

COVARIATES AFFECTING SPATIAL VARIABILITY IN BISON TRAVEL BEHAVIOR IN YELLOWSTONE NATIONAL PARK

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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 (USA), 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. We collected 121 380 locations from 14 female bison with GPS collars in central Yellowstone to examine how topography, habitat type, roads, and elevation affected the probability of bison travel year-round. We also conducted daily winter bison road use surveys (2003–2005) to quantify how topography and habitat type influenced spatial variability in the amount of bison road travel. Using model comparison techniques, we found the probability of bison travel and spatial distribution of travel locations were affected by multiple topographic and habitat type attributes including slope, landscape roughness, habitat type, elevation, and distances to streams, foraging areas, forested habitats, and roads. Streams were the most influential natural landscape feature affecting bison travel, and results suggest 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 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, our findings suggest that many road segments used as travel corridors are overlaid upon natural travel pathways because road segments receiving high amounts of bison travel had similar landscape features as natural travel corridors. We suggest that most spatial patterns in bison road travel are a manifestation of general spatial travel trends. Our research offers novel insights into bison spatial dynamics and provides conceptual and analytical frameworks for examining movement patterns of other species.

Key words: Akaike Information Criterion (AIC); bison; Bison bison; Global Positioning System (GPS); resource selection; road grooming; roads and travel corridors; spatial dynamics; ungulate movements; Yellowstone National Park.

INTRODUCTION

The influence of roads and winter road grooming on bison (*Bison bison*) travel patterns in Yellowstone National Park (YNP), Wyoming, USA, have been debated for more than a decade. Road grooming has been implicated in influencing bison range expansion and population growth because groomed roads purportedly provided routes of energy-efficient travel for bison as an alternative to traveling through deep snow (Meagher 1993). Conversely, Bjornlie and Garrott (2001) and Bruggeman et al. (2006) suggested that groomed roads in the Madison, Gibbon, and Firehole (MGF) drainages in west central YNP were not the cause of the likely density-dependent bison range

expansion (Fuller et al., *in press*). They found no evidence that bison preferentially used groomed roads in winter and that bison road travel 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 because 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. 2006). This debate culminated in a series of court cases challenging YNP's management of winter recreation (NPS [National Park Service] 2000, 2004), though litigation continues at present and management issues remain unresolved. In this work we investigated how topographic and habitat type attributes, and roads, affected spatial patterns in bison travel throughout central Yellowstone during the entire year. Our research offers further insights into mechanisms

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affecting bison travel, both on and off road, and why specific regions of the road network received higher amounts of bison travel than others.

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, Dingle 1996). 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 (Fraser et al. 1995, Ferguson and Elkie 2004). 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 (Johnson et al. 2002). 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, occurs for both migratory and small-scale movements (Sinclair 1983, Haddad 1999, Cronin 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, 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, whereas others avoid them owing to traffic or human presence (Brody and Pelton 1989, Dyer et al. 2002, 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 (Freddy et al. 1986, Borkowski et al. 2006) is particularly debatable, owing to the added physiological stresses of deep snow, restricted forage, and cold temperatures (Moen 1976, Gabrielsen and Smith 1995).

The influence of winter recreation on bison in YNP has been a subject of debate since park staff began grooming (i.e., packing) snow on interior park roads in 1971 to facilitate the passage of visitors on over-snow vehicles (e.g., snowmobiles, coaches) from December to March. Over the decades that followed, motorized winter recreation increased substantially from 2000 to >100 000 riders per winter during the mid-1990s (Gates et al. 2005), and concurrently, counts of central Yellow-

stone bison increased from <500 to >3000 animals (NPS 2000). As the population grew, bison expanded their range into the MGF (Fig. 1A) and beyond YNP boundaries. Meagher (1993) attributed this expansion to purported energy savings from groomed roads, which allowed bison to better survive winters and produce healthy calves in the spring, resulting in an unnatural population increase and alteration of bison spatial dynamics.

Litigation has 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 abiotic and biotic factors 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 MGF foraging areas. As a result, it is impossible to conclusively determine through retrospective analyses why bison use of groomed roads began or if groomed roads facilitated range expansion.

Given these constraints, we explored an alternate approach to quantify the influence of landscape and habitat type attributes on bison spatial use of travel routes in central YNP and to gain insight into how roads may currently affect bison travel year-round. We evaluated competing hypotheses using an information theoretic approach in two modeling exercises to quantify the relative contributions of topography and habitat type attributes in influencing the probability of bison travel using behaviorally based resource selection analyses. We used the top approximating models to predict the probability of bison travel and identify possible high-use travel corridors throughout central YNP. In exploratory analyses, we examined potential effects of roads and elevation on long-distance bison movements to determine whether these effects improved the predictive capability of the model. We also quantified how topography and habitat type characteristics affected spatial variability in the amount of bison road travel in the MGF. Finally, we developed maps to display both predicted and actual bison travel patterns to enhance our understanding of bison spatial ecology in YNP.

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

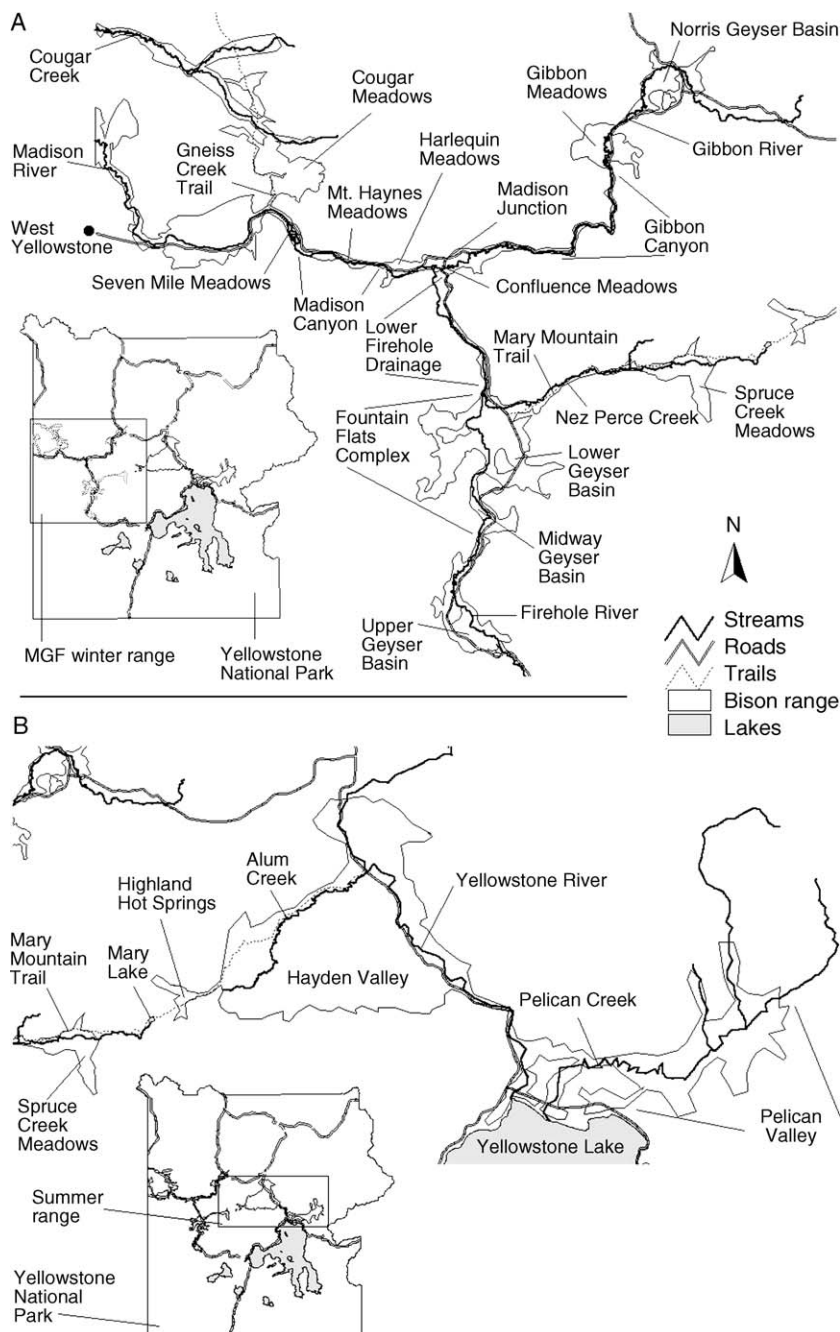


FIG. 1. The study area in Yellowstone National Park, Wyoming and Montana, USA, in (A) the Madison, Gibbon, and Firehole (MGF) drainages in west central Yellowstone and (B) the Hayden and Pelican Valleys in east-central Yellowstone.

(Fig. 1A) and their summer range in the Hayden and Pelican Valleys in east-central YNP (Fig. 1B) as delineated by Hess (2002). Elevations varied between 2000 and 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 returned to the summer range in June (Bruggeman et al. 2006). 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. There were four geothermal areas in the MGF along with smaller pockets of geothermal activity that had reduced snow accumulation and produced longer growing seasons compared to surrounding meadows. There were also some geothermally influenced areas along the Mary Mountain trail and throughout the summer range.

Vegetation and habitat types are described in Bruggeman (2006). A network of paved, two-lane roads paralleled the Madison, Gibbon, Firehole, and Yellowstone Rivers through the study area as described in Bruggeman (2006).

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

METHODS

Data collection

Fifteen GPS/VHF collars (Model TGW 3700, Telonics, Mesa, Arizona, USA) 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 07:00 to 19:00 hours, with fixes also taken at 23:00 and 03:00 hours. From mid-March through October, locations were recorded every 30 minutes from 06:00 to 23:00 hours, with fixes also at 01:00 and 03:00 hours.

Bison spatial use of roads in the MGF was recorded using daily bison road use surveys from November to April during three seasons (2002–2003 through 2004–2005) by four observers traveling independently using snowmobiles or trucks (Bruggeman et al. 2006). 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 (kilometers of road traveled).

Model development and statistical analysis using GPS data

We conducted two modeling exercises using GPS data to examine different aspects of year-round bison travel. The first was designed to investigate spatial patterns in the probability of general bison travel (i.e., movements of all distances), whereas the second examined only long-distance movements. To obtain the most powerful predictive capabilities from our models, we 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, we removed all locations obtained >32 minutes apart to procure the most accurate travel vectors possible that consisted of at least one segment, defined as two consecutive GPS locations. Second, we calculated Euclidean distances (d) for each segment and turning angles (α ; $0^\circ \leq \alpha \leq 180^\circ$) between segments, enabling us to define threshold values of ≥ 800 m and $\leq 90^\circ$, respectively, to indicate a significant movement (Appendix A; Bruggeman 2006). All segments with $d < 800$ m and $\alpha > 90^\circ$ were removed from the data set. After censoring, we identified each remaining individual travel vector, consisting of ≥ 1 segment(s), along with total vector distance and number of segments per vector. These vectors were used for the general bison travel analysis. For the long-distance travel analysis we considered the subset of identified travel vectors with a length ≥ 3200 m, because longer distance movements by bison would be indicative of sustained travel in corridors, and potentially important travel corridors that connected foraging areas were >3 km long.

We mapped each vector into a Geographic Information System (GIS) layer, created nodes at 400-m intervals along each vector beginning at the first GPS location of the vector, and systematically sampled for covariates (detailed below) at each node. Additionally, we created random movement data by taking each original vector and assigning 20 random relocations and orientations of the vector within our 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) vs. availability (0) data using logistic regression techniques (Manly et al. 2002).

Landscape covariates.—We calculated 10 covariates to characterize topography and habitat type attributes for each node location using GIS data layers (Bruggeman 2006). A USGS Digital Elevation Model was used to calculate topography covariates, while habitat type covariates were determined using vegetation cover type and geothermal data layers developed by The Watershed Institute (California State University, Monterey Bay, California, USA). Topography covariates were calculated based on averages of pixel values within a circle of 200 m radius from the node location, as we assumed bison would choose travel paths based on topography at a scale larger than one 28.5×28.5 m pixel. Average slope (SL), slope heterogeneity (SLHG), and average slope tangent (TAN) provided measures of landscape roughness (Bruggeman 2006). Habitat type covariates were calculated based on the habitat at the node point location. We 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, we 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 ≥ 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 we determined the elevation (ELEV) and calculated the nearest distance to road (DRD) for use in an exploratory modeling exercise.

Model development.—We developed and compared a priori hypotheses, expressed as multiple logistic regression models, to estimate the relative contributions of topography and habitat type attributes in influencing the odds of bison travel. While forming our model list, we calculated variance inflation factors (VIFs) to quantify multicollinearity between model predictors, including interactions (Neter et al. 1996). We removed models containing predictors having a VIF > 6 from our a priori list. As a result of multicollinearity, we were unable to include covariate interactions in any of our a priori models. Hypotheses for each modeling exercise were expressed as 255 candidate models, consisting of biologically plausible combinations of covariates (Appendix B). We formulated an a priori hypothesis for each covariate regarding the direction of its effect on the log odds response as detailed in Appendix B.

We used a generalized estimating equation (GEE) approach (Liang and Zeger 1986, Hardin and Hilbe 2003) to examine bison travel patterns (Bruggeman 2006). For each analysis, we 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 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 (Bruggeman et al. 2006). Model fitting (i.e., calibration) was completed using 75% of the original and random vector data. The remaining data were saved for use in model validation per a data-partitioning heuristic given by Fielding and Bell (1997), with model validation techniques described in Bruggeman (2006). For each model, we calculated the quasilikelihood under the independence model information criterion value (QIC; Pan 2001), which is applicable for GEEs and based on Akaike's Information Criterion (AIC). We then ranked and selected the best approximating models for each analysis using Δ QIC values, calculated Akaike weights (w_i) 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). We used the top model from each exercise to develop probability maps of bison travel by evaluating covariates using GIS layers.

Exploratory analyses.—We conducted two exploratory analyses using the 10 most highly supported models from our a priori bison long-distance travel modeling efforts. First, we 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 travel than distance to stream. Second, we added ELEV and DRD to each of the top 10 a priori models to see if these covariates resulted in an improved best approximating model. We 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*

We used data from 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). We 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 kilometers traveled by observers in the segment). We 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 our 52 defined road segments. We calculated the following covariates at each node: SL, SLHG, TAN, DBF, DUF, DST, and PROX, with covariates defined in *Landscape covariates*. For each of the 52 segments, we averaged the node values of each covariate across the segment to obtain one value of each covariate per segment. We did not assign a HBT code to each segment because of difficulty in defining an "average" habitat type surrounding the road that would be meaningful in the final analysis. Finally, we used indicator variables to define a covariate for the year (YEAR; i.e., for 2002–2003, YEAR = 1 if the data were collected in 2002–2003, and YEAR = 0 otherwise).

We developed and compared a priori hypotheses, expressed as multiple regression models, to estimate the effects of topography and habitat type attributes on η_{ij} . While forming our model list, we calculated VIFs and removed models containing predictors having a VIF > 6 from our a priori list (Neter et al. 1996). Hypotheses were expressed as 190 candidate models (Appendix B) in the form of regression equations consisting of covariate main effects. We developed an a priori hypothesis about the effect of each covariate on η_{ij} (Appendix B). We 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 nonconstant error variance and departures from normality in the error terms, so we applied a square-root transform on η_{ij} to stabilize the variance and normalize the errors to remedy these departures from regression assumptions. We calculated a corrected AIC (AIC_c) value for each model, ranked and selected the best approximating models using Δ AIC_c values, and calculated w_i and $w_{+(i)}$ (Burnham and Anderson 2002).

RESULTS

Modeling spatial variation in bison travel

A total of 121 380 locations, spanning late November 2003 through early November 2004, were recorded from 14 collars, with one collar failing to gather data. After censoring the data using the time, angle, and distance criteria for the general travel analysis, we had 3200 locations of primarily diurnal bison travel comprising 1192 vectors with an average length of 2025 ± 51 m (mean and SE) and an average of 1.68 ± 0.04 segments. For the long-distance travel analysis, adding the vector distance criterion left us with 918 locations and 187 vectors (average length of 5373 ± 144 m; average of 3.91 ± 0.11 segments). Further descriptions of data available for model calibration and validation for each analysis are provided in Bruggeman (2006).

General bison travel.—General travel vectors were primarily located throughout the central herd's range, concentrated in major meadow complexes, canyons in the MGF, the lower Firehole drainage, and along the Mary Mountain trail (Fig. 2A). Of all GPS locations obtained, 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, with $w_i = 1.0$, which was 191 QIC units better than the second-best model (Table 1A). Seven of the covariates contained in the best approximating model were significant effects with confidence intervals not spanning zero (Table 2). Additionally, all of the habitat categories, except BF, were significant effects. Because use of scaled covariates facilitated relative 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, slope, proximity to foraging area, distance to stream, and “other” habitat types were negatively correlated with the odds of bison travel, whereas slope heterogeneity, average slope tangent, and “meadow” and “geothermal” habitat types were positively correlated. Contrary to our predictions, distances to burned and unburned forest were positively correlated with the odds of travel. The top approximating model had $AUC = 0.882$, and therefore provided “excellent discrimination” capabilities for predicting the probability of bison travel (Hosmer and Lemeshow 2000). As expected, the top model predicted bison travel along streams and in some canyons (Fig. 3A; Appendices D and E) but 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 (Fig. 3A; Appendices D and E). 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.

Long-distance travel.—Long-distance travel vectors were concentrated in canyons, the lower Firehole drainage, and along two segments of the Mary Mountain trail (Fig. 2B). Of all GPS traveling locations, 9–18% were part of long-distance vectors in meadow complexes; 58–77% were part of long-distance vectors in canyons, and 44–57% were part of long-distance vectors along the Mary Mountain trail. Long-distance vectors overlapped with 27% of roads in central Yellowstone (i.e., 27% of the roads were used for long-distance travel, where a section of road was defined to have been used if it occurred between two consecutive long-distance travel locations that were both within 50 m of a road).

We found one top approximating model in the long-distance travel modeling exercise ($w_i = 0.995$), which was 10.8 QIC units better than the second-best model (Table 1B). Six covariates, plus all habitat types except BF, contained in the top model were significant effects, with DST being the most influential effect (Table 2). As predicted, slope, proximity to foraging area, distance to stream, and “other” habitat types were negatively correlated with the odds of long-distance bison travel, whereas slope heterogeneity, average slope tangent, and “meadow” and “geothermal” habitat types were positively correlated. Contrary to our hypotheses, distance to burned forest was positively correlated with the odds of long-distance travel, and distance to unburned forest and the burned forest habitat type were not significant in the top model ($AUC = 0.876$). The best approximating long-distance travel model predicted travel along streams and offered improved prediction along actual bison travel corridors compared to the top general travel model (Fig. 3B; Appendices D and E). Minimal long-distance travel was predicted in meadow complexes, except along streams. The model failed to predict long-distance travel along known high-use routes in the lower Firehole drainage and central Mary Mountain trail.

Both exploratory modeling efforts resulted in improved models compared to the top 10 a priori long-distance travel models. Contrary to our prediction, adding DRD and removing DST provided significant improvements in the QIC values (Appendix C: Table C1), and provided a top model containing seven significant covariates, with DRD negatively correlated with the odds of bison travel (Appendix C: Table C2). Adding ELEV and DRD lowered the QIC values of the top 10 a priori models (Appendix C: Table C3) 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 C: Table C4). The most influential covariate in the top model was still DST. Probability predictions with the new best approximating model addressed limitations from the top a priori model. Specifically, including ELEV predicted more long-distance bison travel along lower-elevation valley bottoms in the MGF, and minimal travel on high-elevation plateaus (Appendix D: Fig. D1). Models

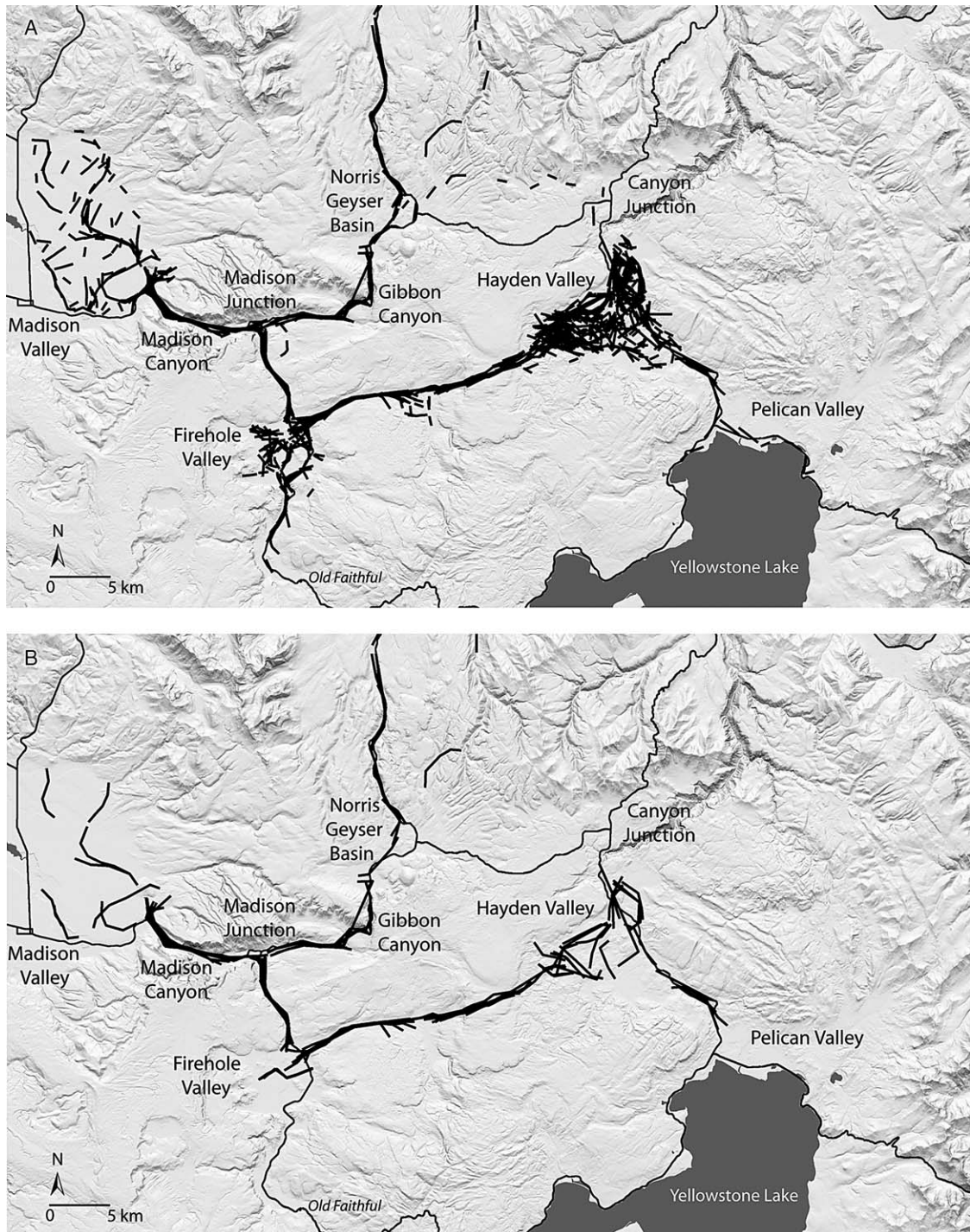


FIG. 2. Maps of the spatial distribution of vectors from GPS collared bison for (A) general bison travel and (B) long-distance bison travel throughout central Yellowstone National Park as determined from data-filtering techniques described in the *Methods*. Short black line segments denote vectors, and thin lines depict the road system.

including DRD improved prediction of long-distance travel along roads in the lower Firehole and Gibbon drainages, but also predicted more travel in meadows near roads (Appendix D: Fig. D1).

Modeling spatial variation in bison road travel

A total of 1444 bison groups were observed traveling on the MGF road system during daily road use surveys in 2002–2005, ranging from a minimum of 285 groups in

TABLE 1. Model selection results for a priori hypothesized models examining the effects of habitat type and topography covariates on spatial variation in the odds of (a) general bison travel and (b) long-distance bison travel.

Model	Structure	<i>K</i>	Δ QIC	w_i
A) General bison travel modeling results				
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
B) Long-distance bison travel modeling results				
CHT213‡	$\beta_0 + \beta_1(\text{HBT}) + \beta_2(\text{DST}) + \beta_3(\text{DBF}) + \beta_4(\text{PROX}) + \beta_5(\text{SL}) + \beta_6(\text{SLHG}) + \beta_7(\text{TAN})$	11	0.00	0.995
CHT217	$\beta_0 + \beta_1(\text{HBT}) + \beta_2(\text{DST}) + \beta_3(\text{DBF}) + \beta_4(\text{DUF}) + \beta_5(\text{PROX}) + \beta_6(\text{SL}) + \beta_7(\text{SLHG}) + \beta_8(\text{TAN})$	12	10.76	0.005

Notes: For each analysis, the best approximating models are presented along with the number of parameters (*K*), the Δ QIC value (quasi-likelihood under the independence model information criterion), and the Akaike weight (w_i)

† QIC value for model HT217 is 29 762.58.

‡ QIC value for model CHT213 is 11 334.35.

2002–2003 to a maximum of 656 groups in 2003–2004 (481 ± 108 groups [mean \pm SE]). Survey effort varied between 25 031 km in 2002–2003 and 34 464 km in 2004–2005 ($29\,307 \pm 2758$ km). Bison spatial use of the road system varied greatly (Fig. 4) with the average three-year amount of bison travel per segment ranging between 0.0 and 11.7 bison groups observed in the segment per 100 km traveled in the segment (3.2 ± 0.4 bison groups). Road segments receiving high amounts of bison travel were primarily located in canyons and the lower Firehole drainage (Fig. 4).

One model received the most support in our road travel modeling exercise with $w_i = 0.274$ and a relative likelihood of 3.7 compared to the second-best model, which differed by 2.6 AIC_c units (Table 3). Six of the covariates contained in the best approximating model were significant effects with confidence intervals not spanning zero, with YEAR and distances to unburned forest and streams having the highest predictor weights (Table 4). In addition, the dichotomous YEAR effect

was significant for the 2002–2003 and 2003–2004 seasons. As predicted, slope heterogeneity and YEAR (for two years) were positively correlated, and distances to streams and unburned forest were negatively correlated with η . Contrary to our hypotheses, proximity to foraging area and distance to burned forest were positively correlated with η , average slope tangent was negatively correlated with η , and slope was not in the top model.

DISCUSSION

Using behaviorally based resource selection analyses, we found the spatial distribution of bison travel locations and the probability of bison travel throughout central Yellowstone year-round were affected by multiple topographic and habitat type attributes. These included slope, landscape roughness, elevation, habitat type, proximity to foraging areas, and distances to streams, burned and unburned forest, and roads. In certain portions of the landscape where rugged topog-

TABLE 2. Coefficient values and lower and upper 95% confidence limits (in parentheses) from the best approximating models for the general bison travel analysis (model HT217) and the long-distance bison travel analysis (model CHT213).

Covariate	General bison travel model		Long-distance bison travel model	
	$w_{+(i)}$	β_i	$w_{+(i)}$	β_i
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	N/A
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)

Notes: Both top models were identified through QIC model comparison techniques examining spatial variability in the odds of bison travel. Boldface type denotes significant coefficients at $\alpha = 0.05$. Predictor weights ($w_{+(i)}$) are presented for each of the modeling exercises.

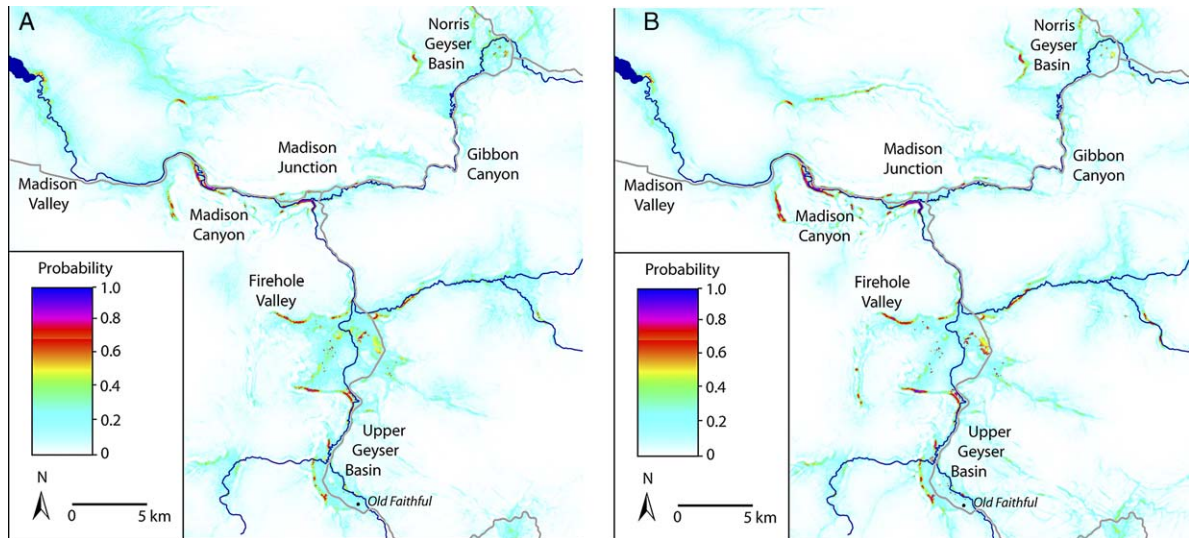


FIG. 3. Probability maps developed from the best approximating a priori models examining the effects of topography and habitat attributes on (A) general bison travel and (B) long-distance bison travel throughout the Madison, Gibbon, and Firehole areas of Yellowstone National Park. White areas represent a travel probability of zero, and travel probability increases as colors darken from light blue to green to red to dark blue (see legend). Roads are depicted in gray shading, and streams in blue. Maps for the entire central Yellowstone area are provided in Appendices D and E.

raphy or habitat types inhibit travel, roads appear to facilitate bison travel. While similar landscape characteristics influence both short- and long-distance bison travel, certain features have effects of different magnitudes on long-distance movements, suggesting specific areas have a higher probability of long-distance, or corridor, travel throughout central Yellowstone. Our findings agree with those of other studies that found habitat type, topography, and landscape heterogeneity to affect the movements of mammals (Geist 1971, Johnson et al. 1992, Bergman et al. 2000, Dickson et al. 2005, Morales et al. 2005), and large herbivores to use corridors to connect feeding areas (Douglas-Hamilton et al. 2005).

Streams were the most influential natural landscape features affecting bison travel. Streams guide animal movements (Noss 1991) and bison regularly establish and use travel routes along them. Our results suggest the bison travel network throughout central Yellowstone is spatially defined largely by the presence of streams that connect foraging areas. Areas receiving the most long-distance bison travel often paralleled major streams, and while segments of some of these streams parallel roads, other portions are located away from any roads, such as streams along 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 snowpack along riverbanks and afford bison easier travel routes and foraging than nearby areas of deep snow.

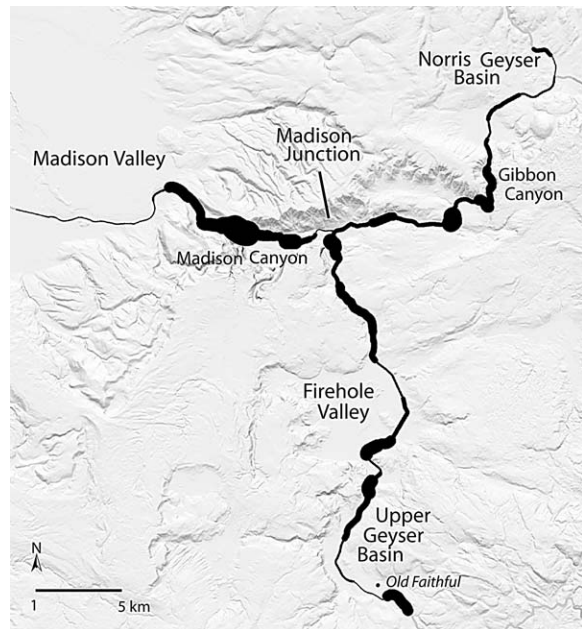


FIG. 4. Map depicting spatial variability in the amount of bison road travel for the Firehole, Gibbon, and Madison drainages in west central Yellowstone National Park. The width of the black lines represents the magnitude in average bison road travel for each road segment for 2002–2003 to 2004–2005, with values ranging between 0.0 and 11.7 bison groups observed in a segment per 100 km traveled in the segment. Roads are depicted in dark gray. Data on bison road use were obtained during winter bison road use surveys conducted from 2002–2003 to 2004–2005 in the Madison, Gibbon, and Firehole drainages.

TABLE 3. Model selection results for a priori hypothesized models examining the effects of habitat type, topography, and year covariates on spatial variation in the amount of bison road travel.

Model	Structure	<i>K</i>	ΔAIC_c	w_i
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

Notes: The four best approximating models are presented along with the number of parameters (*K*), the ΔAIC_c value, and the Akaike weight (w_i).

† The AIC_c value for model RHT150 is 327.73.

Topography affected the probability of bison travel because the odds of travel were negatively correlated with slope and positively correlated with slope heterogeneity and average slope tangent. Further, the odds of long-distance travel were negatively correlated with elevation in the top exploratory model. The negative effect of slope indicates that the probability of bison travel is higher along gentle elevation gradients, and that bison avoid traversing steep slopes when other routes exist. Correspondingly, the probability of travel was higher in areas of variable topography that constrain movements, such as in canyons; this pattern agrees with bison travel corridors that exist throughout the MGF. In these canyons, river corridors, which mostly parallel roads, assist in naturally guiding bison movements along gentle elevation gradients. 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 influences travel routes of species in a variety of environments (Allee and Schmidt 1966, Sinclair 1983). In agreement with our results, Johnson et al. (2002) found that caribou (*Rangifer tarandus*) used the most energy efficient pathways for travel. 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, and Fortin et al. (2005) found elk (*Cervus elaphus*) avoided traveling across steep slopes.

Bison travel was more likely in close proximity to foraging areas, a result suggesting that bison travel more near foraging areas. Additionally, the probability of bison travel increased in meadow and thermal habitats, indicating that bison develop some travel routes through interconnected foraging areas, which is how bison utilize the western part of the Mary Mountain trail that passes through a series of meadows. Thermal areas may also have increased importance as travel corridors because the magnitude of effect of thermal habitats was greater for long-distance 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 long-distance travel vectors reveals that movements in

large meadow complexes are generally of short distance and likely related to travel between patches of suitable forage (Fig. 2). In contrast, bison travel behavior is different in habitats lacking adequate foraging areas (i.e., corridors), with travel consisting of long-distance sustained movements (compare Fig. 2A and 2B). Our 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, 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 that received the most bison travel, suggesting bison primarily use roads when they are part of a natural travel corridor. However, we cannot discount the possibility that roads facilitated the initial discovery of certain routes, even if perhaps they are no longer the determining factor for travel along those routes. Measured high-use travel routes overlapped with roads in canyons and the lower Firehole drainage, and portions of these road segments also received the highest amount of bison travel during our road use surveys. The top road travel model contained significant effects for some of the same

TABLE 4. Coefficient values and lower and upper 95% confidence limits (in parentheses) from the best approximating model (model RHT150) identified through AIC model comparison techniques examining spatial variability in the amount of bison road travel.

Covariate	$w_{+(i)}$	β_i
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 (2003–2004)	0.999	0.599 (0.343, 0.855)
YEAR (2004–2005)	0.999	0.030 (-0.226, 0.286)

Notes: Boldface type denotes significant coefficients at $\alpha = 0.05$. Predictor weights ($w_{+(i)}$) are presented for the overall modeling exercise.

landscape covariates that influenced bison travel, most notably distance to stream and slope heterogeneity. Indeed, road segments that passed through meadow complexes without topographic restrictions or that circumvented important foraging areas received below-average bison travel.

While distance to stream helped predict travel in many actual high-use travel areas, addition of distance to road in the exploratory models improved prediction along certain road segments. Contrary to our hypothesis (Appendix B), including distance to road in models resulted in a lower QIC value than when distance to stream was included, suggesting that the road system is important as part of the bison travel network. When including both DST and DRD covariates together in exploratory models, however, the coefficient for DST was 1.7 times greater than that for DRD with confidence intervals that overlapped slightly. This suggests that streams are more influential on bison travel than roads alone and, given the vector maps (Fig. 2), it is clear that bison also travel far away from roads in areas often containing streams. Overall, results indicate that both streams and roads can affect bison travel patterns and facilitate travel.

Pronounced bison travel corridors existed both in close association with modern roads in parts of the MGF and distant from any roads, such as along the Mary Mountain trail migratory corridor. While portions of corridors through canyons were predicted from the top a priori long-distance 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. It is possible that bison were selecting certain travel routes in response to landscape variables not considered in our analyses. The travel route along the road through the lower Firehole drainage was predicted after including distance to road in exploratory models, indicating road influence on bison 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 (Trombulak and Frissell 2000).

Our 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. Use of spatial memory to revisit foraging areas has been documented for several ungulate species (Bailey et al. 1989, Hewitson et al. 2005) and is likely used by bison

given their well-defined travel corridors. 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 combination of factors including lack of foraging areas and geothermal habitats, route length, and deep snow, 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 through canyons in the MGF 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). Our 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.

Our goal in this study was to quantify how static landscape attributes influenced bison travel throughout summer and winter. Snowpack may only influence bison movements for part of the year, but we examined this effect in our exploratory analysis, and the significance of the elevation covariate suggests snowpack may affect bison spatial travel patterns. Snow affects the foraging behavior, distribution, and temporal travel patterns of bison (e.g., Fortin et al. 2003, Bruggeman 2006, Bruggeman et al. 2006) and other large herbivores (Schaefer and Messier 1995, Doerr et al. 2005). While use of elevation as a surrogate covariate for snowpack provides only a relative estimate of snow depth on rough spatial scales, accurate prediction and estimation of snow conditions on the fine scales necessitated by this study requires a fully validated, spatially explicit snowpack simulation model. Lacking this we felt it was more appropriate to include a rough index of snowpack than to ignore it entirely. Therefore, one limitation of this work is a lack of full understanding of how fine-scale temporal and spatial trends in snowpack affect bison travel patterns.

Although our study cannot fully resolve the debate over effects of roads and 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. (2006) 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. 2006). We 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 type attributes alone predicted the majority of bison travel corridors throughout central Yellowstone. Beyond investigating bison travel in Yellowstone, our study provides conceptual and analytical frameworks for examining animal movement patterns using a behaviorally based resource selection analysis. Given the increasing use of GPS and GIS technology in wildlife research, we anticipate the methodology presented here will be applicable to studies of behaviorally influenced resource selection for a variety of species.

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APPENDIX A

Figures depicting the definition of turning angle between segments, criteria for a significant movement bout, distance vs. turning angle, and a histogram of turning angles (*Ecological Archives* A017-054-A1).

APPENDIX B

A description of a priori hypothesized effects for each covariate on the response variables and tables listing the candidate sets for bison travel analysis (*Ecological Archives* A017-054-A2).

APPENDIX C

Tables listing model results and parameter coefficient estimates for the two exploratory long-distance travel modeling exercises (*Ecological Archives* A017-054-A3).

APPENDIX D

A map of predicted travel probability from the top approximating exploratory model and fine-scale maps of predicted travel probabilities for areas throughout central Yellowstone (*Ecological Archives* A017-054-A4).

APPENDIX E

Maps of predicted travel probability from top approximating models for general and long-distance bison travel throughout central Yellowstone (*Ecological Archives* A017-054-A5).