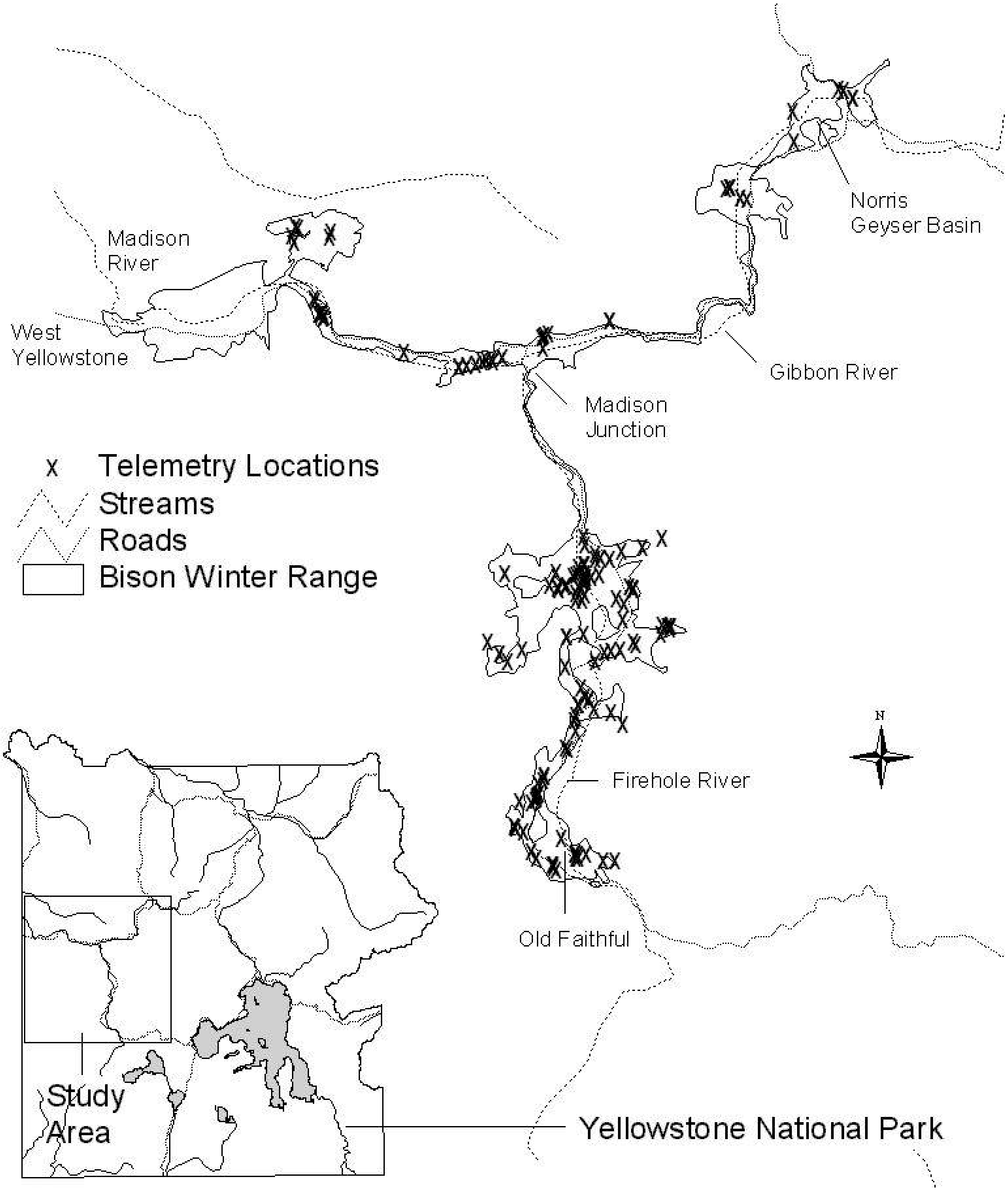
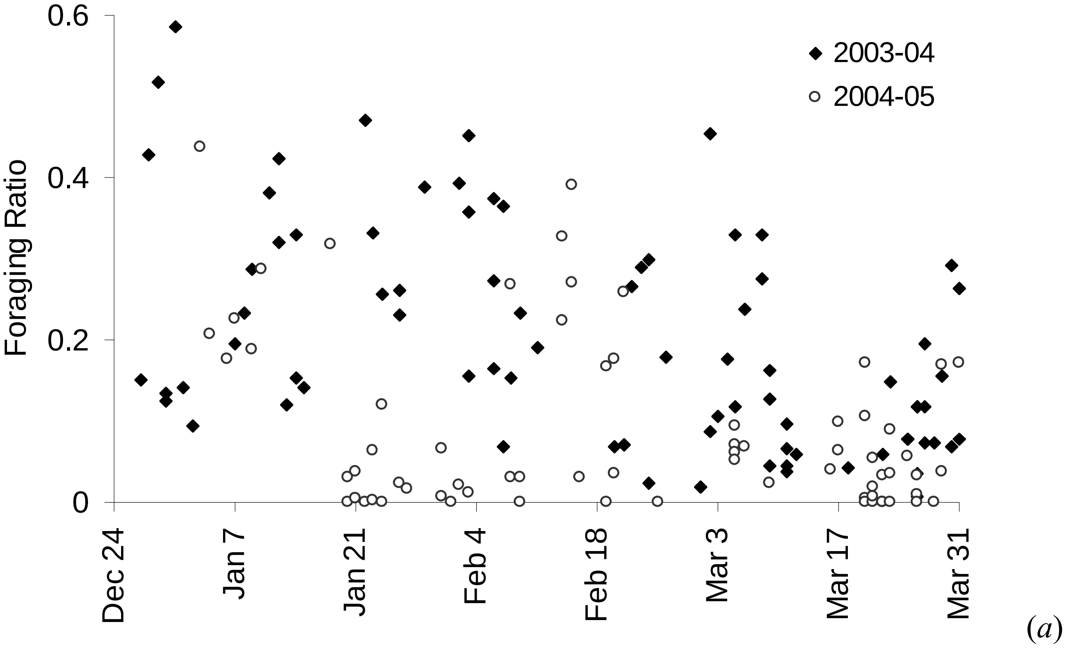


Figure 5.2. The distribution of the 147 telemetry locations throughout the Madison-Gibbon-Firehole study area in Yellowstone National Park obtained from December-March during 2003-04 and 2004-05.



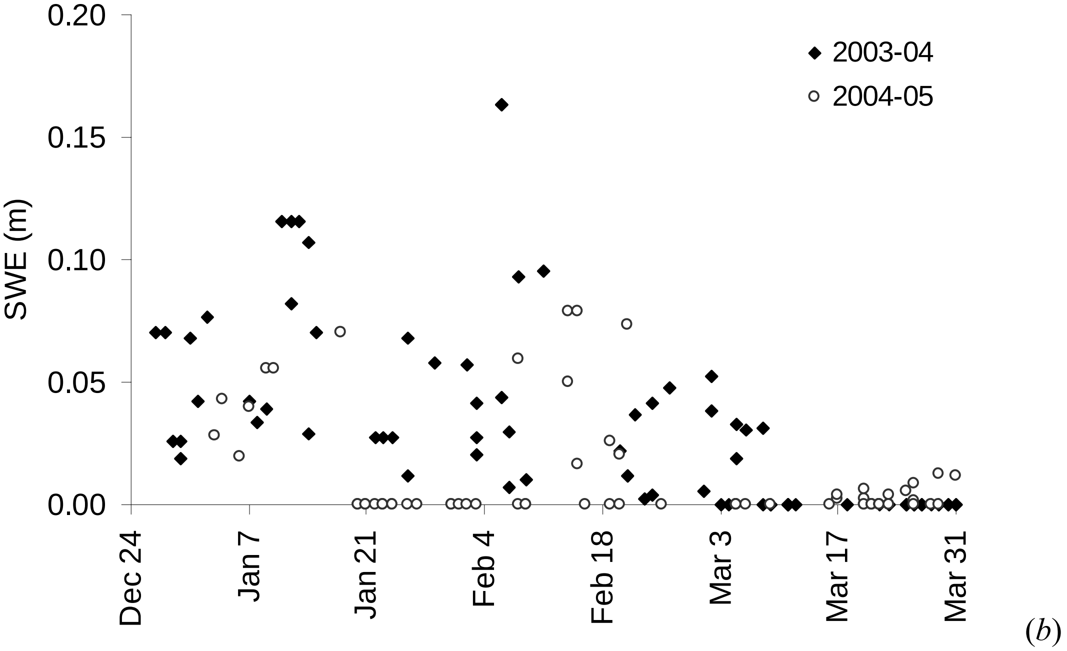


Figure 5.3. Temporal patterns in (*a*) the foraging ratio from bison observations, and (*b*) snowpack snow water equivalent (SWE) for bison locations in the Madison-Gibbon-Firehole area of Yellowstone National Park obtained from December-March during 2003-04 and 2004-05.

Table 5.1. Model selection results for *a priori* hypothesized models examining the effects of snowpack characteristics, forage biomass, and intraspecific competition on ϕ. The five best approximating models are presented along with the number of parameters (K), the ΔAIC_c value, and the Akaike weight (w_k).

Model	**Structure**	**K**	**ΔAIC_c**	**w_k**
W1.37‡	$\beta_0 + \beta_1(SWE+1)^{1/2} + \beta_2(HD+1)^{1/2}$	3	0.000	0.218
W1.32	$\beta_0 + \beta_1(SWE+1)^{1/2}$	2	0.608	0.161
W1.47	$\beta_0 + \beta_1(SWE+1)^{1/2} + \beta_2(HD+1)^{1/2} + \beta_3\exp(-BIO)$	4	1.583	0.099
W1.49	$\beta_0 + \beta_1(SWE+1)^{1/2} + \beta_2(HD+1)^{1/2} + \beta_3\exp(HF)$	4	2.087	0.077
W1.48	$\beta_0 + \beta_1(SWE+1)^{1/2} + \beta_2(HD+1)^{1/2} + \beta_3(BISON+1)^{1/2}$	4	2.114	0.076

‡ AIC_c value for model W1.37 is –266.802

The covariate SWE (Figure 5.4*a*), with moderated form, was significant in all three of the top models with confidence intervals not spanning zero and had the highest predictor weight of 0.999 (Table 5.2). Since the scaled covariates afford efficient comparisons between coefficients, SWE was 3.5 times more influential than HD in the top approximating model. As hypothesized, SWE had a positive effect on ϕ, but contrary to my predictions HD, BIO, BISON and HF had no significant effect in the best approximating models.

Discussion

Bison patch scale foraging behavior in winter was predominantly affected by snowpack, with forage biomass and intraspecific competition having minimal influence. These results indicate that on small spatial and temporal scales in heterogeneous

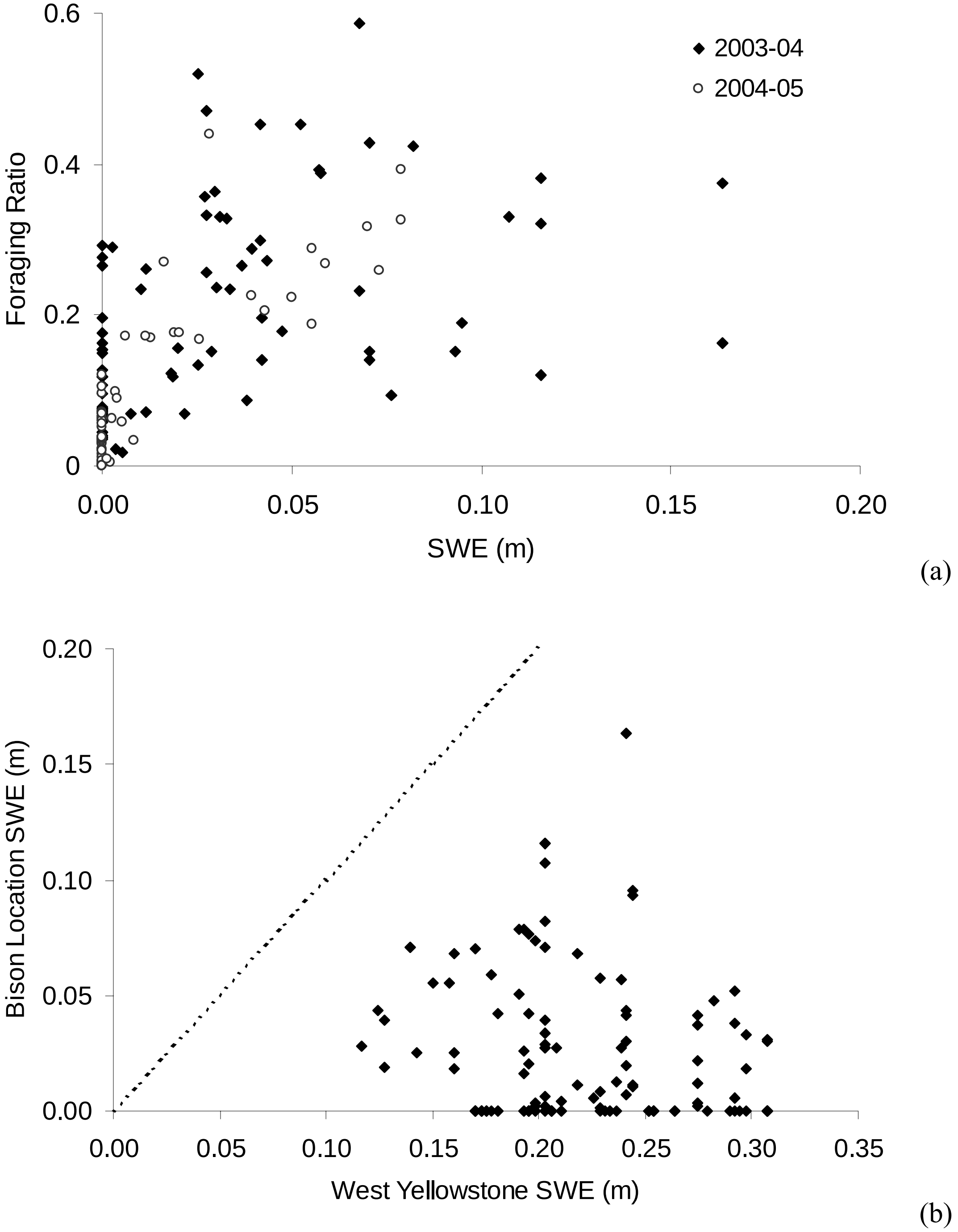


Figure 5.4. The relationship between (*a*) the foraging ratio and snow water equivalent (SWE) for bison locations obtained throughout the Madison-Gibbon-Firehole study area in Yellowstone National Park from December-March during 2003-04 and 2004-05, and (*b*) SWE for bison locations and landscape SWE as indexed by the West Yellowstone SNOTEL site. The line y=x is denoted.

Table 5.2. Coefficient values and lower (LCI) and upper (UCI) 95% confidence limits from the three best approximating models (models W1.37, W1.32, and W1.47) identified through AIC model comparison techniques examining abiotic and biotic effects on ϕ. Bold notation denotes significant coefficients at $\alpha = 0.05$. Predictor weights ($w_{+(i)}$) are presented for the overall modeling exercise.

	Model	**W1.37**	**W1.32**	**W1.47**
Covariate	**$w_{+(i)}$**	**β_i (LCI, UCI)**	**β_i (LCI, UCI)**	**β_i (LCI, UCI)**
Intercept		**0.065 (0.044, 0.085)**	**0.065 (0.044, 0.085)**	0.044 (-0.016, 0.104)
‡ SWE	0.999	**0.206 (0.146, 0.265)**	**0.243 (0.204, 0.282)**	**0.210 (0.149, 0.270)**
§ HD	0.574	0.059 (-0.012, 0.131)		0.061 (-0.011, 0.132)
BIO	0.308			0.011 (-0.018, 0.039)
BISON	0.262			
HF	0.259			

‡ SWE is significant at $P < 0.001$

§ HD is significant at $P < 0.11$

environments, bison forage in response to external stimuli rather than food abundance within a patch. This agrees with other studies that found large herbivore patch selection to be influenced by factors other than forage quantity. Wallace et al. (1995) documented neither elk (*Cervus elaphus*) nor bison in northern Yellowstone selected winter feeding sites or stations based on biomass. Cattle chose grazing sites because of quality and quantity of preferred species, rather than total biomass in an area (Senft et al. 1985). On larger scales, Fortin et al. (2003) found that bison did not select meadows during winter or summer based on biomass or abundance of preferred species. Spatial scale is an important factor determining selection of feeding areas by herbivores since sensitivity of foraging dynamics to abiotic and biotic factors can vary with scale (Gross et al. 1995, Bailey et al. 1996, Johnson et al. 2001). My results, combined with those from Bruggeman et al. (*in review, d*), further support this contention.

As predicted, ϕ was positively correlated with SWE because bison spent proportionately less time foraging in areas of deep, wet, or dense snow. My results indicate that snow is the primary factor that reduces foraging efficiency and patch quality for bison, supporting other studies that found snow to influence the use of foraging areas, foraging behavior, and diet selection by bison (Larter and Gates 1991, Turner et al. 1994, Bjornlie and Garrott 2001, Rutley and Hudson 2001, Fortin et al. 2003). Additionally, the moderated form of SWE was supported in all three top models, suggesting bison will decrease foraging time in a patch only to a certain extent as they are forced to spend proportionately more time displacing snow or searching (Figure 5.4*a*). As this asymptote in ϕ is approached, bison will change their activity or simply leave the patch in search of a more favorable foraging environment. From my two winters of data collection, ϕ was concentrated between 0.0-0.4, indicating bison rarely spent less than 70% of their time eating during a foraging bout within a patch. Further, 94% of our bison locations had SWE<0.08 m, suggesting bison preference for patches with minimal snowpack. However, this study occurred during two mild winters (2003-04 SWE_{ACC} = 2885 cm days; 2004-05 SWE_{ACC} = 2456 cm days; NRCS National Water and Climate Center 2006) relative to the historic average (mean SWE_{ACC} = 3405 cm days from 1966-2005; NRCS National Water and Climate Center 2006). SWE_{ACC}, a measure of annual snowpack severity, is the sum of daily SWE values from October 1-April 30 (Garrott et al. 2003), calculated here using data from the West Yellowstone SNOTEL site. In more severe winters I would expect that bison tolerance for foraging in snow would change in response to landscape conditions.

A herbivore's assessment of patch quality is likely determined by its perception of the patch relative to the surrounding environment (Senft et al. 1987, Bailey et al. 1996). Winter distribution patterns of elk, and their response to small-scale snow conditions, were found to be heavily influenced by landscape scale SWE (Messer 2003). Muskoxen (*Ovibos moschatus*) preferred patches with low snow cover and adjusted their time spent in patches depending on energetic costs of travel through snow to reach other patches (Schaefer and Messier 1995*a*,*b*). Since Yellowstone bison spend the majority of their time finding and eating forage during winter, and nearly one-third of that time displacing snow to reach forage (Bruggeman et al. *in press*), it is reasonable to expect bison to select patches with as favorable snow conditions as possible in which to forage. Field observations indicate that bison select patches in areas of lesser snow relative to the snowpack of the surrounding landscape. This is supported by a comparison of SWE data between my bison locations and the West Yellowstone SNOTEL site (Figure 5.4*b*) that provides an index of landscape snowpack conditions for valley bottoms in the MGF area. In more severe winters I would expect this behavior to continue, but with two possible alterations that may affect large-scale population processes. First, bison may continue to use the same foraging patches as in milder winters, but change their tolerance of snow to allow for greater values of ϕ and reduced foraging efficiency because their choices are constrained and out of necessity for survival. Second, large shifts in bison distributions may occur to low elevation meadows beyond the usual winter range that offer lesser snowpack and more energy efficient foraging. It is likely that this scenario occurred during the harsh winter of 1996-97 (SWE_{ACC} = 5502 cm days; NRCS National Water and Climate Center 2006) when hundreds of bison left Yellowstone in search of forage at lower elevations (National Park Service 2000*a*). Extending this work to encompass a variety of winter severities, and using a spatial snowpack model to study patch resource selection, would lend more insight into bison tolerance of snow and potential modifications in foraging behavior and distribution.

Forage biomass was not a significant effect in the top approximating models. Other studies have found biomass to be a poor predictor of ungulate distribution as red deer (*Cervus elaphus*) foraged on plants of intermediate biomass to obtain the most nutritional benefits (Albon and Langvatn 1992, Langvatn and Hanley 1993). Also, Serengeti wildebeest (*Connochaetes taurinus*) chose local areas because of grass greenness rather than height (Wilmshurst et al. 1999). A similar profitability trade-off may exist between SWE and biomass for bison because of their use of geothermal areas in winter as 35% of my locations were in thermally influenced habitats. These areas, which have no or reduced snow cover, generally contain low biomass and/or poor quality forage, likely resulting in increased ϕ owing to increased search time. The decision for bison becomes whether to forage in thermally influenced habitats without the added time constraint and energetic cost of displacing snow, or to select patches in meadows of high biomass with substantial snowpack. Therefore, constraints are imposed on patch scale foraging behavior by selection of foraging areas on large scales. Results from this study and other work (Bruggeman et al. *in review, d*) suggest snowpack presence and SWE levels are determining factors in optimal foraging area and patch choice for bison.

My findings demonstrate scale dependence for factors influencing bison winter foraging decisions, supporting other large herbivore research (Gross et al. 1995, Wallace et al. 1995, Bailey et al. 1996, Johnson et al. 2001, Fortin et al. 2002, Johnson et al. 2002). On both patch and foraging area scales, snowpack was the most significant effect on foraging behavior as SWE affected not only ϕ, but also foraging area residence times (Bruggeman et al. *in review, d*). However, while I found no influence of local scale competition on ϕ, I did find local and landscape level competition to be prominent in affecting foraging area scale behavior (Bruggeman et al. *in review, d*). These differing effects of density across scales may owe to how bison perceive patch and foraging area quality. On larger scales, abiotic factors and the extent of competition may be most influential (Senft et al. 1987, Bailey et al. 1996) and provide initial estimates of foraging area quality. For example, if a foraging area is covered by deep snow, or there are many animals in an area such that competition is severe, quality may be perceived as low and bison will not remain in the area long. On small scales, however, forage availability and quality may be of increased significance in determining patch value since herbivores may not be able to perceive differences in resource quality on large spatial scales (Bailey et al. 1996). Other studies have proposed that the relative importance of forage properties declines with increasing scale (Senft et al. 1987, Bailey et al. 1996, Fortin et al. 2003). While I found no influence of biomass on either patch or foraging area scale behavior (Bruggeman et al. *in review, d*), the results from my study must be considered in the appropriate context. This work considered foraging behavior in winter, during which forage is senescent and of low quality. Related to this is the importance to bison during winter of geothermal habitats, often containing forage of low biomass. Therefore, vegetation quality has little influence on bison patch scale foraging behavior during winter and the importance of biomass is likely overshadowed by the significant effect of snowpack (or lack thereof), which also affects forage availability.

My results reinforce the role of heterogeneity in affecting large herbivore behavior. Snowpack distribution in Yellowstone is highly variable, influenced by topography, vegetation, habitat, and wind (Watson et al. *in press*). This heterogeneity in snowpack is influential in affecting bison foraging behavior on multiple scales, which has implications on large-scale movements and distribution patterns. Snow has been shown to affect distributions of other large herbivores (Pruitt 1959, Schmidt 1993, Loison and Langvatn 1998, Nellemann 1998, Ball et al. 2001, Ihl and Klein 2001) and it is possible that forage properties are not the predominant factors influencing patch selection in these species. Heterogeneity affects large herbivore behavior on multiple scales. For example, Wallace and Crosthwaite (2005) discovered bison responded to burned versus unburned grasslands by altering foraging behavior. Etzenhouser et al. (1998) documented white-tailed deer (*Odocoileus virginianus*) and Spanish goat (*Capra hircus*) foraging strategies and movements varied in response to landscape heterogeneity. Saïd and Servanty (2005) found that edge density between habitats was the primary factor influencing home range size of female roe deer (*Capreolus capreolus*). Also, Kie et al. (2005) documented large-scale elk movements that were related to variation in topography.

I have defined a new metric, the foraging ratio, for quantifying large herbivore foraging behavior on patch scales that can be applied to species in heterogeneous and dynamic environments. In these complex systems, abiotic factors and the perceived value of patches relative to those in the surrounding landscape may influence a herbivore's discernment of patch quality. My research provides an example of how ϕ can be used to examine large herbivore foraging behavior and presents novel findings on the relative influence of abiotic and biotic mechanisms affecting Yellowstone bison patch scale foraging behavior in winter.

SYNTHESIS

The spatio-temporal dynamics of bison from the central herd in Yellowstone National Park are complex and affected by several interacting density dependent and density independent mechanisms operating across multiple scales. Factors influencing resource availability—including snowpack, population density, and drought—provided the primary impetus for variability in bison distribution, movements, and foraging behavior. Additionally, heterogeneity, in the form of multi-scale biological or landscape complexity, contributed to spatial distribution and movement patterns that may, ultimately, influence population level processes. My results agree with other studies suggesting large herbivore decisions are not independent of either spatial or temporal scale and may be affected by biotic or abiotic factors (Senft et al. 1987, Ward and Saltz 1994, Gross et al. 1995, Wallace et al. 1995, Bailey et al. 1996, Johnson et al. 2001, Fortin et al. 2002, Johnson et al. 2002). Further, the importance of heterogeneity and its scale dependent effects on large herbivore movements and foraging behavior has been previously documented (Senft et al. 1987, Gross et al. 1995, Pearson et al. 1995, Bailey et al. 1996). The seminal publication of Senft et al. (1987) provided a framework for examining large herbivore foraging behavior using hierarchy theory for integrating herbivore decisions across several scales. Bailey et al. (1996) furthered this work by presenting a conceptual model incorporating biotic, abiotic, and animal memory effects to explain distribution patterns of grazers. I apply these concepts below to synthesize my work and understand how bison respond to scale-dependent abiotic and biotic effects and heterogeneity.

Density, drought, and snowpack affected the central herd's annual migration from the summer range in the Hayden and Pelican Valleys to the Madison-Gibbon-Firehole (MGF) winter range. The number of bison migrating each year and the timing of migration were positively influenced by increasing density and drought severity. Snowpack snow water equivalent (SWE) on the summer range was also positively correlated with the timing of migration. Therefore, on regional scales (as defined in Senft et al. (1987)), general trends in the migration are explained by limitations in resource availability that may operate over timeframes ranging from weekly to yearly. These broad scale changes in resources over the summer and winter constrain bison choices on the summer range, affecting decisions on when and whether or not to migrate. Bison responses to these constraints are manifested in changes in large-scale distribution patterns across the central herd's range. Upon deciding to migrate and move, factors affecting spatial patterns in bison movement and choice of travel routes become of importance.

Multiple topographic and habitat attributes—including slope, landscape roughness, elevation, habitat, and distances to streams, roads, foraging areas, and forested habitats—influenced the probability of bison travel and spatial distribution of travel corridors during winter and summer throughout the central herd's range. Streams were the most influential landscape feature affecting bison travel and corridor use as the probability of travel was higher closest to streams. My results suggest the bison travel network throughout central Yellowstone is spatially defined largely by the presence of streams that connect foraging areas. The probability of bison travel and corridor use was also higher in regions of variable topography that constrain movements, such as canyons like those in the Madison, Gibbon, and Firehole drainages. Pronounced travel corridors existed both in close association with roads and distant from any roads, and results indicate that roads may facilitate bison travel in certain areas. Elevation was a negative effect on the probability of travel, suggesting, in part, that greater snowpack accumulation at higher elevations may hinder bison travel in some regions during winter and that some high elevation regions lack suitable foraging areas. Bison travel locations and corridors were more likely in close proximity to foraging areas, a result that suggests bison connect foraging areas using the most direct routes. Additionally, the probability of bison travel and corridors increased in meadow and thermal habitats, indicating bison develop some travel routes through interconnected foraging areas. These results suggest landscape heterogeneity is quite influential in affecting spatial patterns in bison travel. The well-defined bison travel corridors that exist throughout central Yellowstone provide routes for migration and long distance movements throughout and between both ranges.

Temporal trends in bison travel across the MGF winter range are influenced by multiple, interacting effects as snowpack, bison density, and road grooming all were influential factors affecting variability in the amount of bison road travel. Likewise, snowpack, density, and springtime snowmelt were significant in accounting for temporal variation in the amount of bison off-road travel. My results suggest that temporal road travel patterns are likely a manifestation of general bison travel trends since both are affected by similar abiotic and biotic factors. Snowpack had a positive influence on both bison road and off-road travel in the MGF, a result likely more an artifact of high SWE values during spring when bison are actually responding to energy efficient foraging opportunities with increased travel to redistribute themselves to meadows that have partially melted out. Bison road and off-road travel were both positively correlated with the number of bison in the MGF, an anticipated result because redistribution, manifested as a travel bout, should eventually occur as more bison enter an area of limited space and some threshold limit of occupancy is reached. Road travel was negatively correlated with road grooming and I found no evidence that bison preferentially used groomed roads during winter. Overall, the amount of bison travel, both on and off roads, was reduced during winter likely because bison, to conserve energy, decrease movements as snowpack accumulates since foraging areas, with the exception of geothermal meadows, are all covered with deep snow and contain senescent vegetation. Therefore, on a landscape scale in the MGF, temporal variability in the amount of bison travel is influenced by similar factors to those affecting migration, notably snowpack and density, but operating on smaller spatial and temporal scales. These abiotic and biotic effects also impact resource availability and influence bison foraging decisions about where to forage throughout the MGF, and the optimal amount of time to spend in each foraging area.

In the MGF, bison foraging area residence times in winter were affected by the ratio of local to landscape scale snowpack SWE, previous foraging experiences, and both local and landscape scale intraspecific competition. These results indicate that the amount of time bison spend in one foraging area is dependent on a suite of abiotic and biotic factors that affect resource availability, and the perceived value of the area relative to other recently visited areas. Residence times were positively correlated with the ratio of local to landscape scale SWE as a quadratic effect, suggesting bison foraging decisions are made in response to snowpack at local, foraging area scales and to snow conditions in the surrounding landscape. Experiences in previous foraging areas on a landscape scale affected bison foraging behavior and residence time in future areas, indicating that as expectations of value increase from previous experiences, a bison is more likely to select subsequent areas of higher quality and remain in those areas longer. The number of bison in the MGF was negatively correlated with residence time, suggesting competition on a landscape scale can affect foraging behavior. As bison migrate into the MGF throughout the winter, competition will increase in higher quality foraging areas. In theory, the frequency of bison redistribution should increase as density increases (Fretwell and Lucas 1969) resulting in decreased residence time. In turn, the amount of bison travel should increase, which I found in the analysis of temporal travel patterns. On a local scale, however, I found group size had a positive influence on residence time as an interaction with previous experience, suggesting as both group size and foraging area value expectations increase, bison will remain in an area longer. The significance of local and landscape scale snowpack and density related effects on residence time reinforces the idea that foraging by large herbivores may be simultaneously affected by mechanisms operating across multiple spatial and temporal scales. Further, bison choices of foraging areas may also constrain foraging decisions on smaller scales.

Bison patch scale foraging behavior in winter in the MGF was predominantly affected by snowpack, with forage biomass and intraspecific competition having minimal influence. These results indicate that on small spatial and temporal scales in heterogeneous environments, bison forage in response to external stimuli rather than food abundance within a patch. As predicted, the foraging ratio was positively correlated with SWE because bison spent proportionately less time foraging in areas of deep, wet, or dense snow. My results indicate that snow is the primary factor that reduces foraging efficiency and patch quality for bison. Forage biomass was not a significant effect on patch scale foraging behavior and a profitability trade-off might exist between SWE and biomass for bison because of their use of geothermal areas in winter. These areas, which have no or reduced snow cover, generally contain low biomass and/or poor quality forage, likely resulting in an increased foraging ratio owing to increased search time. The decision for bison becomes whether to forage in thermally influenced habitats without the added time constraint and energetic cost of displacing snow, or to select patches in meadows of high biomass with substantial snowpack. Therefore, constraints are imposed on patch scale foraging behavior by selection of foraging areas on large scales.

Overall, my results reinforce the role of heterogeneity in affecting large herbivore behavior, particularly given the pervasiveness of snowpack in affecting all aspects of bison spatio-temporal dynamics examined in this work. Snowpack distribution in Yellowstone is highly variable, influenced by topography, vegetation, habitat, and wind (Watson et al. *in press*). This heterogeneity in snowpack is influential in affecting bison foraging behavior on multiple scales, which has implications on large-scale movements and distribution patterns, and, ultimately, population level processes. In addition to the effects of biological heterogeneity, the complexities of the Yellowstone landscape influence spatial patterns in travel as bison use distinct travel corridors throughout the winter and summer ranges. Streams and canyon bottoms, which at times coincide with roads, provide natural travel pathways for bison to connect foraging areas.

My findings also demonstrate scale dependence for factors influencing bison winter foraging decisions. On both patch and foraging area scales, snowpack was the most significant effect on foraging behavior. However, while I found no influence of local scale competition on patch scale foraging behavior, I did find local and landscape level competition to be prominent in affecting foraging area residence times. These differing effects of density across scales may owe to how bison perceive patch and foraging area quality. On larger scales, abiotic factors and the extent of competition may be most influential (Senft et al. 1987, Bailey et al. 1996) and provide initial estimates of foraging area quality. On small scales, however, forage availability and quality may be of increased significance in determining patch value since herbivores may not be able to perceive differences in resource quality on large spatial scales (Bailey et al. 1996). A herbivore's assessment of patch quality is likely determined by its perception of the patch relative to the surrounding environment (Senft et al. 1987, Bailey et al. 1996) and, therefore, understanding interactions between herbivores and landscapes requires investigations across multiple scales. The challenges, implications, and opportunities presented by multi-scale large herbivore studies were well summarized by Hobbs (2003). The scale of observation affects what is observed and determined to be significant effects through analysis (Hobbs 2003). Further, with scale-dependent phenomena, inferences about large-scale behavior and processes cannot necessarily be made using small-scale studies as decisions made on broad scales are not always the integration of numerous small-scale choices (Hobbs 2003). The ability, therefore, to address important large herbivore management and conservation issues depends critically on amassing and aggregating information from studies conducted across multiple scales (Hobbs 2003).

In this work, I have examined bison spatio-temporal dynamics across multiple scales in relation to scale dependent abiotic and biotic effects. The results from this research offer many new findings regarding Yellowstone bison ecology and provide valuable information for park managers. My work provides a better understanding of the role of road grooming for winter recreation, and roads in general, on bison travel patterns. Bison responses to snowpack are of paramount importance given its role in affecting bison behavior across multiple scales. In extremely harsh winters it is likely these effects will be magnified, resulting in major shifts in distribution to lower elevations and beyond park boundaries as has occurred in the past. Continuing drought in the Greater Yellowstone Area may exacerbate these movements given the significance of drought severity on migration patterns. Also, the importance of population density on bison migration, movements, and foraging behavior is of interest to managers given the rapidly growing Yellowstone bison population. Establishing management guidelines that allow for modifying protocols in response to environmental stochasticity and population variability can provide flexibility to managers in devoting funding and resources to addressing the most pressing concerns.

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APPENDICES

APPENDIX 1A

TABLES OF *A PRIORI* MODELS FOR BISON EXTENT AND TIMING OF MIGRATION MODELING EXERCISES

Table 1A.1. Candidate list of *a priori* regression models for the timing of bison migration modeling exercise. The response variable is the timing of migration (τ). Note: an intercept term was included with each model (not depicted in the model structure).

Model	Structure
T1	BISON
T2	SWES
T3	DROUGHT
T4	BISON + SWES
T5	BISON + DROUGHT
T6	SWES + DROUGHT
T7	BISON + SWES + DROUGHT
T8	BISON + SWES + BISON*SWES
T9	BISON + DROUGHT + BISON*DROUGHT
T10	BISON + SWES + DROUGHT + BISON*SWES
T11	BISON + SWES + DROUGHT + BISON*SWES + BISON*DROUGHT

Table 1A.2. Candidate list of *a priori* regression models for the extent of bison migration modeling exercise. The response variable is the extent of migration (ε). Note: an intercept term was included with each model (not depicted in the model structure).

Model	Structure
E1	BISON
E2	SWE_{acc}
E3	DROUGHT
E4	BISON + SWE_{acc}
E5	BISON + DROUGHT
E6	SWE_{acc} + DROUGHT
E7	BISON + SWE_{acc} + DROUGHT
E8	BISON + SWE_{acc} + BISON* SWE_{acc}
E9	BISON + DROUGHT + BISON*DROUGHT
E10	BISON + SWE_{acc} + DROUGHT + BISON* SWE_{acc}
E11	BISON + SWE_{acc} + DROUGHT + BISON* SWE_{acc} + BISON*DROUGHT

APPENDIX 1B

TABLES OF MODEL RESULTS FOR BISON EXTENT AND TIMING OF MIGRATION MODELING EXERCISES

Table 1B.1. Complete model results for *a priori* candidate models examining the timing of bison migration. The model number, number of parameters (K), the AIC_c value, ΔAIC_c value, and the Akaike weight (w_k) are listed.

Model	**K**	**AIC_c**	**ΔAIC_c**	**w_k**
M11	6	1366.737	0.000	0.9774
M6	3	1375.175	8.438	0.0144
M7	4	1376.903	10.165	0.0061
M10	5	1379.121	12.384	0.0020
M8	4	1385.244	18.506	0.0001
M4	3	1385.343	18.606	0.0001
M2	2	1404.028	37.291	0.0000
M1	2	1407.477	40.740	0.0000
M5	3	1409.594	42.857	0.0000
M9	4	1411.610	44.872	0.0000
M3	2	1418.143	51.406	0.0000

Table 1B.2. Complete model results for *a priori* candidate models examining the extent of bison migration. The model number, number of parameters (K), the AIC_c value, ΔAIC_c value, and the Akaike weight (w_k) are listed.

Model	**K**	**AIC_c**	**ΔAIC_c**	**w_k**
M3	2	115.000	0.000	0.4531
M5	3	115.602	0.602	0.3353
M1	2	118.718	3.718	0.0706
M4	3	119.007	4.006	0.0611
M6	3	119.203	4.203	0.0554
M9	4	122.371	7.370	0.0114
M7	4	122.531	7.531	0.0105
M8	4	125.979	10.979	0.0019
M2	2	127.874	12.874	0.0007
M10	5	134.444	19.443	0.0000
M11	6	157.595	42.594	0.0000

APPENDIX 2A

FIGURES DEPICTING THE DEFINITION OF TURNING ANGLE BETWEEN SEGMENTS, CRITERIA FOR A SIGNIFICANT MOVEMENT BOUT, AND DISTANCE VERSUS TURNING ANGLE

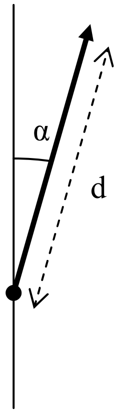


Figure 2A.1. The definition of segment distances (*d*) and turning angle between segments (α) for a bison vector (dark line with arrow). The turning angle between segments, α, ranges between $0^\circ \leq \alpha \leq 180^\circ$.

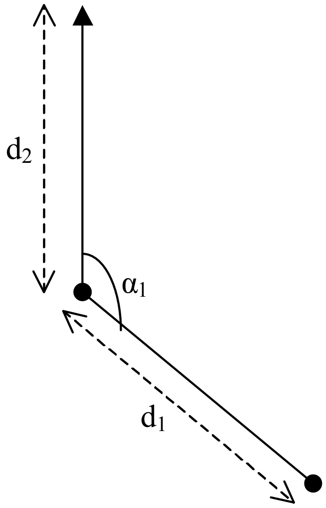


Figure 2A.2. A bison travel vector consisting of two significant movement bouts. By definition, for a significant movement bout the distance of each segment must be ≥800 m (i.e., $d_1 \geq 800$ m; $d_2 \geq 800$ m) and the turning angle must be ≤90° (i.e., $\alpha_1 \leq 90^\circ$).

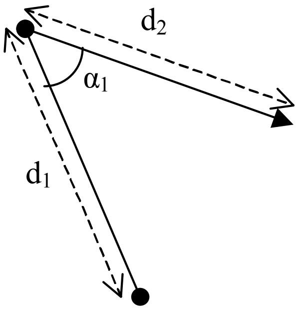


Figure 2A.3. A set of bison vectors that are representative of a foraging or searching trajectory for which the turning angle between segments (α_1) has a value of α_1>90^o and/or segment distances (*d*) are <800 m (i.e., d_1<800 m; d_2<800 m).

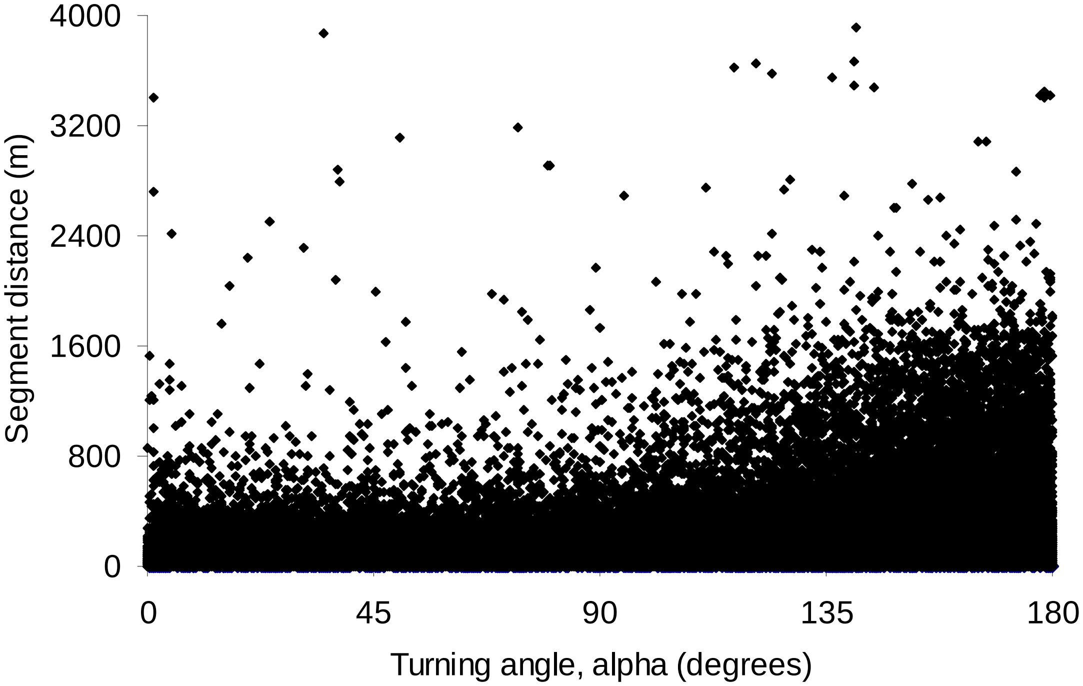


Figure 2A.4. A plot of segment distance (*d*) versus turning angle (α) for consecutive bison GPS locations obtained <32 min apart.

APPENDIX 2B

TABLES OF *A PRIORI* MODELS FOR THE BISON GENERAL TRAVEL, CORRIDOR TRAVEL, AND ROAD TRAVEL MODELING EXERCISES

Table 2B.1. Table of *a priori* models for the general bison travel modeling exercise using GPS vector data. The response variable is the log odds of general bison travel.

Model	Structure
	Suite 1: Static Topography Variables
T1	Bo + B1[SL]
T2	Bo + B1[SLHG]
T3	Bo + B1[TAN]
T4	Bo + B1[SL] + B2[SLHG]
T5	Bo + B1[SL] + B2[TAN]
T6	Bo + B1[SLHG] + B2[TAN]
T7	Bo + B1[SL] + B2[SLHG] + B3[TAN]
	Suite 2: Static Habitat Variables
H1	Bo + B1[HBT]
H2	Bo + B1[DST]
H3	Bo + B1[DBF]
H4	Bo + B1[DUF]
H5	Bo + B1[PROX]
H6	Bo + B1[HBT] + B2[DST]
H7	Bo + B1[HBT] + B2[DBF]
H8	Bo + B1[HBT] + B2[DUF]
H9	Bo + B1[HBT] + B2[PROX]
H10	Bo + B1[DST] + B2[DBF]
H11	Bo + B1[DST] + B2[DUF]
H12	Bo + B1[DST] + B2[PROX]
H13	Bo + B1[DBF] + B2[DUF]
H14	Bo + B1[DBF] + B2[PROX]
H15	Bo + B1[DUF] + B2[PROX]
H16	Bo + B1[HBT] + B2[DST] + B3[DBF]
H17	Bo + B1[HBT] + B2[DST] + B3[DUF]
H18	Bo + B1[HBT] + B2[DST] + B3[PROX]
H19	Bo + B1[HBT] + B2[DBF] + B3[DUF]
H20	Bo + B1[HBT] + B2[DBF] + B3[PROX]
H21	Bo + B1[HBT] + B2[DUF] + B3[PROX]
H22	Bo + B1[DST] + B2[DBF] + B3[DUF]
H23	Bo + B1[DST] + B2[DBF] + B3[PROX]
H24	Bo + B1[DST] + B2[DUF] + B3[PROX]

TABLE 2B.1—CONTINUED

H25	Bo + B1[DBF] + B2[DUF] + B3[PROX]
H26	Bo + B1[HBT] + B2[DST] + B3[DBF] + B4[DUF]
H27	Bo + B1[HBT] + B2[DST] + B3[DBF] + B4[PROX]
H28	Bo + B1[HBT] + B2[DST] + B3[DUF] + B4[PROX]
H29	Bo + B1[HBT] + B2[DBF] + B3[DUF] + B4[PROX]
H30	Bo + B1[DST] + B2[DBF] + B3[DUF] + B4[PROX]
H31	Bo + B1[HBT] + B2[DST] + B3[DBF] + B4[DUF] + B5[PROX]
	Suite 3: Composite Static Topography & Habitat Variables
HT1	Bo + B1[HBT] + B2[SL]
HT2	Bo + B1[DST] + B2[SL]
HT3	Bo + B1[DBF] + B2[SL]
HT4	Bo + B1[DUF] + B2[SL]
HT5	Bo + B1[PROX] + B2[SL]
HT6	Bo + B1[HBT] + B2[DST] + B3[SL]
HT7	Bo + B1[HBT] + B2[DBF] + B3[SL]
HT8	Bo + B1[HBT] + B2[DUF] + B3[SL]
HT9	Bo + B1[HBT] + B2[PROX] + B3[SL]
HT10	Bo + B1[DST] + B2[DBF] + B3[SL]
HT11	Bo + B1[DST] + B2[DUF] + B3[SL]
HT12	Bo + B1[DST] + B2[PROX] + B3[SL]
HT13	Bo + B1[DBF] + B2[DUF] + B3[SL]
HT14	Bo + B1[DBF] + B2[PROX] + B3[SL]
HT15	Bo + B1[DUF] + B2[PROX] + B3[SL]
HT16	Bo + B1[HBT] + B2[DST] + B3[DBF] + B4[SL]
HT17	Bo + B1[HBT] + B2[DST] + B3[DUF] + B4[SL]
HT18	Bo + B1[HBT] + B2[DST] + B3[PROX] + B4[SL]
HT19	Bo + B1[HBT] + B2[DBF] + B3[DUF] + B4[SL]
HT20	Bo + B1[HBT] + B2[DBF] + B3[PROX] + B4[SL]
HT21	Bo + B1[HBT] + B2[DUF] + B3[PROX] + B4[SL]
HT22	Bo + B1[DST] + B2[DBF] + B3[DUF] + B4[SL]
HT23	Bo + B1[DST] + B2[DBF] + B3[PROX] + B4[SL]
HT24	Bo + B1[DST] + B2[DUF] + B3[PROX] + B4[SL]
HT25	Bo + B1[DBF] + B2[DUF] + B3[PROX] + B4[SL]
HT26	Bo + B1[HBT] + B2[DST] + B3[DBF] + B4[DUF] + B5[SL]
HT27	Bo + B1[HBT] + B2[DST] + B3[DBF] + B4[PROX] + B5[SL]
HT28	Bo + B1[HBT] + B2[DST] + B3[DUF] + B4[PROX] + B5[SL]

TABLE 2B.1—CONTINUED

HT29	Bo + B1[HBT] + B2[DBF] + B3[DUF] + B4[PROX] + B5[SL]
HT30	Bo + B1[DST] + B2[DBF] + B3[DUF] + B4[PROX] + B5[SL]
HT31	Bo + B1[HBT] + B2[DST] + B3[DBF] + B4[DUF] + B5[PROX] + B6[SL]
HT32	Bo + B1[HBT] + B2[SLHG]
HT33	Bo + B1[DST] + B2[SLHG]
HT34	Bo + B1[DBF] + B2[SLHG]
HT35	Bo + B1[DUF] + B2[SLHG]
HT36	Bo + B1[PROX] + B2[SLHG]
HT37	Bo + B1[HBT] + B2[DST] + B3[SLHG]
HT38	Bo + B1[HBT] + B2[DBF] + B3[SLHG]
HT39	Bo + B1[HBT] + B2[DUF] + B3[SLHG]
HT40	Bo + B1[HBT] + B2[PROX] + B3[SLHG]
HT41	Bo + B1[DST] + B2[DBF] + B3[SLHG]
HT42	Bo + B1[DST] + B2[DUF] + B3[SLHG]
HT43	Bo + B1[DST] + B2[PROX] + B3[SLHG]
HT44	Bo + B1[DBF] + B2[DUF] + B3[SLHG]
HT45	Bo + B1[DBF] + B2[PROX] + B3[SLHG]
HT46	Bo + B1[DUF] + B2[PROX] + B3[SLHG]
HT47	Bo + B1[HBT] + B2[DST] + B3[DBF] + B4[SLHG]
HT48	Bo + B1[HBT] + B2[DST] + B3[DUF] + B4[SLHG]
HT49	Bo + B1[HBT] + B2[DST] + B3[PROX] + B4[SLHG]
HT50	Bo + B1[HBT] + B2[DBF] + B3[DUF] + B4[SLHG]
HT51	Bo + B1[HBT] + B2[DBF] + B3[PROX] + B4[SLHG]
HT52	Bo + B1[HBT] + B2[DUF] + B3[PROX] + B4[SLHG]
HT53	Bo + B1[DST] + B2[DBF] + B3[DUF] + B4[SLHG]
HT54	Bo + B1[DST] + B2[DBF] + B3[PROX] + B4[SLHG]
HT55	Bo + B1[DST] + B2[DUF] + B3[PROX] + B4[SLHG]
HT56	Bo + B1[DBF] + B2[DUF] + B3[PROX] + B4[SLHG]
HT57	Bo + B1[HBT] + B2[DST] + B3[DBF] + B4[DUF] + B5[SLHG]
HT58	Bo + B1[HBT] + B2[DST] + B3[DBF] + B4[PROX] + B5[SLHG]
HT59	Bo + B1[HBT] + B2[DST] + B3[DUF] + B4[PROX] + B5[SLHG]
HT60	Bo + B1[HBT] + B2[DBF] + B3[DUF] + B4[PROX] + B5[SLHG]
HT61	Bo + B1[DST] + B2[DBF] + B3[DUF] + B4[PROX] + B5[SLHG]
HT62	Bo + B1[HBT] + B2[DST] + B3[DBF] + B4[DUF] + B5[PROX] + B6[SLHG]
HT63	Bo + B1[HBT] + B2[TAN]
HT64	Bo + B1[DST] + B2[TAN]
HT65	Bo + B1[DBF] + B2[TAN]

TABLE 2B.1—CONTINUED

HT66	Bo + B1[DUF] + B2[TAN]
HT67	Bo + B1[PROX] + B2[TAN]
HT68	Bo + B1[HBT] + B2[DST] + B3[TAN]
HT69	Bo + B1[HBT] + B2[DBF] + B3[TAN]
HT70	Bo + B1[HBT] + B2[DUF] + B3[TAN]
HT71	Bo + B1[HBT] + B2[PROX] + B3[TAN]
HT72	Bo + B1[DST] + B2[DBF] + B3[TAN]
HT73	Bo + B1[DST] + B2[DUF] + B3[TAN]
HT74	Bo + B1[DST] + B2[PROX] + B3[TAN]
HT75	Bo + B1[DBF] + B2[DUF] + B3[TAN]
HT76	Bo + B1[DBF] + B2[PROX] + B3[TAN]
HT77	Bo + B1[DUF] + B2[PROX] + B3[TAN]
HT78	Bo + B1[HBT] + B2[DST] + B3[DBF] + B4[TAN]
HT79	Bo + B1[HBT] + B2[DST] + B3[DUF] + B4[TAN]
HT80	Bo + B1[HBT] + B2[DST] + B3[PROX] + B4[TAN]
HT81	Bo + B1[HBT] + B2[DBF] + B3[DUF] + B4[TAN]
HT82	Bo + B1[HBT] + B2[DBF] + B3[PROX] + B4[TAN]
HT83	Bo + B1[HBT] + B2[DUF] + B3[PROX] + B4[TAN]
HT84	Bo + B1[DST] + B2[DBF] + B3[DUF] + B4[TAN]
HT85	Bo + B1[DST] + B2[DBF] + B3[PROX] + B4[TAN]
HT86	Bo + B1[DST] + B2[DUF] + B3[PROX] + B4[TAN]
HT87	Bo + B1[DBF] + B2[DUF] + B3[PROX] + B4[TAN]
HT88	Bo + B1[HBT] + B2[DST] + B3[DBF] + B4[DUF] + B5[TAN]
HT89	Bo + B1[HBT] + B2[DST] + B3[DBF] + B4[PROX] + B5[TAN]
HT90	Bo + B1[HBT] + B2[DST] + B3[DUF] + B4[PROX] + B5[TAN]
HT91	Bo + B1[HBT] + B2[DBF] + B3[DUF] + B4[PROX] + B5[TAN]
HT92	Bo + B1[DST] + B2[DBF] + B3[DUF] + B4[PROX] + B5[TAN]
HT93	Bo + B1[HBT] + B2[DST] + B3[DBF] + B4[DUF] + B5[PROX] + B6[TAN]
HT94	Bo + B1[HBT] + B2[SL] + B3[SLHG]
HT95	Bo + B1[DST] + B2[SL] + B3[SLHG]
HT96	Bo + B1[DBF] + B2[SL] + B3[SLHG]
HT97	Bo + B1[DUF] + B2[SL] + B3[SLHG]
HT98	Bo + B1[PROX] + B2[SL] + B3[SLHG]
HT99	Bo + B1[HBT] + B2[DST] + B3[SL] + B4[SLHG]
HT100	Bo + B1[HBT] + B2[DBF] + B3[SL] + B4[SLHG]
HT101	Bo + B1[HBT] + B2[DUF] + B3[SL] + B4[SLHG]
HT102	Bo + B1[HBT] + B2[PROX] + B3[SL] + B4[SLHG]

TABLE 2B.1—CONTINUED

HT103	Bo + B1[DST] + B2[DBF] + B3[SL] + B4[SLHG]
HT104	Bo + B1[DST] + B2[DUF] + B3[SL] + B4[SLHG]
HT105	Bo + B1[DST] + B2[PROX] + B3[SL] + B4[SLHG]
HT106	Bo + B1[DBF] + B2[DUF] + B3[SL] + B4[SLHG]
HT107	Bo + B1[DBF] + B2[PROX] + B3[SL] + B4[SLHG]
HT108	Bo + B1[DUF] + B2[PROX] + B3[SL] + B4[SLHG]
HT109	Bo + B1[HBT] + B2[DST] + B3[DBF] + B4[SL] + B5[SLHG]
HT110	Bo + B1[HBT] + B2[DST] + B3[DUF] + B4[SL] + B5[SLHG]
HT111	Bo + B1[HBT] + B2[DST] + B3[PROX] + B4[SL] + B5[SLHG]
HT112	Bo + B1[HBT] + B2[DBF] + B3[DUF] + B4[SL] + B5[SLHG]
HT113	Bo + B1[HBT] + B2[DBF] + B3[PROX] + B4[SL] + B5[SLHG]
HT114	Bo + B1[HBT] + B2[DUF] + B3[PROX] + B4[SL] + B5[SLHG]
HT115	Bo + B1[DST] + B2[DBF] + B3[DUF] + B4[SL] + B5[SLHG]
HT116	Bo + B1[DST] + B2[DBF] + B3[PROX] + B4[SL] + B5[SLHG]
HT117	Bo + B1[DST] + B2[DUF] + B3[PROX] + B4[SL] + B5[SLHG]
HT118	Bo + B1[DBF] + B2[DUF] + B3[PROX] + B4[SL] + B5[SLHG]
HT119	Bo + B1[HBT] + B2[DST] + B3[DBF] + B4[DUF] + B5[SL] + B6[SLHG]
HT120	Bo + B1[HBT] + B2[DST] + B3[DBF] + B4[PROX] + B5[SL] + B6[SLHG]
HT121	Bo + B1[HBT] + B2[DST] + B3[DUF] + B4[PROX] + B5[SL] + B6[SLHG]
HT122	Bo + B1[HBT] + B2[DBF] + B3[DUF] + B4[PROX] + B5[SL] + B6[SLHG]
HT123	Bo + B1[DST] + B2[DBF] + B3[DUF] + B4[PROX] + B5[SL] + B6[SLHG]
HT124	Bo + B1[HBT] + B2[DST] + B3[DBF] + B4[DUF] + B5[PROX] + B6[SL] + B7[SLHG]
HT125	Bo + B1[HBT] + B2[SL] + B3[TAN]
HT126	Bo + B1[DST] + B2[SL] + B3[TAN]
HT127	Bo + B1[DBF] + B2[SL] + B3[TAN]
HT128	Bo + B1[DUF] + B2[SL] + B3[TAN]
HT129	Bo + B1[PROX] + B2[SL] + B3[TAN]
HT130	Bo + B1[HBT] + B2[DST] + B3[SL] + B4[TAN]
HT131	Bo + B1[HBT] + B2[DBF] + B3[SL] + B4[TAN]
HT132	Bo + B1[HBT] + B2[DUF] + B3[SL] + B4[TAN]
HT133	Bo + B1[HBT] + B2[PROX] + B3[SL] + B4[TAN]
HT134	Bo + B1[DST] + B2[DBF] + B3[SL] + B4[TAN]
HT135	Bo + B1[DST] + B2[DUF] + B3[SL] + B4[TAN]
HT136	Bo + B1[DST] + B2[PROX] + B3[SL] + B4[TAN]
HT137	Bo + B1[DBF] + B2[DUF] + B3[SL] + B4[TAN]
HT138	Bo + B1[DBF] + B2[PROX] + B3[SL] + B4[TAN]
HT139	Bo + B1[DUF] + B2[PROX] + B3[SL] + B4[TAN]

TABLE 2B.1—CONTINUED

HT140	Bo + B1[HBT] + B2[DST] + B3[DBF] + B4[SL] + B5[TAN]
HT141	Bo + B1[HBT] + B2[DST] + B3[DUF] + B4[SL] + B5[TAN]
HT142	Bo + B1[HBT] + B2[DST] + B3[PROX] + B4[SL] + B5[TAN]
HT143	Bo + B1[HBT] + B2[DBF] + B3[DUF] + B4[SL] + B5[TAN]
HT144	Bo + B1[HBT] + B2[DBF] + B3[PROX] + B4[SL] + B5[TAN]
HT145	Bo + B1[HBT] + B2[DUF] + B3[PROX] + B4[SL] + B5[TAN]
HT146	Bo + B1[DST] + B2[DBF] + B3[DUF] + B4[SL] + B5[TAN]
HT147	Bo + B1[DST] + B2[DBF] + B3[PROX] + B4[SL] + B5[TAN]
HT148	Bo + B1[DST] + B2[DUF] + B3[PROX] + B4[SL] + B5[TAN]
HT149	Bo + B1[DBF] + B2[DUF] + B3[PROX] + B4[SL] + B5[TAN]
HT150	Bo + B1[HBT] + B2[DST] + B3[DBF] + B4[DUF] + B5[SL] + B6[TAN]
HT151	Bo + B1[HBT] + B2[DST] + B3[DBF] + B4[PROX] + B5[SL] + B6[TAN]
HT152	Bo + B1[HBT] + B2[DST] + B3[DUF] + B4[PROX] + B5[SL] + B6[TAN]
HT153	Bo + B1[HBT] + B2[DBF] + B3[DUF] + B4[PROX] + B5[SL] + B6[TAN]
HT154	Bo + B1[DST] + B2[DBF] + B3[DUF] + B4[PROX] + B5[SL] + B6[TAN]
HT155	Bo + B1[HBT] + B2[DST] + B3[DBF] + B4[DUF] + B5[PROX] + B6[SL] + B7[TAN]
HT156	Bo + B1[HBT] + B2[SLHG] + B3[TAN]
HT157	Bo + B1[DST] + B2[SLHG] + B3[TAN]
HT158	Bo + B1[DBF] + B2[SLHG] + B3[TAN]
HT159	Bo + B1[DUF] + B2[SLHG] + B3[TAN]
HT160	Bo + B1[PROX] + B2[SLHG] + B3[TAN]
HT161	Bo + B1[HBT] + B2[DST] + B3[SLHG] + B4[TAN]
HT162	Bo + B1[HBT] + B2[DBF] + B3[SLHG] + B4[TAN]
HT163	Bo + B1[HBT] + B2[DUF] + B3[SLHG] + B4[TAN]
HT164	Bo + B1[HBT] + B2[PROX] + B3[SLHG] + B4[TAN]
HT165	Bo + B1[DST] + B2[DBF] + B3[SLHG] + B4[TAN]
HT166	Bo + B1[DST] + B2[DUF] + B3[SLHG] + B4[TAN]
HT167	Bo + B1[DST] + B2[PROX] + B3[SLHG] + B4[TAN]
HT168	Bo + B1[DBF] + B2[DUF] + B3[SLHG] + B4[TAN]
HT169	Bo + B1[DBF] + B2[PROX] + B3[SLHG] + B4[TAN]
HT170	Bo + B1[DUF] + B2[PROX] + B3[SLHG] + B4[TAN]
HT171	Bo + B1[HBT] + B2[DST] + B3[DBF] + B4[SLHG] + B5[TAN]
HT172	Bo + B1[HBT] + B2[DST] + B3[DUF] + B4[SLHG] + B5[TAN]
HT173	Bo + B1[HBT] + B2[DST] + B3[PROX] + B4[SLHG] + B5[TAN]
HT174	Bo + B1[HBT] + B2[DBF] + B3[DUF] + B4[SLHG] + B5[TAN]
HT175	Bo + B1[HBT] + B2[DBF] + B3[PROX] + B4[SLHG] + B5[TAN]
HT176	Bo + B1[HBT] + B2[DUF] + B3[PROX] + B4[SLHG] + B5[TAN]

TABLE 2B.1—CONTINUED

HT177	Bo + B1[DST] + B2[DBF] + B3[DUF] + B4[SLHG] + B5[TAN]
HT178	Bo + B1[DST] + B2[DBF] + B3[PROX] + B4[SLHG] + B5[TAN]
HT179	Bo + B1[DST] + B2[DUF] + B3[PROX] + B4[SLHG] + B5[TAN]
HT180	Bo + B1[DBF] + B2[DUF] + B3[PROX] + B4[SLHG] + B5[TAN]
HT181	Bo + B1[HBT] + B2[DST] + B3[DBF] + B4[DUF] + B5[SLHG] + B6[TAN]
HT182	Bo + B1[HBT] + B2[DST] + B3[DBF] + B4[PROX] + B5[SLHG] + B6[TAN]
HT183	Bo + B1[HBT] + B2[DST] + B3[DUF] + B4[PROX] + B5[SLHG] + B6[TAN]
HT184	Bo + B1[HBT] + B2[DBF] + B3[DUF] + B4[PROX] + B5[SLHG] + B6[TAN]
HT185	Bo + B1[DST] + B2[DBF] + B3[DUF] + B4[PROX] + B5[SLHG] + B6[TAN]
HT186	Bo + B1[HBT] + B2[DST] + B3[DBF] + B4[DUF] + B5[PROX] + B6[SLHG] + B7[TAN]
HT187	Bo + B1[HBT] + B2[SL] + B3[SLHG] + B4[TAN]
HT188	Bo + B1[DST] + B2[SL] + B3[SLHG] + B4[TAN]
HT189	Bo + B1[DBF] + B2[SL] + B3[SLHG] + B4[TAN]
HT190	Bo + B1[DUF] + B2[SL] + B3[SLHG] + B4[TAN]
HT191	Bo + B1[PROX] + B2[SL] + B3[SLHG] + B4[TAN]
HT192	Bo + B1[HBT] + B2[DST] + B3[SL] + B4[SLHG] + B5[TAN]
HT193	Bo + B1[HBT] + B2[DBF] + B3[SL] + B4[SLHG] + B5[TAN]
HT194	Bo + B1[HBT] + B2[DUF] + B3[SL] + B4[SLHG] + B5[TAN]
HT195	Bo + B1[HBT] + B2[PROX] + B3[SL] + B4[SLHG] + B5[TAN]
HT196	Bo + B1[DST] + B2[DBF] + B3[SL] + B4[SLHG] + B5[TAN]
HT197	Bo + B1[DST] + B2[DUF] + B3[SL] + B4[SLHG] + B5[TAN]
HT198	Bo + B1[DST] + B2[PROX] + B3[SL] + B4[SLHG] + B5[TAN]
HT199	Bo + B1[DBF] + B2[DUF] + B3[SL] + B4[SLHG] + B5[TAN]
HT200	Bo + B1[DBF] + B2[PROX] + B3[SL] + B4[SLHG] + B5[TAN]
HT201	Bo + B1[DUF] + B2[PROX] + B3[SL] + B4[SLHG] + B5[TAN]
HT202	Bo + B1[HBT] + B2[DST] + B3[DBF] + B4[SL] + B5[SLHG] + B6[TAN]
HT203	Bo + B1[HBT] + B2[DST] + B3[DUF] + B4[SL] + B5[SLHG] + B6[TAN]
HT204	Bo + B1[HBT] + B2[DST] + B3[PROX] + B4[SL] + B5[SLHG] + B6[TAN]
HT205	Bo + B1[HBT] + B2[DBF] + B3[DUF] + B4[SL] + B5[SLHG] + B6[TAN]
HT206	Bo + B1[HBT] + B2[DBF] + B3[PROX] + B4[SL] + B5[SLHG] + B6[TAN]
HT207	Bo + B1[HBT] + B2[DUF] + B3[PROX] + B4[SL] + B5[SLHG] + B6[TAN]
HT208	Bo + B1[DST] + B2[DBF] + B3[DUF] + B4[SL] + B5[SLHG] + B6[TAN]
HT209	Bo + B1[DST] + B2[DBF] + B3[PROX] + B4[SL] + B5[SLHG] + B6[TAN]
HT210	Bo + B1[DST] + B2[DUF] + B3[PROX] + B4[SL] + B5[SLHG] + B6[TAN]
HT211	Bo + B1[DBF] + B2[DUF] + B3[PROX] + B4[SL] + B5[SLHG] + B6[TAN]
HT212	Bo + B1[HBT] + B2[DST] + B3[DBF] + B4[DUF] + B5[SL] + B6[SLHG] + B7[TAN]
HT213	Bo + B1[HBT] + B2[DST] + B3[DBF] + B4[PROX] + B5[SL] + B6[SLHG] + B7[TAN]

TABLE 2B.1—CONTINUED

HT214	Bo + B1[HBT] + B2[DST] + B3[DUF] + B4[PROX] + B5[SL] + B6[SLHG] + B7[TAN]
HT215	Bo + B1[HBT] + B2[DBF] + B3[DUF] + B4[PROX] + B5[SL] + B6[SLHG] + B7[TAN]
HT216	Bo + B1[DST] + B2[DBF] + B3[DUF] + B4[PROX] + B5[SL] + B6[SLHG] + B7[TAN]
HT217	Bo + B1[HBT] + B2[DST] + B3[DBF] + B4[DUF] + B5[PROX] + B6[SL] + B7[SLHG] + B8[TAN]

Table 2B.2. Table of *a priori* models for the bison corridor travel modeling exercise using GPS vector data. The response variable is the log odds of bison selection of travel corridors.

Model	Structure
	Suite 1: Static Topography Variables
CT1	Bo + B1[SL]
CT2	Bo + B1[SLHG]
CT3	Bo + B1[TAN]
CT4	Bo + B1[SL] + B2[SLHG]
CT5	Bo + B1[SL] + B2[TAN]
CT6	Bo + B1[SLHG] + B2[TAN]
CT7	Bo + B1[SL] + B2[SLHG] + B3[TAN]
	Suite 2: Static Habitat Variables
CH1	Bo + B1[HBT]
CH2	Bo + B1[DST]
CH3	Bo + B1[DBF]
CH4	Bo + B1[DUF]
CH5	Bo + B1[PROX]
CH6	Bo + B1[HBT] + B2[DST]
CH7	Bo + B1[HBT] + B2[DBF]
CH8	Bo + B1[HBT] + B2[DUF]
CH9	Bo + B1[HBT] + B2[PROX]
CH10	Bo + B1[DST] + B2[DBF]
CH11	Bo + B1[DST] + B2[DUF]
CH12	Bo + B1[DST] + B2[PROX]
CH13	Bo + B1[DBF] + B2[DUF]
CH14	Bo + B1[DBF] + B2[PROX]
CH15	Bo + B1[DUF] + B2[PROX]
CH16	Bo + B1[HBT] + B2[DST] + B3[DBF]
CH17	Bo + B1[HBT] + B2[DST] + B3[DUF]
CH18	Bo + B1[HBT] + B2[DST] + B3[PROX]
CH19	Bo + B1[HBT] + B2[DBF] + B3[DUF]
CH20	Bo + B1[HBT] + B2[DBF] + B3[PROX]
CH21	Bo + B1[HBT] + B2[DUF] + B3[PROX]
CH22	Bo + B1[DST] + B2[DBF] + B3[DUF]
CH23	Bo + B1[DST] + B2[DBF] + B3[PROX]
CH24	Bo + B1[DST] + B2[DUF] + B3[PROX]

TABLE 2B.2—CONTINUED

CH25	Bo + B1[DBF] + B2[DUF] + B3[PROX]
CH26	Bo + B1[HBT] + B2[DST] + B3[DBF] + B4[DUF]
CH27	Bo + B1[HBT] + B2[DST] + B3[DBF] + B4[PROX]
CH28	Bo + B1[HBT] + B2[DST] + B3[DUF] + B4[PROX]
CH29	Bo + B1[HBT] + B2[DBF] + B3[DUF] + B4[PROX]
CH30	Bo + B1[DST] + B2[DBF] + B3[DUF] + B4[PROX]
CH31	Bo + B1[HBT] + B2[DST] + B3[DBF] + B4[DUF] + B5[PROX]
	Suite 3: Composite Static Topography & Habitat Variables
CHT1	Bo + B1[HBT] + B2[SL]
CHT2	Bo + B1[DST] + B2[SL]
CHT3	Bo + B1[DBF] + B2[SL]
CHT4	Bo + B1[DUF] + B2[SL]
CHT5	Bo + B1[PROX] + B2[SL]
CHT6	Bo + B1[HBT] + B2[DST] + B3[SL]
CHT7	Bo + B1[HBT] + B2[DBF] + B3[SL]
CHT8	Bo + B1[HBT] + B2[DUF] + B3[SL]
CHT9	Bo + B1[HBT] + B2[PROX] + B3[SL]
CHT10	Bo + B1[DST] + B2[DBF] + B3[SL]
CHT11	Bo + B1[DST] + B2[DUF] + B3[SL]
CHT12	Bo + B1[DST] + B2[PROX] + B3[SL]
CHT13	Bo + B1[DBF] + B2[DUF] + B3[SL]
CHT14	Bo + B1[DBF] + B2[PROX] + B3[SL]
CHT15	Bo + B1[DUF] + B2[PROX] + B3[SL]
CHT16	Bo + B1[HBT] + B2[DST] + B3[DBF] + B4[SL]
CHT17	Bo + B1[HBT] + B2[DST] + B3[DUF] + B4[SL]
CHT18	Bo + B1[HBT] + B2[DST] + B3[PROX] + B4[SL]
CHT19	Bo + B1[HBT] + B2[DBF] + B3[DUF] + B4[SL]
CHT20	Bo + B1[HBT] + B2[DBF] + B3[PROX] + B4[SL]
CHT21	Bo + B1[HBT] + B2[DUF] + B3[PROX] + B4[SL]
CHT22	Bo + B1[DST] + B2[DBF] + B3[DUF] + B4[SL]
CHT23	Bo + B1[DST] + B2[DBF] + B3[PROX] + B4[SL]
CHT24	Bo + B1[DST] + B2[DUF] + B3[PROX] + B4[SL]
CHT25	Bo + B1[DBF] + B2[DUF] + B3[PROX] + B4[SL]
CHT26	Bo + B1[HBT] + B2[DST] + B3[DBF] + B4[DUF] + B5[SL]
CHT27	Bo + B1[HBT] + B2[DST] + B3[DBF] + B4[PROX] + B5[SL]
CHT28	Bo + B1[HBT] + B2[DST] + B3[DUF] + B4[PROX] + B5[SL]

TABLE 2B.2—CONTINUED

CHT29	Bo + B1[HBT] + B2[DBF] + B3[DUF] + B4[PROX] + B5[SL]
CHT30	Bo + B1[DST] + B2[DBF] + B3[DUF] + B4[PROX] + B5[SL]
CHT31	Bo + B1[HBT] + B2[DST] + B3[DBF] + B4[DUF] + B5[PROX] + B6[SL]
CHT32	Bo + B1[HBT] + B2[SLHG]
CHT33	Bo + B1[DST] + B2[SLHG]
CHT34	Bo + B1[DBF] + B2[SLHG]
CHT35	Bo + B1[DUF] + B2[SLHG]
CHT36	Bo + B1[PROX] + B2[SLHG]
CHT37	Bo + B1[HBT] + B2[DST] + B3[SLHG]
CHT38	Bo + B1[HBT] + B2[DBF] + B3[SLHG]
CHT39	Bo + B1[HBT] + B2[DUF] + B3[SLHG]
CHT40	Bo + B1[HBT] + B2[PROX] + B3[SLHG]
CHT41	Bo + B1[DST] + B2[DBF] + B3[SLHG]
CHT42	Bo + B1[DST] + B2[DUF] + B3[SLHG]
CHT43	Bo + B1[DST] + B2[PROX] + B3[SLHG]
CHT44	Bo + B1[DBF] + B2[DUF] + B3[SLHG]
CHT45	Bo + B1[DBF] + B2[PROX] + B3[SLHG]
CHT46	Bo + B1[DUF] + B2[PROX] + B3[SLHG]
CHT47	Bo + B1[HBT] + B2[DST] + B3[DBF] + B4[SLHG]
CHT48	Bo + B1[HBT] + B2[DST] + B3[DUF] + B4[SLHG]
CHT49	Bo + B1[HBT] + B2[DST] + B3[PROX] + B4[SLHG]
CHT50	Bo + B1[HBT] + B2[DBF] + B3[DUF] + B4[SLHG]
CHT51	Bo + B1[HBT] + B2[DBF] + B3[PROX] + B4[SLHG]
CHT52	Bo + B1[HBT] + B2[DUF] + B3[PROX] + B4[SLHG]
CHT53	Bo + B1[DST] + B2[DBF] + B3[DUF] + B4[SLHG]
CHT54	Bo + B1[DST] + B2[DBF] + B3[PROX] + B4[SLHG]
CHT55	Bo + B1[DST] + B2[DUF] + B3[PROX] + B4[SLHG]
CHT56	Bo + B1[DBF] + B2[DUF] + B3[PROX] + B4[SLHG]
CHT57	Bo + B1[HBT] + B2[DST] + B3[DBF] + B4[DUF] + B5[SLHG]
CHT58	Bo + B1[HBT] + B2[DST] + B3[DBF] + B4[PROX] + B5[SLHG]
CHT59	Bo + B1[HBT] + B2[DST] + B3[DUF] + B4[PROX] + B5[SLHG]
CHT60	Bo + B1[HBT] + B2[DBF] + B3[DUF] + B4[PROX] + B5[SLHG]
CHT61	Bo + B1[DST] + B2[DBF] + B3[DUF] + B4[PROX] + B5[SLHG]
CHT62	Bo + B1[HBT] + B2[DST] + B3[DBF] + B4[DUF] + B5[PROX] + B6[SLHG]
CHT63	Bo + B1[HBT] + B2[TAN]
CHT64	Bo + B1[DST] + B2[TAN]
CHT65	Bo + B1[DBF] + B2[TAN]

TABLE 2B.2—CONTINUED

CHT66	Bo + B1[DUF] + B2[TAN]
CHT67	Bo + B1[PROX] + B2[TAN]
CHT68	Bo + B1[HBT] + B2[DST] + B3[TAN]
CHT69	Bo + B1[HBT] + B2[DBF] + B3[TAN]
CHT70	Bo + B1[HBT] + B2[DUF] + B3[TAN]
CHT71	Bo + B1[HBT] + B2[PROX] + B3[TAN]
CHT72	Bo + B1[DST] + B2[DBF] + B3[TAN]
CHT73	Bo + B1[DST] + B2[DUF] + B3[TAN]
CHT74	Bo + B1[DST] + B2[PROX] + B3[TAN]
CHT75	Bo + B1[DBF] + B2[DUF] + B3[TAN]
CHT76	Bo + B1[DBF] + B2[PROX] + B3[TAN]
CHT77	Bo + B1[DUF] + B2[PROX] + B3[TAN]
CHT78	Bo + B1[HBT] + B2[DST] + B3[DBF] + B4[TAN]
CHT79	Bo + B1[HBT] + B2[DST] + B3[DUF] + B4[TAN]
CHT80	Bo + B1[HBT] + B2[DST] + B3[PROX] + B4[TAN]
CHT81	Bo + B1[HBT] + B2[DBF] + B3[DUF] + B4[TAN]
CHT82	Bo + B1[HBT] + B2[DBF] + B3[PROX] + B4[TAN]
CHT83	Bo + B1[HBT] + B2[DUF] + B3[PROX] + B4[TAN]
CHT84	Bo + B1[DST] + B2[DBF] + B3[DUF] + B4[TAN]
CHT85	Bo + B1[DST] + B2[DBF] + B3[PROX] + B4[TAN]
CHT86	Bo + B1[DST] + B2[DUF] + B3[PROX] + B4[TAN]
CHT87	Bo + B1[DBF] + B2[DUF] + B3[PROX] + B4[TAN]
CHT88	Bo + B1[HBT] + B2[DST] + B3[DBF] + B4[DUF] + B5[TAN]
CHT89	Bo + B1[HBT] + B2[DST] + B3[DBF] + B4[PROX] + B5[TAN]
CHT90	Bo + B1[HBT] + B2[DST] + B3[DUF] + B4[PROX] + B5[TAN]
CHT91	Bo + B1[HBT] + B2[DBF] + B3[DUF] + B4[PROX] + B5[TAN]
CHT92	Bo + B1[DST] + B2[DBF] + B3[DUF] + B4[PROX] + B5[TAN]
CHT93	Bo + B1[HBT] + B2[DST] + B3[DBF] + B4[DUF] + B5[PROX] + B6[TAN]
CHT94	Bo + B1[HBT] + B2[SL] + B3[SLHG]
CHT95	Bo + B1[DST] + B2[SL] + B3[SLHG]
CHT96	Bo + B1[DBF] + B2[SL] + B3[SLHG]
CHT97	Bo + B1[DUF] + B2[SL] + B3[SLHG]
CHT98	Bo + B1[PROX] + B2[SL] + B3[SLHG]
CHT99	Bo + B1[HBT] + B2[DST] + B3[SL] + B4[SLHG]
CHT100	Bo + B1[HBT] + B2[DBF] + B3[SL] + B4[SLHG]
CHT101	Bo + B1[HBT] + B2[DUF] + B3[SL] + B4[SLHG]
CHT102	Bo + B1[HBT] + B2[PROX] + B3[SL] + B4[SLHG]

TABLE 2B.2—CONTINUED

CHT103	Bo + B1[DST] + B2[DBF] + B3[SL] + B4[SLHG]
CHT104	Bo + B1[DST] + B2[DUF] + B3[SL] + B4[SLHG]
CHT105	Bo + B1[DST] + B2[PROX] + B3[SL] + B4[SLHG]
CHT106	Bo + B1[DBF] + B2[DUF] + B3[SL] + B4[SLHG]
CHT107	Bo + B1[DBF] + B2[PROX] + B3[SL] + B4[SLHG]
CHT108	Bo + B1[DUF] + B2[PROX] + B3[SL] + B4[SLHG]
CHT109	Bo + B1[HBT] + B2[DST] + B3[DBF] + B4[SL] + B5[SLHG]
CHT110	Bo + B1[HBT] + B2[DST] + B3[DUF] + B4[SL] + B5[SLHG]
CHT111	Bo + B1[HBT] + B2[DST] + B3[PROX] + B4[SL] + B5[SLHG]
CHT112	Bo + B1[HBT] + B2[DBF] + B3[DUF] + B4[SL] + B5[SLHG]
CHT113	Bo + B1[HBT] + B2[DBF] + B3[PROX] + B4[SL] + B5[SLHG]
CHT114	Bo + B1[HBT] + B2[DUF] + B3[PROX] + B4[SL] + B5[SLHG]
CHT115	Bo + B1[DST] + B2[DBF] + B3[DUF] + B4[SL] + B5[SLHG]
CHT116	Bo + B1[DST] + B2[DBF] + B3[PROX] + B4[SL] + B5[SLHG]
CHT117	Bo + B1[DST] + B2[DUF] + B3[PROX] + B4[SL] + B5[SLHG]
CHT118	Bo + B1[DBF] + B2[DUF] + B3[PROX] + B4[SL] + B5[SLHG]
CHT119	Bo + B1[HBT] + B2[DST] + B3[DBF] + B4[DUF] + B5[SL] + B6[SLHG]
CHT120	Bo + B1[HBT] + B2[DST] + B3[DBF] + B4[PROX] + B5[SL] + B6[SLHG]
CHT121	Bo + B1[HBT] + B2[DST] + B3[DUF] + B4[PROX] + B5[SL] + B6[SLHG]
CHT122	Bo + B1[HBT] + B2[DBF] + B3[DUF] + B4[PROX] + B5[SL] + B6[SLHG]
CHT123	Bo + B1[DST] + B2[DBF] + B3[DUF] + B4[PROX] + B5[SL] + B6[SLHG]
CHT124	Bo + B1[HBT] + B2[DST] + B3[DBF] + B4[DUF] + B5[PROX] + B6[SL] + B7[SLHG]
CHT125	Bo + B1[HBT] + B2[SL] + B3[TAN]
CHT126	Bo + B1[DST] + B2[SL] + B3[TAN]
CHT127	Bo + B1[DBF] + B2[SL] + B3[TAN]
CHT128	Bo + B1[DUF] + B2[SL] + B3[TAN]
CHT129	Bo + B1[PROX] + B2[SL] + B3[TAN]
CHT130	Bo + B1[HBT] + B2[DST] + B3[SL] + B4[TAN]
CHT131	Bo + B1[HBT] + B2[DBF] + B3[SL] + B4[TAN]
CHT132	Bo + B1[HBT] + B2[DUF] + B3[SL] + B4[TAN]
CHT133	Bo + B1[HBT] + B2[PROX] + B3[SL] + B4[TAN]
CHT134	Bo + B1[DST] + B2[DBF] + B3[SL] + B4[TAN]
CHT135	Bo + B1[DST] + B2[DUF] + B3[SL] + B4[TAN]
CHT136	Bo + B1[DST] + B2[PROX] + B3[SL] + B4[TAN]
CHT137	Bo + B1[DBF] + B2[DUF] + B3[SL] + B4[TAN]
CHT138	Bo + B1[DBF] + B2[PROX] + B3[SL] + B4[TAN]
CHT139	Bo + B1[DUF] + B2[PROX] + B3[SL] + B4[TAN]

TABLE 2B.2—CONTINUED

CHT140	Bo + B1[HBT] + B2[DST] + B3[DBF] + B4[SL] + B5[TAN]
CHT141	Bo + B1[HBT] + B2[DST] + B3[DUF] + B4[SL] + B5[TAN]
CHT142	Bo + B1[HBT] + B2[DST] + B3[PROX] + B4[SL] + B5[TAN]
CHT143	Bo + B1[HBT] + B2[DBF] + B3[DUF] + B4[SL] + B5[TAN]
CHT144	Bo + B1[HBT] + B2[DBF] + B3[PROX] + B4[SL] + B5[TAN]
CHT145	Bo + B1[HBT] + B2[DUF] + B3[PROX] + B4[SL] + B5[TAN]
CHT146	Bo + B1[DST] + B2[DBF] + B3[DUF] + B4[SL] + B5[TAN]
CHT147	Bo + B1[DST] + B2[DBF] + B3[PROX] + B4[SL] + B5[TAN]
CHT148	Bo + B1[DST] + B2[DUF] + B3[PROX] + B4[SL] + B5[TAN]
CHT149	Bo + B1[DBF] + B2[DUF] + B3[PROX] + B4[SL] + B5[TAN]
CHT150	Bo + B1[HBT] + B2[DST] + B3[DBF] + B4[DUF] + B5[SL] + B6[TAN]
CHT151	Bo + B1[HBT] + B2[DST] + B3[DBF] + B4[PROX] + B5[SL] + B6[TAN]
CHT152	Bo + B1[HBT] + B2[DST] + B3[DUF] + B4[PROX] + B5[SL] + B6[TAN]
CHT153	Bo + B1[HBT] + B2[DBF] + B3[DUF] + B4[PROX] + B5[SL] + B6[TAN]
CHT154	Bo + B1[DST] + B2[DBF] + B3[DUF] + B4[PROX] + B5[SL] + B6[TAN]
CHT155	Bo + B1[HBT] + B2[DST] + B3[DBF] + B4[DUF] + B5[PROX] + B6[SL] + B7[TAN]
CHT156	Bo + B1[HBT] + B2[SLHG] + B3[TAN]
CHT157	Bo + B1[DST] + B2[SLHG] + B3[TAN]
CHT158	Bo + B1[DBF] + B2[SLHG] + B3[TAN]
CHT159	Bo + B1[DUF] + B2[SLHG] + B3[TAN]
CHT160	Bo + B1[PROX] + B2[SLHG] + B3[TAN]
CHT161	Bo + B1[HBT] + B2[DST] + B3[SLHG] + B4[TAN]
CHT162	Bo + B1[HBT] + B2[DBF] + B3[SLHG] + B4[TAN]
CHT163	Bo + B1[HBT] + B2[DUF] + B3[SLHG] + B4[TAN]
CHT164	Bo + B1[HBT] + B2[PROX] + B3[SLHG] + B4[TAN]
CHT165	Bo + B1[DST] + B2[DBF] + B3[SLHG] + B4[TAN]
CHT166	Bo + B1[DST] + B2[DUF] + B3[SLHG] + B4[TAN]
CHT167	Bo + B1[DST] + B2[PROX] + B3[SLHG] + B4[TAN]
CHT168	Bo + B1[DBF] + B2[DUF] + B3[SLHG] + B4[TAN]
CHT169	Bo + B1[DBF] + B2[PROX] + B3[SLHG] + B4[TAN]
CHT170	Bo + B1[DUF] + B2[PROX] + B3[SLHG] + B4[TAN]
CHT171	Bo + B1[HBT] + B2[DST] + B3[DBF] + B4[SLHG] + B5[TAN]
CHT172	Bo + B1[HBT] + B2[DST] + B3[DUF] + B4[SLHG] + B5[TAN]
CHT173	Bo + B1[HBT] + B2[DST] + B3[PROX] + B4[SLHG] + B5[TAN]
CHT174	Bo + B1[HBT] + B2[DBF] + B3[DUF] + B4[SLHG] + B5[TAN]
CHT175	Bo + B1[HBT] + B2[DBF] + B3[PROX] + B4[SLHG] + B5[TAN]
CHT176	Bo + B1[HBT] + B2[DUF] + B3[PROX] + B4[SLHG] + B5[TAN]

TABLE 2B.2—CONTINUED

CHT177	Bo + B1[DST] + B2[DBF] + B3[DUF] + B4[SLHG] + B5[TAN]
CHT178	Bo + B1[DST] + B2[DBF] + B3[PROX] + B4[SLHG] + B5[TAN]
CHT179	Bo + B1[DST] + B2[DUF] + B3[PROX] + B4[SLHG] + B5[TAN]
CHT180	Bo + B1[DBF] + B2[DUF] + B3[PROX] + B4[SLHG] + B5[TAN]
CHT181	Bo + B1[HBT] + B2[DST] + B3[DBF] + B4[DUF] + B5[SLHG] + B6[TAN]
CHT182	Bo + B1[HBT] + B2[DST] + B3[DBF] + B4[PROX] + B5[SLHG] + B6[TAN]
CHT183	Bo + B1[HBT] + B2[DST] + B3[DUF] + B4[PROX] + B5[SLHG] + B6[TAN]
CHT184	Bo + B1[HBT] + B2[DBF] + B3[DUF] + B4[PROX] + B5[SLHG] + B6[TAN]
CHT185	Bo + B1[DST] + B2[DBF] + B3[DUF] + B4[PROX] + B5[SLHG] + B6[TAN]
CHT186	Bo + B1[HBT] + B2[DST] + B3[DBF] + B4[DUF] + B5[PROX] + B6[SLHG] + B7[TAN]
CHT187	Bo + B1[HBT] + B2[SL] + B3[SLHG] + B4[TAN]
CHT188	Bo + B1[DST] + B2[SL] + B3[SLHG] + B4[TAN]
CHT189	Bo + B1[DBF] + B2[SL] + B3[SLHG] + B4[TAN]
CHT190	Bo + B1[DUF] + B2[SL] + B3[SLHG] + B4[TAN]
CHT191	Bo + B1[PROX] + B2[SL] + B3[SLHG] + B4[TAN]
CHT192	Bo + B1[HBT] + B2[DST] + B3[SL] + B4[SLHG] + B5[TAN]
CHT193	Bo + B1[HBT] + B2[DBF] + B3[SL] + B4[SLHG] + B5[TAN]
CHT194	Bo + B1[HBT] + B2[DUF] + B3[SL] + B4[SLHG] + B5[TAN]
CHT195	Bo + B1[HBT] + B2[PROX] + B3[SL] + B4[SLHG] + B5[TAN]
CHT196	Bo + B1[DST] + B2[DBF] + B3[SL] + B4[SLHG] + B5[TAN]
CHT197	Bo + B1[DST] + B2[DUF] + B3[SL] + B4[SLHG] + B5[TAN]
CHT198	Bo + B1[DST] + B2[PROX] + B3[SL] + B4[SLHG] + B5[TAN]
CHT199	Bo + B1[DBF] + B2[DUF] + B3[SL] + B4[SLHG] + B5[TAN]
CHT200	Bo + B1[DBF] + B2[PROX] + B3[SL] + B4[SLHG] + B5[TAN]
CHT201	Bo + B1[DUF] + B2[PROX] + B3[SL] + B4[SLHG] + B5[TAN]
CHT202	Bo + B1[HBT] + B2[DST] + B3[DBF] + B4[SL] + B5[SLHG] + B6[TAN]
CHT203	Bo + B1[HBT] + B2[DST] + B3[DUF] + B4[SL] + B5[SLHG] + B6[TAN]
CHT204	Bo + B1[HBT] + B2[DST] + B3[PROX] + B4[SL] + B5[SLHG] + B6[TAN]
CHT205	Bo + B1[HBT] + B2[DBF] + B3[DUF] + B4[SL] + B5[SLHG] + B6[TAN]
CHT206	Bo + B1[HBT] + B2[DBF] + B3[PROX] + B4[SL] + B5[SLHG] + B6[TAN]
CHT207	Bo + B1[HBT] + B2[DUF] + B3[PROX] + B4[SL] + B5[SLHG] + B6[TAN]
CHT208	Bo + B1[DST] + B2[DBF] + B3[DUF] + B4[SL] + B5[SLHG] + B6[TAN]
CHT209	Bo + B1[DST] + B2[DBF] + B3[PROX] + B4[SL] + B5[SLHG] + B6[TAN]
CHT210	Bo + B1[DST] + B2[DUF] + B3[PROX] + B4[SL] + B5[SLHG] + B6[TAN]
CHT211	Bo + B1[DBF] + B2[DUF] + B3[PROX] + B4[SL] + B5[SLHG] + B6[TAN]
CHT212	Bo + B1[HBT] + B2[DST] + B3[DBF] + B4[DUF] + B5[SL] + B6[SLHG] + B7[TAN]
CHT213	Bo + B1[HBT] + B2[DST] + B3[DBF] + B4[PROX] + B5[SL] + B6[SLHG] + B7[TAN]

TABLE 2B.2—CONTINUED

CHT214	Bo + B1[HBT] + B2[DST] + B3[DUF] + B4[PROX] + B5[SL] + B6[SLHG] + B7[TAN]
CHT215	Bo + B1[HBT] + B2[DBF] + B3[DUF] + B4[PROX] + B5[SL] + B6[SLHG] + B7[TAN]
CHT216	Bo + B1[DST] + B2[DBF] + B3[DUF] + B4[PROX] + B5[SL] + B6[SLHG] + B7[TAN]
CHT217	Bo + B1[HBT] + B2[DST] + B3[DBF] + B4[DUF] + B5[PROX] + B6[SL] + B7[SLHG] + B8[TAN]

Table 2B.3. Table of *a priori* models for the bison road travel modeling exercise using data from bison road use surveys. The response variable is the η, the amount of bison travel per road segment.

Model	**Structure**
	Suite 1: Static Topography Variables & Year Effect
RT1	Bo + B1[SL]
RT2	Bo + B1[SLHG]
RT3	Bo + B1[TAN]
RT4	Bo + B1[SL] + B2[SLHG]
RT5	Bo + B1[SLHG] + B2[TAN]
RT6	Bo + B1[SL] + B2[YEAR]
RT7	Bo + B1[SLHG] + B2[YEAR]
RT8	Bo + B1[TAN] + B2[YEAR]
RT9	Bo + B1[SL] + B2[SLHG] + B3[YEAR]
RT10	Bo + B1[SLHG] + B2[TAN] + B3[YEAR]
	Suite 2: Static Habitat Variables & Year Effect
RH1	Bo + B1[DST]
RH2	Bo + B1[DBF]
RH3	Bo + B1[DUF]
RH4	Bo + B1[PROX]
RH5	Bo + B1[DST] + B2[DBF]
RH6	Bo + B1[DST] + B2[DUF]
RH7	Bo + B1[DST] + B2[PROX]
RH8	Bo + B1[DBF] + B2[DUF]
RH9	Bo + B1[DBF] + B2[PROX]
RH10	Bo + B1[DUF] + B2[PROX]
RH11	Bo + B1[DST] + B2[DBF] + B3[DUF]
RH12	Bo + B1[DST] + B2[DBF] + B3[PROX]
RH13	Bo + B1[DST] + B2[DUF] + B3[PROX]
RH14	Bo + B1[DBF] + B2[DUF] + B3[PROX]
RH15	Bo + B1[DST] + B2[DBF] + B3[DUF] + B4[PROX]
RH16	Bo + B1[DST] + B2[YEAR]
RH17	Bo + B1[DBF] + B2[YEAR]
RH18	Bo + B1[DUF] + B2[YEAR]
RH19	Bo + B1[PROX] + B2[YEAR]
RH20	Bo + B1[DST] + B2[DBF] + B3[YEAR]
RH21	Bo + B1[DST] + B2[DUF] + B3[YEAR]

TABLE 2B.3—CONTINUED

RH22	Bo + B1[DST] + B2[PROX] + B3[YEAR]
RH23	Bo + B1[DBF] + B2[DUF] + B3[YEAR]
RH24	Bo + B1[DBF] + B2[PROX] + B3[YEAR]
RH25	Bo + B1[DUF] + B2[PROX] + B3[YEAR]
RH26	Bo + B1[DST] + B2[DBF] + B3[DUF] + B4[YEAR]
RH27	Bo + B1[DST] + B2[DBF] + B3[PROX] + B4[YEAR]
RH28	Bo + B1[DST] + B2[DUF] + B3[PROX] + B4[YEAR]
RH29	Bo + B1[DBF] + B2[DUF] + B3[PROX] + B4[YEAR]
RH30	Bo + B1[DST] + B2[DBF] + B3[DUF] + B4[PROX] + B5[YEAR]
	Suite 3: Composite Static Topography & Habitat Variables
RHT1	Bo + B1[DST] + B2[SL]
RHT2	Bo + B1[DBF] + B2[SL]
RHT3	Bo + B1[DUF] + B2[SL]
RHT4	Bo + B1[PROX] + B2[SL]
RHT5	Bo + B1[DST] + B2[DBF] + B3[SL]
RHT6	Bo + B1[DST] + B2[DUF] + B3[SL]
RHT7	Bo + B1[DST] + B2[PROX] + B3[SL]
RHT8	Bo + B1[DBF] + B2[DUF] + B3[SL]
RHT9	Bo + B1[DBF] + B2[PROX] + B3[SL]
RHT10	Bo + B1[DUF] + B2[PROX] + B3[SL]
RHT11	Bo + B1[DST] + B2[DBF] + B3[DUF] + B4[SL]
RHT12	Bo + B1[DST] + B2[DBF] + B3[PROX] + B4[SL]
RHT13	Bo + B1[DST] + B2[DUF] + B3[PROX] + B4[SL]
RHT14	Bo + B1[DBF] + B2[DUF] + B3[PROX] + B4[SL]
RHT15	Bo + B1[DST] + B2[DBF] + B3[DUF] + B4[PROX] + B5[SL]
RHT16	Bo + B1[DST] + B2[SLHG]
RHT17	Bo + B1[DBF] + B2[SLHG]
RHT18	Bo + B1[DUF] + B2[SLHG]
RHT19	Bo + B1[PROX] + B2[SLHG]
RHT20	Bo + B1[DST] + B2[DBF] + B3[SLHG]
RHT21	Bo + B1[DST] + B2[DUF] + B3[SLHG]
RHT22	Bo + B1[DST] + B2[PROX] + B3[SLHG]
RHT23	Bo + B1[DBF] + B2[DUF] + B3[SLHG]
RHT24	Bo + B1[DBF] + B2[PROX] + B3[SLHG]
RHT25	Bo + B1[DUF] + B2[PROX] + B3[SLHG]
RHT26	Bo + B1[DST] + B2[DBF] + B3[DUF] + B4[SLHG]

TABLE 2B.3—CONTINUED

RHT27	Bo + B1[DST] + B2[DBF] + B3[PROX] + B4[SLHG]
RHT28	Bo + B1[DST] + B2[DUF] + B3[PROX] + B4[SLHG]
RHT29	Bo + B1[DBF] + B2[DUF] + B3[PROX] + B4[SLHG]
RHT30	Bo + B1[DST] + B2[DBF] + B3[DUF] + B4[PROX] + B5[SLHG]
RHT31	Bo + B1[DST] + B2[TAN]
RHT32	Bo + B1[DBF] + B2[TAN]
RHT33	Bo + B1[DUF] + B2[TAN]
RHT34	Bo + B1[PROX] + B2[TAN]
RHT35	Bo + B1[DST] + B2[DBF] + B3[TAN]
RHT36	Bo + B1[DST] + B2[DUF] + B3[TAN]
RHT37	Bo + B1[DST] + B2[PROX] + B3[TAN]
RHT38	Bo + B1[DBF] + B2[DUF] + B3[TAN]
RHT39	Bo + B1[DBF] + B2[PROX] + B3[TAN]
RHT40	Bo + B1[DUF] + B2[PROX] + B3[TAN]
RHT41	Bo + B1[DST] + B2[DBF] + B3[DUF] + B4[TAN]
RHT42	Bo + B1[DST] + B2[DBF] + B3[PROX] + B4[TAN]
RHT43	Bo + B1[DST] + B2[DUF] + B3[PROX] + B4[TAN]
RHT44	Bo + B1[DBF] + B2[DUF] + B3[PROX] + B4[TAN]
RHT45	Bo + B1[DST] + B2[DBF] + B3[DUF] + B4[PROX] + B5[TAN]
RHT46	Bo + B1[DST] + B2[SL] + B3[SLHG]
RHT47	Bo + B1[DBF] + B2[SL] + B3[SLHG]
RHT48	Bo + B1[DUF] + B2[SL] + B3[SLHG]
RHT49	Bo + B1[PROX] + B2[SL] + B3[SLHG]
RHT50	Bo + B1[DST] + B2[DBF] + B3[SL] + B4[SLHG]
RHT51	Bo + B1[DST] + B2[DUF] + B3[SL] + B4[SLHG]
RHT52	Bo + B1[DST] + B2[PROX] + B3[SL] + B4[SLHG]
RHT53	Bo + B1[DBF] + B2[DUF] + B3[SL] + B4[SLHG]
RHT54	Bo + B1[DBF] + B2[PROX] + B3[SL] + B4[SLHG]
RHT55	Bo + B1[DUF] + B2[PROX] + B3[SL] + B4[SLHG]
RHT56	Bo + B1[DST] + B2[DBF] + B3[DUF] + B4[SL] + B5[SLHG]
RHT57	Bo + B1[DST] + B2[DBF] + B3[PROX] + B4[SL] + B5[SLHG]
RHT58	Bo + B1[DST] + B2[DUF] + B3[PROX] + B4[SL] + B5[SLHG]
RHT59	Bo + B1[DBF] + B2[DUF] + B3[PROX] + B4[SL] + B5[SLHG]
RHT60	Bo + B1[DST] + B2[DBF] + B3[DUF] + B4[PROX] + B5[SL] + B6[SLHG]
RHT61	Bo + B1[DST] + B2[SLHG] + B3[TAN]
RHT62	Bo + B1[DBF] + B2[SLHG] + B3[TAN]
RHT63	Bo + B1[DUF] + B2[SLHG] + B3[TAN]

TABLE 2B.3—CONTINUED

RHT64	Bo + B1[PROX] + B2[SLHG] + B3[TAN]
RHT65	Bo + B1[DST] + B2[DBF] + B3[SLHG] + B4[TAN]
RHT66	Bo + B1[DST] + B2[DUF] + B3[SLHG] + B4[TAN]
RHT67	Bo + B1[DST] + B2[PROX] + B3[SLHG] + B4[TAN]
RHT68	Bo + B1[DBF] + B2[DUF] + B3[SLHG] + B4[TAN]
RHT69	Bo + B1[DBF] + B2[PROX] + B3[SLHG] + B4[TAN]
RHT70	Bo + B1[DUF] + B2[PROX] + B3[SLHG] + B4[TAN]
RHT71	Bo + B1[DST] + B2[DBF] + B3[DUF] + B4[SLHG] + B5[TAN]
RHT72	Bo + B1[DST] + B2[DBF] + B3[PROX] + B4[SLHG] + B5[TAN]
RHT73	Bo + B1[DST] + B2[DUF] + B3[PROX] + B4[SLHG] + B5[TAN]
RHT74	Bo + B1[DBF] + B2[DUF] + B3[PROX] + B4[SLHG] + B5[TAN]
RHT75	Bo + B1[DST] + B2[DBF] + B3[DUF] + B4[PROX] + B5[SLHG] + B6[TAN]
RHT76	Bo + B1[DST] + B2[SL] + B3[YEAR]
RHT77	Bo + B1[DBF] + B2[SL] + B3[YEAR]
RHT78	Bo + B1[DUF] + B2[SL] + B3[YEAR]
RHT79	Bo + B1[PROX] + B2[SL] + B3[YEAR]
RHT80	Bo + B1[DST] + B2[DBF] + B3[SL] + B4[YEAR]
RHT81	Bo + B1[DST] + B2[DUF] + B3[SL] + B4[YEAR]
RHT82	Bo + B1[DST] + B2[PROX] + B3[SL] + B4[YEAR]
RHT83	Bo + B1[DBF] + B2[DUF] + B3[SL] + B4[YEAR]
RHT84	Bo + B1[DBF] + B2[PROX] + B3[SL] + B4[YEAR]
RHT85	Bo + B1[DUF] + B2[PROX] + B3[SL] + B4[YEAR]
RHT86	Bo + B1[DST] + B2[DBF] + B3[DUF] + B4[SL] + B5[YEAR]
RHT87	Bo + B1[DST] + B2[DBF] + B3[PROX] + B4[SL] + B5[YEAR]
RHT88	Bo + B1[DST] + B2[DUF] + B3[PROX] + B4[SL] + B5[YEAR]
RHT89	Bo + B1[DBF] + B2[DUF] + B3[PROX] + B4[SL] + B5[YEAR]
RHT90	Bo + B1[DST] + B2[DBF] + B3[DUF] + B4[PROX] + B5[SL] + B6[YEAR]
RHT91	Bo + B1[DST] + B2[SLHG] + B3[YEAR]
RHT92	Bo + B1[DBF] + B2[SLHG] + B3[YEAR]
RHT93	Bo + B1[DUF] + B2[SLHG] + B3[YEAR]
RHT94	Bo + B1[PROX] + B2[SLHG] + B3[YEAR]
RHT95	Bo + B1[DST] + B2[DBF] + B3[SLHG] + B4[YEAR]
RHT96	Bo + B1[DST] + B2[DUF] + B3[SLHG] + B4[YEAR]
RHT97	Bo + B1[DST] + B2[PROX] + B3[SLHG] + B4[YEAR]
RHT98	Bo + B1[DBF] + B2[DUF] + B3[SLHG] + B4[YEAR]
RHT99	Bo + B1[DBF] + B2[PROX] + B3[SLHG] + B4[YEAR]
RHT100	Bo + B1[DUF] + B2[PROX] + B3[SLHG] + B4[YEAR]

TABLE 2B.3—CONTINUED

RHT101	Bo + B1[DST] + B2[DBF] + B3[DUF] + B4[SLHG] + B5[YEAR]
RHT102	Bo + B1[DST] + B2[DBF] + B3[PROX] + B4[SLHG] + B5[YEAR]
RHT103	Bo + B1[DST] + B2[DUF] + B3[PROX] + B4[SLHG] + B5[YEAR]
RHT104	Bo + B1[DBF] + B2[DUF] + B3[PROX] + B4[SLHG] + B5[YEAR]
RHT105	Bo + B1[DST] + B2[DBF] + B3[DUF] + B4[PROX] + B5[SLHG] + B6[YEAR]
RHT106	Bo + B1[DST] + B2[TAN] + B3[YEAR]
RHT107	Bo + B1[DBF] + B2[TAN] + B3[YEAR]
RHT108	Bo + B1[DUF] + B2[TAN] + B3[YEAR]
RHT109	Bo + B1[PROX] + B2[TAN] + B3[YEAR]
RHT110	Bo + B1[DST] + B2[DBF] + B3[TAN] + B4[YEAR]
RHT111	Bo + B1[DST] + B2[DUF] + B3[TAN] + B4[YEAR]
RHT112	Bo + B1[DST] + B2[PROX] + B3[TAN] + B4[YEAR]
RHT113	Bo + B1[DBF] + B2[DUF] + B3[TAN] + B4[YEAR]
RHT114	Bo + B1[DBF] + B2[PROX] + B3[TAN] + B4[YEAR]
RHT115	Bo + B1[DUF] + B2[PROX] + B3[TAN] + B4[YEAR]
RHT116	Bo + B1[DST] + B2[DBF] + B3[DUF] + B4[TAN] + B5[YEAR]
RHT117	Bo + B1[DST] + B2[DBF] + B3[PROX] + B4[TAN] + B5[YEAR]
RHT118	Bo + B1[DST] + B2[DUF] + B3[PROX] + B4[TAN] + B5[YEAR]
RHT119	Bo + B1[DBF] + B2[DUF] + B3[PROX] + B4[TAN] + B5[YEAR]
RHT120	Bo + B1[DST] + B2[DBF] + B3[DUF] + B4[PROX] + B5[TAN] + B6[YEAR]
RHT121	Bo + B1[DST] + B2[SL] + B3[SLHG] + B4[YEAR]
RHT122	Bo + B1[DBF] + B2[SL] + B3[SLHG] + B4[YEAR]
RHT123	Bo + B1[DUF] + B2[SL] + B3[SLHG] + B4[YEAR]
RHT124	Bo + B1[PROX] + B2[SL] + B3[SLHG] + B4[YEAR]
RHT125	Bo + B1[DST] + B2[DBF] + B3[SL] + B4[SLHG] + B5[YEAR]
RHT126	Bo + B1[DST] + B2[DUF] + B3[SL] + B4[SLHG] + B5[YEAR]
RHT127	Bo + B1[DST] + B2[PROX] + B3[SL] + B4[SLHG] + B5[YEAR]
RHT128	Bo + B1[DBF] + B2[DUF] + B3[SL] + B4[SLHG] + B5[YEAR]
RHT129	Bo + B1[DBF] + B2[PROX] + B3[SL] + B4[SLHG] + B5[YEAR]
RHT130	Bo + B1[DUF] + B2[PROX] + B3[SL] + B4[SLHG] + B5[YEAR]
RHT131	Bo + B1[DST] + B2[DBF] + B3[DUF] + B4[SL] + B5[SLHG] + B6[YEAR]
RHT132	Bo + B1[DST] + B2[DBF] + B3[PROX] + B4[SL] + B5[SLHG] + B6[YEAR]
RHT133	Bo + B1[DST] + B2[DUF] + B3[PROX] + B4[SL] + B5[SLHG] + B6[YEAR]
RHT134	Bo + B1[DBF] + B2[DUF] + B3[PROX] + B4[SL] + B5[SLHG] + B6[YEAR]
RHT135	Bo + B1[DST] + B2[DBF] + B3[DUF] + B4[PROX] + B5[SL] + B6[SLHG] + B7[YEAR]
RHT136	Bo + B1[DST] + B2[SLHG] + B3[TAN] + B4[YEAR]
RHT137	Bo + B1[DBF] + B2[SLHG] + B3[TAN] + B4[YEAR]

TABLE 2B.3—CONTINUED

RHT138	Bo + B1[DUF] + B2[SLHG] + B3[TAN] + B4[YEAR]
RHT139	Bo + B1[PROX] + B2[SLHG] + B3[TAN] + B4[YEAR]
RHT140	Bo + B1[DST] + B2[DBF] + B3[SLHG] + B4[TAN] + B5[YEAR]
RHT141	Bo + B1[DST] + B2[DUF] + B3[SLHG] + B4[TAN] + B5[YEAR]
RHT142	Bo + B1[DST] + B2[PROX] + B3[SLHG] + B4[TAN] + B5[YEAR]
RHT143	Bo + B1[DBF] + B2[DUF] + B3[SLHG] + B4[TAN] + B5[YEAR]
RHT144	Bo + B1[DBF] + B2[PROX] + B3[SLHG] + B4[TAN] + B5[YEAR]
RHT145	Bo + B1[DUF] + B2[PROX] + B3[SLHG] + B4[TAN] + B5[YEAR]
RHT146	Bo + B1[DST] + B2[DBF] + B3[DUF] + B4[SLHG] + B5[TAN] + B6[YEAR]
RHT147	Bo + B1[DST] + B2[DBF] + B3[PROX] + B4[SLHG] + B5[TAN] + B6[YEAR]
RHT148	Bo + B1[DST] + B2[DUF] + B3[PROX] + B4[SLHG] + B5[TAN] + B6[YEAR]
RHT149	Bo + B1[DBF] + B2[DUF] + B3[PROX] + B4[SLHG] + B5[TAN] + B6[YEAR]
RHT150	Bo + B1[DST] + B2[DBF] + B3[DUF] + B4[PROX] + B5[SLHG] + B6[TAN] + B7[YEAR]

APPENDIX 2C

TABLES OF MODEL RESULTS FOR THE BISON GENERAL TRAVEL, CORRIDOR TRAVEL, AND ROAD TRAVEL MODELING EXERCISES

Table 2C.1. Modeling results for general bison travel analysis using GPS vector data. For each model the model number, number of parameters (K), QIC value, ΔQIC value, and Akaike weight (w_k) are presented.

Model	K	QIC	ΔQIC	w_k
HT217	12	29762.584	0.000	1.0000
HT213	11	29953.604	191.020	0.0000
HT214	11	29983.843	221.259	0.0000
HT124	11	30132.116	369.532	0.0000
HT204	10	30174.638	412.054	0.0000
HT216	8	30243.170	480.586	0.0000
HT120	10	30317.918	555.334	0.0000
HT121	10	30335.360	572.776	0.0000
HT209	7	30461.781	699.197	0.0000
HT111	9	30521.052	758.468	0.0000
HT210	7	30527.828	765.244	0.0000
HT123	7	30628.451	865.867	0.0000
HT198	6	30749.460	986.876	0.0000
HT116	6	30849.047	1086.463	0.0000
HT117	6	30897.114	1134.530	0.0000
HT215	11	31109.872	1347.288	0.0000
HT105	5	31120.543	1357.959	0.0000
HT206	10	31223.600	1461.016	0.0000
HT212	11	31413.432	1650.848	0.0000
HT207	10	31436.941	1674.357	0.0000
HT203	10	31449.907	1687.323	0.0000
HT186	11	31540.518	1777.934	0.0000
HT195	9	31556.815	1794.231	0.0000
HT122	10	31570.294	1807.710	0.0000
HT183	10	31591.080	1828.496	0.0000
HT211	7	31613.775	1851.191	0.0000
HT202	10	31645.302	1882.718	0.0000
HT155	11	31654.637	1892.053	0.0000
HT113	9	31677.858	1915.274	0.0000
HT192	9	31686.735	1924.151	0.0000
HT151	10	31737.917	1975.333	0.0000
HT152	10	31744.291	1981.707	0.0000
HT119	10	31760.516	1997.932	0.0000
HT200	6	31771.336	2008.752	0.0000

TABLE 2C.1—CONTINUED

HT110	9	31790.649	2028.065	0.0000
HT142	9	31830.103	2067.519	0.0000
HT93	10	31875.082	2112.498	0.0000
HT114	9	31876.230	2113.646	0.0000
HT90	9	31926.305	2163.721	0.0000
HT62	10	31935.913	2173.329	0.0000
HT182	10	31975.903	2213.319	0.0000
HT59	9	31977.092	2214.508	0.0000
HT109	9	31988.670	2226.086	0.0000
HT102	8	31990.225	2227.641	0.0000
HT173	9	32017.703	2255.119	0.0000
HT99	8	32023.738	2261.154	0.0000
HT201	6	32044.838	2282.254	0.0000
HT118	6	32095.394	2332.810	0.0000
HT89	9	32111.919	2349.335	0.0000
HT80	8	32156.112	2393.528	0.0000
HT154	7	32171.298	2408.714	0.0000
HT191	5	32208.638	2446.054	0.0000
HT107	5	32251.799	2489.215	0.0000
HT147	6	32271.201	2508.617	0.0000
HT31	10	32291.943	2529.359	0.0000
HT148	6	32303.318	2540.734	0.0000
HT58	9	32357.766	2595.182	0.0000
HT27	9	32360.585	2598.001	0.0000
HT28	9	32363.873	2601.289	0.0000
HT185	7	32370.004	2607.420	0.0000
HT49	8	32391.537	2628.953	0.0000
HT136	5	32407.910	2645.326	0.0000
H31	9	32414.110	2651.526	0.0000
HT179	6	32420.985	2658.401	0.0000
HT18	8	32434.768	2672.184	0.0000
H28	8	32458.491	2695.907	0.0000
HT108	5	32509.965	2747.381	0.0000
HT92	6	32550.781	2788.197	0.0000
H27	8	32597.247	2834.663	0.0000
HT86	5	32612.164	2849.580	0.0000
H18	7	32635.510	2872.926	0.0000

TABLE 2C.1—CONTINUED

HT98	4	32672.805	2910.221	0.0000
HT61	6	32795.497	3032.913	0.0000
HT30	6	32829.209	3066.625	0.0000
HT55	5	32838.355	3075.771	0.0000
HT23	5	32921.497	3158.913	0.0000
HT85	5	32939.862	3177.278	0.0000
HT24	5	32943.901	3181.317	0.0000
HT178	6	32947.192	3184.608	0.0000
HT74	4	32984.555	3221.971	0.0000
HT167	5	32984.733	3222.149	0.0000
HT12	4	33040.498	3277.914	0.0000
H30	5	33084.372	3321.788	0.0000
H24	4	33142.869	3380.285	0.0000
HT205	10	33298.979	3536.395	0.0000
HT141	9	33358.738	3596.154	0.0000
HT150	10	33374.048	3611.464	0.0000
HT54	5	33374.059	3611.475	0.0000
HT194	9	33383.033	3620.449	0.0000
HT43	4	33404.882	3642.298	0.0000
H23	4	33415.668	3653.084	0.0000
HT172	9	33433.087	3670.503	0.0000
HT181	10	33446.229	3683.645	0.0000
HT193	9	33451.976	3689.392	0.0000
H12	3	33458.276	3695.692	0.0000
HT130	8	33481.878	3719.294	0.0000
HT140	9	33495.774	3733.190	0.0000
HT197	6	33522.788	3760.204	0.0000
HT208	7	33537.991	3775.407	0.0000
HT187	8	33543.027	3780.443	0.0000
HT188	5	33607.843	3845.259	0.0000
HT196	6	33617.226	3854.642	0.0000
HT153	10	33638.916	3876.332	0.0000
HT184	10	33646.965	3884.381	0.0000
HT144	9	33661.905	3899.321	0.0000
HT79	8	33692.585	3930.001	0.0000
HT88	9	33706.688	3944.104	0.0000
HT176	9	33729.929	3967.345	0.0000

TABLE 2C.1—CONTINUED

HT112	9	33765.219	4002.635	0.0000
HT48	8	33790.152	4027.568	0.0000
HT57	9	33803.788	4041.204	0.0000
HT145	9	33811.273	4048.689	0.0000
HT133	8	33839.369	4076.785	0.0000
HT101	8	33840.787	4078.203	0.0000
HT104	5	33879.450	4116.866	0.0000
HT115	6	33896.320	4133.736	0.0000
HT100	8	33913.834	4151.250	0.0000
HT17	8	33949.863	4187.279	0.0000
HT161	8	33963.122	4200.538	0.0000
HT26	9	33968.244	4205.660	0.0000
HT95	4	33973.505	4210.921	0.0000
HT171	9	33975.118	4212.534	0.0000
HT103	5	33984.701	4222.117	0.0000
HT94	7	33996.466	4233.882	0.0000
HT68	7	34025.903	4263.319	0.0000
HT175	9	34031.687	4269.103	0.0000
HT78	8	34038.834	4276.250	0.0000
HT6	7	34059.061	4296.477	0.0000
HT91	9	34062.320	4299.736	0.0000
HT16	8	34076.202	4313.618	0.0000
HT164	8	34112.779	4350.195	0.0000
HT60	9	34148.920	4386.336	0.0000
HT83	8	34159.087	4396.503	0.0000
H17	7	34168.079	4405.495	0.0000
H26	8	34183.239	4420.655	0.0000
HT149	6	34189.181	4426.597	0.0000
HT52	8	34222.604	4460.020	0.0000
HT82	8	34235.324	4472.740	0.0000
HT138	5	34240.086	4477.502	0.0000
HT37	7	34306.200	4543.616	0.0000
HT47	8	34318.465	4555.881	0.0000
HT71	7	34328.279	4565.695	0.0000
HT29	9	34375.129	4612.545	0.0000
HT20	8	34389.864	4627.280	0.0000
HT139	5	34442.156	4679.572	0.0000

TABLE 2C.1—CONTINUED

H6	6	34443.699	4681.115	0.0000
H16	7	34457.404	4694.820	0.0000
HT129	4	34499.609	4737.025	0.0000
HT51	8	34515.600	4753.016	0.0000
HT21	8	34531.863	4769.279	0.0000
HT9	7	34550.882	4788.298	0.0000
HT180	6	34582.997	4820.413	0.0000
HT40	7	34588.824	4826.240	0.0000
HT170	5	34672.166	4909.582	0.0000
H29	8	34683.155	4920.571	0.0000
H21	7	34777.204	5014.620	0.0000
H20	7	34813.022	5050.438	0.0000
HT87	5	34818.324	5055.740	0.0000
H9	6	34903.569	5140.985	0.0000
HT77	4	34936.311	5173.727	0.0000
HT25	5	34951.280	5188.696	0.0000
HT14	4	34995.530	5232.946	0.0000
HT56	5	35123.256	5360.672	0.0000
HT169	5	35153.586	5391.002	0.0000
HT76	4	35171.017	5408.433	0.0000
HT15	4	35192.147	5429.563	0.0000
HT46	4	35206.378	5443.794	0.0000
HT160	4	35230.456	5467.872	0.0000
HT5	3	35242.445	5479.861	0.0000
HT67	3	35267.347	5504.763	0.0000
H25	4	35445.031	5682.447	0.0000
H15	3	35567.190	5804.606	0.0000
HT146	6	35579.579	5816.995	0.0000
HT135	5	35584.221	5821.637	0.0000
HT126	4	35591.608	5829.024	0.0000
HT134	5	35594.049	5831.465	0.0000
HT45	4	35685.759	5923.175	0.0000
H14	3	35747.962	5985.378	0.0000
HT36	3	35758.601	5996.017	0.0000
HT190	5	35789.979	6027.395	0.0000
HT199	6	35791.661	6029.077	0.0000
H5	2	35848.867	6086.283	0.0000

TABLE 2C.1—CONTINUED

HT189	5	35869.197	6106.613	0.0000
T7	4	35878.794	6116.210	0.0000
HT132	8	35986.577	6223.993	0.0000
HT143	9	35987.410	6224.826	0.0000
HT131	8	36037.784	6275.200	0.0000
HT125	7	36039.645	6277.061	0.0000
HT163	8	36185.403	6422.819	0.0000
HT22	5	36199.529	6436.945	0.0000
HT174	9	36200.557	6437.973	0.0000
HT11	4	36205.050	6442.466	0.0000
HT2	3	36214.985	6452.401	0.0000
HT10	4	36216.789	6454.205	0.0000
HT177	6	36294.223	6531.639	0.0000
HT97	4	36299.103	6536.519	0.0000
HT106	5	36303.624	6541.040	0.0000
HT84	5	36336.979	6574.395	0.0000
HT96	4	36390.206	6627.622	0.0000
T4	3	36397.063	6634.479	0.0000
HT166	5	36417.009	6654.425	0.0000
HT73	4	36444.329	6681.745	0.0000
HT70	7	36530.578	6767.994	0.0000
HT81	8	36546.089	6783.505	0.0000
HT72	4	36660.235	6897.651	0.0000
HT39	7	36672.122	6909.538	0.0000
HT53	5	36679.665	6917.081	0.0000
HT156	7	36686.039	6923.455	0.0000
HT50	8	36688.426	6925.842	0.0000
HT162	8	36700.702	6938.118	0.0000
HT8	7	36710.827	6948.243	0.0000
HT19	8	36714.458	6951.874	0.0000
HT165	5	36715.802	6953.218	0.0000
HT64	3	36744.323	6981.739	0.0000
HT1	6	36754.556	6991.972	0.0000
HT7	7	36755.749	6993.165	0.0000
H22	4	36783.460	7020.876	0.0000
HT63	6	36801.474	7038.890	0.0000
HT157	4	36804.261	7041.677	0.0000

TABLE 2C.1—CONTINUED

HT42	4	36804.773	7042.189	0.0000
HT69	7	36816.371	7053.787	0.0000
H11	3	36885.403	7122.819	0.0000
H10	3	37071.700	7309.116	0.0000
HT41	4	37117.717	7355.133	0.0000
H8	6	37122.642	7360.058	0.0000
H19	7	37138.567	7375.983	0.0000
H2	2	37153.505	7390.921	0.0000
HT32	6	37154.453	7391.869	0.0000
HT38	7	37170.052	7407.468	0.0000
HT33	3	37207.403	7444.819	0.0000
H1	5	37342.874	7580.290	0.0000
H7	6	37358.066	7595.482	0.0000
HT128	4	38619.681	8857.097	0.0000
T5	3	38629.275	8866.691	0.0000
HT137	5	38632.454	8869.870	0.0000
HT127	4	38645.274	8882.690	0.0000
HT4	3	39409.266	9646.682	0.0000
T1	2	39421.614	9659.030	0.0000
HT13	4	39423.078	9660.494	0.0000
HT3	3	39438.550	9675.966	0.0000
HT168	5	39590.893	9828.309	0.0000
HT75	4	39687.317	9924.733	0.0000
HT159	4	39710.598	9948.014	0.0000
HT66	3	39782.014	10019.430	0.0000
HT65	3	40049.778	10287.194	0.0000
HT158	4	40100.962	10338.378	0.0000
T3	2	40131.449	10368.865	0.0000
HT44	4	40146.715	10384.131	0.0000
T6	3	40191.534	10428.950	0.0000
HT35	3	40264.769	10502.185	0.0000
H13	3	40298.803	10536.219	0.0000
H4	2	40384.527	10621.943	0.0000
H3	2	40632.661	10870.077	0.0000
HT34	3	40668.270	10905.686	0.0000
T2	2	40756.490	10993.906	0.0000

Table 2C.2. Modeling results for bison corridor travel analysis using GPS vector data. For each model the model number, number of parameters (K), QIC value, ΔQIC value, and Akaike weight (w_k) are presented.

Model	K	QIC	ΔQIC	w_k
CHT213	11	11334.345	0.000	0.9954
CHT217	12	11345.106	10.761	0.0046
CHT204	10	11403.056	68.711	0.0000
CHT214	11	11415.304	80.959	0.0000
CHT209	7	11429.220	94.875	0.0000
CHT216	8	11442.738	108.392	0.0000
CHT198	6	11499.677	165.332	0.0000
CHT210	7	11513.640	179.295	0.0000
CHT120	10	11576.849	242.504	0.0000
CHT124	11	11587.850	253.505	0.0000
CHT111	9	11640.843	306.498	0.0000
CHT121	10	11653.152	318.807	0.0000
CHT116	6	11675.562	341.217	0.0000
CHT202	10	11681.991	347.646	0.0000
CHT123	7	11687.930	353.585	0.0000
CHT212	11	11693.139	358.793	0.0000
CHT192	9	11696.900	362.555	0.0000
CHT203	10	11708.558	374.213	0.0000
CHT105	5	11741.958	407.612	0.0000
CHT117	6	11754.892	420.547	0.0000
CHT109	9	11916.310	581.965	0.0000
CHT119	10	11927.655	593.310	0.0000
CHT99	8	11929.196	594.851	0.0000
CHT110	9	11941.024	606.678	0.0000
CHT186	11	11947.685	613.340	0.0000
CHT182	10	11966.810	632.465	0.0000
CHT183	10	11970.806	636.461	0.0000
CHT173	9	11986.378	652.033	0.0000
CHT188	5	11995.253	660.908	0.0000
CHT196	6	11998.265	663.920	0.0000
CHT197	6	12009.327	674.982	0.0000
CHT208	7	12012.183	677.838	0.0000
CHT185	7	12181.284	846.939	0.0000

TABLE 2C.2—CONTINUED

CHT62	10	12189.957	855.612	0.0000
CHT179	6	12190.927	856.582	0.0000
CHT58	9	12206.793	872.447	0.0000
CHT178	6	12207.753	873.408	0.0000
CHT59	9	12210.866	876.521	0.0000
CHT167	5	12214.843	880.498	0.0000
CHT49	8	12224.503	890.158	0.0000
CHT95	4	12231.540	897.194	0.0000
CHT103	5	12235.684	901.339	0.0000
CHT104	5	12245.296	910.951	0.0000
CHT115	6	12249.391	915.046	0.0000
CHT206	10	12290.436	956.091	0.0000
CHT89	9	12294.039	959.694	0.0000
CHT151	10	12294.535	960.190	0.0000
CHT215	11	12300.942	966.597	0.0000
CHT93	10	12304.523	970.178	0.0000
CHT80	8	12304.950	970.605	0.0000
CHT155	11	12305.316	970.971	0.0000
CHT142	9	12308.781	974.436	0.0000
CHT90	9	12315.507	981.162	0.0000
CHT152	10	12319.252	984.907	0.0000
CHT172	9	12365.598	1031.253	0.0000
CHT181	10	12373.785	1039.439	0.0000
CHT161	8	12390.748	1056.403	0.0000
CHT147	6	12398.007	1063.662	0.0000
CHT195	9	12398.174	1063.829	0.0000
CHT171	9	12399.233	1064.888	0.0000
CHT207	10	12408.914	1074.568	0.0000
CHT154	7	12409.129	1074.783	0.0000
CHT200	6	12410.164	1075.819	0.0000
CHT136	5	12411.724	1077.378	0.0000
CHT211	7	12420.832	1086.487	0.0000
CHT148	6	12422.664	1088.319	0.0000
CHT85	5	12428.824	1094.479	0.0000
CHT61	6	12429.092	1094.747	0.0000
CHT74	4	12434.498	1100.153	0.0000
CHT55	5	12437.340	1102.994	0.0000

TABLE 2C.2—CONTINUED

CHT92	6	12439.303	1104.958	0.0000
CHT86	5	12445.208	1110.863	0.0000
CHT54	5	12456.810	1122.465	0.0000
CHT43	4	12462.703	1128.357	0.0000
CHT191	5	12529.905	1195.560	0.0000
CHT201	6	12540.991	1206.646	0.0000
CHT48	8	12597.566	1263.221	0.0000
CHT57	9	12606.379	1272.034	0.0000
CHT37	7	12620.387	1286.041	0.0000
CHT47	8	12629.368	1295.023	0.0000
CHT113	9	12637.282	1302.937	0.0000
CHT122	10	12647.067	1312.722	0.0000
CHT130	8	12676.629	1342.284	0.0000
CHT140	9	12683.466	1349.121	0.0000
CHT141	9	12687.738	1353.392	0.0000
CHT68	7	12693.259	1358.913	0.0000
CHT150	10	12694.514	1360.169	0.0000
CHT78	8	12700.752	1366.407	0.0000
CHT79	8	12704.525	1370.179	0.0000
CHT88	9	12711.996	1377.651	0.0000
CH27	8	12737.721	1403.376	0.0000
CHT102	8	12738.356	1404.011	0.0000
CH31	9	12741.616	1407.271	0.0000
CH18	7	12745.699	1411.354	0.0000
CHT114	9	12748.285	1413.940	0.0000
CH28	8	12748.897	1414.552	0.0000
CHT27	9	12757.717	1423.371	0.0000
CHT107	5	12765.104	1430.759	0.0000
CHT31	10	12765.430	1431.085	0.0000
CHT18	8	12765.718	1431.372	0.0000
CHT28	9	12773.197	1438.852	0.0000
CHT118	6	12774.438	1440.093	0.0000
CHT193	9	12810.611	1476.266	0.0000
CHT205	10	12820.849	1486.504	0.0000
CHT187	8	12838.337	1503.992	0.0000
CHT194	9	12848.924	1514.578	0.0000
CH23	4	12850.251	1515.905	0.0000

TABLE 2C.2—CONTINUED

CH12	3	12855.523	1521.178	0.0000
CH30	5	12858.637	1524.292	0.0000
CH24	4	12863.376	1529.031	0.0000
CHT23	5	12864.461	1530.115	0.0000
CHT12	4	12872.534	1538.188	0.0000
CHT30	6	12874.395	1540.049	0.0000
CHT98	4	12880.380	1546.035	0.0000
CHT24	5	12882.445	1548.100	0.0000
CHT108	5	12890.139	1555.794	0.0000
CHT177	6	12929.650	1595.304	0.0000
CHT166	5	12937.443	1603.097	0.0000
CHT165	5	12942.082	1607.737	0.0000
CHT157	4	12948.441	1614.096	0.0000
CHT135	5	13023.094	1688.749	0.0000
CHT146	6	13023.583	1689.238	0.0000
CHT134	5	13031.687	1697.342	0.0000
CHT126	4	13033.910	1699.565	0.0000
CH6	6	13106.582	1772.237	0.0000
CHT72	4	13113.437	1779.092	0.0000
CH16	7	13114.666	1780.321	0.0000
CH17	7	13114.926	1780.581	0.0000
CH26	8	13122.898	1788.553	0.0000
CHT84	5	13123.003	1788.657	0.0000
CHT64	3	13123.205	1788.860	0.0000
CHT6	7	13125.120	1790.775	0.0000
CHT73	4	13132.438	1798.093	0.0000
CHT16	8	13132.773	1798.427	0.0000
CHT17	8	13133.886	1799.541	0.0000
CHT26	9	13141.503	1807.158	0.0000
CHT100	8	13156.262	1821.917	0.0000
CHT112	9	13166.069	1831.724	0.0000
CHT53	5	13168.877	1834.532	0.0000
CHT42	4	13177.307	1842.962	0.0000
CHT94	7	13181.139	1846.794	0.0000
CHT41	4	13184.322	1849.977	0.0000
CHT33	3	13191.197	1856.852	0.0000
CHT101	8	13191.250	1856.905	0.0000

TABLE 2C.2—CONTINUED

CHT189	5	13247.920	1913.575	0.0000
CT7	4	13251.040	1916.694	0.0000
CHT199	6	13259.083	1924.738	0.0000
CHT190	5	13262.166	1927.821	0.0000
CHT184	10	13324.278	1989.933	0.0000
CHT175	9	13344.489	2010.144	0.0000
CHT176	9	13345.738	2011.393	0.0000
CHT164	8	13363.727	2029.382	0.0000
CHT22	5	13481.091	2146.745	0.0000
CHT11	4	13482.356	2148.011	0.0000
CHT10	4	13486.927	2152.582	0.0000
CHT2	3	13491.303	2156.957	0.0000
CH10	3	13497.797	2163.452	0.0000
CH22	4	13503.494	2169.149	0.0000
CH2	2	13506.668	2172.323	0.0000
CH11	3	13511.663	2177.318	0.0000
CHT96	4	13609.802	2275.457	0.0000
CT4	3	13611.323	2276.978	0.0000
CHT106	5	13620.198	2285.853	0.0000
CHT97	4	13621.529	2287.184	0.0000
CHT180	6	13630.443	2296.098	0.0000
CHT170	5	13636.701	2302.355	0.0000
CHT169	5	13673.305	2338.960	0.0000
CHT160	4	13676.465	2342.119	0.0000
CHT60	9	13691.780	2357.434	0.0000
CHT51	8	13710.852	2376.506	0.0000
CHT52	8	13711.039	2376.694	0.0000
CHT40	7	13728.345	2394.000	0.0000
CHT153	10	13824.837	2490.492	0.0000
CHT144	9	13833.445	2499.099	0.0000
CHT145	9	13852.738	2518.393	0.0000
CHT133	8	13861.025	2526.680	0.0000
CHT82	8	13876.124	2541.779	0.0000
CHT91	9	13882.055	2547.710	0.0000
CHT71	7	13891.956	2557.611	0.0000
CHT83	8	13897.548	2563.203	0.0000
CHT163	8	13943.490	2609.145	0.0000

TABLE 2C.2—CONTINUED

CHT174	9	13953.872	2619.527	0.0000
CHT149	6	13956.656	2622.310	0.0000
CHT138	5	13958.007	2623.662	0.0000
CHT156	7	13978.154	2643.808	0.0000
CHT162	8	13988.053	2653.708	0.0000
CHT139	5	13991.111	2656.766	0.0000
CHT129	4	13992.370	2658.025	0.0000
CHT56	5	14011.275	2676.930	0.0000
CHT46	4	14016.738	2682.393	0.0000
CHT76	4	14052.276	2717.931	0.0000
CHT45	4	14056.090	2721.745	0.0000
CHT36	3	14058.824	2724.479	0.0000
CHT87	5	14060.529	2726.184	0.0000
CHT67	3	14062.590	2728.244	0.0000
CHT77	4	14071.373	2737.028	0.0000
CHT39	7	14308.412	2974.067	0.0000
CHT50	8	14319.021	2984.675	0.0000
CHT32	6	14341.720	3007.375	0.0000
CHT38	7	14351.832	3017.487	0.0000
CHT132	8	14417.954	3083.609	0.0000
CHT125	7	14421.998	3087.653	0.0000
CHT143	9	14425.621	3091.276	0.0000
CHT131	8	14429.880	3095.534	0.0000
CHT29	9	14453.525	3119.180	0.0000
CH29	8	14456.496	3122.150	0.0000
CH20	7	14459.327	3124.982	0.0000
CHT20	8	14466.763	3132.418	0.0000
CH21	7	14474.162	3139.816	0.0000
CHT21	8	14478.144	3143.799	0.0000
CH9	6	14478.164	3143.819	0.0000
CHT63	6	14489.015	3154.670	0.0000
CHT9	7	14490.943	3156.598	0.0000
CHT69	7	14497.047	3162.702	0.0000
CHT70	7	14497.441	3163.095	0.0000
CHT81	8	14505.374	3171.029	0.0000
CHT25	5	14599.603	3265.257	0.0000
CHT14	4	14601.524	3267.179	0.0000

TABLE 2C.2—CONTINUED

CH14	3	14620.073	3285.728	0.0000
CH25	4	14627.662	3293.317	0.0000
CHT15	4	14632.597	3298.252	0.0000
CHT5	3	14634.420	3300.075	0.0000
CH5	2	14638.010	3303.664	0.0000
CH15	3	14644.902	3310.557	0.0000
CHT168	5	14696.948	3362.603	0.0000
CHT159	4	14726.281	3391.936	0.0000
CHT158	4	14738.783	3404.438	0.0000
CT6	3	14767.617	3433.272	0.0000
CHT128	4	14901.217	3566.872	0.0000
CHT137	5	14902.725	3568.380	0.0000
CHT127	4	14912.865	3578.520	0.0000
CT5	3	14913.367	3579.022	0.0000
CHT8	7	15039.718	3705.372	0.0000
CHT1	6	15047.123	3712.778	0.0000
CHT19	8	15048.031	3713.685	0.0000
CH1	5	15051.628	3717.282	0.0000
CH8	6	15055.325	3720.980	0.0000
CHT7	7	15055.716	3721.371	0.0000
CH7	6	15060.387	3726.041	0.0000
CH19	7	15063.907	3729.562	0.0000
CHT65	3	15071.951	3737.605	0.0000
CHT75	4	15079.620	3745.275	0.0000
CHT44	4	15086.248	3751.902	0.0000
CT3	2	15094.083	3759.737	0.0000
CHT66	3	15101.703	3767.358	0.0000
CHT35	3	15116.499	3782.154	0.0000
CHT34	3	15132.664	3798.318	0.0000
CT2	2	15162.057	3827.712	0.0000
CHT4	3	15552.682	4218.337	0.0000
CHT13	4	15554.092	4219.747	0.0000
CHT3	3	15560.770	4226.424	0.0000
CT1	2	15561.328	4226.983	0.0000
CH3	2	15624.170	4289.824	0.0000
CH13	3	15632.133	4297.788	0.0000
CH4	2	15647.438	4313.093	0.0000

Table 2C.3. Modeling results for bison road travel spatial analysis. For each model the model number, number of parameters (K), AIC_c value, ΔAIC_c value, and Akaike weight (w_k) are presented.

Model	**K**	**AIC_c**	**ΔAIC_c**	**w_k**
RHT150	9	327.733	0.000	0.2744
RHT148	8	330.375	2.642	0.0733
RH30	7	330.568	2.835	0.0665
RHT135	9	330.631	2.898	0.0644
RHT120	8	331.168	3.435	0.0493
RH21	5	331.387	3.654	0.0442
RHT133	8	331.435	3.702	0.0431
RH28	6	331.548	3.815	0.0407
RH26	6	331.797	4.064	0.0360
RHT146	8	331.860	4.127	0.0349
RHT141	7	331.981	4.248	0.0328
RHT90	8	332.270	4.537	0.0284
RHT118	7	332.432	4.699	0.0262
RHT105	8	332.561	4.828	0.0246
RHT96	6	333.030	5.297	0.0194
RHT88	7	333.092	5.358	0.0188
RHT126	7	333.224	5.491	0.0176
RHT101	7	333.249	5.515	0.0174
RHT111	6	333.264	5.531	0.0173
RHT81	6	333.523	5.790	0.0152
RHT103	7	333.577	5.843	0.0148
RHT116	7	333.755	6.022	0.0135
RHT131	8	333.912	6.179	0.0125
RHT86	7	333.988	6.255	0.0120
RHT145	7	339.738	12.005	0.0007
RHT149	8	340.816	13.083	0.0004
RHT130	7	341.312	13.579	0.0003
RHT100	6	341.885	14.152	0.0002
RHT93	5	342.523	14.789	0.0002
RHT138	6	342.659	14.926	0.0002
RHT134	8	343.073	15.340	0.0001
RHT104	7	343.471	15.738	0.0001
RH25	5	343.832	16.099	0.0001
RHT123	6	343.977	16.244	0.0001

TABLE 2C.3—CONTINUED

RHT98	6	344.609	16.876	0.0001
RHT143	7	344.749	17.016	0.0001
RHT85	6	345.129	17.396	0.0000
RHT115	6	345.792	18.059	0.0000
RH29	6	345.838	18.105	0.0000
RHT78	5	345.968	18.235	0.0000
RHT128	7	346.151	18.418	0.0000
RHT89	7	346.983	19.250	0.0000
RHT108	5	347.637	19.904	0.0000
RH18	4	347.651	19.918	0.0000
RHT119	7	347.799	20.066	0.0000
RHT83	6	348.106	20.373	0.0000
RHT75	7	349.314	21.581	0.0000
RH23	5	349.574	21.841	0.0000
RHT113	6	349.776	22.043	0.0000
RHT147	8	349.839	22.106	0.0000
RH15	5	351.166	23.433	0.0000
RHT73	6	351.273	23.540	0.0000
RH6	3	351.345	23.612	0.0000
RHT132	8	351.431	23.698	0.0000
RH13	4	351.739	24.006	0.0000
RHT60	7	351.770	24.037	0.0000
RHT45	6	351.948	24.215	0.0000
RH11	4	351.951	24.218	0.0000
RHT58	6	352.175	24.442	0.0000
RHT66	5	352.371	24.638	0.0000
RHT71	6	352.537	24.804	0.0000
RHT43	5	352.756	25.023	0.0000
RHT15	6	352.886	25.153	0.0000
RHT21	4	353.006	25.273	0.0000
RHT102	7	353.117	25.384	0.0000
RHT30	6	353.134	25.401	0.0000
RHT36	4	353.206	25.473	0.0000
RHT13	5	353.319	25.586	0.0000
RHT6	4	353.428	25.695	0.0000
RHT51	5	353.432	25.699	0.0000
RHT26	5	353.453	25.720	0.0000

TABLE 2C.3—CONTINUED

RHT28	5	353.733	26.000	0.0000
RHT41	5	353.886	26.153	0.0000
RHT11	5	354.086	26.352	0.0000
RHT56	6	354.286	26.553	0.0000
RH27	6	355.890	28.157	0.0000
RHT87	7	357.344	29.610	0.0000
RHT117	7	357.915	30.182	0.0000
RHT127	7	358.192	30.458	0.0000
RHT95	6	358.875	31.142	0.0000
RHT70	5	359.014	31.281	0.0000
RHT142	7	359.321	31.588	0.0000
RHT140	7	359.741	32.007	0.0000
RHT97	6	360.191	32.458	0.0000
RHT74	6	360.194	32.461	0.0000
RHT55	5	360.367	32.634	0.0000
RHT125	7	360.535	32.802	0.0000
RHT25	4	360.616	32.883	0.0000
RHT18	3	360.929	33.196	0.0000
RHT144	7	360.969	33.236	0.0000
RHT63	4	361.284	33.551	0.0000
RH10	3	362.062	34.329	0.0000
RHT59	6	362.134	34.400	0.0000
RHT129	7	362.224	34.491	0.0000
RHT29	5	362.227	34.494	0.0000
RHT48	4	362.422	34.689	0.0000
RHT99	6	362.537	34.804	0.0000
RHT91	5	362.922	35.189	0.0000
RHT23	4	362.969	35.236	0.0000
RHT68	5	363.330	35.597	0.0000
RHT10	4	363.418	35.685	0.0000
RHT80	6	363.580	35.847	0.0000
RH22	5	363.648	35.915	0.0000
RHT3	3	363.913	36.180	0.0000
RHT124	6	363.990	36.256	0.0000
RHT40	4	363.992	36.259	0.0000
RH14	4	364.032	36.299	0.0000
RHT121	6	364.098	36.365	0.0000

TABLE 2C.3—CONTINUED

RHT136	6	364.259	36.526	0.0000
RHT139	6	364.368	36.635	0.0000
RHT53	5	364.541	36.808	0.0000
RHT94	5	364.743	37.010	0.0000
RHT82	6	364.921	37.187	0.0000
RHT112	6	365.066	37.333	0.0000
RH3	2	365.151	37.418	0.0000
RHT14	5	365.260	37.527	0.0000
RHT33	3	365.362	37.629	0.0000
RHT110	6	365.412	37.679	0.0000
RHT44	5	365.967	38.234	0.0000
RHT8	4	365.998	38.265	0.0000
RH8	3	367.045	39.312	0.0000
RHT38	4	367.447	39.714	0.0000
RH20	5	367.451	39.718	0.0000
RHT72	6	367.972	40.239	0.0000
RHT76	5	368.144	40.411	0.0000
RHT106	5	368.743	41.009	0.0000
RT7	4	368.778	41.045	0.0000
RHT92	5	368.823	41.090	0.0000
RHT57	6	369.351	41.618	0.0000
RHT137	6	370.435	42.702	0.0000
RT10	5	370.486	42.753	0.0000
RHT27	5	370.580	42.847	0.0000
RT9	5	370.614	42.881	0.0000
RHT122	6	370.876	43.143	0.0000
RHT84	6	371.048	43.315	0.0000
RH16	4	371.162	43.429	0.0000
RH12	4	372.772	45.038	0.0000
RHT79	5	372.947	45.214	0.0000
RHT114	6	373.321	45.588	0.0000
RHT109	5	374.057	46.324	0.0000
RHT12	5	374.261	46.528	0.0000
RHT42	5	374.760	47.027	0.0000
RHT52	5	375.002	47.268	0.0000
RHT20	4	375.381	47.647	0.0000
RHT67	5	375.988	48.255	0.0000

TABLE 2C.3—CONTINUED

RHT65	5	376.355	48.622	0.0000
RHT77	5	376.379	48.646	0.0000
RT6	4	376.507	48.774	0.0000
RHT22	4	376.533	48.800	0.0000
RH24	5	376.539	48.806	0.0000
RHT50	5	377.049	49.316	0.0000
RH19	4	377.342	49.608	0.0000
RHT69	5	377.430	49.697	0.0000
RHT54	5	378.528	50.795	0.0000
RHT24	4	378.590	50.857	0.0000
RHT16	3	378.723	50.990	0.0000
RT8	4	378.744	51.011	0.0000
RH7	3	379.361	51.628	0.0000
RHT5	4	379.506	51.773	0.0000
RHT49	4	379.866	52.133	0.0000
RHT107	5	379.926	52.193	0.0000
RHT46	4	379.961	52.228	0.0000
RHT61	4	380.102	52.369	0.0000
RHT64	4	380.199	52.465	0.0000
RHT19	3	380.325	52.592	0.0000
RHT7	4	380.684	52.951	0.0000
RHT37	4	380.812	53.079	0.0000
RHT35	4	381.116	53.383	0.0000
RH5	3	382.712	54.979	0.0000
RHT1	3	383.324	55.591	0.0000
RT2	2	383.692	55.959	0.0000
RHT31	3	383.853	56.120	0.0000
RHT17	3	383.924	56.191	0.0000
RT5	3	385.394	57.661	0.0000
RT4	3	385.507	57.774	0.0000
RHT62	4	385.544	57.810	0.0000
RH1	2	385.803	58.070	0.0000
RHT47	4	385.933	58.200	0.0000
RHT9	4	386.085	58.352	0.0000
RHT4	3	387.573	59.840	0.0000
RHT39	4	388.095	60.361	0.0000
RHT34	3	388.556	60.823	0.0000

TABLE 2C.3—CONTINUED

RT1	2	390.550	62.817	0.0000
RHT2	3	390.617	62.884	0.0000
RH9	3	390.759	63.026	0.0000
RH4	2	391.292	63.559	0.0000
RT3	2	392.541	64.808	0.0000
RHT32	3	393.772	66.039	0.0000
RH17	4	396.182	68.449	0.0000
RH2	2	408.173	80.439	0.0000

APPENDIX 2D

TABLES OF MODEL RESULTS AND PARAMETER COEFFICIENT ESTIMATES FOR THE TWO EXPLORATORY BISON CORRIDOR TRAVEL MODELING EXERCISES

Table 2D.1. Model results for exploratory analysis of adding DRD and removing DST from the top ten *a priori* approximating models from the bison corridor travel analysis. The exploratory model structure is presented with the model number corresponding to the original *a priori* model that was modified. The suffix "e" after the original model number denotes an exploratory model. For each model the QIC value from the exploratory modeling exercise is presented (QIC_{ex}) along with the number of parameters in the exploratory model (K) and the change in QIC from the original value (QIC_{ex}-QIC).

Model	**Structure**	**K**	**QIC_{ex}**	**QIC_{ex}-QIC**
CHT213e	$\beta_0 + \beta_1(HBT) + \beta_2(DRD) + \beta_3(DBF) + \beta_4(PROX) + \beta_5(SL) + \beta_6(SLHG) + \beta_7(TAN)$	11	10607.79	-726.55
CHT217e	$\beta_0 + \beta_1(HBT) + \beta_2(DRD) + \beta_3(DBF) + \beta_4(DUF) + \beta_5(PROX) + \beta_6(SL) + \beta_7(SLHG) + \beta_8(TAN)$	12	10626.14	-718.97
CHT204e	$\beta_0 + \beta_1(HBT) + \beta_2(DRD) + \beta_3(PROX) + \beta_4(SL) + \beta_5(SLHG) + \beta_6(TAN)$	10	10641.71	-761.34
CHT214e	$\beta_0 + \beta_1(HBT) + \beta_2(DRD) + \beta_3(DUF) + \beta_4(PROX) + \beta_5(SL) + \beta_6(SLHG)$	11	10661.39	-753.91
CHT209e	$\beta_0 + \beta_1(DRD) + \beta_2(DBF) + \beta_3(PROX) + \beta_4(SL) + \beta_5(SLHG) + \beta_6(TAN)$	7	10698.35	-730.87
CHT216e	$\beta_0 + \beta_1(DRD) + \beta_2(DBF) + \beta_3(DUF) + \beta_4(PROX) + \beta_5(SL) + \beta_6(SLHG) + \beta_7(TAN)$	8	10717.70	-725.04
CHT198e	$\beta_0 + \beta_1(DRD) + \beta_2(PROX) + \beta_3(SL) + \beta_4(SLHG) + \beta_5(TAN)$	6	10734.57	-765.11
CHT210e	$\beta_0 + \beta_1(DRD) + \beta_2(DUF) + \beta_3(PROX) + \beta_4(SL) + \beta_5(SLHG) + \beta_6(TAN)$	7	10755.30	-758.35
CHT120e	$\beta_0 + \beta_1(HBT) + \beta_2(DRD) + \beta_3(DBF) + \beta_4(PROX) + \beta_5(SL) + \beta_6(SLHG)$	10	10874.10	-702.75
CHT124e	$\beta_0 + \beta_1(HBT) + \beta_2(DRD) + \beta_3(DBF) + \beta_4(DUF) + \beta_5(PROX) + \beta_6(SL) + \beta_7(SLHG)$	11	10891.82	-696.03

Table 2D.2. Coefficient values and lower (LCI) and upper (UCI) 95% confidence limits from the best exploratory model (model CHT213e) identified through QIC model comparison techniques examining the effect of substituting distance to road (DRD) for distance to stream (DST) on spatial variability in the odds of bison selection of travel corridors. Bold notation denotes significant coefficients at α=0.05.

Covariate	**β_i (LCI, UCI)**
Intercept (HBT=UF)	**-11.385 (-13.423, -9.346)**
HBT=BF	0.161 (-0.136, 0.458)
HBT=MD	**0.565 (0.344, 0.787)**
HBT=OT	**-0.337 (-0.669, -0.005)**
HBT=TH	**2.709 (1.096, 4.323)**
DBF	**0.680 (0.273, 1.088)**
PROX	**-2.946 (-4.170, -1.721)**
SL	**-4.651 (-6.217, -3.085)**
SLHG	**4.073 (3.388, 4.758)**
TAN	**3.332 (2.922, 3.741)**
DRD	**-6.450 (-8.680, -4.220)**

Table 2D.3. Model results for exploratory analysis of adding DRD and ELEV to the top ten *a priori* approximating models for bison corridor travel. The exploratory model structure is presented with the model number corresponding to the original *a priori* model that was modified. The suffix e after the original model number denotes an exploratory model. For each model the number of parameters (K) and the ΔQIC value for the exploratory modeling exercise are presented.

Model	**Structure**	**K**	**ΔQIC**
‡CHT204e	$\beta_0 + \beta_1(\text{HBT}) + \beta_2(\text{DST}) + \beta_3(\text{PROX}) + \beta_4(\text{SL}) + \beta_5(\text{SLHG}) + \beta_6(\text{TAN}) + \beta_7(\text{DRD}) + \beta_8(\text{ELEV})$	12	0.00
CHT213e	$\beta_0 + \beta_1(\text{HBT}) + \beta_2(\text{DST}) + \beta_3(\text{DBF}) + \beta_4(\text{PROX}) + \beta_5(\text{SL}) + \beta_6(\text{SLHG}) + \beta_7(\text{TAN}) + \beta_8(\text{DRD}) + \beta_9(\text{ELEV})$	13	16.43
CHT214e	$\beta_0 + \beta_1(\text{HBT}) + \beta_2(\text{DST}) + \beta_3(\text{DUF}) + \beta_4(\text{PROX}) + \beta_5(\text{SL}) + \beta_6(\text{SLHG}) + \beta_7(\text{TAN}) + \beta_8(\text{DRD}) + \beta_9(\text{ELEV})$	13	19.58
CHT217e	$\beta_0 + \beta_1(\text{HBT}) + \beta_2(\text{DST}) + \beta_3(\text{DBF}) + \beta_4(\text{DUF}) + \beta_5(\text{PROX}) + \beta_6(\text{SL}) + \beta_7(\text{SLHG}) + \beta_8(\text{TAN}) + \beta_9(\text{DRD}) + \beta_{10}(\text{ELEV})$	14	33.70
CHT198e	$\beta_0 + \beta_1(\text{DST}) + \beta_2(\text{PROX}) + \beta_3(\text{SL}) + \beta_4(\text{SLHG}) + \beta_5(\text{TAN}) + \beta_6(\text{DRD}) + \beta_7(\text{ELEV})$	8	44.19
CHT209e	$\beta_0 + \beta_1(\text{DST}) + \beta_2(\text{DBF}) + \beta_3(\text{PROX}) + \beta_4(\text{SL}) + \beta_5(\text{SLHG}) + \beta_6(\text{TAN}) + \beta_7(\text{DRD}) + \beta_8(\text{ELEV})$	9	61.94
CHT210e	$\beta_0 + \beta_1(\text{DST}) + \beta_2(\text{DUF}) + \beta_3(\text{PROX}) + \beta_4(\text{SL}) + \beta_5(\text{SLHG}) + \beta_6(\text{TAN}) + \beta_7(\text{DRD}) + \beta_8(\text{ELEV})$	9	68.52
CHT216e	$\beta_0 + \beta_1(\text{DST}) + \beta_2(\text{DBF}) + \beta_3(\text{DUF}) + \beta_4(\text{PROX}) + \beta_5(\text{SL}) + \beta_6(\text{SLHG}) + \beta_7(\text{TAN}) + \beta_8(\text{DRD}) + \beta_9(\text{ELEV})$	10	85.18
CHT120e	$\beta_0 + \beta_1(\text{HBT}) + \beta_2(\text{DST}) + \beta_3(\text{DBF}) + \beta_4(\text{PROX}) + \beta_5(\text{SL}) + \beta_6(\text{SLHG}) + \beta_7(\text{DRD}) + \beta_8(\text{ELEV})$	12	88.05
CHT124e	$\beta_0 + \beta_1(\text{HBT}) + \beta_2(\text{DST}) + \beta_3(\text{DBF}) + \beta_4(\text{DUF}) + \beta_5(\text{PROX}) + \beta_6(\text{SL}) + \beta_7(\text{SLHG}) + \beta_8(\text{DRD}) + \beta_8(\text{PROX})$	13	105.52

‡ QIC value for model CHT204e is 9071.22

Table 2D.4. Coefficient values and lower (LCI) and upper (UCI) 95% confidence limits from the best exploratory model (model CHT204e) identified through QIC model comparison techniques examining the additional effect of distance to road (DRD) and elevation (ELEV) covariates on spatial variability in the odds of bison selection of travel corridors. Bold notation denotes significant coefficients at α=0.05.

Covariate	**β_i (LCI, UCI)**
Intercept (HBT=UF)	**-16.365 (-18.014, -14.716)**
HBT=BF	0.041 (-0.255, 0.338)
HBT=MD	**0.349 (0.067, 0.632)**
HBT=OT	**-0.479 (-0.899, -0.060)**
HBT=TH	**2.976 (1.504, 4.449)**
DST	**-7.430 (-9.363, -5.498)**
PROX	**-1.710 (-2.678, -0.742)**
SL	**-3.715 (-4.923, -2.506)**
SLHG	**2.935 (2.458, 3.412)**
TAN	**1.923 (1.531, 2.315)**
DRD	**-4.513 (-6.218, -2.808)**
ELEV	**-3.821 (-4.815, -2.827)**

APPENDIX 2E

FINE SCALE MAPS OF PREDICTED TRAVEL PROBABILITIES FOR AREAS THROUGHOUT CENTRAL YELLOWSTONE

Maps of travel probabilities from the (*a*) top approximating general travel *a priori* model; (*b*) top approximating corridor travel *a priori* model, and (*c*) top approximating exploratory corridor travel model for important travel regions throughout central Yellowstone.

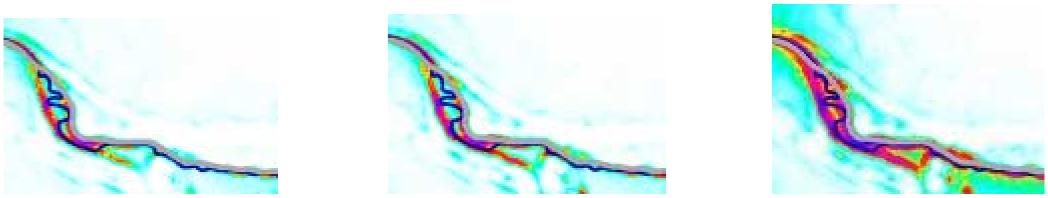

(a) (b) (c)

Figure 2E.1. Predicted travel probabilities in the Madison Canyon

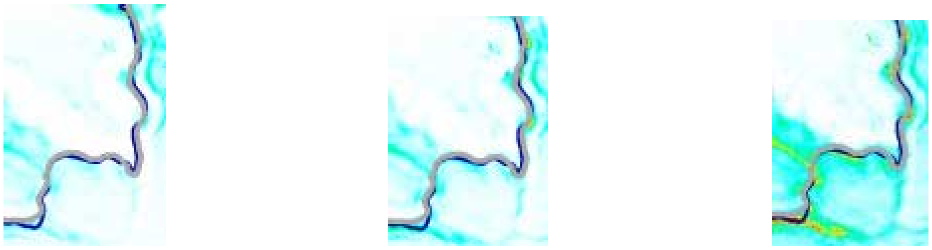

(a) (b) (c)

Figure 2E.2. Predicted travel probabilities in the Gibbon Canyon.

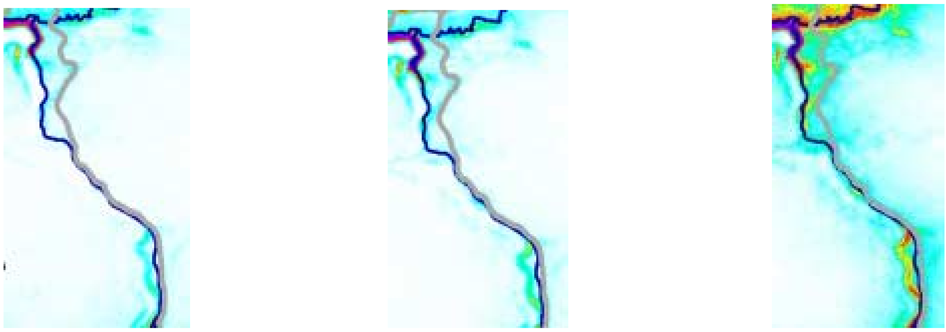
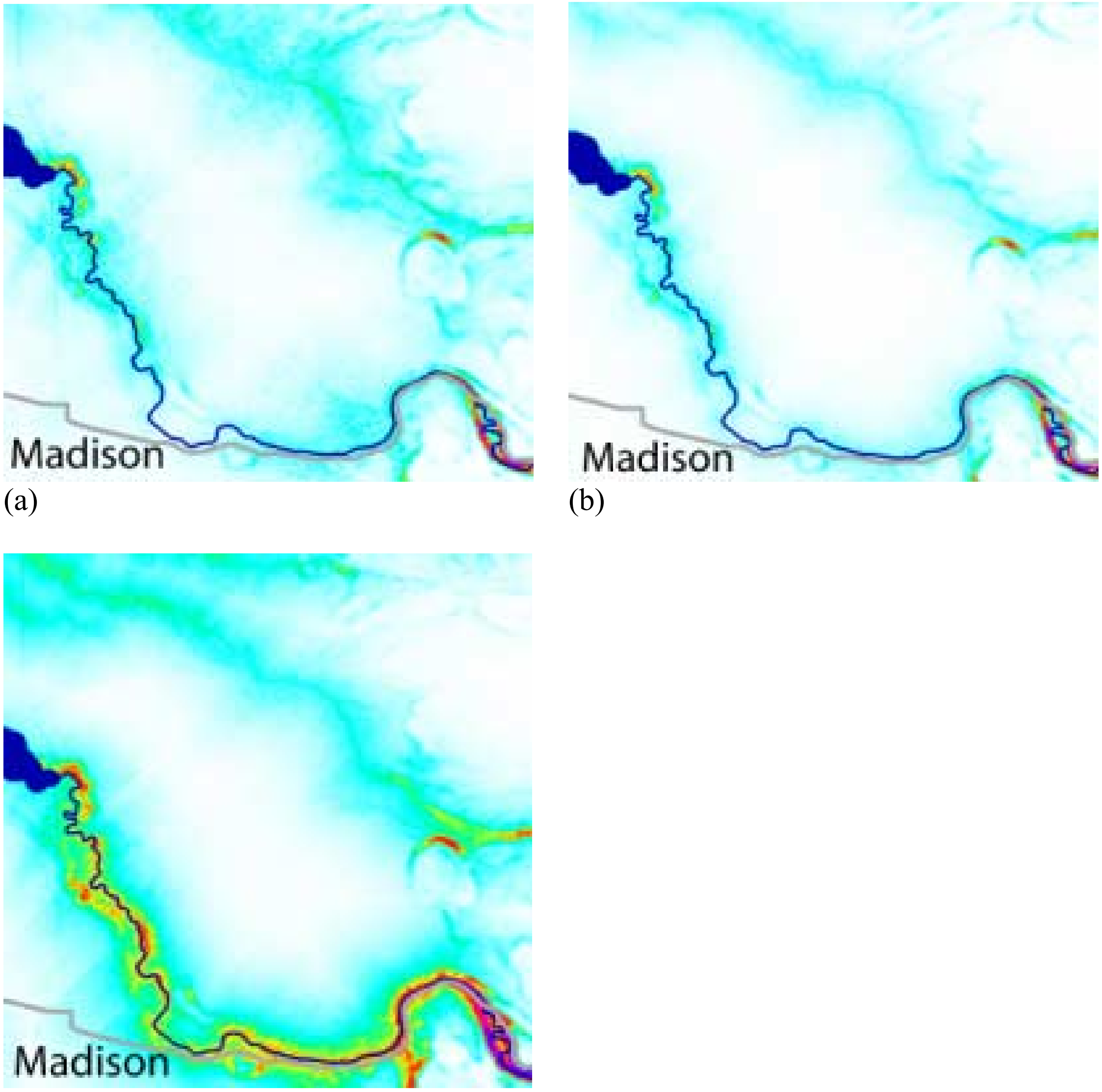

(a) (b) (c)

Figure 2E.3. Predicted travel probabilities in the lower Firehole drainage.

Maps of travel probabilities from the (*a*) top approximating general travel *a priori* model; (*b*) top approximating corridor travel *a priori* model, and (*c*) top approximating exploratory corridor travel model for important travel regions throughout central Yellowstone.



(a)

(b)

(c)

Figure 2E.4. Predicted travel probabilities in the Madison Valley, Cougar Creek, and west park boundary region.

Maps of travel probabilities from the (*a*) top approximating general travel *a priori* model; (*b*) top approximating corridor travel *a priori* model, and (*c*) top approximating exploratory corridor travel model for important travel regions throughout central Yellowstone.

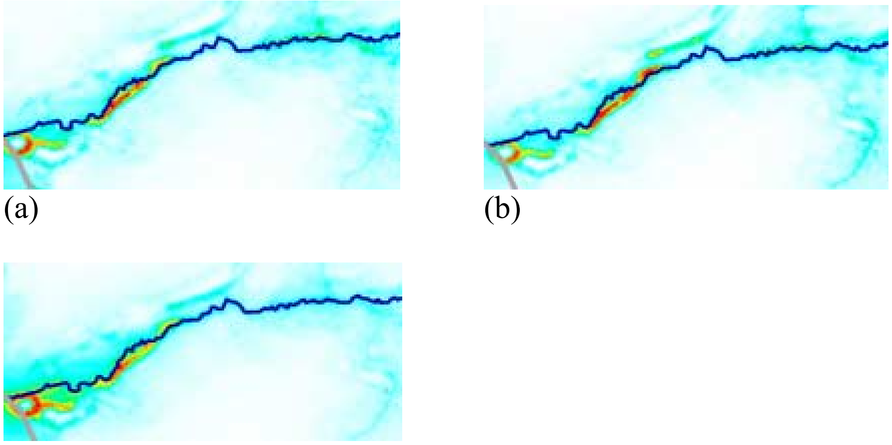

(a)
(b)
(c)

Figure 2E.5. Predicted travel probabilities along Nez Perce Creek and the western portion of the Mary Mountain trail.

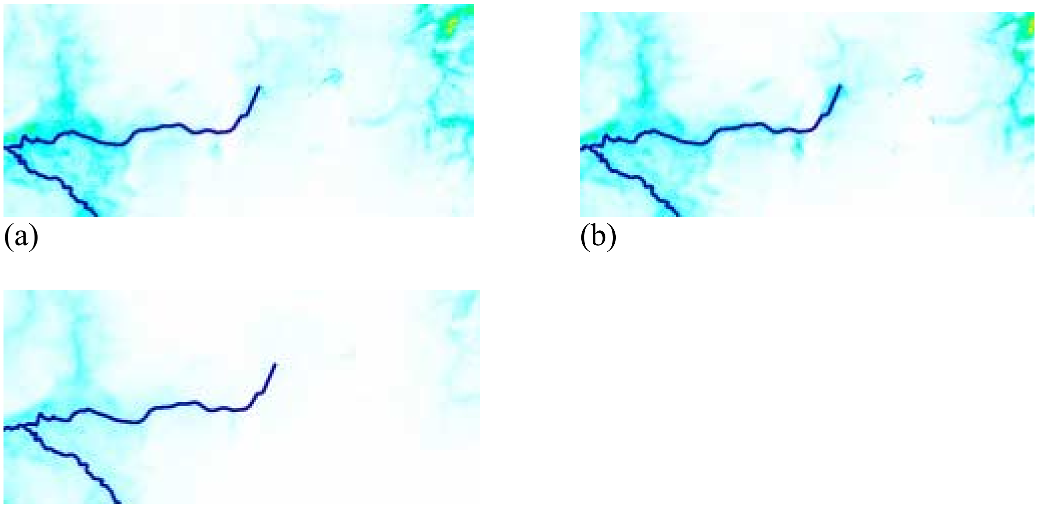

(a)
(b)
(c)

Figure 2E.6. Predicted travel probabilities along the central Mary Mountain trail.

Maps of travel probabilities from the (*a*) top approximating general travel *a priori* model; (*b*) top approximating corridor travel *a priori* model, and (*c*) top approximating exploratory corridor travel model for important travel regions throughout central Yellowstone.

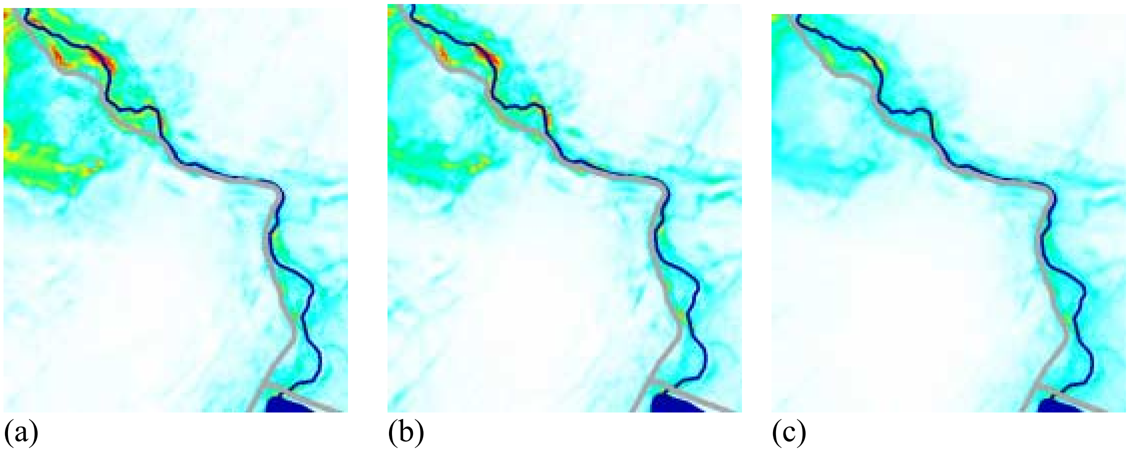

(a) (b) (c)

Figure 2E.7. Predicted travel probabilities along the Yellowstone River corridor between the Hayden Valley and Pelican Valley.

APPENDIX 3A

TABLES OF *A PRIORI* MODELS FOR BISON ROAD AND BISON OFF-ROAD TRAVEL MODELING EXERCISES

Table 3A.1. Candidate list of *a priori* regression models for the extent of bison road travel modeling exercise. The response variable is the amount of bison road travel (ρ). Note: an intercept term was included with each model (not depicted in the model structure).

Model	Model Structure
	Suite 1: Biotic + Abiotic Factors
r1.1	[BISON]
r1.2	[SWE]
r1.3	[TEMP]
r1.4	[SWE] + [BISON]
r1.5	[SWE] + [BISON] + [SWE]*[BISON]
r1.6	[TEMP] + [BISON]
r1.7	[TEMP] + [BISON] + [BISON]*[TEMP]
r1.8	[SWE] + [TEMP]
r1.9	[SWE] + [BISON] + [TEMP]
r1.10	[SWE] + [BISON] + [TEMP] + [SWE]*[BISON] + [BISON]*[TEMP]
r1.11	[BISON] + [MELT]
r1.12	[BISON] + [MELT] + [BISON]*[MELT]
r1.13	[SWE] + [MELT]
r1.14	[SWE] + [MELT] + [SWE]*[MELT]
r1.15	[TEMP] + [MELT]
r1.16	[TEMP] + [MELT] + [TEMP]*[MELT]
r1.17	[SWE] + [BISON] + [MELT]
r1.18	[SWE] + [BISON] + [MELT] + [SWE]*[BISON]
r1.19	[SWE] + [BISON] + [MELT] + [BISON]*[MELT]
r1.20	[SWE] + [BISON] + [MELT] + [SWE]*[MELT]
r1.21	[SWE] + [BISON] + [MELT] + [SWE]*[BISON] + [SWE]*[MELT]
r1.22	[SWE] + [BISON] + [MELT] + [SWE]*[BISON] + [BISON]*[MELT]
r1.23	[SWE] + [BISON] + [MELT] + [SWE]*[BISON] + [BISON]*[MELT] + [SWE]*[MELT]
r1.24	[TEMP] + [BISON] + [MELT]
r1.25	[TEMP] + [BISON] + [MELT] + [BISON]*[TEMP]
r1.26	[TEMP] + [BISON] + [MELT] + [BISON]*[MELT]
r1.27	[TEMP] + [BISON] + [MELT] + [BISON]*[TEMP] + [BISON]*[MELT]
r1.28	[TEMP] + [BISON] + [MELT] + [BISON]*[TEMP] + [BISON]*[MELT] + [TEMP]*[MELT]
r1.29	[SWE] + [BISON] + [TEMP] + [MELT]
r1.30	[SWE] + [BISON] + [TEMP] + [MELT] + [SWE]*[BISON]
r1.31	[SWE] + [BISON] + [TEMP] + [MELT] + [BISON]*[TEMP]
r1.32	[SWE] + [BISON] + [TEMP] + [MELT] + [BISON]*[MELT]
r1.33	[SWE] + [BISON] + [TEMP] + [MELT] + [TEMP]*[MELT]
r1.34	[SWE] + [BISON] + [TEMP] + [MELT] + [SWE]*[BISON] + [BISON]*[TEMP]
r1.35	[SWE] + [BISON] + [TEMP] + [MELT] + [SWE]*[BISON] + [BISON]*[MELT]
r1.36	[SWE] + [BISON] + [TEMP] + [MELT] + [SWE]*[BISON] + [TEMP]*[MELT]
r1.37	[SWE] + [BISON] + [TEMP] + [MELT] + [SWE]*[BISON] + [BISON]*[TEMP] + [BISON]*[MELT] + [TEMP]*[MELT]

TABLE 3A.1—CONTINUED

	Suite 2: Composite Factors (Biotic + Abiotic + Anthropogenic)
r2.1	[BISON] + [GROOM]
r2.2	[BISON] + [GROOM] + [GROOM]*[BISON]
r2.3	[SWE] + [GROOM]
r2.4	[SWE] + [GROOM] + [GROOM]*[SWE]
r2.5	[SWE] + [BISON] + [GROOM]
r2.6	[SWE] + [BISON] + [GROOM] + [GROOM]*[BISON]
r2.7	[SWE] + [BISON] + [GROOM] + [GROOM]*[SWE]
r2.8	[SWE] + [BISON] + [GROOM] + [SWE]*[BISON]
r2.9	[SWE] + [BISON] + [GROOM] + [SWE]*[BISON] + [GROOM]*[BISON]
r2.10	[SWE] + [BISON] + [GROOM] + [SWE]*[BISON] + [GROOM]*[BISON] + [GROOM]*[SWE]
r2.11	[SWE] + [BISON] + [GROOM] + [MELT] + [BISON]*[MELT]
r2.12	[SWE] + [BISON] + [GROOM] + [MELT] + [SWE]*[MELT]
r2.13	[SWE] + [BISON] + [GROOM] + [MELT] + [GROOM]*[BISON]
r2.14	[SWE] + [BISON] + [GROOM] + [MELT] + [SWE]*[BISON]
r2.15	[SWE] + [BISON] + [GROOM] + [MELT] + [GROOM]*[SWE]
r2.16	[SWE] + [BISON] + [GROOM] + [TEMP] + [BISON]*[TEMP]
r2.17	[SWE] + [BISON] + [GROOM] + [TEMP] + [SWE]*[TEMP]
r2.18	[SWE] + [BISON] + [GROOM] + [TEMP] + [GROOM]*[BISON]
r2.19	[SWE] + [BISON] + [GROOM] + [TEMP] + [SWE]*[BISON]
r2.20	[SWE] + [BISON] + [GROOM] + [TEMP] + [GROOM]*[SWE]
r2.21	[SWE] + [BISON] + [GROOM] + [MELT] + [TEMP]
r2.22	[SWE] + [BISON] + [GROOM] + [MELT] + [TEMP] + [BISON]*[MELT]
r2.23	[SWE] + [BISON] + [GROOM] + [MELT] + [TEMP] + [SWE]*[MELT]
r2.24	[SWE] + [BISON] + [GROOM] + [MELT] + [TEMP] + [GROOM]*[BISON]
r2.25	[SWE] + [BISON] + [GROOM] + [MELT] + [TEMP] + [SWE]*[BISON]
r2.26	[SWE] + [BISON] + [GROOM] + [MELT] + [TEMP] + [BISON]*[TEMP]
r2.27	[SWE] + [BISON] + [GROOM] + [MELT] + [TEMP] + [GROOM]*[SWE]
r2.28	[TRAFFIC]
r2.29	[BISON] + [TRAFFIC]
r2.30	[BISON] + [TRAFFIC] + [TRAFFIC]*[BISON]
r2.31	[SWE] + [TRAFFIC]
r2.32	[SWE] + [TRAFFIC] + [TRAFFIC]*[SWE]
r2.33	[SWE] + [BISON] + [TRAFFIC]
r2.34	[SWE] + [BISON] + [TRAFFIC] + [TRAFFIC]*[BISON]
r2.35	[SWE] + [BISON] + [TRAFFIC] + [TRAFFIC]*[SWE]
r2.36	[SWE] + [BISON] + [TRAFFIC] + [SWE]*[BISON]
r2.37	[SWE] + [BISON] + [TRAFFIC] + [SWE]*[BISON] + [TRAFFIC]*[BISON]
r2.39	[SWE] + [BISON] + [TRAFFIC] + [MELT] + [BISON]*[MELT]
r2.40	[SWE] + [BISON] + [TRAFFIC] + [MELT] + [SWE]*[MELT]
r2.41	[SWE] + [BISON] + [TRAFFIC] + [MELT] + [TRAFFIC]*[BISON]
r2.42	[SWE] + [BISON] + [TRAFFIC] + [MELT] + [SWE]*[BISON]
r2.43	[SWE] + [BISON] + [TRAFFIC] + [MELT] + [TRAFFIC]*[SWE]
r2.44	[SWE] + [BISON] + [TRAFFIC] + [TEMP] + [BISON]*[TEMP]

TABLE 3A.1—CONTINUED

r2.45	[SWE] + [BISON] + [TRAFFIC] + [TEMP] + [SWE]*[TEMP]
r2.46	[SWE] + [BISON] + [TRAFFIC] + [TEMP] + [TRAFFIC]*[BISON]
r2.47	[SWE] + [BISON] + [TRAFFIC] + [TEMP] + [SWE]*[BISON]
r2.48	[SWE] + [BISON] + [TRAFFIC] + [TEMP] + [TRAFFIC]*[SWE]
r2.49	[SWE] + [BISON] + [TRAFFIC] + [MELT] + [TEMP]
r2.50	[SWE] + [BISON] + [TRAFFIC] + [MELT] + [TEMP] + [BISON]*[MELT]
r2.51	[SWE] + [BISON] + [TRAFFIC] + [MELT] + [TEMP] + [SWE]*[MELT]
r2.52	[SWE] + [BISON] + [TRAFFIC] + [MELT] + [TEMP] + [TRAFFIC]*[BISON]
r2.53	[SWE] + [BISON] + [TRAFFIC] + [MELT] + [TEMP] + [SWE]*[BISON]
r2.54	[SWE] + [BISON] + [TRAFFIC] + [MELT] + [TEMP] + [BISON]*[TEMP]
r2.55	[SWE] + [BISON] + [TRAFFIC] + [MELT] + [TEMP] + [TRAFFIC]*[SWE]
r2.56	[TRAFFIC] + [GROOM]
r2.57	[BISON] + [GROOM] + [TRAFFIC]
r2.58	[BISON] + [GROOM] + [TRAFFIC] + [GROOM]*[BISON]
r2.59	[SWE] + [GROOM] + [TRAFFIC]
r2.60	[SWE] + [GROOM] + [TRAFFIC] + [GROOM]*[SWE]
r2.61	[SWE] + [BISON] + [GROOM] + [TRAFFIC]
r2.62	[SWE] + [BISON] + [GROOM] + [TRAFFIC] + [GROOM]*[BISON]
r2.64	[SWE] + [BISON] + [GROOM] + [TRAFFIC] + [GROOM]*[SWE]
r2.65	[SWE] + [BISON] + [GROOM] + [TRAFFIC] + [TRAFFIC]*[SWE]
r2.66	[SWE] + [BISON] + [GROOM] + [TRAFFIC] + [SWE]*[BISON]
r2.67	[SWE] + [BISON] + [GROOM] + [TRAFFIC] + [SWE]*[BISON] + [GROOM]*[BISON]
r2.68	[SWE] + [BISON] + [GROOM] + [TRAFFIC] + [SWE]*[BISON] + [GROOM]*[BISON] + [GROOM]*[SWE]
r2.69	[SWE] + [BISON] + [GROOM] + [TRAFFIC] + [MELT] + [BISON]*[MELT]
r2.70	[SWE] + [BISON] + [GROOM] + [TRAFFIC] + [MELT] + [SWE]*[MELT]
r2.71	[SWE] + [BISON] + [GROOM] + [TRAFFIC] + [MELT] + [GROOM]*[BISON]
r2.73	[SWE] + [BISON] + [GROOM] + [TRAFFIC] + [MELT] + [SWE]*[BISON]
r2.74	[SWE] + [BISON] + [GROOM] + [TRAFFIC] + [MELT] + [GROOM]*[SWE]
r2.75	[SWE] + [BISON] + [GROOM] + [TRAFFIC] + [MELT] + [TRAFFIC]*[SWE]
r2.76	[SWE] + [BISON] + [GROOM] + [TEMP] + [TRAFFIC] + [BISON]*[TEMP]
r2.77	[SWE] + [BISON] + [GROOM] + [TEMP] + [TRAFFIC] + [SWE]*[TEMP]
r2.78	[SWE] + [BISON] + [GROOM] + [TEMP] + [TRAFFIC] + [GROOM]*[BISON]
r2.79	[SWE] + [BISON] + [GROOM] + [TEMP] + [TRAFFIC] + [SWE]*[BISON]
r2.80	[SWE] + [BISON] + [GROOM] + [TEMP] + [TRAFFIC] + [GROOM]*[SWE]
r2.81	[SWE] + [BISON] + [GROOM] + [MELT] + [TEMP] + [TRAFFIC]
r2.82	[SWE] + [BISON] + [GROOM] + [MELT] + [TEMP] + [TRAFFIC] + [BISON]*[MELT]
r2.83	[SWE] + [BISON] + [GROOM] + [MELT] + [TEMP] + [TRAFFIC] + [SWE]*[MELT]
r2.84	[SWE] + [BISON] + [GROOM] + [MELT] + [TEMP] + [TRAFFIC] + [GROOM]*[BISON]
r2.85	[SWE] + [BISON] + [GROOM] + [MELT] + [TEMP] + [TRAFFIC] + [SWE]*[BISON]
r2.86	[SWE] + [BISON] + [GROOM] + [MELT] + [TEMP] + [TRAFFIC] + [BISON]*[TEMP]
r2.87	[SWE] + [BISON] + [GROOM] + [MELT] + [TEMP] + [TRAFFIC] + [GROOM]*[SWE]

Table 3A.2. Candidate list of *a priori* regression models for the bison off-road travel modeling exercise. The response variable is the amount of bison off-road travel (τ). Note: an intercept term was included with each model (not depicted in the model structure).

Model	**Model Structure**
o1.1	[BISON]
o1.2	[SWE]
o1.3	[TEMP]
o1.4	[SWE] + [BISON]
o1.5	[SWE] + [BISON] + [SWE]*[BISON]
o1.6	[TEMP] + [BISON]
o1.7	[TEMP] + [BISON] + [BISON]*[TEMP]
o1.8	[SWE] + [TEMP]
o1.9	[SWE] + [BISON] + [TEMP]
o1.10	[SWE] + [BISON] + [TEMP] + [SWE]*[BISON] + [BISON]*[TEMP]
o1.11	[BISON] + [MELT]
o1.12	[BISON] + [MELT] + [BISON]*[MELT]
o1.13	[SWE] + [MELT]
o1.14	[SWE] + [MELT] + [SWE]*[MELT]
o1.15	[TEMP] + [MELT]
o1.16	[TEMP] + [MELT] + [TEMP]*[MELT]
o1.17	[SWE] + [BISON] + [MELT]
o1.18	[SWE] + [BISON] + [MELT] + [SWE]*[BISON]
o1.19	[SWE] + [BISON] + [MELT] + [BISON]*[MELT]
o1.20	[SWE] + [BISON] + [MELT] + [SWE]*[MELT]
o1.21	[SWE] + [BISON] + [MELT] + [SWE]*[BISON] + [SWE]*[MELT]
o1.22	[SWE] + [BISON] + [MELT] + [SWE]*[BISON] + [BISON]*[MELT]
o1.23	[SWE] + [BISON] + [MELT] + [SWE]*[BISON] + [BISON]*[MELT] + [SWE]*[MELT]
o1.24	[TEMP] + [BISON] + [MELT]
o1.25	[TEMP] + [BISON] + [MELT] + [BISON]*[TEMP]
o1.26	[TEMP] + [BISON] + [MELT] + [BISON]*[MELT]
o1.27	[TEMP] + [BISON] + [MELT] + [BISON]*[TEMP] + [BISON]*[MELT]
o1.28	[TEMP] + [BISON] + [MELT] + [BISON]*[TEMP] + [BISON]*[MELT] + [TEMP]*[MELT]
o1.29	[SWE] + [BISON] + [TEMP] + [MELT]
o1.30	[SWE] + [BISON] + [TEMP] + [MELT] + [SWE]*[BISON]
o1.31	[SWE] + [BISON] + [TEMP] + [MELT] + [BISON]*[TEMP]
o1.32	[SWE] + [BISON] + [TEMP] + [MELT] + [BISON]*[MELT]
o1.33	[SWE] + [BISON] + [TEMP] + [MELT] + [TEMP]*[MELT]
o1.34	[SWE] + [BISON] + [TEMP] + [MELT] + [SWE]*[BISON] + [BISON]*[TEMP]
o1.35	[SWE] + [BISON] + [TEMP] + [MELT] + [SWE]*[BISON] + [BISON]*[MELT]
o1.36	[SWE] + [BISON] + [TEMP] + [MELT] + [SWE]*[BISON] + [TEMP]*[MELT]
o1.37	[SWE] + [BISON] + [TEMP] + [MELT] + [SWE]*[BISON] + [BISON]*[TEMP] + [BISON]*[MELT] + [TEMP]*[MELT]

APPENDIX 3B

TABLES OF MODEL RESULTS FOR BISON ROAD TRAVEL AND BISON OFF-ROAD TRAVEL MODELING EXERCISES

Table 3B.1. Modeling results for bison road travel analysis. Covariate functional forms are denoted as linear (L), square root (SQ), pseudothreshold (PT), or exponential (EX). The model number, number of parameters (K), ΔAIC_c value, and the Akaike weight (w_k) are listed.

	Covariate Functional Form						
Model	SWE	BISON	TEMP	TRAFFIC	**K**	**ΔAICc**	w_k
r2.8	L	L			5	0.000	0.2201
r2.10	L	L			7	0.851	0.1438
r2.14	SQ	L			6	1.841	0.0877
r2.66	L	L		PT	6	1.997	0.0811
r2.9	L	L			6	2.032	0.0797
r2.19	L	L	L		6	2.318	0.0690
r2.68	L	L		PT	8	3.167	0.0452
r2.7	L	SQ			5	3.443	0.0394
r2.5	SQ	SQ			4	3.635	0.0358
r2.25	L	L	L		7	3.889	0.0315
r2.73	L	L		PT	7	4.005	0.0297
r2.67	L	L		L	7	4.084	0.0286
r2.13	SQ	PT			6	4.262	0.0261
r2.79	L	L	L	L	7	4.496	0.0232
r2.6	SQ	PT			5	4.788	0.0201
r2.85	L	L	L	L	8	6.091	0.0105
r2.15	L	PT			6	6.808	0.0073
r2.20	L	L	L		6	10.295	0.0013
r2.61	L	L		L	5	10.318	0.0013
r2.17	L	L	L		6	10.363	0.0012
r2.62	L	L		L	6	10.421	0.0012
r2.18	L	L	L		6	10.541	0.0011
r2.64	L	L		L	6	10.662	0.0011
r2.11	L	L			6	10.676	0.0011
r2.37	L	L		L	6	10.805	0.0010
r2.12	L	L			6	11.124	0.0008
r2.42	L	L		L	6	11.141	0.0008
r2.65	L	L		L	6	11.262	0.0008
r2.36	L	L		L	5	11.339	0.0008
r2.21	L	L	L		6	11.495	0.0007
r2.74	L	L		L	7	11.776	0.0006
r2.27	L	L	L		7	11.801	0.0006

TABLE 3B.1—CONTINUED

r2.71	L	L		L	7	12.145	0.0005
r2.16	L	L	L		6	12.262	0.0005
r2.75	L	L		L	7	12.270	0.0005
r2.24	L	L	L		7	12.396	0.0004
r2.22	L	L	L		7	12.413	0.0004
r2.78	L	L	L	L	7	12.681	0.0004
r2.80	L	L	L	L	7	12.682	0.0004
r2.77	L	L	L	L	7	12.740	0.0004
r2.47	L	L	L	L	6	13.045	0.0003
r2.69	L	L		L	7	13.071	0.0003
r2.23	L	L	L		7	13.259	0.0003
r2.26	L	L	L		7	13.400	0.0003
r2.70	L	L		L	7	13.485	0.0003
r2.53	L	L	L	L	7	13.518	0.0003
r2.81	L	L	L	L	7	13.852	0.0002
r2.87	L	L	L	L	8	14.241	0.0002
r2.84	L	L	L	L	8	14.601	0.0001
r2.76	L	L	L	L	7	14.658	0.0001
r2.41	L	L		L	6	14.828	0.0001
r2.82	L	L	L	L	8	14.872	0.0001
r2.34	L	L		L	5	15.103	0.0001
r2.83	L	L	L	L	8	15.648	0.0001
r2.46	L	L	L	L	6	15.678	0.0001
r2.86	L	L	L	L	8	15.861	0.0001
r2.43	L	L		L	6	16.476	0.0001
r2.33	L	L		L	4	16.737	0.0001
r2.52	L	L	L	L	7	17.013	0.0000
r2.48	L	L	L	L	6	17.741	0.0000
r2.35	L	L		L	5	17.791	0.0000
r2.39	L	L		L	6	17.831	0.0000
r2.40	L	L		L	6	17.891	0.0000
r2.49	L	L	L	L	6	18.051	0.0000
r2.55	L	L	L	L	7	18.585	0.0000
r1.18	L	L			5	19.286	0.0000
r2.44	L	L	L	L	6	19.827	0.0000
r2.45	L	L	L	L	6	19.860	0.0000
r2.50	L	L	L	L	7	20.220	0.0000
r2.51	L	L	L	L	7	20.290	0.0000

TABLE 3B.1—CONTINUED

r1.22	L	L			6	20.443	0.0000
r2.54	L	L	L	L	7	20.447	0.0000
r1.17	L	L			4	20.481	0.0000
r1.30	L	L	L		6	20.881	0.0000
r1.36	L	L	L		7	20.914	0.0000
r1.23	L	L			7	20.997	0.0000
r1.21	L	L			6	21.119	0.0000
r1.19	L	L			5	21.612	0.0000
r1.29	L	L	L		5	21.904	0.0000
r1.33	L	L	L		6	21.922	0.0000
r1.9	L	L	L		4	21.953	0.0000
r1.37	L	L	L		9	22.079	0.0000
r1.20	L	L			5	22.728	0.0000
r1.35	L	L	L		7	22.732	0.0000
r1.10	L	L	L		6	22.976	0.0000
r1.34	L	L	L		7	23.230	0.0000
r1.32	L	L	L		6	23.775	0.0000
r1.5	L	L			4	24.134	0.0000
r1.31	L	L	L		6	24.239	0.0000
r2.59	L			L	4	25.050	0.0000
r1.4	L	L			3	25.449	0.0000
r2.3	L				3	26.017	0.0000
r2.60	L			L	5	26.955	0.0000
r2.4	L				4	27.971	0.0000
r1.8	L		L		3	29.425	0.0000
r2.31	L			L	3	29.644	0.0000
r1.13	L				3	31.682	0.0000
r2.32	L			L	4	31.815	0.0000
r1.14	L				4	32.628	0.0000
r2.1		L			3	33.540	0.0000
r2.2		L			4	35.072	0.0000
r2.57		L		L	4	35.634	0.0000
r1.1		L			2	35.906	0.0000
r2.29		L		L	3	36.020	0.0000
r1.11		L			3	37.259	0.0000
r2.58		L		L	5	37.318	0.0000
r1.6		L	L		3	37.594	0.0000
r1.12		L			4	37.796	0.0000

TABLE 3B.1—CONTINUED

r1.28		L	L		7	37.875	0.0000
r2.30		L		L	4	38.067	0.0000
r1.7		L	L		4	38.847	0.0000
r1.24		L	L		4	39.465	0.0000
r1.26		L	L		5	39.618	0.0000
r1.25		L	L		5	40.327	0.0000
r1.27		L	L		6	41.941	0.0000
r1.16			L		4	43.575	0.0000
r1.2	L				2	58.090	0.0000
r1.3			L		2	60.295	0.0000
r1.15			L		3	61.913	0.0000
r2.28				L	2	64.853	0.0000
r2.56				L	3	66.481	0.0000

Table 3B.2. Modeling results for bison off-road travel analysis. Covariate functional forms are denoted as linear (L), square root (SQ), pseudothreshold (PT), or exponential (EX). The model number, number of parameters (K), ΔAIC_c value, and the Akaike weight (w_k) are listed.

	Covariate Functional Form					
Model	SWE	BISON	TEMP	**K**	**ΔAICc**	$\mathbf{w_k}$
o1.19	SQ	L		5	0.000	0.2667
o1.23	L	L		7	1.041	0.1584
o1.4	L	L		3	2.040	0.0962
o1.32	SQ	L	L	6	2.205	0.0886
o1.9	L	L	SQ	4	3.160	0.0549
o1.22	L	L		6	3.248	0.0526
o1.31	SQ	L	L	6	3.700	0.0419
o1.17	L	L		4	3.717	0.0416
o1.5	L	L		4	3.856	0.0388
o1.10	L	L	L	6	4.673	0.0258
o1.20	EX	L		5	5.000	0.0219
o1.35	L	L	L	7	5.222	0.0196
o1.29	L	L	PT	5	5.254	0.0193
o1.18	L	L		5	5.600	0.0162
o1.37	L	L	L	8	5.909	0.0139
o1.34	L	L	L	7	6.565	0.0100
o1.33	L	L	PT	6	7.134	0.0075
o1.21	L	L		6	7.134	0.0075
o1.30	L	L	PT	6	7.230	0.0072
o1.7		L	L	4	8.818	0.0032
o1.36	L	L	PT	7	9.096	0.0028
o1.12		L		4	10.400	0.0015
o1.25		L	L	5	11.040	0.0011
o1.26		L	L	5	11.553	0.0008
o1.1		L		2	12.238	0.0006
o1.27		L	L	6	12.732	0.0005
o1.28		L	L	7	13.469	0.0003
o1.11		L		3	13.842	0.0003
o1.6		L	L	3	14.280	0.0002
o1.24		L	L	4	15.982	0.0001
o1.8	L		L	3	33.099	0.0000
o1.13	L			3	38.463	0.0000

TABLE 3B.2—CONTINUED

o1.14	L		4	39.365	0.0000
o1.16		L	4	46.303	0.0000
o1.2	L		2	60.861	0.0000
o1.3		L	2	61.577	0.0000
o1.15		L	3	63.714	0.0000

APPENDIX 3C

DESCRIPTIONS OF RESPONSE VARIABLES WITH SUPPORTING FIGURES FOR BISON ROAD AND BISON OFF-ROAD TRAVEL MODELING EXERCISES

Road Travel Response Variable (ρ_{ij})

To offer more insight into how we defined and calculated our road travel response variable (ρ_{ij}) we examine each component of the response variable and provide plots of the data. Using data from our bison road use surveys we calculated the response as $\rho_{ij} = \beta_{ij}\sigma_{ij}$ for each time interval (i) and year (j) to quantify the amount of bison road travel in units of bison groups observed per 100 km of road surveyed. We calculated β_{ij} by summing the number of bison groups observed traveling on roads for the ij^{th} period and dividing by the total distance of road surveyed for that period. A plot of bison groups observed on roads over time for each period and for all eight years is presented in Figure 3C.1. Since varying amounts of survey effort between periods could lead to observing more (or fewer) groups, we divided the number of groups observed per period by the distance of road surveyed per period to obtain β_{ij}. A plot of β_{ij} versus time is provided in Figure 3C.2.

Using β_{ij} alone as the response variable was not sufficient because the size of traveling bison groups can vary throughout the season as bison migrate into the Madison-Firehole area (Figure 3C.3) and all groups would be treated equivalently whether the size of the group was one or 50 bison. Based upon our field observations we felt that β_{ij} alone did not provide an accurate representation and quantification of the variability in the amount of bison road travel between periods. Therefore, we multiplied β_{ij} by a unitless road use weighting factor (σ_{ij}) to account for the potential variability in group size over time. We calculated σ_{ij} as the total number of individual bison in road traveling groups for the ij^{th} period divided by the total number of individual bison documented in road traveling groups for the entire season. A plot of σ_{ij} over time is presented in Figure 3C.4. Our final road travel response variable (ρ_{ij}) accounted for the number of traveling road groups observed, variability in group size, and survey effort as depicted in Figure 3C.5.

Given this background on how we calculated our response variable, we now examine the alternatives that we did not use. Two possibilities for the response were the number of individual bison traveling roads (Figure 3C.6) or the number of individual bison traveling roads per survey effort (Figure 3C.7). However, these would have given an overestimation of the amount of road travel because bison in groups do not travel independently. In large groups it is often the case that a few bison will begin traveling and the remainder of the group will follow until the lead animals stop. By this rationale we did not calculate σ_{ij} as the average group size per period because this σ_{ij}, when multiplied by β_{ij}, would have given a response variable of number of individual bison per survey effort.

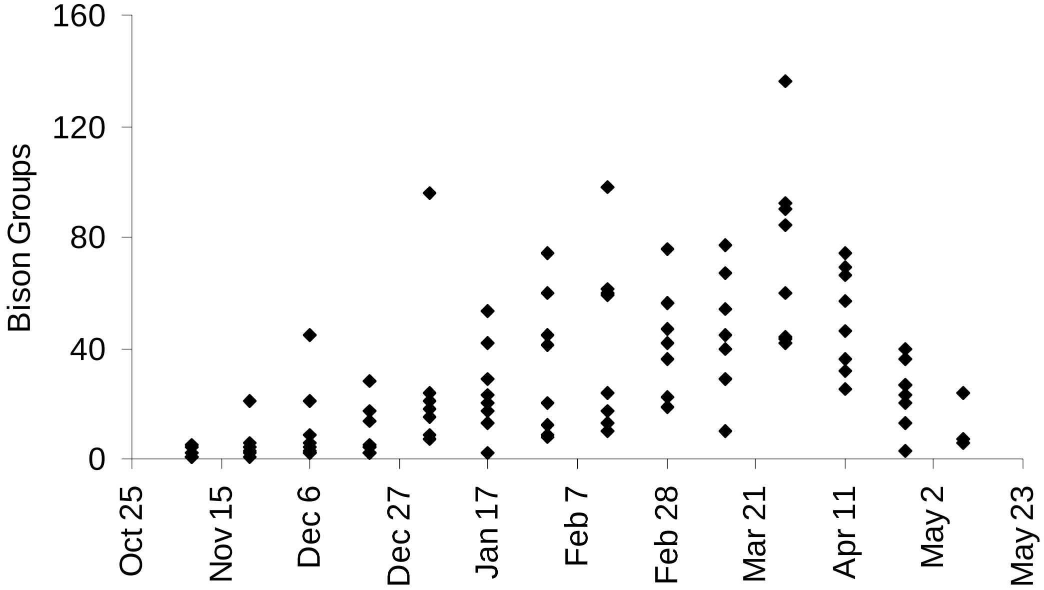


Figure 3C.1. The number of bison groups observed traveling on roads for each period and year during bison road use surveys from 1997-98 through 2004-05.

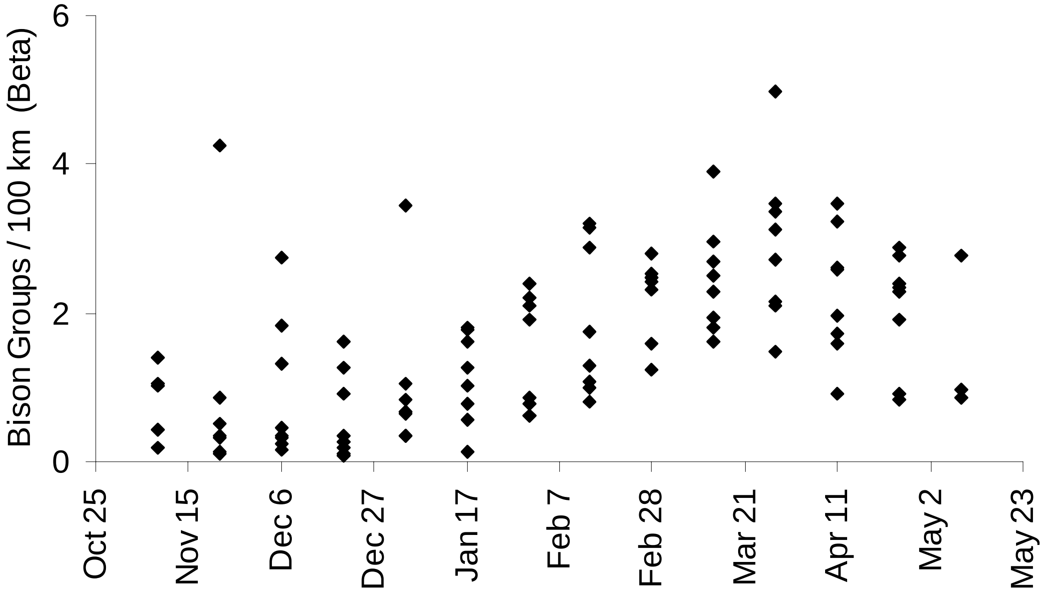


Figure 3C.2. The number of bison groups observed traveling on roads per 100 km of road survey effort (β_{ij}) for each period and year during bison road use surveys from 1997-98 through 2004-05.

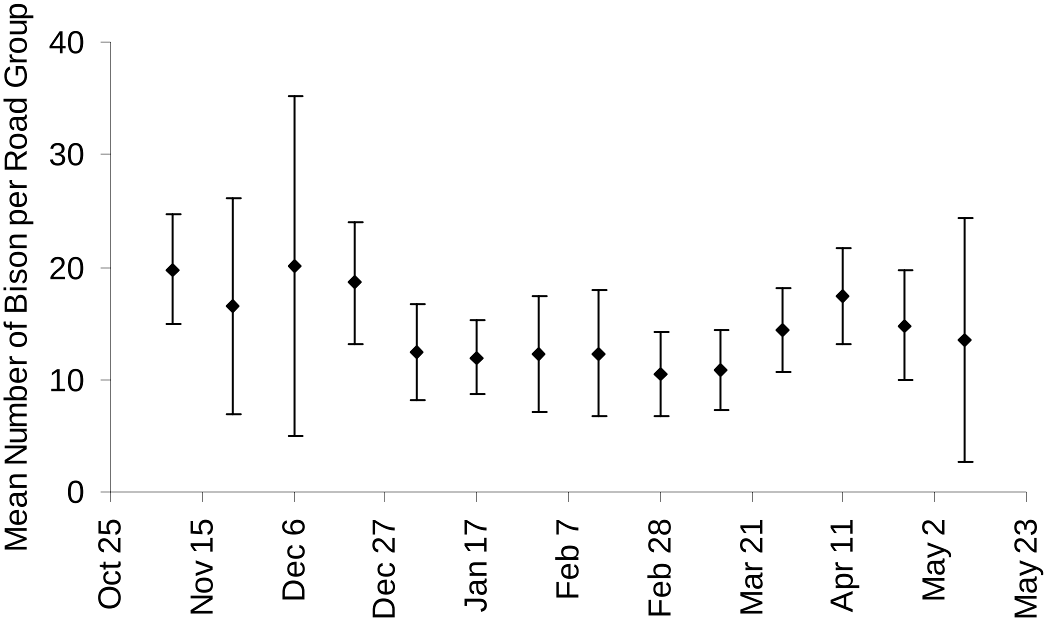


Figure 3C.3. The mean number of bison per group traveling on roads per period as observed during bison road use surveys from 1997-98 through 2004-05. The 95% confidence intervals about the mean for each year are presented.

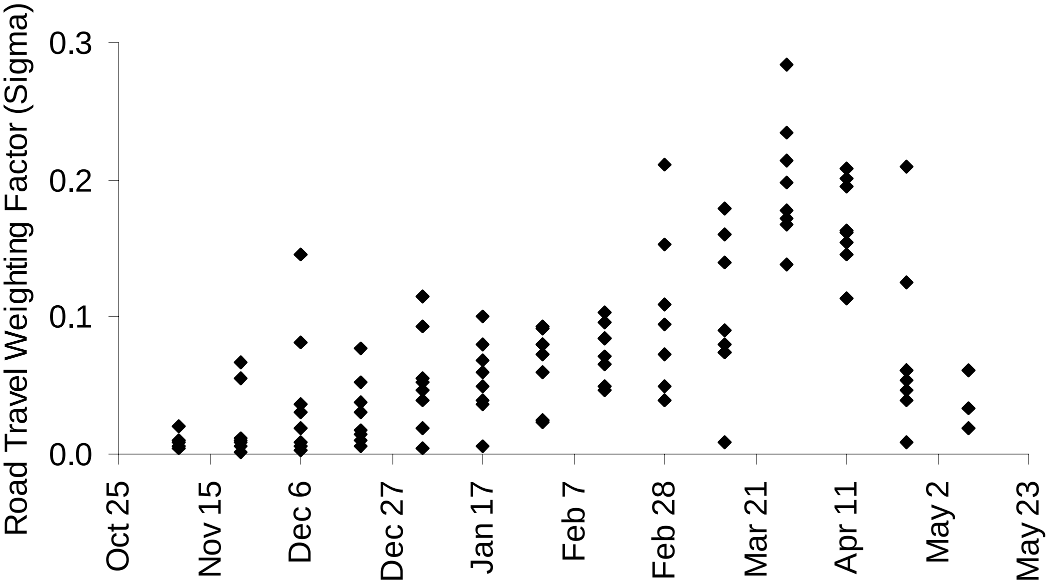


Figure 3C.4. The road travel weighting factor (σ_{ij}) for each period and year as calculated using data from bison road use surveys from 1997-98 through 2004-05.

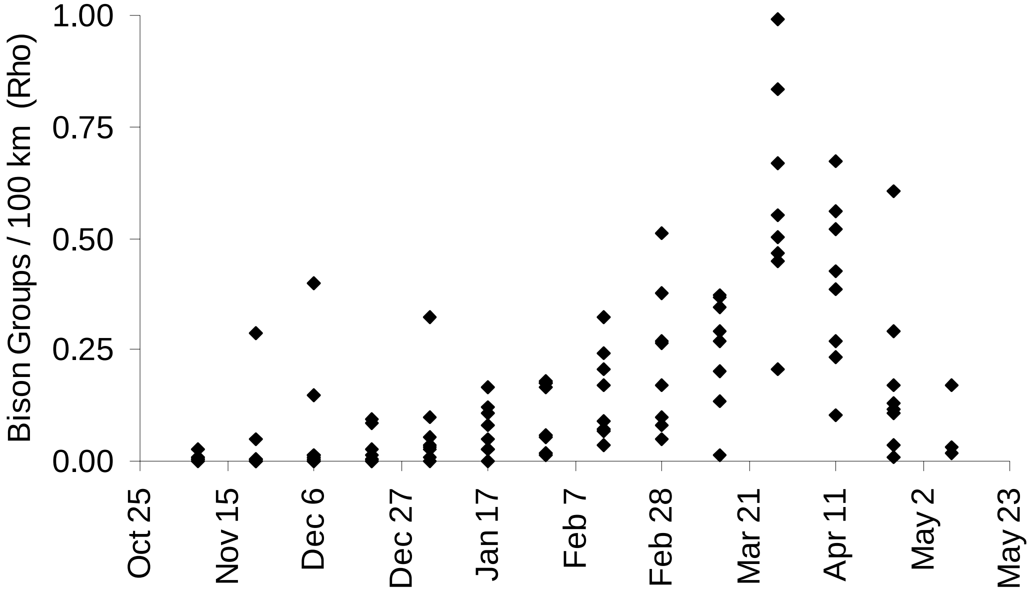


Figure 3C.5. The bison road travel response variable (ρ_{ij}) for each period and year as calculated using data from bison road use surveys from 1997-98 through 2004-05.

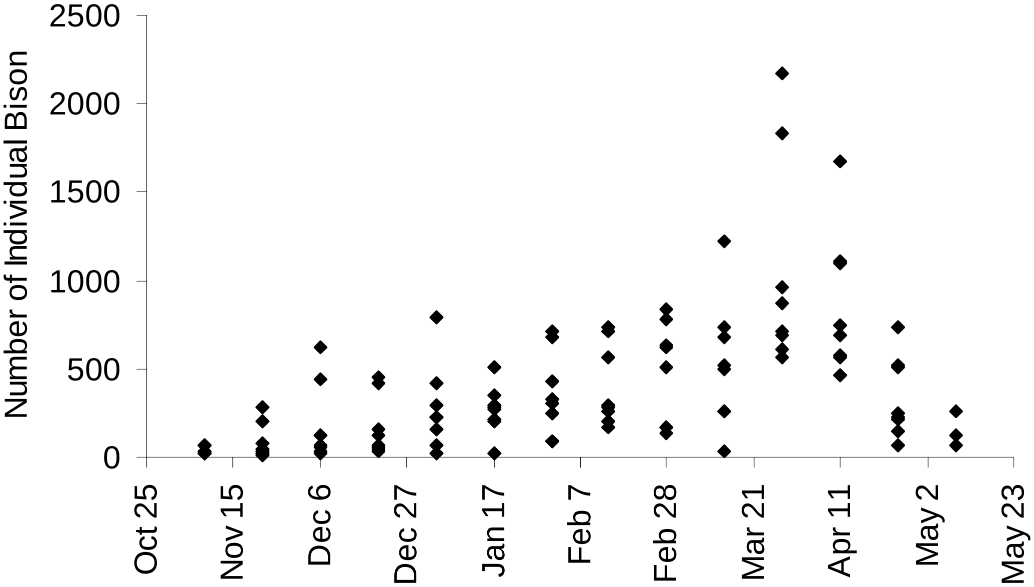


Figure 3C.6. The number of individual bison observed traveling on roads for each period and year during bison road use surveys from 1997-98 through 2004-05.

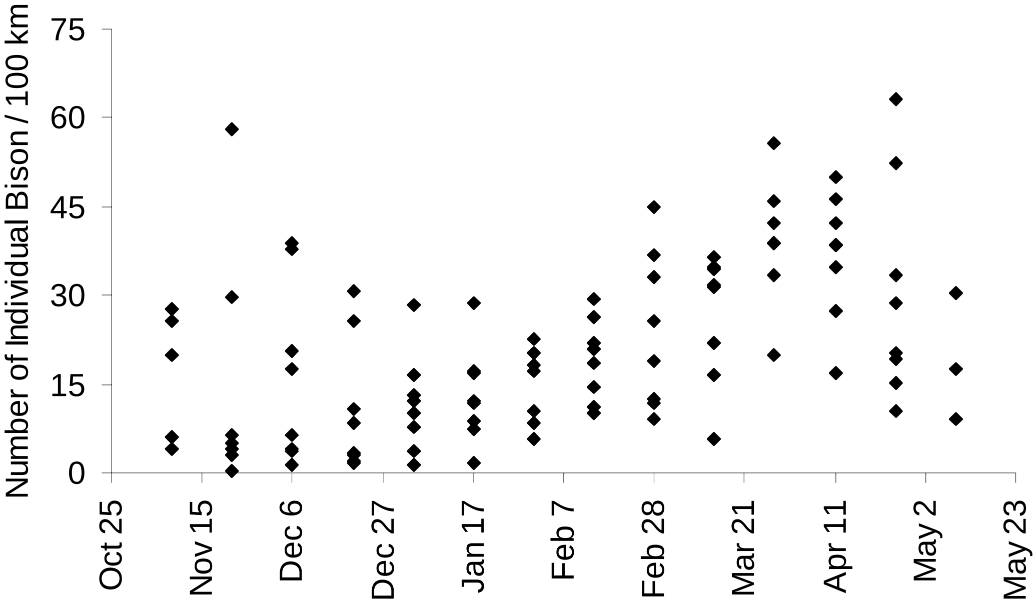


Figure 3C.7. The number of individual bison observed traveling on roads per 100 km of road survey effort for each period and year during bison road use surveys from 1997-98 through 2004-05.

Off-Road Travel Response Variable (τ_{ij})

We defined and calculated our off-road travel response variable (τ_{ij}) using the same rationale as for ρ_{ij}. Using travel data from our ground distribution surveys, we quantified the amount of bison off-road travel for each period by defining an off-road travel response variable as τ_{ij}, having units of bison groups observed traveling off-road per survey. We defined the off-road response as $\tau_{ij} = \alpha_{ij}\gamma_{ij}$, where α_{ij} is the total number of bison groups observed traveling off-road per ground distribution survey for the ijth period, calculated as the sum of off-road/off-trail and off-road/on-trail traveling groups. A plot of α_{ij} over time for each period and for all eight years is presented in Figure 3C.8.

Again, using α_{ij} alone as the response variable was not sufficient because the size of off-road traveling bison groups can vary throughout the season (Figure 3C.9). Therefore, we multiplied α_{ij} by a unitless off-road travel weighting factor (γ_{ij}) to account for the potential variability in group size over time. We calculated γ_{ij} as the number of bison observed traveling off-road during ground distribution surveys during the ijth period divided by the total number of bison observed traveling off-road for the entire season during ground distribution surveys. A plot of γ_{ij} over time is presented in Figure 3C.10. Our final off-road travel response variable (τ_{ij}) accounted for the number of off-road traveling groups observed, variability in group size, and survey effort as depicted in Figure 3C.11.

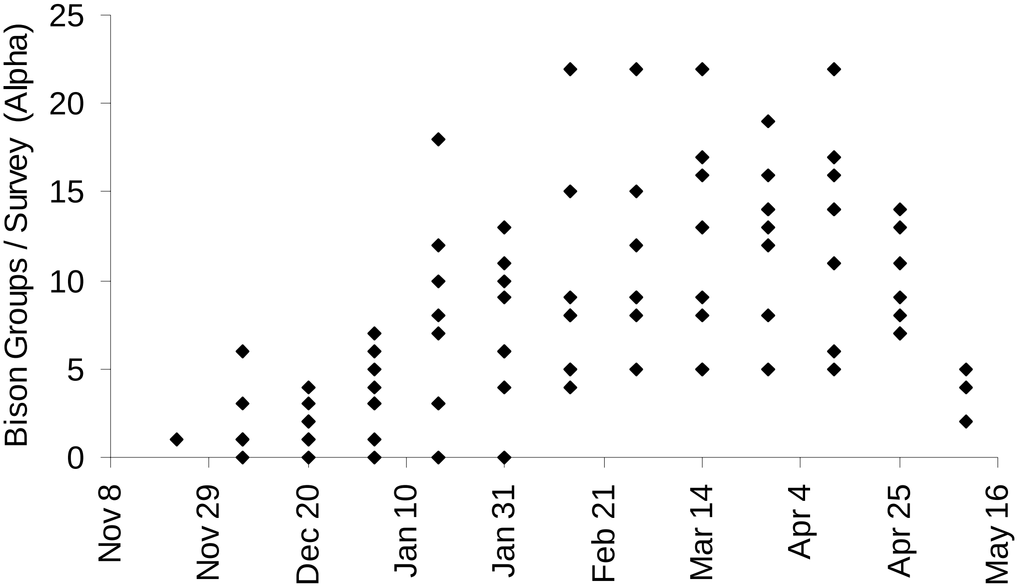


Figure 3C.8. The number of bison groups observed traveling off-roads per survey effort (α_{ij}) for each period and year during bison ground distribution surveys from 1997-98 through 2004-05.

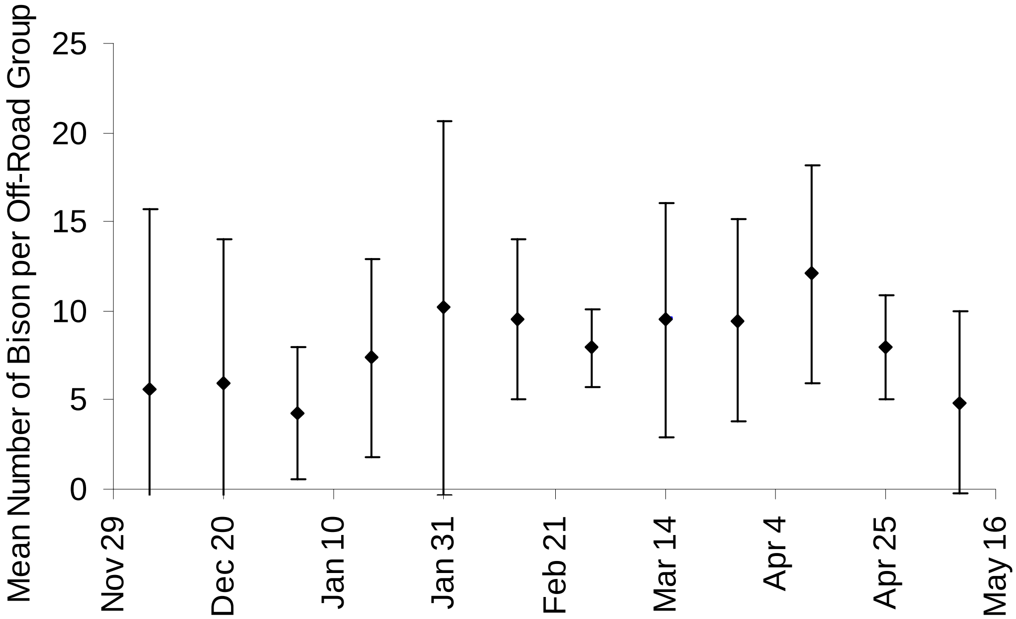


Figure 3C.9. The mean number of bison per group traveling off-roads per period as observed during bison ground distribution surveys from 1997-98 through 2004-05. The 95% confidence intervals about the mean for each year are presented.

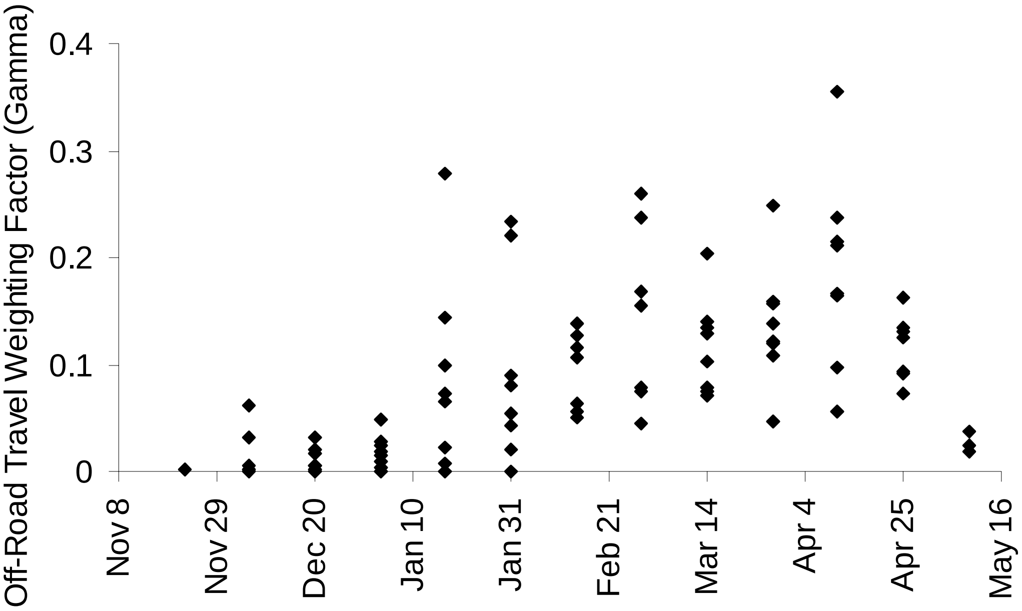


Figure 3C.10. The off-road travel weighting factor (γ_{ij}) for each period and year as calculated using data from bison ground distribution surveys from 1997-98 through 2004-05.

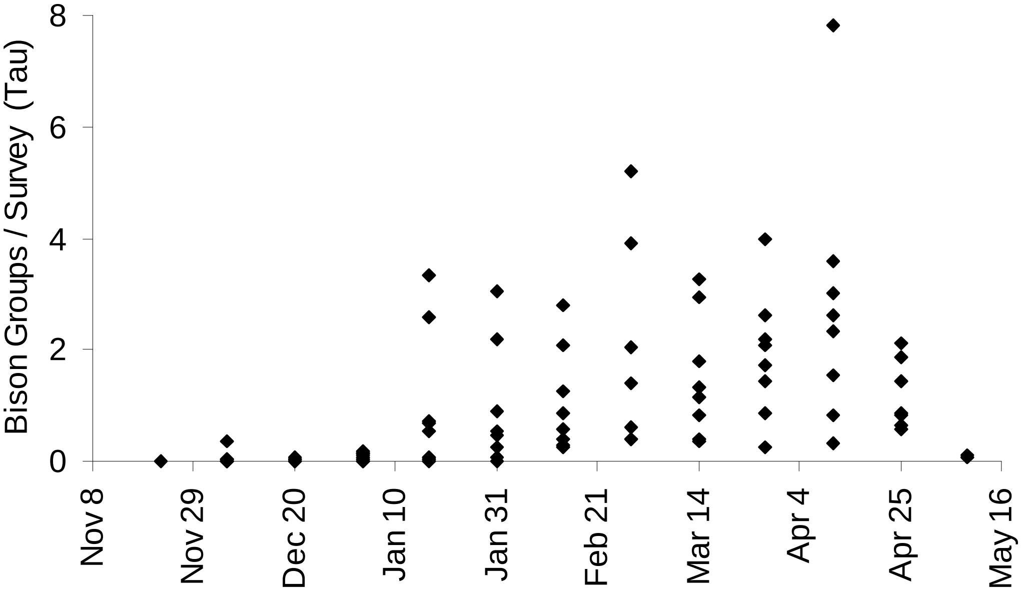


Figure 3C.11. The bison off-road travel response variable (τ_{ij}) for each period and year as calculated using data from bison ground distribution surveys from 1997-98 through 2004-05.

APPENDIX 4A

TABLE OF A PRIORI MODELS FOR BISON FORAGING AREA RESIDENCE TIME MODELING EXERCISE

Table 4A.1. Candidate list of 70 *a priori* mixed-effects regression models for the bison foraging area residence time modeling exercise. The response variable is the residence time (τ). Covariates are described in the main text.

Model	Structure
M1	SWERATIO + ID
M2	BIO + ID
M3	BISONMGF + ID
M4	BISON + ID
M5	τ_{ref} + ID
M6	SWERATIO + BIO + ID
M7	SWERATIO + BISONMGF + ID
M8	SWERATIO + BISON + ID
M9	SWERATIO + τ_{ref} + ID
M10	BIO + BISONMGF + ID
M11	BIO + BISON + ID
M12	BIO + τ_{ref} + ID
M13	BISONMGF + BISON + ID
M14	BISONMGF + τ_{ref} + ID
M15	BISON + τ_{ref} + ID
M16	SWERATIO + τ_{ref} + SWERATIO*τ_{ref} + ID
M17	BIO + BISONMGF + BIO*BISONMGF + ID
M18	BISON + τ_{ref} + BISON*τ_{ref} + ID
M19	SWERATIO + BIO + BISONMGF + ID
M20	SWERATIO + BIO + BISON + ID
M21	SWERATIO + BIO + τ_{ref} + ID
M22	SWERATIO + BISONMGF + BISON + ID
M23	SWERATIO + BISONMGF + τ_{ref} + ID
M24	SWERATIO + BISON + τ_{ref} + ID
M25	BIO + BISONMGF + BISON + ID
M26	BIO + BISONMGF + τ_{ref} + ID
M27	BIO + BISON + τ_{ref} + ID
M28	BISONMGF + BISON + τ_{ref} + ID
M29	SWERATIO + BIO + BISONMGF + BIO*BISONMGF + ID
M30	SWERATIO + BIO + τ_{ref} + SWERATIO*τ_{ref} + ID
M31	SWERATIO + BISONMGF + τ_{ref} + SWERATIO*τ_{ref} + ID
M32	SWERATIO + BISON + τ_{ref} + BISON*τ_{ref} + ID
M33	BIO + BISONMGF + BISON + BIO*BISONMGF + ID

TABLE 4A.1—CONTINUED

M34	BIO + BISONMGF + τ_{ref} + BIO*BISONMGF + ID
M35	BIO + BISON + τ_{ref} + BISON*τ_{ref} + ID
M36	BISONMGF + BISON + τ_{ref} + BISON*τ_{ref} + ID
M37	SWERATIO + BIO + BISONMGF + BISON + ID
M38	SWERATIO + BIO + BISONMGF + τ_{ref} + ID
M39	SWERATIO + BIO + BISON + τ_{ref} + ID
M40	SWERATIO + BISONMGF + BISON + τ_{ref} + ID
M41	BIO + BISONMGF + BISON + τ_{ref} + ID
M42	SWERATIO + BIO + BISONMGF + τ_{ref} + BIO*BISONMGF + ID
M43	SWERATIO + BIO + BISON + τ_{ref} + BISON*τ_{ref} + ID
M44	BIO + BISONMGF + BISON + τ_{ref} + BISON*τ_{ref} + ID
M45	SWERATIO + BIO + BISONMGF + BISON + τ_{ref} + BISON*τ_{ref} + ID
M46	SWE + ID
M47	SWE + BIO + ID
M48	SWE + BISONMGF + ID
M49	SWE + BISON + ID
M50	SWE + τ_{ref} + ID
M51	SWE + τ_{ref} + SWE*τ_{ref} + ID
M52	SWE + BIO + BISONMGF + ID
M53	SWE + BIO + BISON + ID
M54	SWE + BIO + τ_{ref} + ID
M55	SWE + BISONMGF + BISON + ID
M56	SWE + BISONMGF + τ_{ref} + ID
M57	SWE + BISON + τ_{ref} + ID
M58	SWE + BIO + BISONMGF + BIO*BISONMGF + ID
M59	SWE + BIO + τ_{ref} + SWE*τ_{ref} + ID
M60	SWE + BISONMGF + TAVG + SWE*τ_{ref} + ID
M61	SWE + BISON + τ_{ref} + BISON*τ_{ref} + ID
M62	SWE + BIO + BISONMGF + BISON + ID
M63	SWE + BIO + BISONMGF + τ_{ref} + ID
M64	SWE + BIO + BISON + τ_{ref} + ID
M65	SWE + BISONMGF + BISON + τ_{ref} + ID
M66	SWE + BIO + BISONMGF + τ_{ref} + BIO*BISONMGF + ID
M67	SWE + BIO + BISON + τ_{ref} + BISON*τ_{ref} + ID
M68	SWE + BISONMGF + BISON + τ_{ref} + BISON*τ_{ref} + ID
M69	SWE + BIO + BISONMGF + BISON + τ_{ref} + ID

TABLE 4A.1—CONTINUED

M70	SWE + BIO + BISONMGF + BISON + τ_{ref} + BISON*τ_{ref} + ID

APPENDIX 4B

TABLE OF MODEL RESULTS FOR BISON FORAGING AREA RESIDENCE TIME MODELING EXERCISE

Table 4B.1. Complete model results for bison residence time modeling exercise. For each model the model number, number of parameters (K), ΔAIC_c value, and Akaike weight (w_k) are listed. Covariate functional forms are denoted as linear (L) or quadratic (Q) and are provided for covariates included in each model.

	Covariate Functional Form								
Model	SWERATIO	SWE	τ_{ref}	BIO	BISONMGF	BISON	**K**	**ΔAIC_c**	**w_k**
M32	Q		L			L	7	0.000	0.0931
M23	Q		Q		L		7	0.481	0.0732
M7	Q				L		5	1.042	0.0553
M9	Q		L				5	1.487	0.0443
M1	Q						4	2.017	0.0340
M42	Q		Q	L	Q		11	2.112	0.0324
M43	Q		L	L		L	8	2.124	0.0322
M29	Q			L	Q		9	2.399	0.0281
M24	Q		Q			L	7	2.805	0.0229
M21	Q		Q	L			7	3.402	0.0170
M8	Q					L	5	3.818	0.0138
M6	Q			L			5	3.996	0.0126
M16	L		L				5	5.353	0.0064
M61		Q	L			L	7	5.604	0.0057
M31	L		L		L		6	6.812	0.0031
M50		L	L				4	7.300	0.0024
M30	L		L	L			6	7.354	0.0024
M48		L			L		4	7.533	0.0022
M19	L			L	L		5	7.709	0.0020
M22	L				L	L	5	7.730	0.0020
M46		L					3	7.756	0.0019
M68		L	L		L	L	7	7.757	0.0019
M45	L		L	L	L	L	8	7.900	0.0018
M56		L	L		L		5	8.059	0.0017
M51		L	L				5	8.094	0.0016
M40	L		L		L	L	6	8.158	0.0016
M38	L		L	L	L		6	8.275	0.0015
M39	L		L	L		L	6	8.543	0.0013
M20	L			L		L	5	8.679	0.0012
M58		L		L	L		6	8.754	0.0012
M60		L	L		L		6	8.833	0.0011
M57		L	L			L	5	8.886	0.0011

TABLE 4B.1—CONTINUED

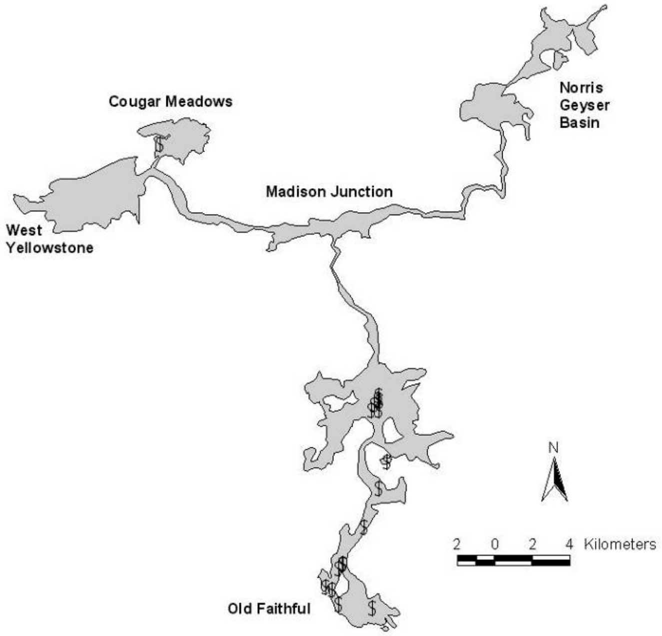
M67		L	L	L		L	7	8.913	0.0011
M66		L	L	L	L		7	9.037	0.0010
M54		L	L			L	5	9.278	0.0009
M49		L				L	4	9.440	0.0008
M52		L		L	L		5	9.504	0.0008
M55		L		L	L		5	9.555	0.0008
M47		L		L			4	9.700	0.0007
M37	L			L	L	L	6	9.744	0.0007
M70		L	L	L	L	L	8	9.786	0.0007
M65		L	L		L	L	6	9.992	0.0006
M63		L	L	L	L		6	10.063	0.0006
M59		L	L	L			6	10.093	0.0006
M64		L	L	L	L		6	10.901	0.0004
M36			L		L	L	6	11.132	0.0004
M53		L	L	L			5	11.417	0.0003
M62		L		L	L	L	6	11.555	0.0003
M69		L	L	L	L	L	7	12.029	0.0002
M14			L		L		4	12.121	0.0002
M18			L			L	5	12.603	0.0002
M34			L	L	L		6	12.965	0.0001
M44			L	L	L	L	7	13.176	0.0001
M3					L		3	13.255	0.0001
M5			L				3	13.974	0.0001
M28			L		L	L	5	14.019	0.0001
M26			L	L	L		5	14.038	0.0001
M17				L	L		5	14.422	0.0001
M35			L	L		L	6	14.526	0.0001
M10				L	L		4	15.071	0.0000
M15			L			L	4	15.172	0.0000
M13					L	L	4	15.208	0.0000
M12			L	L			4	15.739	0.0000
M41			L	L	L	L	6	15.960	0.0000
M33				L	L	L	6	16.382	0.0000
M27			L	L		L	5	16.954	0.0000
M25				L	L	L	5	17.053	0.0000
M4						L	3	20.917	0.0000

TABLE 4B.1—CONTINUED

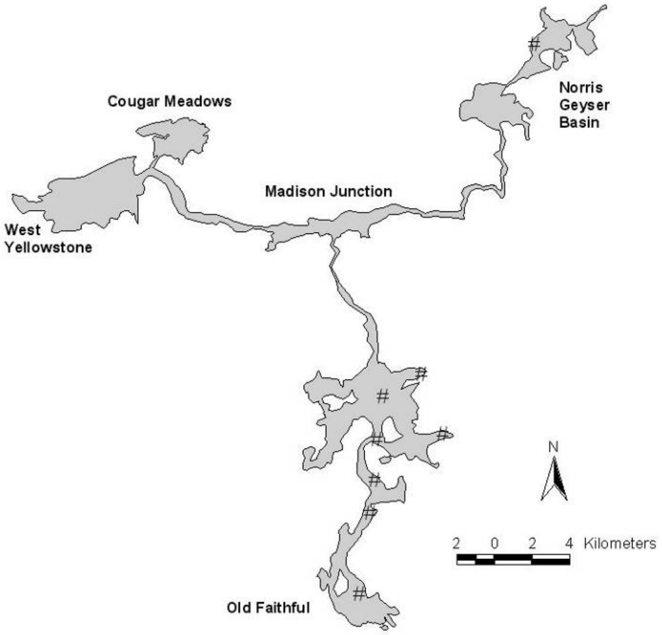
M2	L		3	20.969	0.0000
M11	L	L	4	22.353	0.0000

APPENDIX 4C

MAPS OF MONTHLY RELATIVE PERCEIVED VALUES FOR FORAGING AREAS

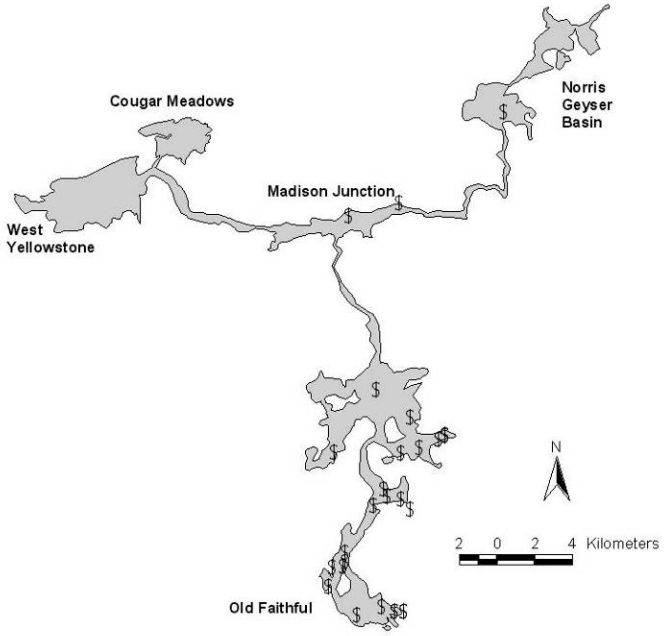


(a)

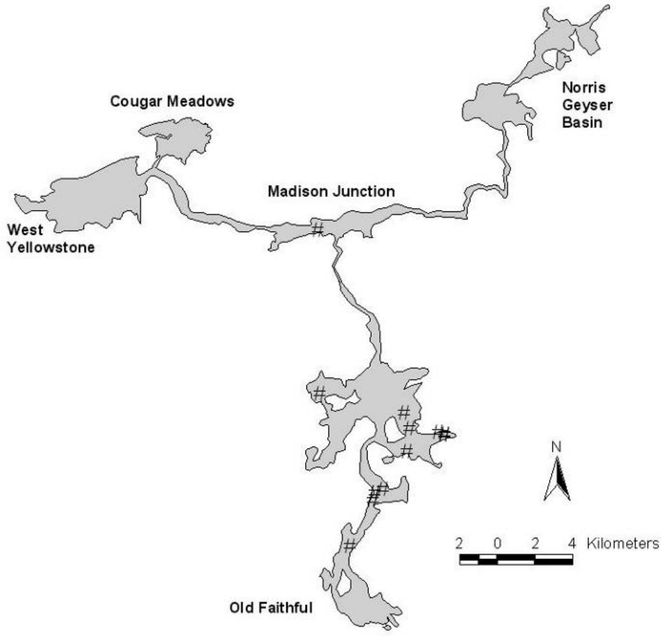


(b)

Figure 4C.1. Maps of (a) positive and (b) negative relative perceived value for bison foraging areas during January 2004 and 2005.



(a)



(b)

Figure E2. Maps of (a) positive and (b) negative relative perceived value for bison foraging areas during February 2004 and 2005.

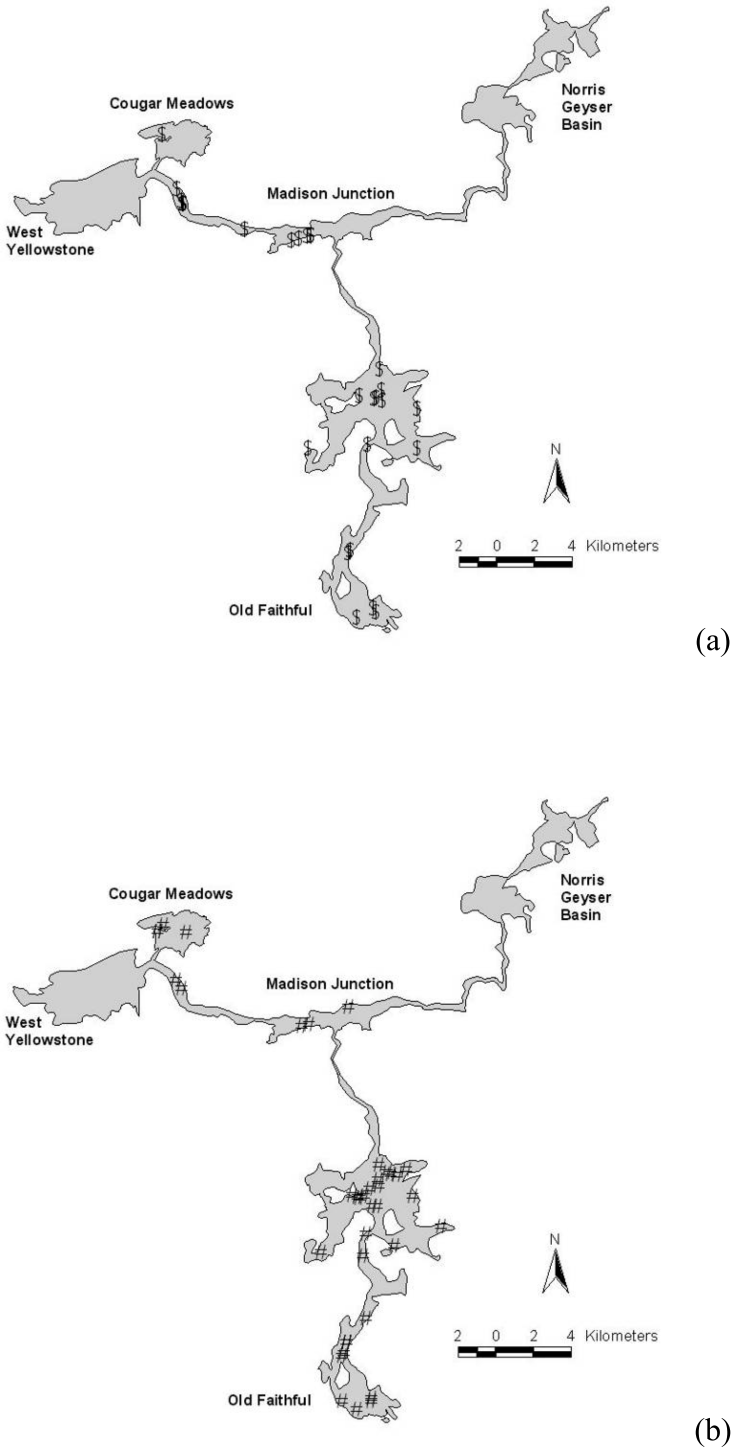


Figure E3. Maps of (a) positive and (b) negative relative perceived value for bison foraging areas during March 2004 and 2005.

APPENDIX 5A

TABLE OF A PRIORI MODELS FOR BISON PATCH SCALE FORAGING MODELING EXERCISE

Table 5A.1. Candidate list of *a priori* regression models for the bison patch scale foraging modeling exercise. The response variable is the foraging ratio (ϕ). Note: an intercept term was included with each model (not depicted in the model structure).

Model	**Model Structure**
W1.1	SWE
W1.2	HD
W1.3	BIO
W1.4	BISON
W1.5	HF
W1.6	SWE + HD
W1.7	SWE + BIO
W1.8	SWE + BISON
W1.9	SWE + HF
W1.10	HD + BIO
W1.11	HD + BISON
W1.12	HD + HF
W1.13	BIO + BISON
W1.14	BIO + HF
W1.15	BISON + HF
W1.16	SWE + HD + BIO
W1.17	SWE + HD + BISON
W1.18	SWE + HD + HF
W1.19	SWE + BIO + BISON
W1.20	SWE + BIO + HF
W1.21	SWE + BISON + HF
W1.22	HD + BIO + BISON
W1.23	HD + BIO + HF
W1.24	HD + BISON + HF
W1.25	BIO + BISON + HF
W1.26	SWE + HD + BIO + BISON
W1.27	SWE + HD + BIO + HF
W1.28	SWE + HD + BISON + HF
W1.29	SWE + BIO + BISON + HF
W1.30	HD + BIO + BISON + HF
W1.31	SWE + HD + BIO + BISON + HF
W1.32	$(\mathrm{SWE}+1)^{1/2}$
W1.33	$(\mathrm{HD}+1)^{1/2}$
W1.34	exp(-BIO)

TABLE 5A.1—CONTINUED

W1.35	$(\mathrm{BISON}+1)^{1/2}$
W1.36	$\exp(\mathrm{HF})$
W1.37	$(\mathrm{SWE}+1)^{1/2} + (\mathrm{HD}+1)^{1/2}$
W1.38	$(\mathrm{SWE}+1)^{1/2} + \exp(-\mathrm{BIO})$
W1.39	$(\mathrm{SWE}+1)^{1/2} + (\mathrm{BISON}+1)^{1/2}$
W1.40	$(\mathrm{SWE}+1)^{1/2} + \exp(\mathrm{HF})$
W1.41	$(\mathrm{HD}+1)^{1/2} + \exp(-\mathrm{BIO})$
W1.42	$(\mathrm{HD}+1)^{1/2} + (\mathrm{BISON}+1)^{1/2}$
W1.43	$(\mathrm{HD}+1)^{1/2} + \exp(\mathrm{HF})$
W1.44	$\exp(-\mathrm{BIO}) + (\mathrm{BISON}+1)^{1/2}$
W1.45	$\exp(-\mathrm{BIO}) + \exp(\mathrm{HF})$
W1.46	$(\mathrm{BISON}+1)^{1/2} + \exp(\mathrm{HF})$
W1.47	$(\mathrm{SWE}+1)^{1/2} + (\mathrm{HD}+1)^{1/2} + \exp(-\mathrm{BIO})$
W1.48	$(\mathrm{SWE}+1)^{1/2} + (\mathrm{HD}+1)^{1/2} + (\mathrm{BISON}+1)^{1/2}$
W1.49	$(\mathrm{SWE}+1)^{1/2} + (\mathrm{HD}+1)^{1/2} + \exp(\mathrm{HF})$
W1.50	$(\mathrm{SWE}+1)^{1/2} + \exp(-\mathrm{BIO}) + (\mathrm{BISON}+1)^{1/2}$
W1.51	$(\mathrm{SWE}+1)^{1/2} + \exp(-\mathrm{BIO}) + \exp(\mathrm{HF})$
W1.52	$(\mathrm{SWE}+1)^{1/2} + (\mathrm{BISON}+1)^{1/2} + \exp(\mathrm{HF})$
W1.53	$(\mathrm{HD}+1)^{1/2} + \exp(-\mathrm{BIO}) + (\mathrm{BISON}+1)^{1/2}$
W1.54	$(\mathrm{HD}+1)^{1/2} + \exp(-\mathrm{BIO}) + \exp(\mathrm{HF})$
W1.55	$(\mathrm{HD}+1)^{1/2} + (\mathrm{BISON}+1)^{1/2} + \exp(\mathrm{HF})$
W1.56	$\exp(-\mathrm{BIO}) + (\mathrm{BISON}+1)^{1/2} + \exp(\mathrm{HF})$
W1.57	$(\mathrm{SWE}+1)^{1/2} + (\mathrm{HD}+1)^{1/2} + \exp(-\mathrm{BIO}) + (\mathrm{BISON}+1)^{1/2}$
W1.58	$(\mathrm{SWE}+1)^{1/2} + (\mathrm{HD}+1)^{1/2} + \exp(-\mathrm{BIO}) + \exp(\mathrm{HF})$
W1.59	$(\mathrm{SWE}+1)^{1/2} + (\mathrm{HD}+1)^{1/2} + (\mathrm{BISON}+1)^{1/2} + \exp(\mathrm{HF})$
W1.60	$(\mathrm{SWE}+1)^{1/2} + \exp(-\mathrm{BIO}) + (\mathrm{BISON}+1)^{1/2} + \exp(\mathrm{HF})$
W1.61	$(\mathrm{HD}+1)^{1/2} + \exp(-\mathrm{BIO}) + (\mathrm{BISON}+1)^{1/2} + \exp(\mathrm{HF})$
W1.62	$(\mathrm{SWE}+1)^{1/2} + (\mathrm{HD}+1)^{1/2} + \exp(-\mathrm{BIO}) + (\mathrm{BISON}+1)^{1/2} + \exp(\mathrm{HF})$

APPENDIX 5B

TABLE OF MODEL RESULTS FOR BISON PATCH SCALE FORAGING MODELING EXERCISE

Table 5B.1. Model results for the bison patch scale foraging modeling exercise. The number of parameters (K), the AIC_c value, ΔAIC_c value, and the Akaike weight (w_k) are listed.

Model	K	AIC_c	ΔAIC_c	w_k
W1.37	3	-266.802	0.000	0.2175
W1.32	2	-266.194	0.608	0.1606
W1.47	4	-265.219	1.583	0.0986
W1.49	4	-264.714	2.087	0.0766
W1.48	4	-264.688	2.114	0.0756
W1.38	3	-264.532	2.270	0.0699
W1.39	3	-264.184	2.617	0.0588
W1.40	3	-264.110	2.692	0.0566
W1.58	5	-263.095	3.707	0.0341
W1.57	5	-263.089	3.712	0.0340
W1.59	5	-262.571	4.231	0.0262
W1.50	4	-262.563	4.239	0.0261
W1.51	4	-262.419	4.382	0.0243
W1.52	4	-262.073	4.729	0.0205
W1.62	6	-260.930	5.872	0.0115
W1.60	5	-260.427	6.374	0.0090
W1.6	3	-232.910	33.892	0.0000
W1.18	4	-231.162	35.639	0.0000
W1.17	4	-230.934	35.868	0.0000
W1.16	4	-230.796	36.006	0.0000
W1.1	2	-230.433	36.369	0.0000
W1.28	5	-229.220	37.581	0.0000
W1.27	5	-229.018	37.783	0.0000
W1.8	3	-228.968	37.834	0.0000
W1.9	3	-228.850	37.952	0.0000
W1.26	5	-228.792	38.010	0.0000
W1.7	3	-228.366	38.435	0.0000
W1.33	2	-228.104	38.698	0.0000
W1.43	3	-227.690	39.111	0.0000
W1.21	4	-227.494	39.308	0.0000
W1.31	6	-227.051	39.751	0.0000
W1.19	4	-226.855	39.947	0.0000
W1.20	4	-226.748	40.054	0.0000

TABLE 5B.1—CONTINUED

W1.42	3	-226.209	40.592	0.0000
W1.41	3	-226.155	40.647	0.0000
W1.55	4	-225.960	40.841	0.0000
W1.54	4	-225.712	41.089	0.0000
W1.29	5	-225.351	41.451	0.0000
W1.53	4	-224.283	42.519	0.0000
W1.61	5	-224.027	42.775	0.0000
W1.2	2	-195.661	71.141	0.0000
W1.12	3	-194.287	72.514	0.0000
W1.10	3	-194.011	72.791	0.0000
W1.11	3	-193.607	73.195	0.0000
W1.23	4	-192.620	74.182	0.0000
W1.24	4	-192.241	74.561	0.0000
W1.22	4	-191.967	74.835	0.0000
W1.30	5	-190.600	76.202	0.0000
W1.45	3	-168.318	98.484	0.0000
W1.34	2	-168.277	98.525	0.0000
W1.44	3	-166.433	100.369	0.0000
W1.56	4	-166.288	100.514	0.0000
W1.36	2	-166.095	100.707	0.0000
W1.3	2	-165.634	101.168	0.0000
W1.5	2	-165.394	101.408	0.0000
W1.14	3	-165.019	101.782	0.0000
W1.4	2	-164.637	102.165	0.0000
W1.35	2	-164.624	102.177	0.0000
W1.46	3	-164.411	102.390	0.0000
W1.13	3	-163.975	102.827	0.0000
W1.15	3	-163.816	102.986	0.0000
W1.25	4	-163.178	103.624	0.0000