Grand Teton National Park Pathway Elk Study

Final Report

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Abstract: *Planned construction of a multi-use pathway along the Teton Park Road (TPR) from Moose Junction to Jenny Lake raised concerns over potential impacts to elk and the opportunity of visitors to view elk. We equipped 42 elk with GPS-radio collars that collected locations every 3 hours during the summers of 2007 through 2010. We used fine-scale movement data to evaluate elk response to the pathway before (2007), during (2008), and after (2009–2010) construction. Following construction of the pathway, elk continued to cross the TPR at rates observed before construction. Elk habitat use and the proportion of high-use elk habitat visible from TPR were similar before, during, and after construction of the pathway. Overall, our results suggest that the multi-use pathway did not affect how elk utilize the area or reduce the opportunity of visitors to view elk from the TPR.*

INTRODUCTION

After completing an environmental impact statement (USDI-NPS 2006) in 2006, the U.S. Department of Interior (USDI) and National Park Service (NPS) approved construction of a multi-use pathway in Grand Teton National Park (GTNP) along the Teton Park Road (TPR) between Dornan's in Moose and the South Jenny Lake visitor facilities (USDI-NPS 2007). This section of pathway was proposed to be the first in a phased development of several pathways (totaling up to 38 miles) connecting the southern boundary of GTNP with the Colter Bay developed area (USDI-NPS 2007). Constructed in 2008, the two-lane, 10-ft. wide paved pathway runs parallel with TPR and was designed for pedestrian, bicycle, and other non-motorized use. Hundreds of elk occupy GTNP during the summer, and the opportunity to view them from TPR is considered a valuable resource to visitors. Of concern here was whether the multi-use pathway would affect the movement and distribution patterns of elk. Elk response to the multi-use pathway could potentially affect the way in which they utilize GTNP, but also reduce the opportunity of visitors to view elk from TPR. The purpose of this study was to determine whether the multi-use pathway affected the spatial or temporal distribution of elk within the vicinity of the pathway.

The effects of roads on ungulates, and elk in particular, are well-documented (e.g., Cole et al. 1997, Rowland et al. 2000, Frair et al. 2008, Shanley and Pyare 2011). In general, elk tend to avoid roads open to vehicular traffic (Lyon 1983, Grover and Thompson 1986, Preisler et al. 2006), however the degree of avoidance can be influenced by topography and forest cover (Edge and Marcum 1991, Rowland et al. 2005, Sawyer et al. 2007). Additionally, animals in national parks and other protected areas tend to be more habituated to roads and vehicle traffic compared to areas open to hunting[1]. This behavior is especially evident in Yellowstone and GTNP, where large ungulates such as elk, moose, and bison are commonly observed on or near roadways. Emerging evidence indicates that the response of animals to anthropogenic disturbance is a function of their perceived risk of the disturbance (Gill et al. 1996, Frid and Dill 2002). Accordingly, elk response to bicycle and pedestrian use may be different than their response to vehicle traffic. For example, Papouchis et al. (2001) found bighorn sheep response to hikers was greater than to vehicles and mountain bikers. In contrast, Naylor et al. (2009) found elk response to mountain bikers was greater than to hikers, but both forms of disturbance were lower compared to the response to motorized-use (i.e., ATVs). In addition, Taylor and Knight (2003)

[1]elk hunting is restricted to the east side of Snake River in GTNP and does not occur in the vicinity (~ 4 km) of the pathway

found that the responses of mule deer to hikers and mountain bikers were essentially the same. Although these studies provide conflicting results of how ungulates may respond to pedestrian and bicycle use versus motorized use, there is general agreement that on-trail pedestrian and bicycle activity has less of an effect on wildlife compared to off-trail activity (Hicks and Elder 1979, Miller et al. 2001, Papouchis et al. 2001, Taylor and Knight 2003). Our goal was to determine how, or if, elk in a national park respond to pedestrian, bicycle, and other non-motorized use associated with a paved pathway adjacent to an existing road. To address this question, we used fine-scale movement data collected from a sample of GPS-collared elk before, during, and after construction of the Phase I GTNP pathway.

METHODS

Animal Capture and Data Collection

We used helicopter net-gunning to capture adult (>1.5 years) female elk during the summers of 2007, 2008, and 2009. We attempted to capture elk within 2 km of TPR, from the southern boundary north to Jenny Lake. We captured a total of 42 elk, including 34 on July 26, 2007, two in the summer of 2008, and six in the summer of 2009. Elk captured south of Moose Junction were intended to provide baseline data in case of proposed pathway construction between Moose Junction and Teton Village, but were not analyzed in this report. Elk captured north of Moose Junction were the focus of this study. All elk were equipped with store-on-board GPS collars (GEN 3 Telonics, Inc.) programmed to collect one location every 3 hours from April 1 through November 30, and one location every 25 hours December 1 through March 31. This data collection schedule was designed to collect frequent locations during summer periods when elk occupy GTNP, and during spring and fall migrations to and from GTNP. Importantly, this data collection schedule prolonged battery life and allowed us to keep collars on the same animals for the entire 4-year study period (2007-2010).

Response to Pathway

We examined three different metrics to evaluate potential elk response to the multi-use pathway. First, we evaluated elk habitat use patterns before, during, and after pathway construction. Second, we examined whether the permeability of TPR was affected by the pathway. (i.e., did elk cross TPR at the same rate as prior to pathway construction?). And third, we completed a viewshed analysis to determine if the proportion of high-use elk habitat visible from TPR changed after the pathway was constructed.

<u>Elk Habitat Use</u>

We assumed that potential pathway effects would not extend beyond 4 km, so our study area was delineated by buffering the pathway by 4 km. We identified five landscape variables known to influence the elk habitat use, including slope, elevation, aspect, distance to cover, and distance to pathway (Wisdom et al. 1986, Edge et al. 1987, Sawyer et al. 2007). Elevation was calculated from a 30 x 30-m resolution digital elevation model (DEM). We used the DEM to calculate slope and north (315-45°), east (45-135°), south (135-225°), and west (225-315°) aspect categories. Cover was defined as vegetation characterized by any tree type (conifer and deciduous), as derived from digital vegetation maps provided by National Park Service. We measured habitat variables at 5,000 random points in the study area. Because slope and elevation were highly correlated (r=0.80), we did not allow both variables in the same model to avoid potential colinearity issues.

We followed the modeling procedures of Sawyer et al. (2009*a*) to estimate habitat use models and create predictive maps. This approach uses the number of animal locations (within a 100-m buffer of each of the 5,000 random points) as the response variable, treats the animal as the experimental unit, and estimates a population-level habitat use model by averaging coefficients across individual animals. Because GPS fix-rate success was high (99%), we were not concerned with missing locations biasing results (Nielson et al. 2009). We restricted our analysis to elk that collected data before (2007), during (2008), and at least one year after (2009 or 2009 and 2010) pathway construction. Additionally, we restricted this analysis to the summer (June 15–September 15) of each year, when pathway use by visitors and elk use of the study area were at peak levels. Because elk were not captured until July 27 of 2007, this summer period was shorter than other years. Our model selection process consisted of two steps. First, we used Akaike's Information Criterion (AIC; Burnham and Anderson 2002) to rank an *a priori* set of eight candidate models that excluded the distance to pathway variable (Table 1). This required that we fit each of the eight candidate models to each animal and then sum the AIC values across animals to identify the most appropriate model (i.e., model with lowest AIC sum) not containing the variable for distance to the pathway. Once this model was identified, the second and final step was to add the distance to pathway variable, along with a quadratic for distance to pathway, and assess whether the inclusion of these variables improved model fit by lowering the sum of AIC values across elk. We assumed that the relationship between probability of use and distance to pathway was non-linear (e.g., elk use may increase as distance from the pathway increases to some distance, but then the effect of the pathway may diminish), so we included both linear and quadratic forms of the distance to pathway variable. It is important to note that because the pathway was constructed adjacent to the TPR, the two features were highly correlated and inclusion of the distance to pathway variable was essentially the same as adding a distance to road variable.

Table 1. Eight candidate models considered in habitat use analysis, excluding the distance to pathway variable.

Candidate Model	Variables
1	elevation + cover
2	elevation + elevation^2 + cover
3	elevation + cover + south + east + west + north
4	elevation + elevation^2 + cover + south + east + west + north
5	slope + cover
6	slope + slope^2 + cover
7	slope + cover + south + east + west + north
8	slope + slope^2 + cover + south + east + west + north

Our elk habitat use models took the form:

$$\ln(E[l_i]) = \ln(total) + \beta_0 + \beta_1 X_1 + \ldots + \beta_p X_p, \quad [1]$$

which is equivalent to:

$$\ln(E[l_i/total]) = \ln(E[\text{Relative Frequency}_i]) = \beta_0 + \beta_1 X_1 + \ldots + \beta_p X_p, \quad [2]$$

where l_i is the number of locations for a GPS-collared elk within sampling unit *i* (i = 1, 2, …, 4500), *total* is the total number of locations recorded for elk *i* within the study area, β_o is an intercept term, $\beta_1,\ldots,\beta_p$ are unknown coefficients to be estimated for habitat variables $X_1,\ldots,X_p$, and E[.] denotes the expected value. The offset term, ln(*total*), simply converts the response variable from an integer count (e.g., 0, 1, 2) to a relative frequency (e.g., 0, 0.003, 0.005) by dividing the number of elk locations in each sampling unit (l_i) by the total number of locations for the individual elk (*total*). At the level of an individual animal, this approach estimates the true probability of use as a function of predictor variables, and is referred to as a resource selection probability function (RSPF; Manly et al. 2002). However, it is important to note that once coefficients from individual elk RSPFs are averaged to obtain a population-level model, the predictions become relative probabilities rather than true probabilities.

We mapped predictions of final population-level models for each year on a 50 × 50 m grid that covered the study area. The model prediction for each grid cell was then assigned a value of 1 to 5 based on the 20^{th}, 40^{th}, 60^{th}, and 80^{th} quantiles of the distribution of predictions for each map, progressing from low to high-use categories. Thus, each of the five prediction classes represented 20% of the landscape. To illustrate the estimated effect of each habitat variable on habitat use by elk we created relative probability plots that illustrate how elk use changed as a function of each variable. To quantify and illustrate the changes in predictive maps from pre-development to subsequent years, we generated change-in-use maps that show which areas had negative, positive, or no change in their predicted level of habitat use relative to pre-development (2007).

We evaluated the predictive ability of each population-level model (2007 – 2010) using an independent sample (i.e., elk not used to estimate the habitat use models) of GPS-collared elk. The independent sample consisted of animals that did not collect data before, during, and after pathway construction. For example, GPS locations collected from eight elk in 2007 were not used in the 2007 model because those elk died prior to 2009. For each year, we made maps based on 20 habitat use prediction classes and calculated the proportion of the independent elk locations that occurred in each class. The model prediction for each grid cell in the predictive map was assigned a value of 1 to 20 based on the percentiles of the distribution of predictions for that map (a value of 20 was highest). We then used a Spearman's rank correlation (r_s) statistic to quantify the relationship between the number of GPS locations that occurred in each of the 20 equal-sized bins and the bin ranks (Sawyer et al. 2009*a*). A high positive correlation indicates the model accurately predicted locations of the independent sample of elk.

To evaluate how well the pre-pathway model (2007) predicted elk habitat use during (2008) and after construction (2009 and 2010), we repeated the same validation procedure using predictions from the 2007 model and independent elk data from 2008 to 2010 not used to estimate habitat use models. All elk habitat use modeling and validation was performed in the R language and environment for statistical computing (R Development Core Team 2011).

<u>Permeability of Teton Park Road</u>

Elk commonly cross TPR and presumably rely on habitats located on both sides of the road. Accordingly, we evaluated whether the permeability of TPR during summer (June 15 – September 15) was affected by the pathway. Because the most powerful approach to evaluate the potential effect of the pathway is to monitor the response of individual animals through time, we treated individual elk as the experimental unit (Thomas and Taylor 2006) and restricted our analysis to elk that provided data before (2007), during (2008), and at least one year after (2009 and 2010) pathway construction. Restricting our analysis to these elk allowed for a straightforward comparison of permeability before, during, and after pathway construction. For each elk, we estimated the number of times it crossed TPR between July 27 (1st day after initial capture in 2007) and September 15 of each year, by connecting consecutive GPS locations in a geographic information system (GIS). Although GPS-collared elk collected locations prior to July 27 in 2008 – 2010, inclusion of those data would have resulted in unequal sampling periods and complicated the analysis.

In order to evaluate differences in the average number of crossings per elk each summer, we fit an analysis-of-variance (ANOVA) with random effects to account for the variability among individual elk (i.e., treat the elk as the experimental unit).. The hierarchical model contained fixed effects for each year and random effects for individual elk. We fit this model using Markov chain Monte Carlo methods (MCMC; Gelmen et al. 2004). The response variable was the total number of crossings per summer period. To evaluate potential changes in temporal patterns, we also fit a model where the response variable was the total number of crossings per summer period that occurred during daylight hours (i.e., sunrise to sunset). For elk *j* in year *i*, the number of crossings (c_{ij}) was modeled as

$$c_{ij} = \alpha + \beta_i + \gamma_j + \varepsilon_{ij}, \qquad [3]$$

where α was the mean number of crossings per summer per elk across all years, β_i were year (fixed) effects, γ_j were individual elk (random) effects, and ε_{ij} were normal random errors. The model was fit using WinBUGS (v1.4.3, Lunn et al. 2000) and R (R Development Core Team 2011).

We used vague prior distributions (Link et al. 2002) to begin the MCMC sampling. Parameters for the overall mean (α), year effects (β_i), and elk effects (γ_j) were assigned relatively flat normal distributions with mean zero and variance of 1000. The standard deviation (SD) of effects for individual elk was modeled as SD ~ uniform (0, 100). This estimate encompassed variation between sampled elk and uncertainty associated with unobserved values from the entire elk population (Gelman and Hill 2007). Errors (ε_{ij}) were assigned a mean zero normal distribution with SD ~ uniform (0, 100). Parameters for both year and elk effects were centered on their respective means to improve convergence during the MCMC process (Gelman and Hill 2007).

We determined an appropriate burn-in and chain length (Link et al. 2002) by visual inspection of trace plots using three chains and 40,000 iterations. Final models were fit using one chain containing 30,000 iterations following a 10,000-iteration burn-in (Gelman et al. 2004). To evaluate model fit, posterior predictive checks were made by comparing histograms of replicated data statistics to observed statistics (e.g., median value; Gelman et al. 2004). Ninety-percent Bayesian confidence intervals (BCIs were used to evaluate the precision of the final estimates of the average number of crossing per elk, per year, during the summer period. Ninety-percent BCIs were also used to test for differences between years. If a 90% BCI for a difference in the average number of crossings per elk in 2007 versus 2008 contained zero we concluded that there was not a statistically significant difference (at the $\alpha = 0.10$ level).

Viewshed Analysis

To determine whether the multi-use pathway influenced the opportunity of visitors to view elk from TPR, we conducted a viewshed analysis to calculate the total area (km^2) of high-use elk habitat visible from TPR before, during, and after construction of the pathway. The viewshed model was provided by GTNP (K. Mellander and S. Cain, unpublished data, Grand Teton National Park, Moose, Wyoming) and was intended to identify areas visible from TPR (Fig. 1). High-use elk habitat was identified each summer from the elk habitat use models. We calculated the amount (km^2) of visible high-use elk habitat 1-km, 2-km, and 3-km from the pathway.

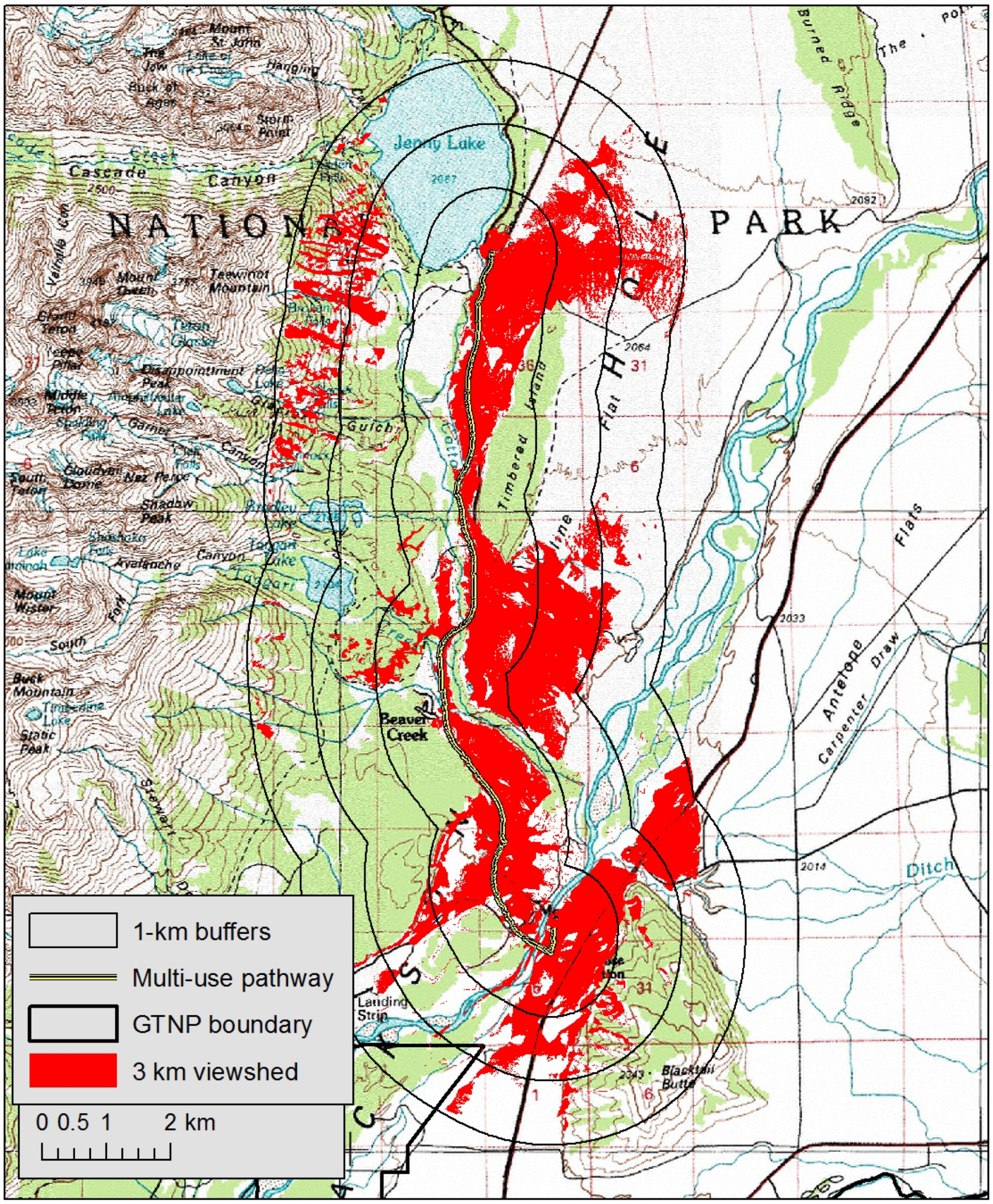

Figure 1. Viewshed model identifies areas visible (red) within 3 km of Teton Park Road (TPR).

<u>Traffic Monitoring</u>

We summarized traffic monitoring data collected at 10 sites using MetroCount traffic counters. For the purposes of this report, we focused on four counters (TPR 1-4) situated between Windy Hill and the Lupine Meadows Road (Fig. 2). Because our elk analyses rely on making comparisons across years, it was of important to determine if traffic levels were similar across years, otherwise the effects of the pathway would be confounded with increased traffic volume on TPR. We plotted the mean number of traffic hits for June, July, August, and September of each year to evaluate traffic levels across years at four monitoring stations along TPR.

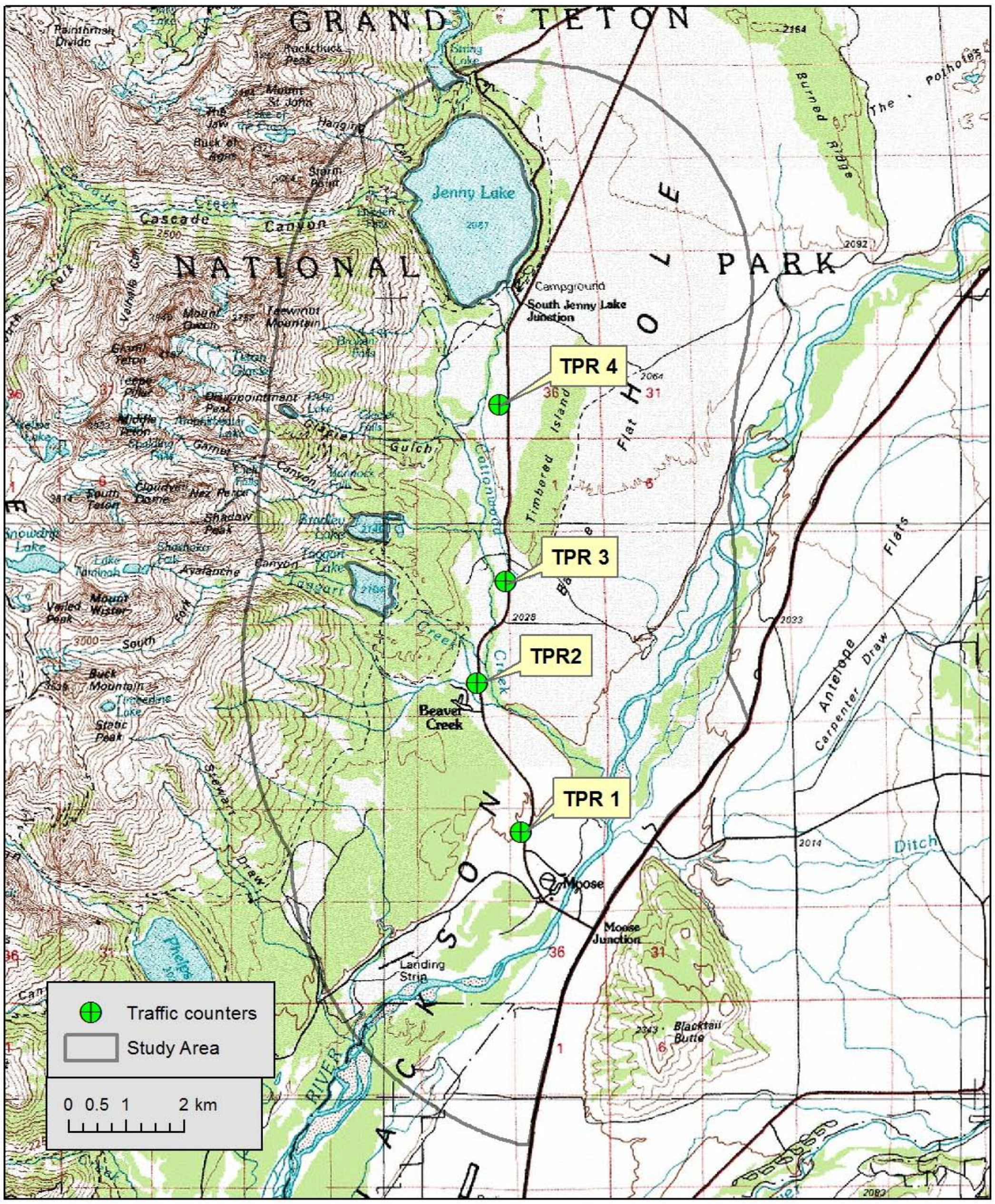

Figure 2. Location of traffic counters TPR 1- 4 in the study area delineated for habitat use analysis.

Elk Migration

Although the primary goal of this study was to evaluate elk response to the multi-use pathway, summarizing the fine-scale migration data to and from GTNP was also of interest to GTNP, the National Elk Refuge, and Wyoming Game and Fish Department. Migration routes are typically depicted by simply connecting-the-dots between consecutive GPS locations (Fig. 3A). While this approach can be used to identify the timing and general location of migration routes (e.g., Sawyer et al. 2005, Berger et al. 2006, White et al. 2007), a major shortcoming of this approach is that it produces a line that has no area associated with it (i.e., is the route 10 feet wide or a mile wide?), which makes it difficult to consider in land-use plans or on-the-ground management (Sawyer et al. 2009*b*). A second shortcoming is there is no means to combine routes of individual animals to assess migration at the population-level. Typically, managers are interested in the migration routes of a population, rather than an individual. To account for these two shortcomings, we used a new method of estimating migration routes, referred to as the Brownian bridge movement model (BBMM; Horne et al. 2007). The BBMM estimates the probability of use, or a utilization distribution (UD), along a migration route. The UDs from individual animals can be combined to estimate a population-level migration route (Sawyer et al. 2009*b*). This approach allows route segments used as stopover sites (i.e., foraging and resting habitat) to be discerned from those used primarily for movement (Fig. 3B).

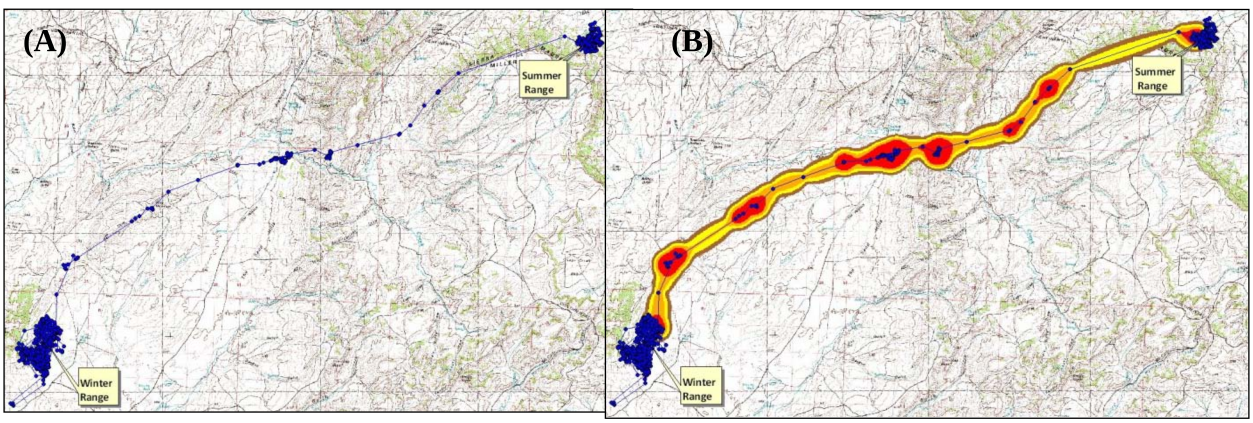

Figure 3. (A) Example of estimating a migration route by connecting-the-dots and (B) with the brownian bridge movement model (BBMM), where stopover sites (red) can be distinguished from movement corridors (orange and yellow).

We used migration data collected from 36 GPS-collared elk to estimate population-level migration routes for spring and fall. Because elk that reside north and south of Moose Junction utilize different migration routes, we created population-level migration routes for each of these sub-populations. We restricted our analysis to migrations that occurred between April 1 and November 30, when GPS collars collected locations every 3 hours. We followed the methods outlined by Sawyer et al. (2009*b*) where: 1) the BBMM (Horne et al. 2007) was used to estimate migration routes of individual elk, and 2) individual routes were then combined to estimate a population-level migration route. We used the R contributed package BBMM v2.2 (Nielson et al. 2011) to estimate migration routes.

RESULTS

GPS Data

We recovered 41 of the 42 GPS collars (Table 2). The release mechanism on the collar of elk #2 did not work and it has not yet been recovered. Of the 41 collars recovered, 38 functioned properly. Collar #24 collected data for approximately one year, Collar #30 collected data intermittently, and Collar #22 was damaged by a hunter and no data was recoverable. Overall, we collected 168,489 locations from 40 elk. Our habitat use analysis was restricted to 14 elk that collected data before, during, and after pathway construction.

Table 2. ID, capture date, status, summer area, and number of GPS locations of 42 GPS-collared elk in Grand Teton National Park, 2007-2010.

Elk	Capture	Status	Area	GPS Locations
1	7/26/2007	Collar removed by NER March 2010, replaced w/Lotek	South	5,110
2	7/26/2007	NO DROP	South	0
3	7/26/2007	Hunter Killed on 12-1-08	South	2,916
4	7/26/2007	Died 5-3-10, in gravel bar	North	5,378
5	7/26/2007	Hunter Killed on 11-10-07	North	809
6	7/26/2007	Hunter Killed on 11-5-08	North	2,788
7	7/26/2007	Recovered November 2010	North	6,571
8	7/26/2007	Hunter Killed on 11-09-08	North	2,848
9	7/26/2007	Collar removed from SP feedground Feb.09, went to Idaho	South	3,021
10	7/26/2007	Hunter Killed on 11-18-09	North	4,851
11	7/26/2007	Recovered November 2010	North	6,810
12	7/26/2007	Recovered November 2010	North	6,826
13	7/26/2007	Recovered November 2010	North	6,763
14	7/26/2007	Hunter killed on 11-19-09	North	4,960
15	7/26/2007	Hunter Killed on 11-15-08	North	2,885
16	7/26/2007	Died 5-29-09 in GTNP, unknown cause	North	3,562
17	7/26/2007	Recovered November 2010	South	6,833
18	7/26/2007	Hunter Killed on 11-08-09	North	4,837
19	7/26/2007	Hunter Killed on 11-25-07	North	905
20	7/26/2007	Died 5-21-10 in NER, unknown cause	North	5,521
21	7/26/2007	Downloaded data @ NER, Recovered November 2010	South	6,866
22	7/26/2007	Hunter killed 11-9-09 (sent to Telonics)-damaged no data	North	0
23	7/26/2007	Recovered November 2010	South	6,762
24	7/26/2007	Hunter killed on 10-16-09 (sent to Telonics)-only 1 year data	South	1,092
25	7/26/2007	Recovered November 2010	North	6,830
26	7/26/2007	Recovered November 2010	South	6,800
27	7/26/2007	Hunter Killed on 9-24-08, switched summer range	North	2,489
28	7/26/2007	Died 10-11-10, likely predation	North	6,658
29	7/26/2007	Wolf kill on 5-18-09	North	3,432
30	7/26/2007	Recovered November 2010, intermittent after 12-02-08	South	2,861
31	7/26/2007	Hunter killed 12-04-09, switched summer range in 2009	North	5,032
32	7/26/2007	Recovered November 2010	South	6,805
33	7/26/2007	Recovered November 2010	North	6,787
34	7/26/2007	Recovered November 2010	North	6,775
35	7/7/2008	Recovered November 2010	North	4,953
36	7/7/2008	Wolf kill on 8-7-09	North	2,245
37	7/15/2009	Recovered November 2010, quit working 3-24-10	North	1,187
38	7/15/2009	Wounding loss (11-27-09)	North	1,047
39	7/15/2009	Hunter killed on 10-19-09	North	732
40	7/15/2009	Hunter killed on 12-07-09	North	1,079
41	7/15/2009	Recovered November 2010	North	2,825
42	7/15/2009	Hunter killed on 11-27-09	North	1,038

Response to Pathway

Elk Habitat Use

The model not containing the distance to pathway variable that had the lowest sum of AIC values was consistent across years and included elevation, cover, and aspect variables (Table 3). The addition of the distance to pathway variable substantially improved the fit of this model in each year and was considered the best overall model (Table 3). We used 5,222 locations collected from 14 GPS-collared elk to estimate individual and population-level models for the summer of 2007 (Table 4, Fig. 4A), 9,679 locations from 14 GPS-collared for summer 2008 (Table 5, Fig. 4B), 9,186 locations from 13 elk for summer of 2009 (Table 6, Fig. 4C), and 5,649 locations from 8 elk for the summer of 2010 (Table 7, Fig. 4D).

Coefficients from the average or population-level model suggest that elk selected for areas with a narrow and relatively low elevation range, close to tree cover, and a moderate distance from the pathway (Tables 4-7). Based on the coefficients and associated predictive maps (Fig. 4), elk habitat use patterns were similar across all four years (2007 – 2010). Figs. 5-7 illustrate where changes occurred between 2007 and each of the following three years. In 2008 for example, 80% of the study area was classified as the same habitat use level as 2007. Similarly, in 2009 and 2010, 86% and 78% of the study area was classified the same as in 2007. In areas where changes occurred (Figs. 5-7), the differences never exceeded one habitat use category (i.e., cell may change from high-use to moderate-use, but not from high-use to low-use).We note that the sample size of elk was considerably smaller in 2010 compared to other years. To assess whether the observed differences between 2009 and 2010 were a response to pathway or a function of reduced sample size, we evaluated the pathway effect (i.e., optimal distance from pathway) in 2009 and 2010 using only the elk (*n*=8) that were included in both the analysis both years. The 90% confidence intervals of the difference contained zero and suggests the subtle differences observed between years was not related to the pathway.

Table 3. AIC values of candidate models considered in habitat use analyses. Excluding the distance to pathway variable, Model #4 was the best model in each year. Adding distance to pathway improved model fit and resulted in the final model.

		AIC sums			
Model	Variables	2007	2008	2009	2010
1	elevation + cover	43365	66352	62030	36103
2	elevation + elevation^2 + cover	36646	56501	52316	32074
3	elevation + cover + south + east + west + north	42162	63776	59467	35023
4	elevation + elevation^2 + cover + south + east + west + north	**36063**	**55207**	**51047**	**31496**
5	slope + cover	43231	67691	62489	36796
6	slope + slope^2 + cover	42657	66434	60782	35844
7	slope + cover + south + east + west + north	41999	65150	60082	36282
8	slope + slope^2 + cover + south + east + west + north	41685	64420	59104	35161
Final	elevation +elevation^2 + cover + south + east + west + north + pathway + pathway^2	**30540**	**47347**	**42241**	**28069**

Table 4. Estimated coefficients for individual (*n*=14) and population-level (or average) elk habitat use models during the summer of 2007.

Elk	Intercept	elevation	elevation^2	cover	pathway	pathway^2	south	east	west	north
04	-3559.48	3.516	-0.00087	-0.014	0.0037	-0.0000019	0.075	-0.150	-0.354	0.369
07	-105.66	0.082	-0.00002	0.001	0.0007	-0.0000004	0.178	1.111	0.527	0.417
10	-4130.84	4.097	-0.00102	-0.003	0.0038	-0.0000022	0.027	-0.022	-0.045	0.302
11	-2393.42	2.353	-0.00058	-0.015	0.0041	-0.0000020	0.519	-0.160	-0.066	0.211
12	-4594.39	4.551	-0.00113	-0.007	0.0031	-0.0000015	0.510	0.446	0.272	-0.114
13	-1139.22	1.098	-0.00027	-0.010	0.0017	-0.0000010	1.439	1.485	0.687	0.863
14	-209.13	0.203	-0.00005	-0.006	0.0003	-0.0000005	0.054	0.540	-0.533	0.983
18	-5495.50	5.443	-0.00135	-0.006	0.0033	-0.0000024	0.551	0.012	0.258	0.504
20	-150.65	0.117	-0.00002	-0.007	0.0014	-0.0000013	-0.216	-0.068	-0.989	-0.636
25	-356.07	0.312	-0.00007	-0.009	0.0004	-0.0000003	0.193	-0.072	-0.563	-0.165
28	-4427.56	4.387	-0.00109	-0.005	0.0022	-0.0000016	0.032	-0.237	0.029	0.370
31	-2803.66	2.787	-0.00069	-0.002	-0.0009	0.0000003	-0.731	-0.882	-0.670	-1.875
33	-5277.05	5.228	-0.00130	-0.008	0.0032	-0.0000020	0.244	-0.401	-0.160	0.108
34	-4647.79	4.606	-0.00114	-0.007	0.0021	-0.0000013	0.293	-0.140	0.049	0.554
Average	-2806.46	2.770	-0.00069	-0.0069	0.0021	-0.0000013	0.226	0.104	-0.111	0.135
SE	549.32	0.547	0.000	0.001	<0.001	<0.001	0.128	0.163	0.126	0.190
P-value	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	0.101	0.533	0.394	0.489

Table 5. Estimated coefficients for individual (*n*=14) and population-level (or average) elk habitat use models during the summer of 2008.

Elk	Intercept	elevation	elevation^2	cover	pathway	pathway^2	south	east	west	north
04	-4193.56	4.136	-0.00102	-0.009	0.001	-0.0000006	0.095	0.470	-0.448	0.990
07	-79.49	0.057	-0.00001	0.001	0.001	-0.0000005	0.246	0.817	-0.391	0.185
10	-3663.51	3.623	-0.00090	-0.002	0.002	-0.0000008	0.229	0.112	-0.417	0.589
11	-2597.39	2.547	-0.00063	-0.003	0.002	-0.0000010	0.617	0.787	-0.061	0.856
12	-3020.49	2.987	-0.00074	-0.003	0.004	-0.0000019	0.022	0.406	-0.287	0.639
13	-907.69	0.879	-0.00021	-0.005	0.003	-0.0000014	0.710	0.854	-0.250	0.809
14	-3101.33	3.094	-0.00077	-0.003	0.002	-0.0000013	-0.113	0.137	-0.761	0.471
18	-4617.75	4.570	-0.00113	-0.001	0.000	-0.0000004	-0.203	0.180	-0.399	0.601
20	-95.43	0.067	-0.00001	-0.004	0.002	-0.0000015	-0.241	-0.162	-1.082	-1.040
25	-260.02	0.228	-0.00005	-0.008	0.001	-0.0000003	0.411	0.437	-0.402	0.438
28	-3918.97	3.899	-0.00097	-0.004	0.002	-0.0000015	-0.172	0.226	-0.570	0.655
31	-1412.26	1.403	-0.00035	-0.002	0.001	-0.0000002	-0.212	-0.673	0.485	-0.143
33	-4573.20	4.523	-0.00112	-0.002	0.001	-0.0000006	0.472	0.571	0.035	1.089
34	-2970.72	2.940	-0.00073	-0.004	0.004	-0.0000017	0.097	0.331	-0.869	0.319
Average	-2529.41	2.497	-0.0006	-0.0035	0.0018	-0.0000009	0.140	0.321	-0.387	0.461
SE	446.27	0.444	<0.001	0.001	0.000	<0.001	0.085	0.109	0.104	0.144
P-value	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	0.124	0.011	0.002	0.006

Table 6. Estimated coefficients for individual (*n*=13) and population-level (or average) elk habitat use models during the summer of 2009.

Elk	Intercept	elevation	elevation^2	cover	pathway	pathway^2	south	east	west	north
04	-196.54	0.184	-0.00005	-0.006	0.001	-0.000001	0.122	0.754	-0.149	0.820
07	-91.15	0.062	-0.00001	-0.003	0.002	-0.000001	-0.183	-0.266	-0.864	-1.152
10	-4532.34	4.506	-0.00112	-0.004	0.003	-0.000001	-0.187	0.081	-0.552	0.192
11	-774.07	0.736	-0.00018	-0.005	0.001	-0.000001	0.733	0.670	0.355	0.697
12	-2094.20	2.042	-0.00050	-0.007	0.001	-0.000001	1.076	1.074	0.378	1.110
13	-796.32	0.750	-0.00018	-0.009	0.000	-0.000001	1.504	2.049	-0.056	1.278
14	-941.30	0.939	-0.00024	-0.006	0.001	-0.000001	-0.170	0.510	-0.412	0.919
18	-4702.88	4.674	-0.00116	-0.006	0.003	-0.000002	0.270	0.240	-0.336	0.584
20	-272.52	0.220	-0.00004	-0.003	0.003	-0.000002	-0.525	-0.394	-1.752	-1.919
25	-239.34	0.206	-0.00005	-0.009	0.002	-0.000001	0.150	0.201	0.223	0.157
28	-3502.91	3.480	-0.00087	-0.004	0.001	-0.000001	0.057	0.336	-0.148	0.555
33	-2939.51	2.903	-0.00072	-0.002	0.001	-0.000001	0.703	0.542	0.036	0.551
34	-2832.46	2.793	-0.00069	-0.007	0.002	-0.000001	-0.150	0.258	-0.801	0.201
Average	-1839.66	1.807	-0.00045	-0.005	0.002	-0.000001	0.262	0.466	-0.314	0.307
SE	468.77	0.469	<0.001	0.001	<0.001	<0.001	0.162	0.172	0.163	0.249
P-value	0.002	0.002	0.001	<0.001	<0.001	<0.001	0.131	0.019	0.078	0.241

Table 7. Estimated coefficients for individual (*n*=8) and population-level (or average) elk habitat use models during the summer of 2010.

Elk	Intercept	elevation	elevation^2	cover	pathway	pathway^2	south	east	west	north
07	-56.40	0.039	-0.00001	-0.004	0.001	-0.0000004	-0.548	-0.328	-0.586	-0.494
11	-339.39	0.330	-0.00008	-0.003	0.002	-0.0000008	0.732	1.012	0.528	0.962
12	-1321.98	1.288	-0.00032	-0.005	0.000	-0.0000005	0.998	1.033	0.016	1.023
13	-641.83	0.614	-0.00015	-0.004	0.003	-0.0000019	0.607	1.064	-0.246	0.934
25	-230.70	0.198	-0.00004	-0.011	0.001	-0.0000003	0.033	0.195	-0.428	0.189
28	-3799.76	3.783	-0.00094	-0.005	0.001	-0.0000006	0.094	0.029	-0.851	-0.100
33	-2668.22	2.661	-0.00067	-0.003	0.001	-0.0000007	0.022	0.265	-0.668	0.351
34	-1954.90	1.924	-0.00048	-0.006	0.001	-0.0000007	0.454	0.619	-0.237	0.938
Average	-1376.65	1.355	-0.00034	-0.005	0.001	-0.0000007	0.299	0.486	-0.309	0.475
SE	473.38	0.474	<0.001	0.001	<0.001	<0.001	0.174	0.186	0.154	0.204
P-value	0.022	0.024	0.019	<0.001	0.005	<0.001	0.130	0.034	0.085	0.052

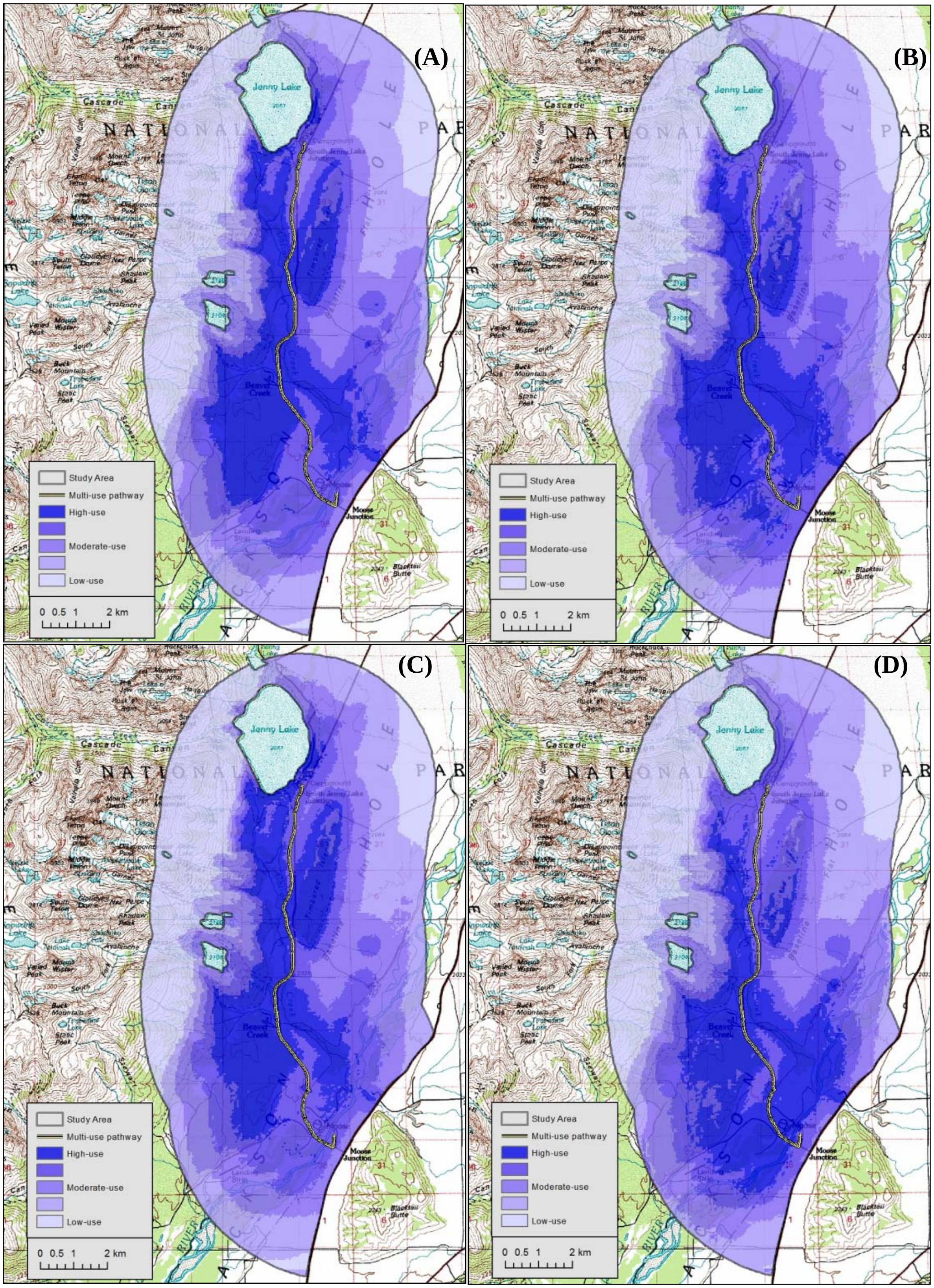

Figure 4. Predictive maps showing relative probability of elk use during the summers of (A) 2007, (B) 2008, (C) 2009, and (D) 2010.

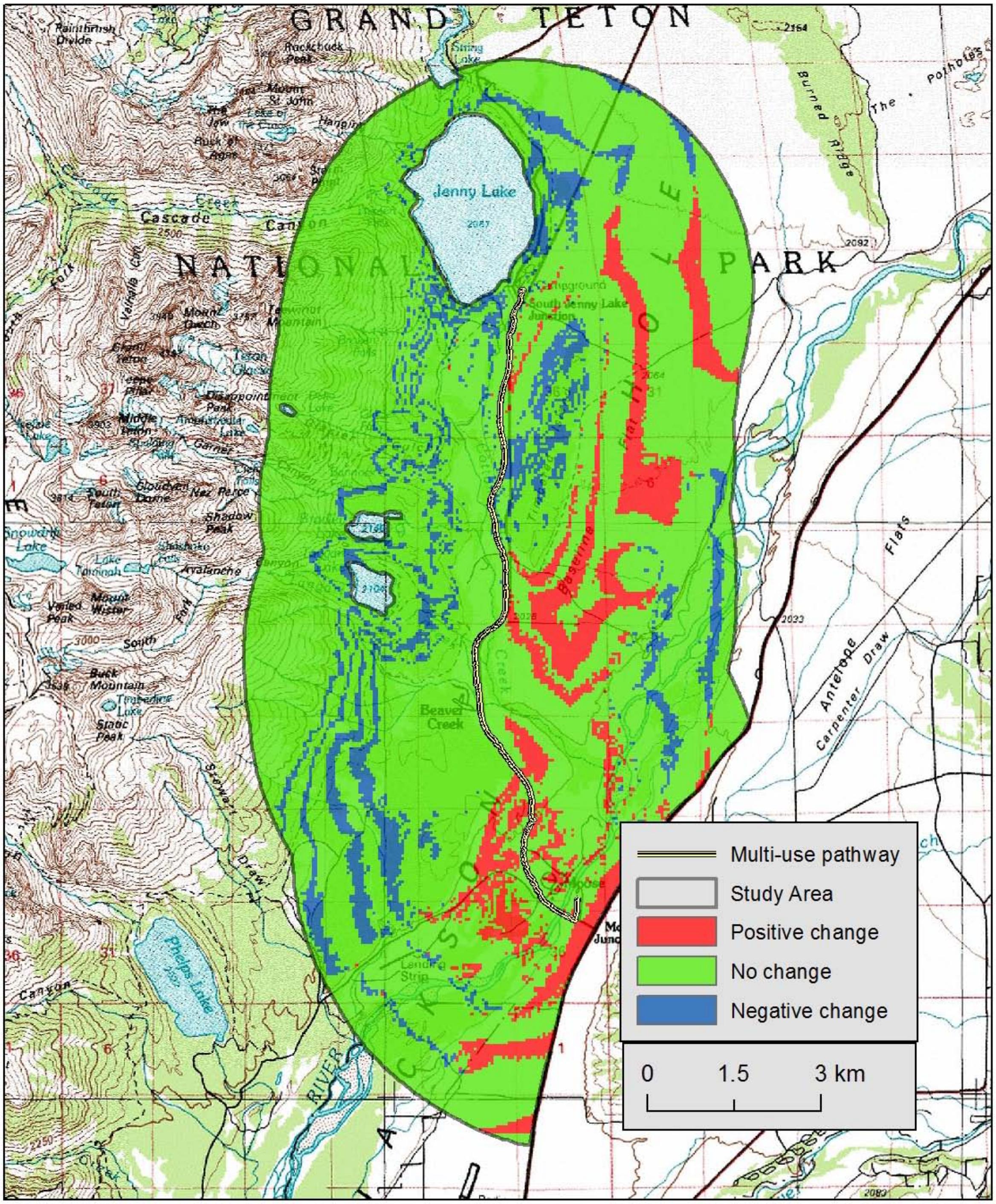

Figure 5. Change in habitat use categories from 2007 to 2008. In 2008, 80% of the study area was classified the same as in 2007.

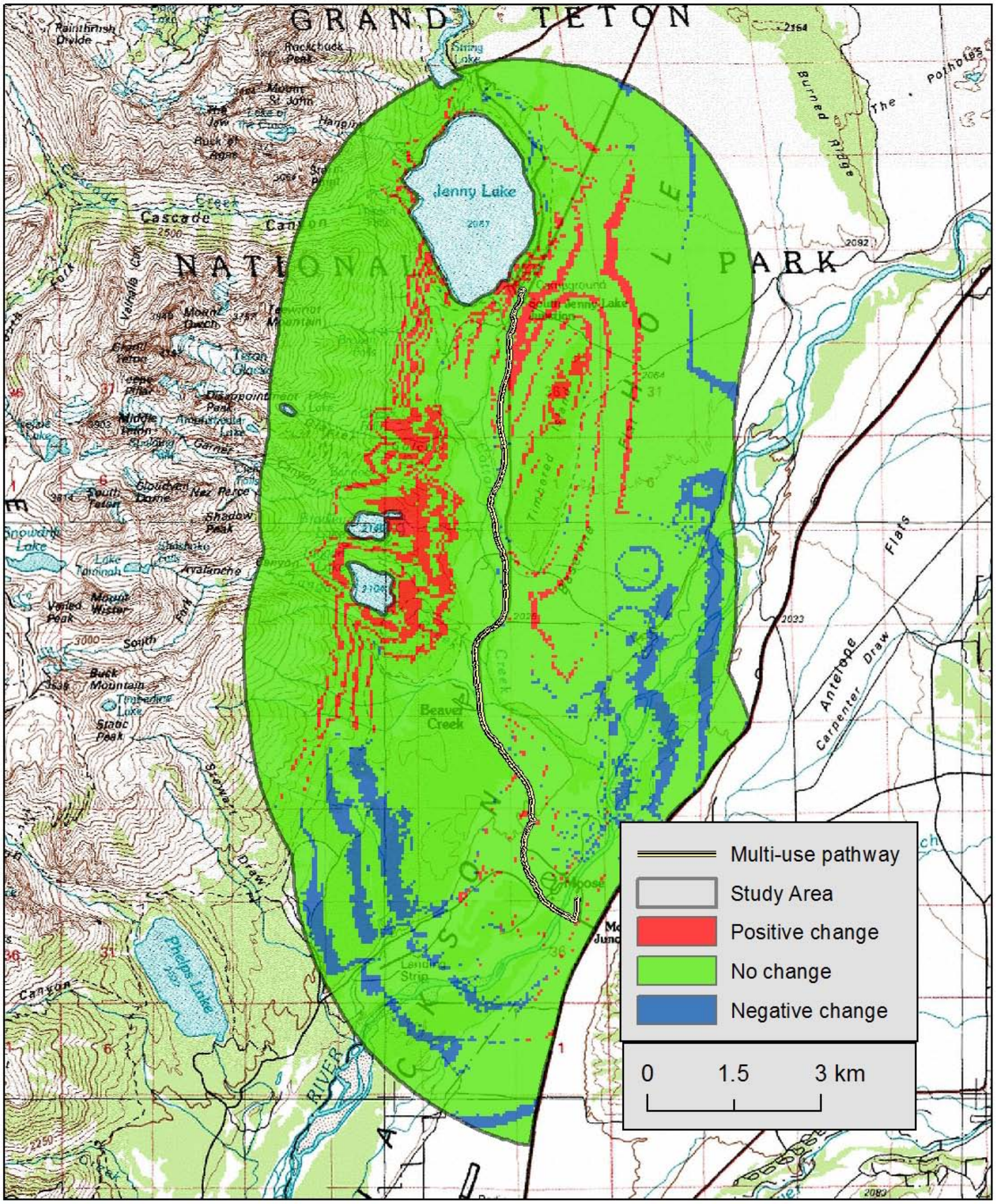

Figure 6. Change in habitat use categories from 2007 to 2009. In 2009, 86% of the study area was classified the same as in 2007.

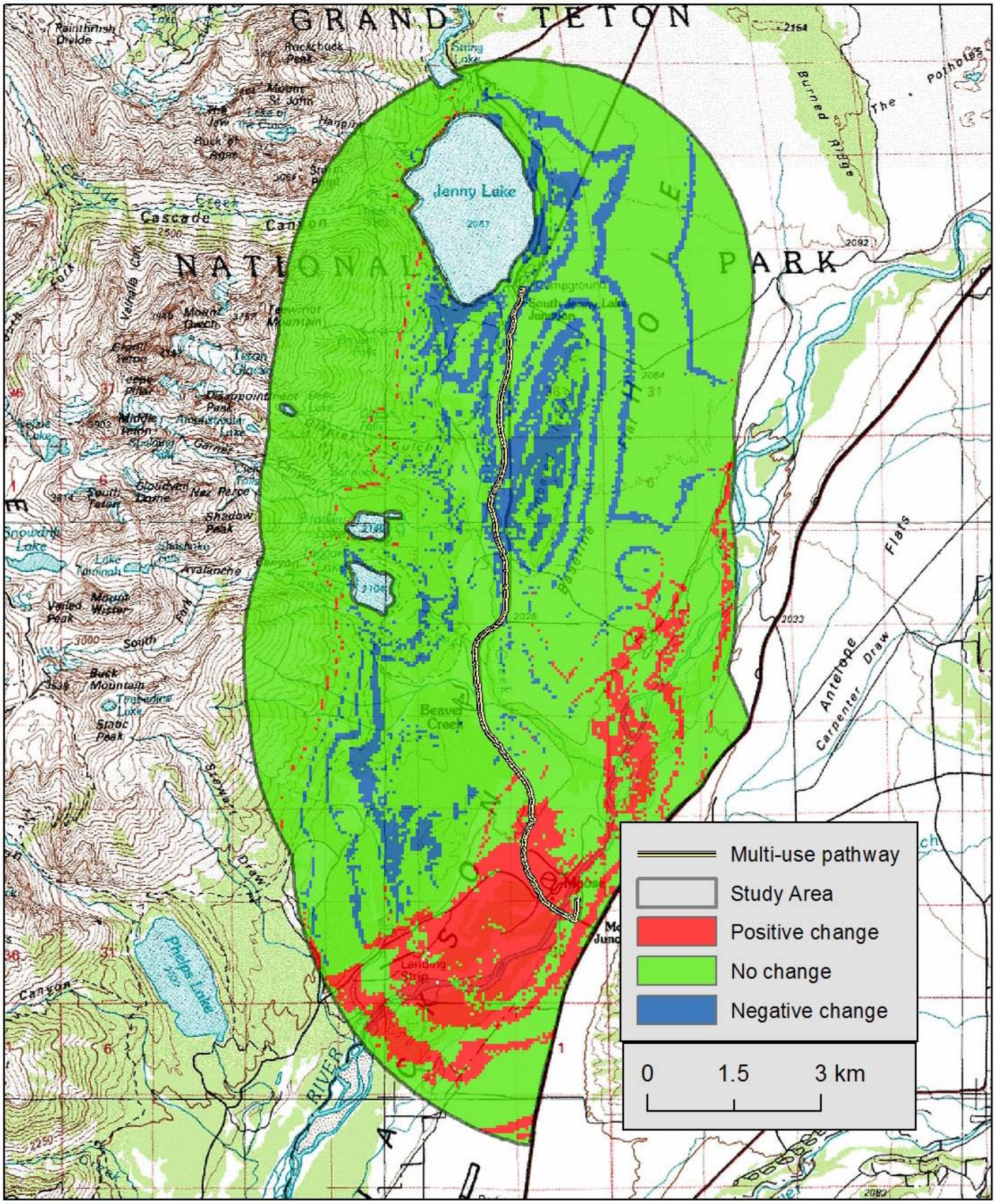

Figure 7. Change in habitat use categories from 2007 to 2010. In 2010, 78% of the study area was classified the same as in 2007.

Relative Probability Plots

In addition to viewing predictive maps (Fig. 4) and interpreting model coefficients (Tables 4-7), plots that illustrate how relative probability of use changes with different values of habitat variables can help discern habitat use patterns and how those patterns may have changed over time (Fig. 8). For example, Fig. 8A shows elk selected for a narrow elevation range (1975 - 2050 m) during all years of study. We note that elevation and slope were highly correlated (*r* = 0.80), so the elevation range corresponds to slopes preferred by elk within the study area. Fig. 8B shows that elk rarely selected habitats >150 m from tree cover. And, based the optimal values, Fig. 8C shows that elk preferred to be approximately 900 m from the pathway during all years.

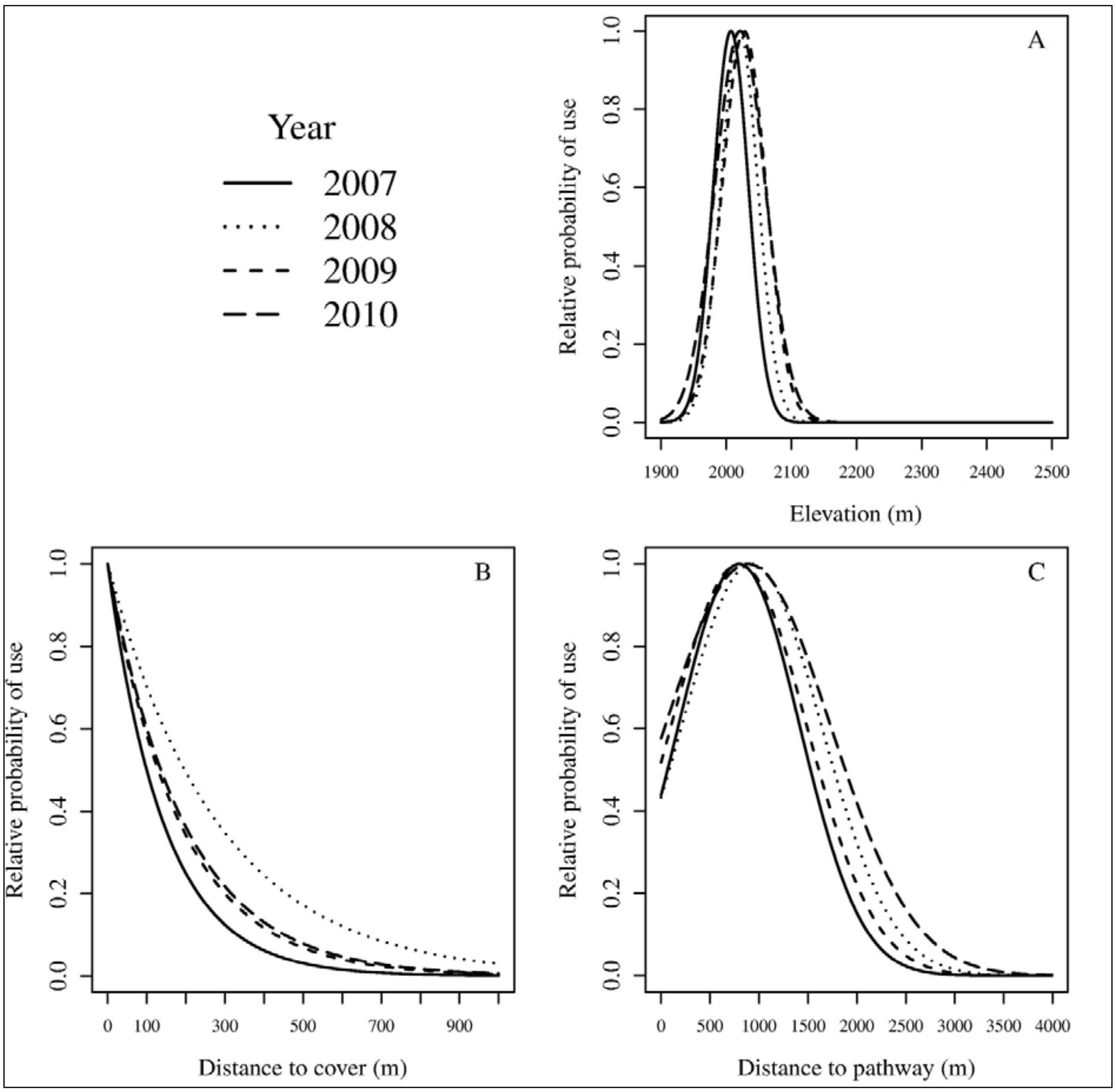

Figure 8. Influence of (A) elevation, (B) distance to cover, and (C) distance to pathway on the predicted relative probability of elk use (scaled so maximum = 1) during summers 2007, 2008, 2009, and 2010. Variables not represented in a plot were held constant at their median values.

Model Validation

Model validation was based on GPS locations from eight elk in 2007 (#'s 5, 6, 8, 15, 16, 19, 27, 29), eight elk in 2008 (#'s 6, 8, 15, 16, 27, 29, 35, 36), seven elk in 2009 (#'s 35, 36, 38, 39, 40, 41, 42), and two elk in 2010 (#'s 35, 41). The 2007, 2008, 2009 and 2010 model predictions produced Spearman rank correlations (r_s) of 0.84, 0.61, 0.88 and 0.80, respectively. The high r_s values indicated that all models accurately predicted the distribution of independent elk locations.

Testing for differences in habitat use pre-development versus during and post-development was based on a total of 49,313 locations collected from 38 GPS-collared elk between June 15 and September 15, 2008 – 2010. When the 2007 model predictions were compared to these locations, the Spearman rank correlation (r_s) was 0.93. This high r_s value indicated that habitat use by elk within the study area during 2008 – 2010 closely resembled elk habitat use prior to pathway development in 2007.

<u>Permeability of Teton Park Road</u>

Permeability analysis was restricted to 13 GPS-collared elk that collected data before, during, and at least one year after construction. Parameter estimates from the hierarchical model indicated that the average number of TPR crossings per summer for each elk was 32.3 ± 2.5 (mean ± 90% BCI; Table 8). This equates to approximately one crossing every 1.5 days. As indicated by β_{year} estimates, the average elk crossed TPR more often in 2007 compared to 2008 through 2010 (Table 8, Fig.9A), however the 90% BCIs for the differences between 2007 and later years contained zero (Fig. 10A), indicating the differences were not statistically significant.

The hierarchical model using daytime only data indicated that the number of summer TPR crossings by the average elk was 19.4 ± 1.6 (mean ± 90% BCI; Table 8). Although the estimated number of elk crossings was higher in 2007 compared to 2008 through 2010 (Table 8, Fig. 9B), the 90% BCIs for the differences between 2007 and later years contained zero (Fig. 10B), indicating the differences were not statistically significant.

Table 8. Parameter estimates and 90% Bayesian confidence intervals (BCI) for the number of times elk crossed TPR during summers (July 27 – Sept. 15) 2007 through 2010. β_{year} estimates reflect the number of TPR crossings relative to the average (α).

Model with all TPR crossings				Model with daytime-only TPR crossings			
Parameter	Estimate	90% CI		Parameter	Estimate	90% CI	
β_{2007}	4.52	-0.15	8.33	β_{2007}	1.29	-0.62	3.72
β_{2008}	-3.04	-6.71	0.60	β_{2008}	-1.05	-3.32	0.87
β_{2009}	-0.77	-4.20	2.52	β_{2009}	0.10	-1.79	2.07
β_{2010}	-0.71	-4.78	3.29	β_{2010}	-0.35	-2.71	1.79
α	32.30	29.85	34.69	α	19.43	17.80	21.06
s_β	3.83	0.80	6.59	s_β	1.51	0.003	2.89

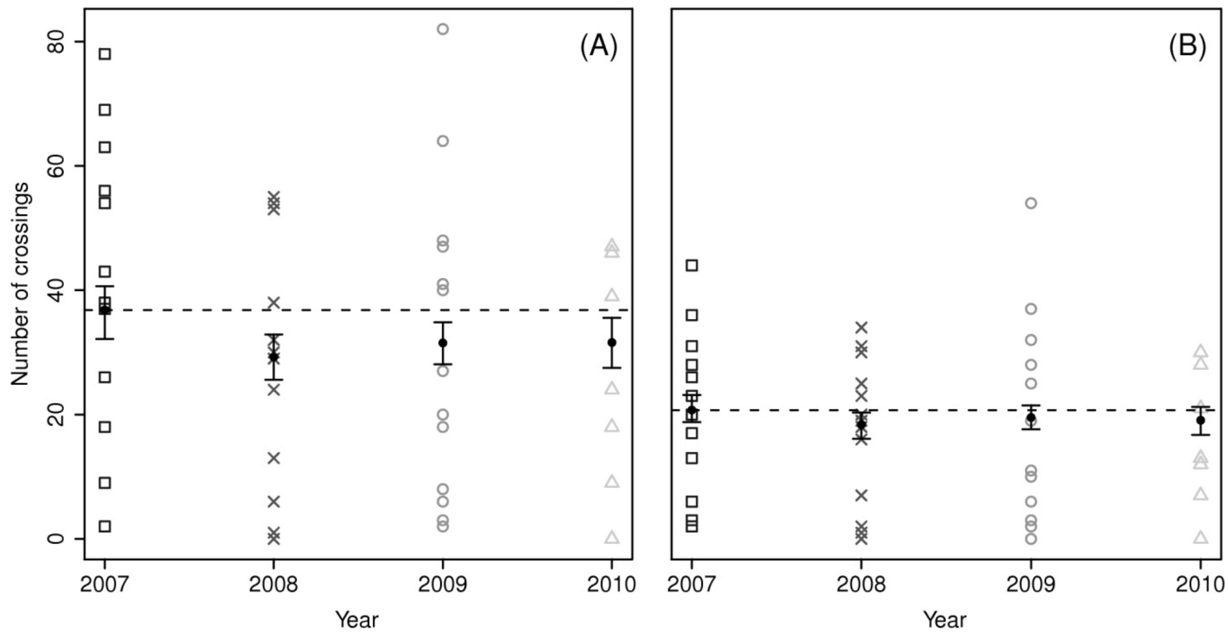

Figure 9. (A) Estimated number of TPR crossings per elk in each summer (July 27 – Sept. 15) and 90% Bayesian confidence intervals (BCI). (B) Estimated number of TPR daylight-only crossings per elk in each summer and 90% BCI. Symbols depict the observed number of crossings for individual elk and dashed line represents the estimated number of crossings in 2007.

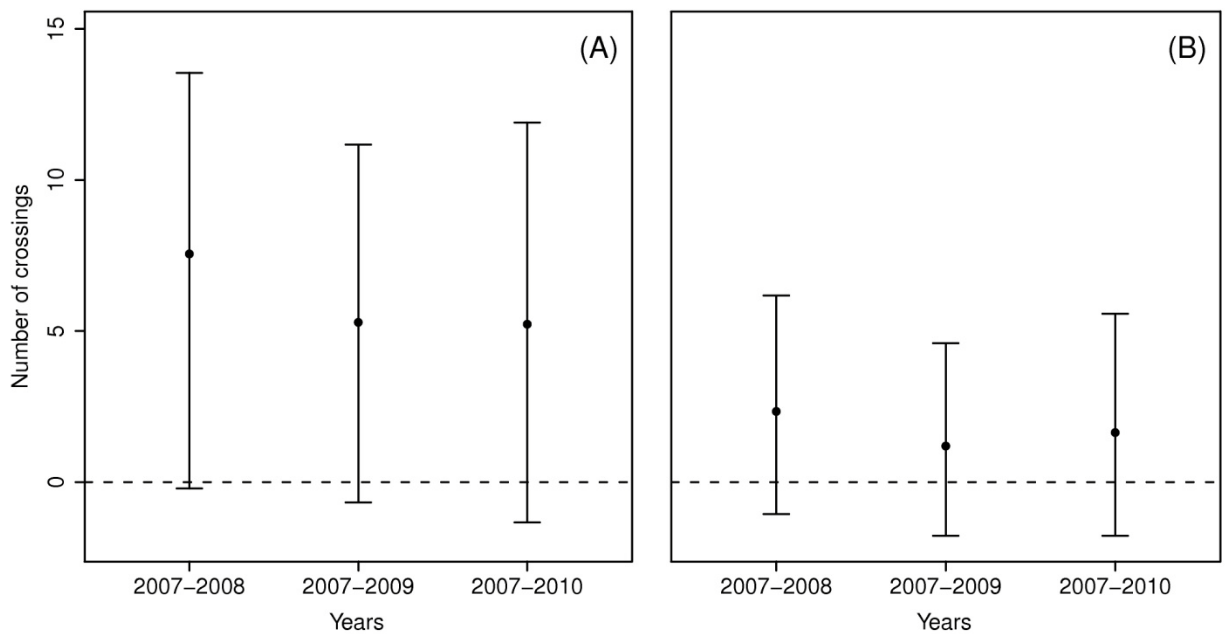

Figure 10. (A) Estimated differences in the number of TPR elk crossings during summer 2007 and later years, with 90% Bayesian confidence intervals (BIC). (B) Estimated differences in the number of TPR daylight-only elk crossings during summer 2007 and later years, with 90% BIC. Confidence intervals encompassing zero indicate the difference was not statistically significant.

On average, elk crossed TPR once every 1.5 days during the summer. Fig. 11 shows the median number of crossings per summer during 3-hr intervals. Although there was some variation in number of crossings across years at 3-hr intervals, the total number of crossings, and those that occur in daylight hours, did not differ between years.

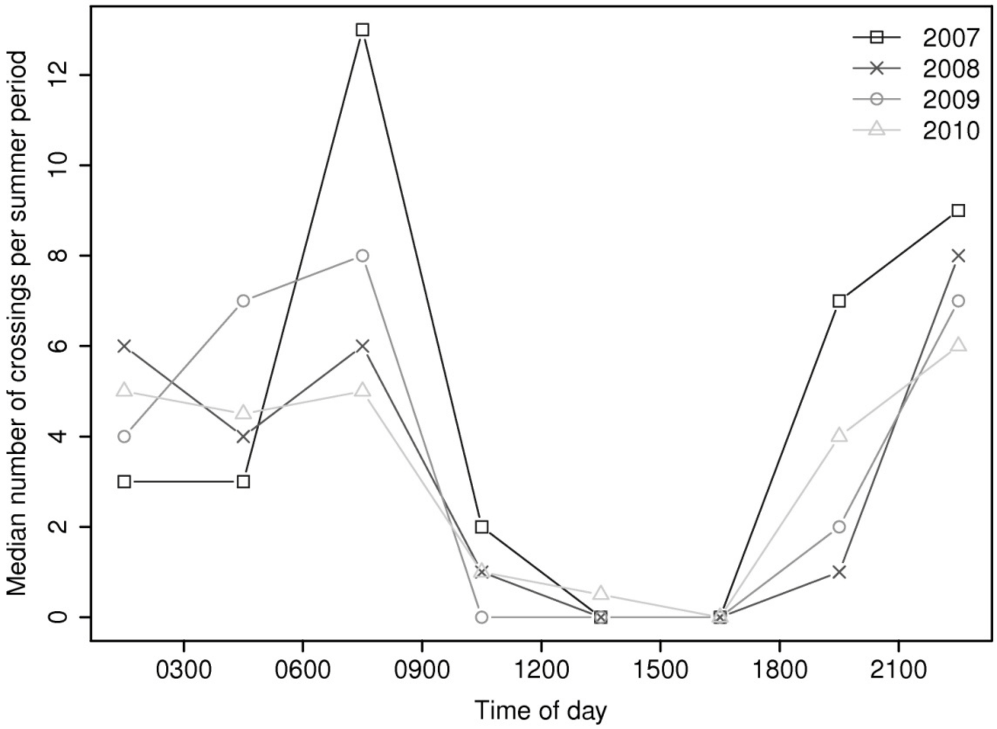

Figure 11. Median number of Teton Park Road (TPR) crossings by elk at 3-hr intervals during the summer, 2007 – 2010.

Viewshed Analysis

The amount of high-use elk habitat visible from TPR was consistent before (2007) and after (2009-10) pathway construction in each of the three distance bands (1, 2, and 3-km; Fig. 12).

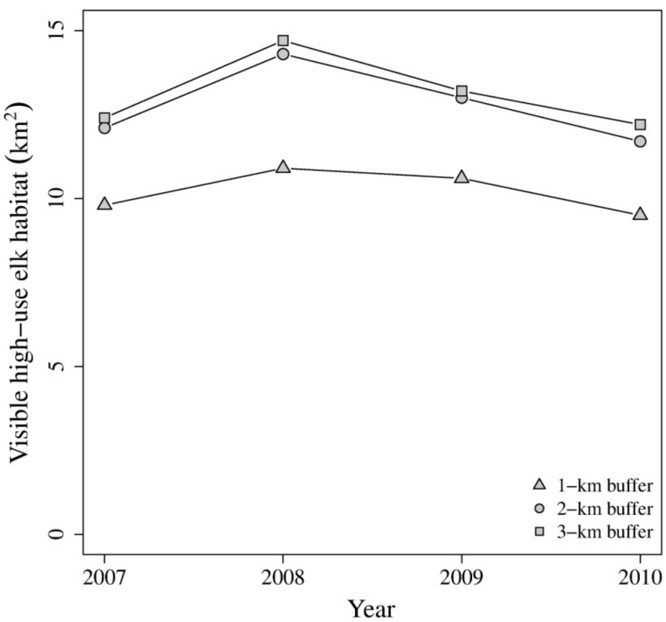

Figure 12. The amount (km^2) of high-use elk habitat visible from Teton Park Road (TPR) during the summers of 2007, 2008, 2009, and 2010.

Traffic Monitoring

Traffic counts measured at four locations (TPR1, 2, 3, and 4) in the study area indicated that traffic volume was consistent across years (Fig.13). In most months, traffic volume ranged between 150-200 counts per day. Accurate data were not collected during the summer of 2009.

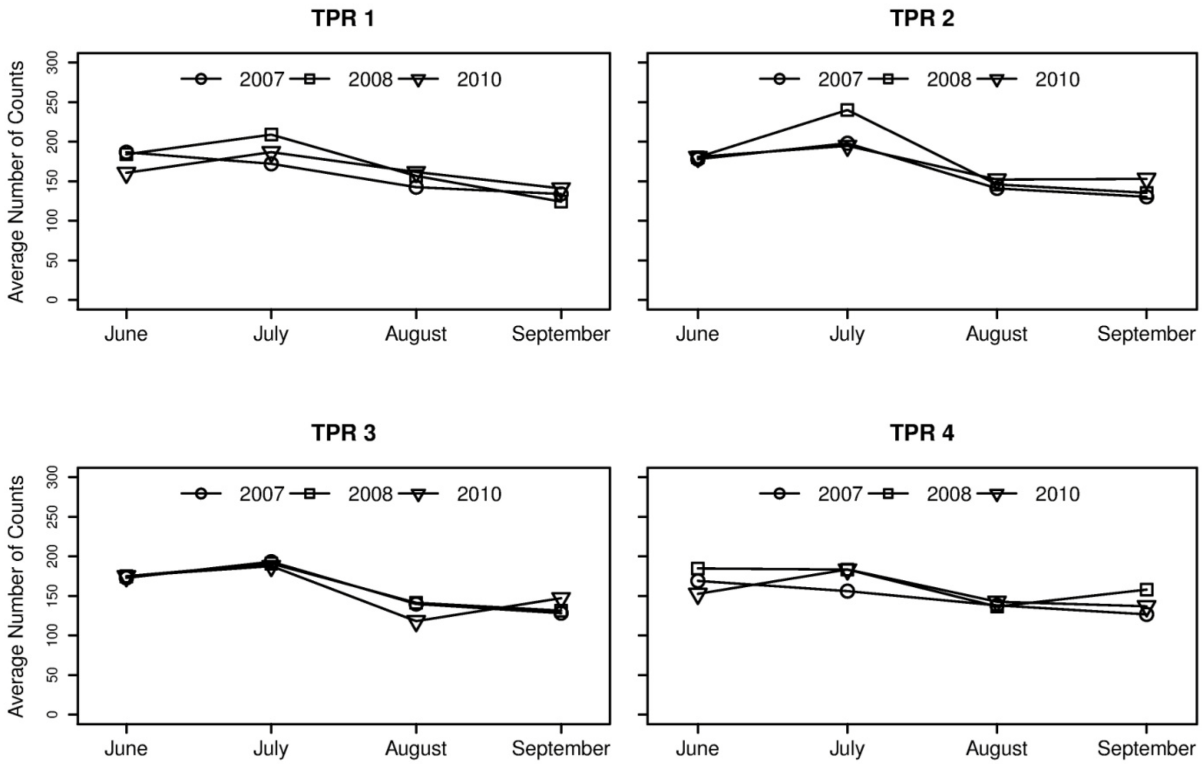

Figure 13. Mean daily traffic rates calculated for summer months of 2007, 2008, and 2010 at four locations along the Teton Park Road (TPR).

Elk Migration

We calculated population-level migration routes for elk that summer north and south of Moose Junction (Figs. 14-17). The migration of the northern sub-population was estimated from 98 migrations (48 spring and 50 fall) collected from 27 GPS-collared elk between 2007 and 2010 (Table 9). The migration of the southern sub-population was estimated from 23 migrations (18 spring and 5 fall) collected from 8 GPS-collared elk between 2007 and 2010. The seasonal migration routes of both sub-populations were markedly different between spring and fall. Spring migrations were characterized by larger, contiguous areas of high-use (or stopover habitat) that reflect slower and less directed movement (Figs. 14 & 16). In contrast, the fall migrations were characterized by distinct pockets of high-use (or stopover) habitat, connected by distinct movement corridors to and from the National Elk Refuge (NER; Figs. 15 & 17). Fall patterns appeared to be influenced by hunting season, as many elk delayed their migration from GTNP until hunting season was over, or migrated to NER during hunting season and made several trips back and forth to GTNP, presumably in response to hunting pressure.

Most elk from the northern sub-population migrated across US 89 approximately 1-2 km south of Moose Junction, near the south end of Blacktail Butte. Most elk from the southern sub-population crossed US 89 at Gros Ventre Junction, presumably along the Gros Ventre River. With the exception of elk #9 and #36, all elk wintered on the NER. Elk #9 spent one winter in Idaho, approximately 22 miles northwest of Pallisades, and was recaptured the following winter (2009) in the South Park Feedground where her collar was removed. Elk #36 wintered in the upper end of Game Creek.

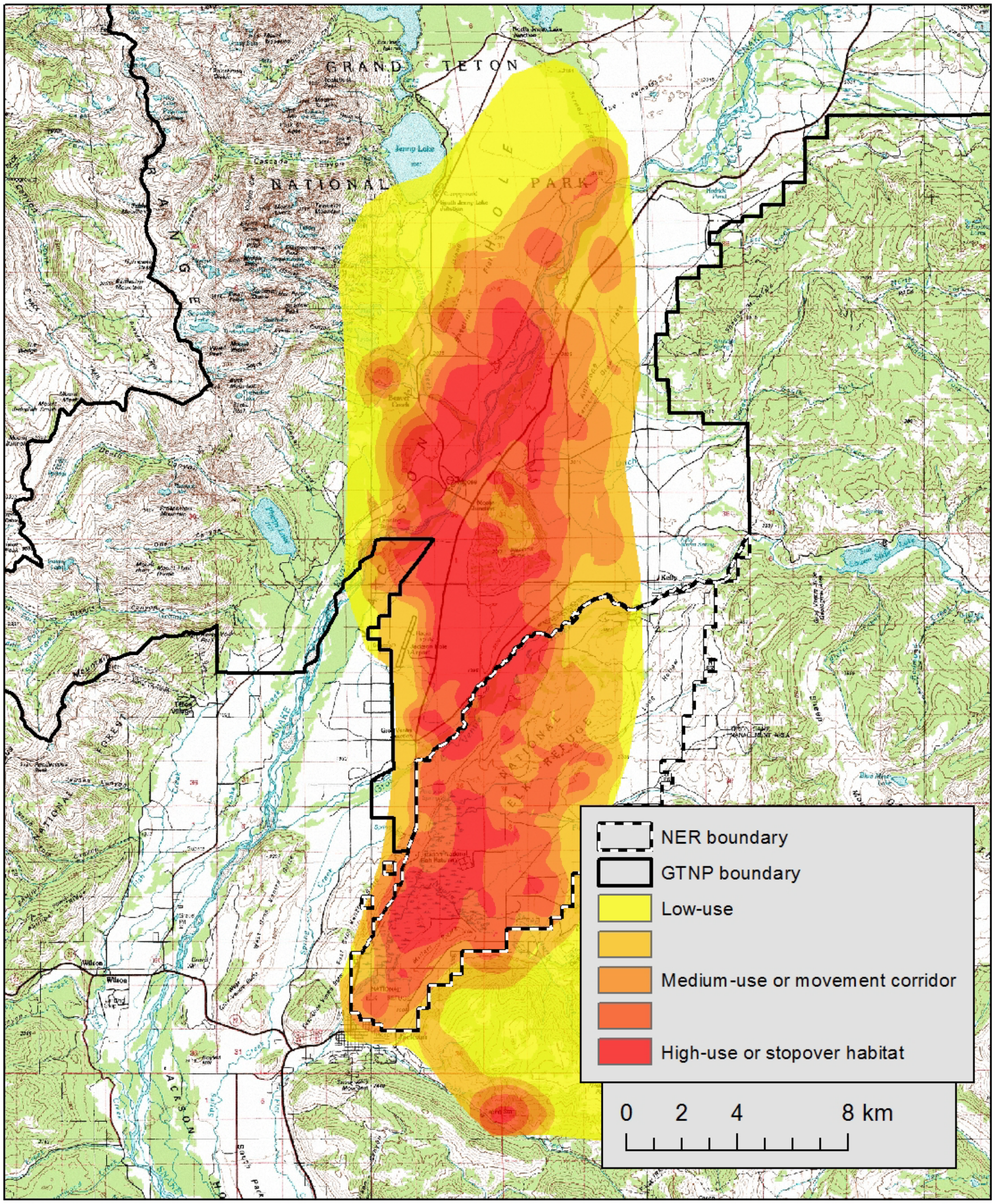

Figure 14. Spring population-level migration route of elk migrating to areas north of Moose, in Grand Teton National Park.

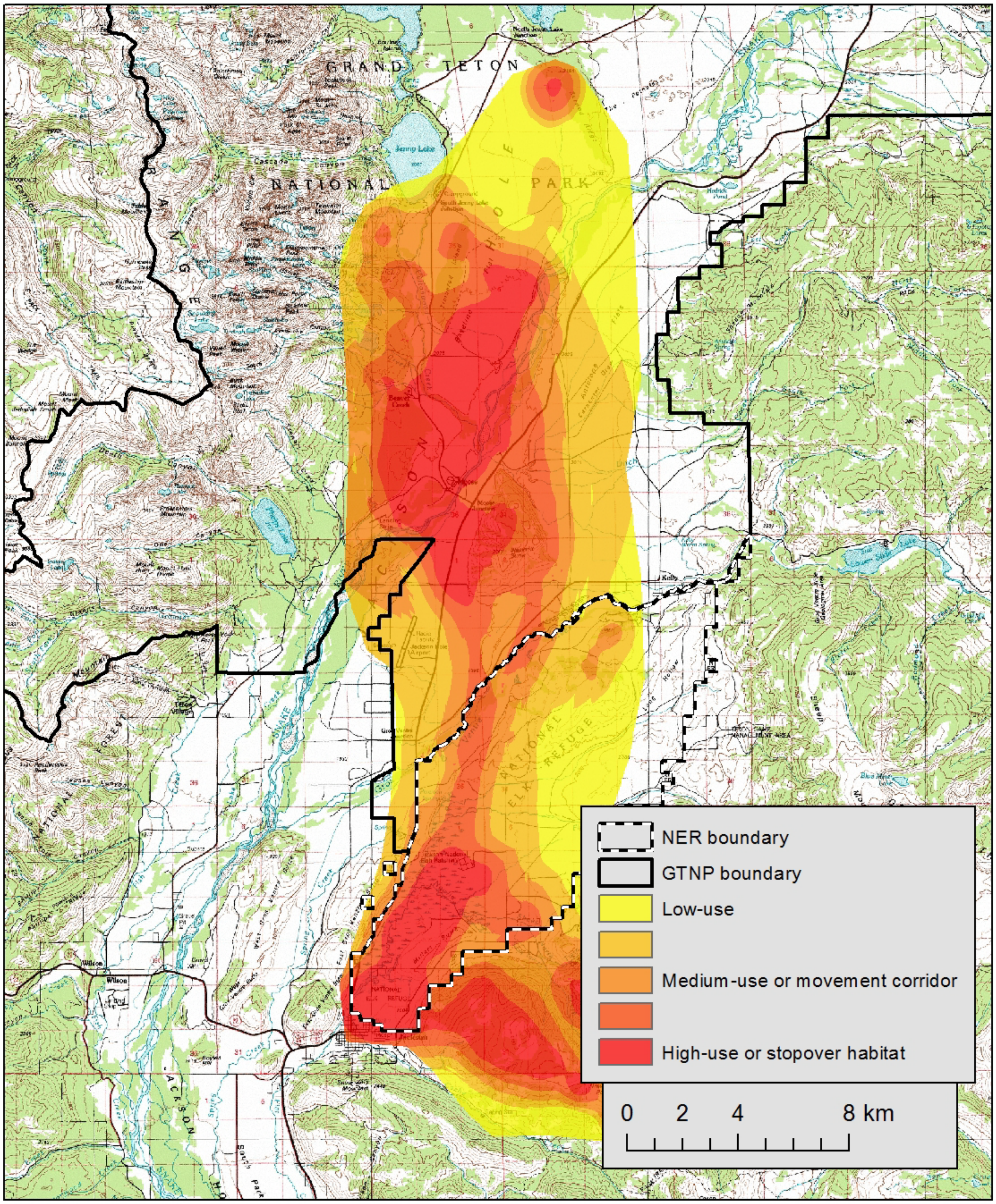

Figure 15. Fall population-level migration route of elk migrating to areas north of Moose, in Grand Teton National Park.

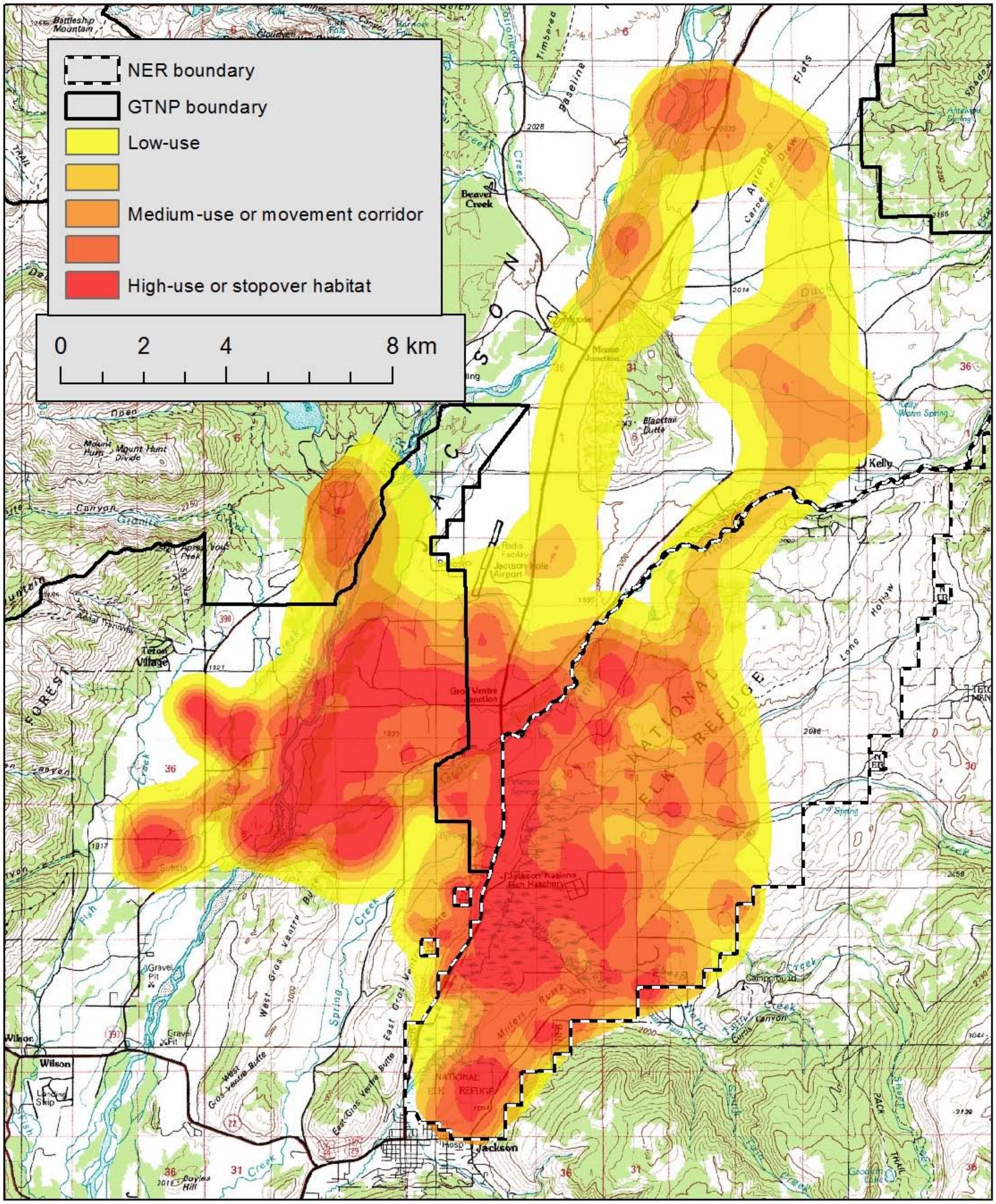

Figure 16. Spring population-level migration route of elk migrating to areas south of Moose, in Grand Teton National Park.

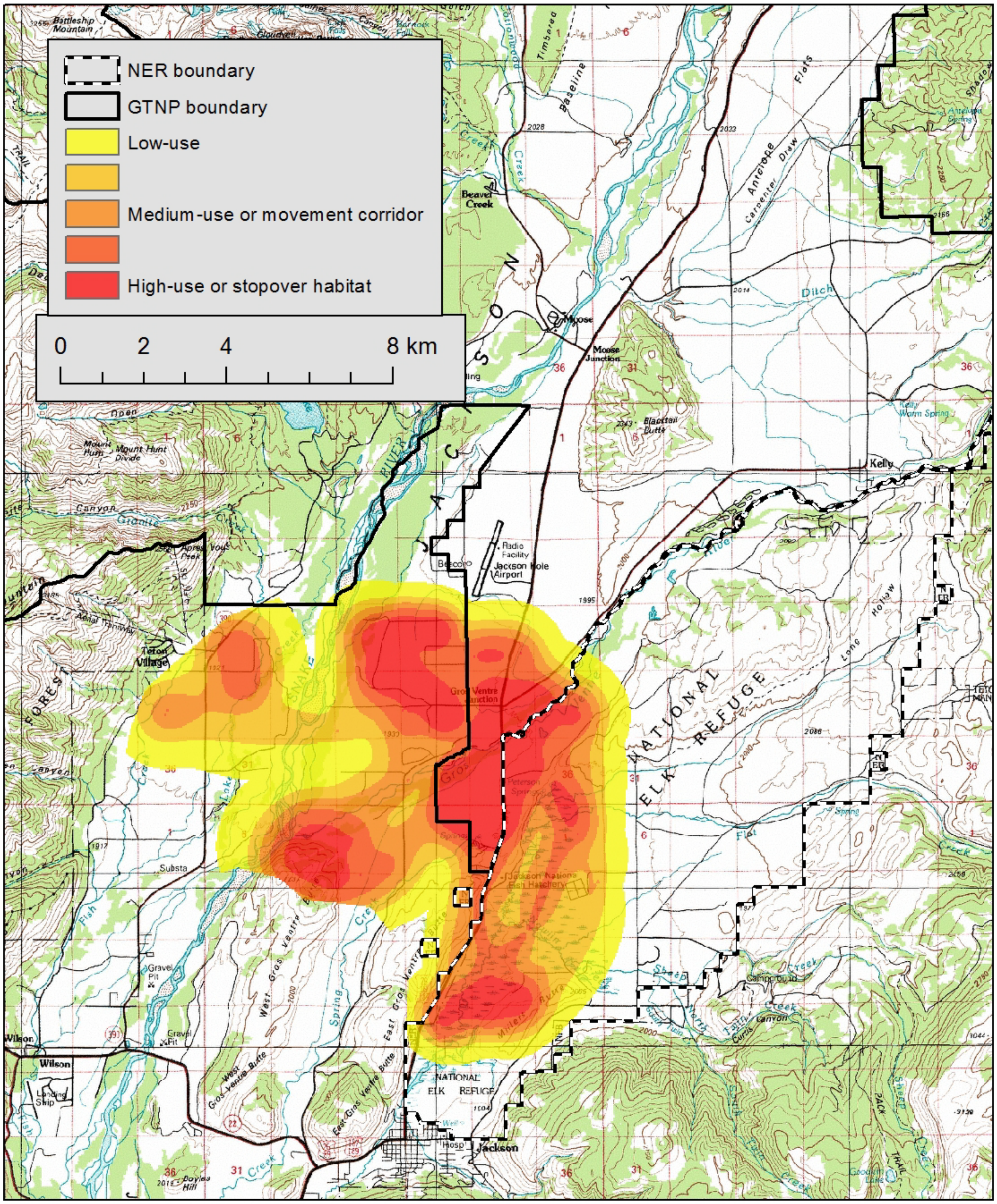

Figure 17. Fall population-level migration route of elk migrating to areas south of Moose, in Grand Teton National Park.

Table 9. Summer range location relative to Moose (north or south) and seasonal migration data available for each GPS-collared elk.

Elk ID	Area	Fall 07	Spring 08	Fall 08	Spring 09	Fall 09	Spring 10
1	South	NO	YES	NO	YES	NO	---
2	South	---	---	---	---	---	---
3	South	NO	YES	YES	---	---	---
4	North	NO	YES	YES	YES	YES	YES
5	North	---	---	---	---	---	---
6	North	YES	YES	YES	---	---	---
7	North	YES	YES	NO	YES	YES	YES
8	North	YES	YES	YES	---	---	---
9	South	---	---	---	---	---	---
10	North	YES	YES	YES	YES	YES	---
11	North	YES	YES	YES	YES	YES	NO
12	North	YES	YES	NO	YES	NO	YES
13	North	YES	YES	NO	YES	YES	YES
14	North	YES	YES	NO	YES	YES	---
15	North	YES	YES	YES	---	---	---
16	North	YES	YES	YES	YES	---	---
17	South	NO	YES	NO	YES	NO	YES
18	North	YES	YES	YES	YES	---	---
19	North	YES	---	---	---	---	---
20	North	YES	YES	YES	YES	YES	---
21	South	NO	YES	NO	YES	YES	
22	North	---	---	---	---	---	---
23	South	NO	YES	NO	YES	YES	YES
24	South	NO	---	---	---	---	---
25	North	YES	YES	YES	YES	YES	YES
26	South	NO	YES	NO	YES	YES	YES
27	North	YES	YES	---	---	---	---
28	North	YES	YES	YES	YES	NO	YES
29	North	YES	YES	YES	YES	---	---
30	South	NO	YES	NO	NO	NO	NO
31	North	YES	YES	YES	YES	---	---
32	South	NO	YES	NO	YES	YES	---
33	North	YES	YES	NO	YES	YES	YES
34	North	YES	YES	YES	YES	YES	YES
35	North	---	---	NO	YES	YES	YES
36	North	---	---	YES	YES	---	---
37	North	---	---	---	---	YES	---
38	North	---	---	---	---	NO	---
39	North	---	---	---	---	YES	---
40	North	---	---	---	---	NO	---
41	North	---	---	---	---	YES	YES
42	North	---	---	---	---	YES	---

--- indicate no data were available and “NO” indicate data were available, but elk did not migrate before December 1 and could not be used in analysis because of few GPS locations (i.e., only 1 location per day).

Elk Survival

Of the 42 elk that were collared 18 survived, 17 were killed by hunters, 3 were killed by wolves, 3 died of unknown causes, and 1 had its collar removed before the study ended (Table 2). Elk mortality was relatively low during 2007 and 2008, with only 2 and 5 elk harvested each year, respectively. However, elk mortality increased considerably during 2009 when 10 elk were harvested, 2 killed by wolves, and 1 died of unknown causes (Table 2). Compared to elk south of Moose Junction, the elk captured north of Moose appeared to be more susceptible to harvest. Of the 10 elk harvested in 2009, 9 were captured north of Moose Junction.

DISCUSSION

Grand Teton National Park (GTNP) is home to one of the largest and most visible elk herds in the world. Sustaining this elk herd and maintaining watchable wildlife opportunities are top priorities for GTNP. Although the multi-use pathway was constructed parallel to the existing Teton Park Road (TPR), there was concern that this new form of human disturbance (i.e., bicycles, pedestrians) could affect the habitat use patterns of elk and reduce the opportunity of visitors to view elk from TPR. Our analysis of fine-scale movement data collected before, during, and after construction of the multi-use pathway suggest that the habitat use patterns of elk were not affected by the pathway during construction and two years afterward.

Many studies of how ungulates respond to human disturbance focus specifically on flight distances (Freddy et al. 1986, Papouchis et al. 2001, Taylor and Knight 2003, Preisler et al. 2006). However, our interest here was to evaluate whether the multi-use pathway affected the overall habitat use patterns of elk, including their ability to move back and forth across TPR. Using fine-scale GPS data to develop elk habitat use models before, during, and after pathway construction provided a direct and rigorous method for assessing potential pathway effects. The fact that model coefficients and predictive maps were similar across years provides compelling evidence that pathway construction and subsequent two years of use did not influence the habitat use patterns of elk. Had the pathway elicited a greater flight or avoidance response than the existing TPR, we would have expected those changes to be evident in the habitat use models. During and after pathway construction, 78-86% of the study area was classified at the same habitat-use level as before construction. Given how similar the predictive maps were across years, it is not surprising that the amount of high-use elk habitat visible from TPR did not change noticeably from 2007 to 2010. These results suggest that visitor opportunities to view elk from TPR were similar before, during, and after pathway construction.

A second concern we addressed was whether the permeability of TPR was affected by the multi-use pathway. Elk are known to utilize habitats on both sides of TPR and are commonly observed crossing the TPR near Windy Point and Timbered Island. Although elk have traditionally crossed TPR with no problems, it was possible that the added disturbance of the pathway may reduce its permeability. At first glance, comparing the number of elk crossings each summer seems like a straight-forward analysis that could be addressed with standard techniques such as analysis-of-variance (ANOVA). However, to test for annual differences and treat the elk as the experimental unit, required that we use a more complex hierarchical modeling approach and MCMC methods. The hierarchical models estimated the average number of elk crossings each year and confidence intervals indicated there was no significance differences in the number the number of times elk crossed TPR before, during, and after pathway construction. Because the temporal patterns (night vs. day) of TPR crossings could potentially change without the total number of crossings change, we also tested for differences in daytime only crossings. Again, we found no evidence that the number of daytime only TPR crossings changed before, during, or after pathway construction. An important assumption in our before, during, and after analysis was that traffic volume was similar across years. Based on traffic data collected at four sites within the elk study area, this appeared to be a reasonable assumption as traffic volume was consistent throughout the 4-year study period.

Although our study relies on spatial data to make inferences about elk behavior, we recognize that behavioral responses depicted or modeled by GPS data may not reflect all the potential consequences of human disturbance (Gill et al. 2001), such as stress or subtle changes in activity budgets. However, a companion study focused specifically on the behavioral ecology of elk in relation to the GTNP pathway and found no evidence that the pathway affected elk behavior, group size, or visibility (Hardy and Crooks 2011).

Between July 2007 and November 2010 we collected >168,000 locations from 40 elk. In addition to the pathway analysis, these data also provide valuable information on the survival and year-around movement patterns of GTNP elk. Although not directly related to the pathway, we summarized elk survival and the migration patterns of elk that summer north and south of Moose Junction. The predominant cause of elk mortality was harvest, although the herd segment north of Moose Junction appeared more susceptible to harvest than those south of Moose Junction. With the exception of one elk that moved to Idaho and another that wintered on Game Creek, all collared elk spent the winter months on the National Elk Refuge (NER). Elk summering north of Moose Junction utilized different migration routes to and from the NER, compared to elk that summer south of Moose Junction. Recognizing where these different herd segments cross US 89 or private lands may improve the ability of GTNP, NER, and Wyoming Game and Fish Department to manage this elk herd. Spring migrations patterns were markedly different from fall, presumably because of hunting pressure. Unlike the spring routes, the fall routes were characterized by well-defined movement corridors to NER. These narrow corridors reflect quick elk movement to and from GTNP.

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