GRADIENTS OF PREDATION RISK AFFECT DISTRIBUTION AND MIGRATION OF A LARGE HERBIVORE

by

Jamin Lyle Grigg

A thesis submitted in partial fulfillment
of the requirements for the degree

of

Master of Science

in

Fish & Wildlife Management

MONTANA STATE UNIVERSITY
Bozeman, Montana

November 2007

APPROVAL

of a thesis submitted by

Jamin Lyle Grigg

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

Dr. Robert A. Garrott

Approved for the Department of Ecology

Dr. Dave W. Roberts

Approved for the Division of Graduate Education

Dr. Carl A. Fox

STATEMENT OF PERMISSION TO USE

In presenting this thesis in partial fulfillment of the requirements for a master's degree at Montana State University, I agree that the Library shall make it available to borrowers under the rules of the Library.

If I have indicated my intention to copyright this thesis by including a copyright notice page, copying is allowable only for scholarly purposes, consistent with "fair use" as prescribed in the U. S. Copyright Law. Only the copyright holder may grant requests for permission for extended quotation from or reproduction of this thesis in whole or in parts.

Jamin Grigg

November 2007

ACKNOWLEDGMENTS

This project was completed with funding and logistical support from Montana Fish Wildlife & Parks, Denver Zoological Foundation, and multiple landowners in the Madison Valley, particularly the Sun Ranch. I would like to thank Jesse Rawson for his work on the project – I couldn't have asked for better field help tracking animals and working with landowners under often tough conditions. I sincerely thank the many people at Montana Fish Wildlife & Parks, particularly Ken Hamlin, Craig Jourdonnais, Kurt Alt, Mike Ross, and Mark Atkinson, who assisted with this research and made it possible. Thanks to Andy Pils with USFS for his help and advice with road and trail data. I thank Adam Messer and Linda Phillips for GIS assistance. Todd Graham made me feel welcome on the Sun Ranch and has become a good friend and I am thankful for both. With much appreciation I thank my graduate committee – Ken Hamlin, Rick Lawrence, and Bob Garrott. I owe a tremendous debt of gratitude to my advisor in particular, Bob Garrott, for the opportunity he provided me and for his wisdom and insights, guidance, and professionalism. I would like to thank my fellow graduate students, particularly Matt Becker, Claire Gower, Kelly Proffitt, Jason Bruggeman, Steph McGinnis, Chris Forristal, and Julia Nelson. I thank Justin Gude and Julie Fuller for laying much of the groundwork that led to this research. I sincerely thank Tom Beck, Chad Bishop, Rick Kahn, Mark Hurley, and David Petersen for their influence in my continued development as a biologist. Their advice and example have been invaluable. And, of course, I owe a special thanks to Emily Harrington and my family for their support throughout this process.

TABLE OF CONTENTS

TABLE OF CONTENTS – CONTINUED

LIST OF TABLES

Table Page

LIST OF FIGURES

ABSTRACT

Few studies have placed wildlife behavioral responses to human disturbance and hunting pressure within the larger ecological context of predator-prey theory. Given that large herbivores respond behaviorally to the presence of wolves and other predators, we should expect similar adaptive behavioral responses when large herbivores are presented with risk in the form of human disturbance and hunting pressure. One index of human access, disturbance, and thus potential predation risk to large herbivores from hunters are road and trail networks bisecting large herbivore ranges. I evaluated the effects of human disturbance and predation pressure in the forms of motorized and total combined access networks on elk (*Cervus elaphus*) summer home range size, timing of fall migration, and movement rates by placing 49 GPS radio-collars on adult female elk on a winter range in the Madison Valley, MT over the course of a two-year study. I found evidence that elk responded to motorized access during the summer by increasing summer home range size. Further, regional variation in predation risk from human hunters resulted in elk subjected to the highest levels of hunting pressure initiating fall migration from summer ranges to winter ranges earlier than elk subjected to lower levels or no hunting pressure. These winter ranges are mostly privately-owned ranchlands that provide relative refuge from hunting pressure. All elk in this study summered on public lands, yet most elk summering in heavily hunted regions were unavailable to public-land hunters for large portions of the hunting seasons due to early fall migration patterns. Movement rate models were ambiguous and I was unable to detect differences associated with motorized and total access levels, though movement rates during the hunting seasons were correlated with varying regional predation risk. This research potentially provides valuable knowledge to biologists across the western United States managing large herbivore populations that summer on public lands and winter in privately-owned agricultural valleys, and provides insight into general predator-prey behavioral relationships.

INTRODUCTION

Adaptive behavioral responses to both predation risk and human influences exerted through encroachment upon and modification of habitats as well as through hunting pressure (predation risk) have important implications for animal distribution and survival (Caro 1998, Houston and McNamara 1999, Geist 2002, Mitchell and Lima 2002). Given this, the drivers of wildlife behavior, and the spatial and temporal scales at which behavioral influences occur, remain important and studied aspects of wildlife ecology and management. Further, identification and protection of corridors used by migrating species is a paramount component of wildlife conservation and population genetics (Soule and Terborgh 1999, Berger 2004). Because many mammal species require large and diverse habitat areas (Skovlin et al. 2002, Festa-Bianchet and Apollonio 2003, Kerley et al. 2003), it is important for wildlife managers to evaluate effects of disturbance on wildlife population dynamics and behavior as humans become an increasingly pervasive influence on landscapes where these populations reside. Understanding how varying levels and forms of human activity interact with climate and other landscape attributes to affect distribution, spatial dynamics, and migration of wildlife populations will provide knowledge to assist in the development of appropriate wildlife conservation and management.

As human development reshapes western landscapes (Hansen et al. 2002), impacts to ecological systems include increasingly pervasive threats to wildlife populations. Decades of research have documented potentially deleterious effects of

roads, trails, and human use of the landscape on ungulate habitat availability and use (see review in Lyon and Christensen 2002). Studies evaluating effects of human infrastructure and transportation networks on ungulates have documented wildlife avoidance of roads and trails and associated changes in habitat use (e.g., Lyon 1979, Rost and Bailey 1979, Rowland et al. 2000, Wisdom et al. 2005), as well as potential increases in vulnerability to hunters (e.g., Hurley and Sargeant 1991, Unsworth and Kuck 1991, Hayes et al. 2002, McCorquodale et al. 2003). Although previous research has provided knowledge of a variety of human impacts on wildlife for informing public policy and management of potential conflicts, questions remain that have yet to be well-evaluated regarding large herbivore distribution and migration.

Biologists in the western United States face the task of managing wildlife populations that migrate across a wide expanse of terrain, often crossing multiple political boundaries where ownership and land management practices and objectives differ (Knight and Landres 1998, Barham 2001). For example, many large herbivore populations use summer ranges consisting largely of high elevation, publicly-owned lands where human activity levels and uses can vary considerably depending on accessibility, recreational use, and management objectives. During late autumn these populations migrate to lower elevation, privately-owned valleys and agricultural lands to winter to avoid the deep snow pack and harsh conditions of the high-elevation ranges (Irwin 2002). If large herbivores respond to landscape heterogeneity in human activities and hunting pressure, one potential adaptive strategy involves altering their spatial distribution (e.g., migration) and moving to less risky areas, similar to how we might

expect animals to behave when faced with any other type of predation risk (e.g., Mitchell and Lima 2002). Given this, there is increasing interest and concern among management agencies that as ownership, land uses, and access levels change, large herbivore populations are "prematurely" migrating to privately-owned wintering areas. Because public access to these wintering grounds is increasingly limited, such areas potentially serve as refuges during fall hunting seasons (Burcham et al. 1999, Conner et al. 2001, Vieira et al. 2003). Consequently, potential changes in spatial distribution and timing of migration of large herbivores have significant consequences on management objectives and societal expectations of herd management.

I evaluated the drivers of movement and fall migration in a large herbivore population exposed to varying management policies and levels of human access and risk by studying a migratory elk (*Cervus elaphus*) population from 2005-2007 that occupied a mosaic of publicly and privately-owned lands in southwestern Montana. An increasing elk herd numbering approximately 5,000 individuals use winter ranges in the eastern portion of the Madison Valley of Montana (pers. comm., MTFWP). Wintering mostly on privately-owned agricultural ranchlands, the summer distribution of this herd spans multiple political boundaries, including Yellowstone National Park and National Forest lands where management varies from non-motorized wilderness to relatively accessible and heavily used areas where motorized travel is prevalent. While on summer ranges, these elk encounter a broad gradient of human recreation and fall hunting activities. Thus, this elk population provides a model system for examining management issues common to many large herbivore populations throughout the western United States.

I hypothesized that summer home range size, timing of fall migration, and movement rates of elk were affected by varying levels of human access and hunting pressure facilitated by motorized and total (combination of motorized and non-motorized) access to summer ranges. With this research, I expand upon previous research efforts on general anti-predator strategies and, more specifically, on human disturbance effects on large herbivore movement and distribution. Better understanding of elk spatial dynamics and variation in movement patterns associated with exposure to differing gradients of human disturbance and risk in the form of motorized and total trail access could improve management of large herbivore populations across the western United States. Further, this research also provided insight into the anti-predator strategy of avoidance as animals seek areas of relative refuge from predation risk.

STUDY AREA

The Madison Valley is located between the Gravelly and Madison mountain ranges in southwest Montana, 32 km west of Yellowstone National Park (YNP) along the eastern edge of the Central Rocky Mountains (44°58' N, 111°36' W). The portion of the Madison Valley east of the Madison River and south of Ennis, MT (Figure 1) is winter range for a migratory herd of approximately 5,000 elk that has increased in size by approximately 400% since the mid 1960s (pers. comm., MTFWP). This increase is largely associated with changes in land ownership that resulted in the loss of traditional ranching and the subsequent changes to increased tolerance of wintering elk and reduced tolerance for hunter access to this herd during this time (pers. comm., MTFWP). The East Madison winter range is an approximately 300 km^2 area consisting mostly of private ranchlands surrounded by National Forest, BLM, and state-owned lands. Another winter range, the state-owned Wall Creek Wildlife Management Area, is located west of the Madison River, directly across from the East Madison winter range and winters an additional several thousand elk. The Madison River and U.S. Highway 287 act as a "soft" boundary to elk movements, though some interchange of elk does occur (pers. comm., MTFWP). The winter climate in the valley is characterized by long, cold winters with infrequent warmer weather caused by Chinook winds. Persistent strong winds scour snow from low-elevation benches and higher-elevation ridges, facilitating energy efficient foraging by large herbivores. Elevations in this region range from 1736 m to 2743 m and the area contains similar native plant communities to those found in and

around YNP (Despain 1990, Gude 2004). The valley and low elevation benches along the river consist primarily of grassland (e.g. *Festuca idahoensis* and *Agropyron spicatum*), sagebrush (*Artemisia sp.*), and irrigated agricultural pastures. Riparian communities dominated by willow (*Salix sp*.) are found along most streams and the Madison River. The west-facing slopes of the Madison range contain a mix of native grasslands at lower elevations and coniferous forests (e.g. *Pinus contorta, Pinus flexilis, Abies lasiocarpa, Picea engelmannii,* and *Pseudotsuga menziesii*) at higher elevations, with aspen (*Populous tremuloides*) woodlands interspersed throughout.

Summer ranges for this elk herd include the mountainous, primarily publicly-owned lands to the south and east of the winter range. Topography is rugged with elevations ranging from 1975-3555 m. Valley bottoms consist primarily of sagebrush, grassland, and riparian areas, while slopes above are dominated by primarily coniferous forests and inter-mixed meadows (Despain 1990). Other large herbivores inhabiting the area include mule deer (*Odocoileus hemionus*), white-tailed deer (*Odocoileus virginianis*), pronghorn (*Antilocapra americana*), moose (*Alces alces*), bighorn sheep (*Ovis canadensis*), and mountain goat (*Oreamnos americanus*), though all species occur at lower densities than elk (pers. comm., MTFWP). Non-human predators occurring in the region include wolves (*Canis lupus*), mountain lions (*Felis concolor*), coyotes (*Canis latrans*), and black (*Ursus americanus*) and grizzly (*Ursus arctos horribilius*) bears.

Elk summer ranges span multiple use National Forest lands, two large wilderness areas, and the western edge of Yellowstone National Park (Figure 2). Consequently, considerable variation exists in road and trail densities, ranging from remote areas that

are not easily accessed to areas popular with recreationists that contain high densities of motorized and non-motorized trail networks. Similarly, fall hunting activity varies, from areas close to metropolitan areas containing extensive road and trail networks, to remote areas with restricted access, and National Park lands closed to hunting. Hunting seasons in this region include an archery season spanning early September through the middle of October and a 5-week general rifle season spanning late October through late November.

The Taylor Fork drainage is within 80 km of the towns of Bozeman (population 27509; U.S. census data from year 2000) and Big Sky (population 1221; U.S. census data from year 2000) and is a popular recreational and hunting area, bisected by approximately 30 km of arterial roads and high densities of secondary roads and both motorized and non-motorized-use trails. The southern portion of the Madison range, including the Cabin Creek Wildlife Management Area, is nearly twice as distant (150 km) from Bozeman and contains only a few short road segments providing access to the area and moderate trail densities. The Henry's Mountains are south of the Madison range, forming the continental divide in this region and extending south into Idaho. Trail networks in this area are generally similar to the Cabin Creek WMA region and terrain is generally steep and rugged. Hunting license allotments in the Idaho portion of this region are more limited and seasons are shorter than in Montana. In contrast to the previous three regions, YNP and the adjacent Bacon Rind portion of the Lee Metcalf Wilderness contain moderate to low trail densities available only to foot and horse traffic, and were closed to human hunting.

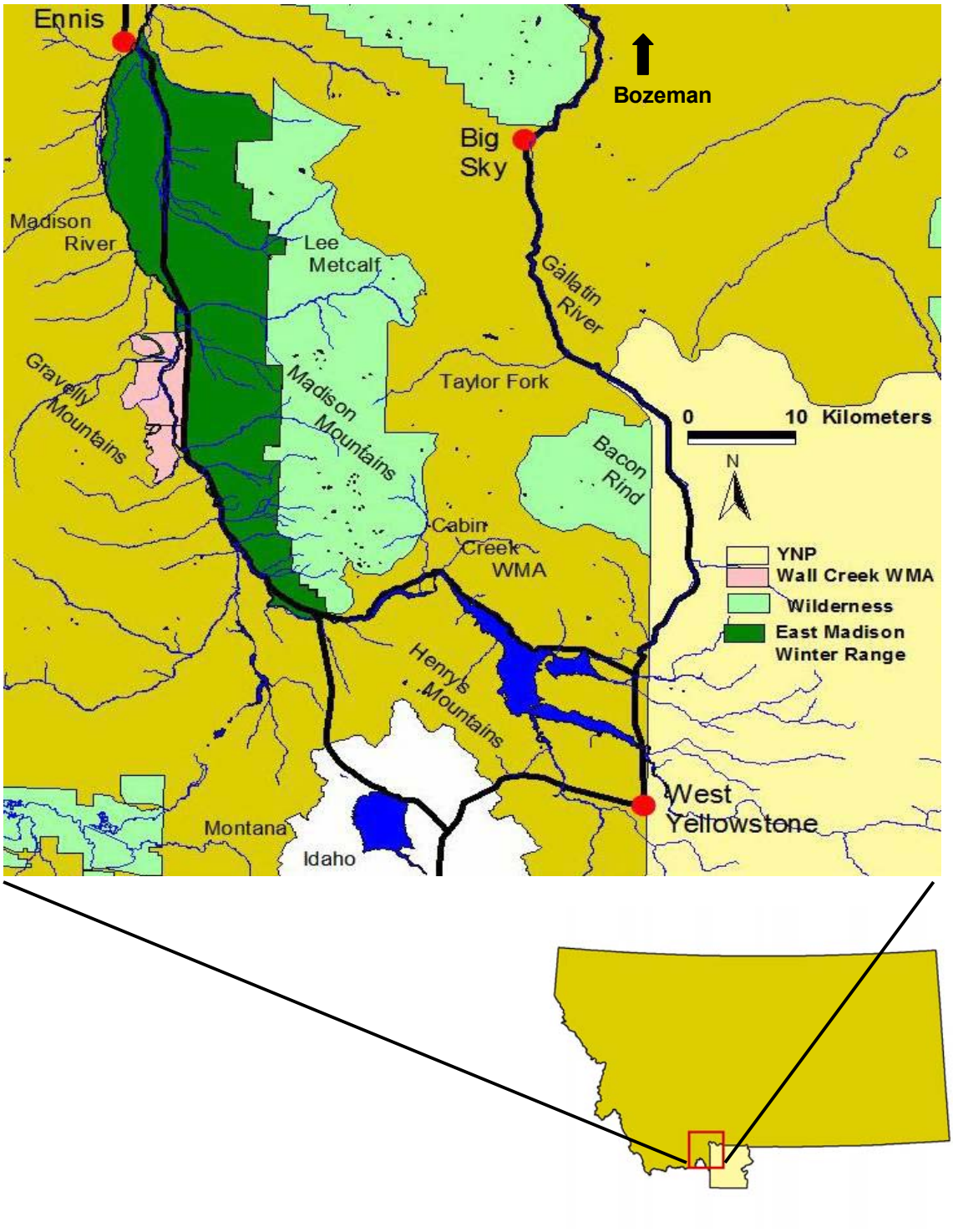


Figure 1. The Lower Madison winter range in SW Montana, consisting mostly of private ranchlands, with the surrounding area primarily comprised of public lands managed by state and federal agencies.

METHODS

Collection of Movement Data

I obtained data on the distribution and seasonal movements of the study population by fitting combination GPS/VHF radio-collars (Model GPS3300L, Lotek®; Newmarket, Ontario) on 49 adult female elk over a two-year period. Twenty collars were deployed in February 2005, followed by an additional 29 collars in February 2006. Elk were immobilized with 50 mg Xylazine and 12 mg Thiafentanil (A-3080) using dart-gunning techniques from a helicopter and Tolazoline and Naltrexone were used as the reversal agents. Collars were programmed to record locations continuously at 30-min intervals and were equipped with a "blow-off" release mechanism to drop the collar 48 (Year 1) and 52 (Year 2) weeks after deployment. Locations retrieved from collars were converted to the Universal Transverse Mercator (UTM), NAD 27, coordinate system and imported into a vector-based geographic information system (GIS; ArcView®; ESRI, Redlands, CA). Positional dilution of precision (PDOP) is a 3-dimensional measure of the quality of GPS data where lower values generally indicate higher location accuracy. I censored locations with PDOP values >10 ($\bar{x}$ = 3.8%; range 2.2% – 6.3%) as locations with PDOP values $\leq$10 rarely exceed 50 m in location error (D'eon and Delparte 2005). Because terrain and landscape attributes can influence GPS location accuracy and, thus, PDOP values, I did not use a censor threshold below 10 due to the potential for systematically introducing bias when deleting a large percentage of non-random locations (D'eon and Delparte 2005).

Defining Seasonal Movements

Elk are seasonal migrants (Irwin 2002), defined as "...a regular, round-trip movement of individuals between two or more areas or seasonal ranges" (White and Garrott 1990). Movements of collared elk were divided into 4 discernable seasonal categories: winter, spring migration, summer, and fall migration. Generally fine-scale movements without persistent directional tendency over long periods of time or distances resulted in dense clusters of locations that readily defined the summer and winter ranges. Similarly, spring and fall migration paths were discernable by the linear series of locations resulting in broader-scale, directional movements from winter to summer ranges and vice versa. More specifically, I considered initiation of spring migration beginning on the date that each animal exited the defined winter range boundary for the final time that season and ending when the directional movement of the animal joined the cluster of points representing her summer home-range polygon. The same delineation procedures were used to define the fall migration. I defined summer home range polygons based on the cluster of locations produced between 15 July and 31 August. Because the last collared elk to arrive on its summer home range did so on 12 July, I chose 15 July as the start date for summer locations to standardize number of days used to calculate summer home range. Also, variation in elk redistribution due to phenological change in plants during the summer season was a source of potential bias had I included all available locations on summer ranges, regardless of an individual's arrival date (Mysterud et al. 2001). Further, a start date of mid-July alleviated potential bias

pertaining to differential movements during the mid-May through mid-June calving season (Cook et al. 2004) for animals caring for relatively non-mobile neonates.

Defining Summer Home Range Size

For each elk, I calculated a summer home range polygon to be used as the response variable in multiple regression analyses evaluating effects of motorized and total (combined motorized and non-motorized) road and trail access networks on elk summer home range size. Home range size can vary considerably within local populations and can be an important indicator of the ability of a particular range to meet an animal's biological requirements of nutrient intake and shelter from disturbance (Nicholson et al. 1997). I defined summer home range polygons using 90% adaptive kernels (Worton 1989, Rodgers and Carr 1998). Adaptive kernel techniques were selected based on goodness-of-fit simulations for the summer location data (Horne and Garton 2006). Because our summer location datasets were too large ($\bar{x}$ = 2155) to be accommodated by the program, I used a systematic sample of every third location for goodness-of-fit simulations. However, once I selected the adaptive kernel home range estimator, I used every acceptable location to produce summer home range polygons. Adaptive and fixed kernel techniques ranked as the top two competing home-range estimators for each of the 42 summer-location datasets. Since both adaptive and fixed kernel techniques were ranked highly by the home range model estimator, and because there is considerable debate over which home range estimator is preferred (Silverman 1986, Worton 1989, Seaman and Powell 1996, Blundell et al. 2001), I calculated a home

range using both methods for each collared elk. Because minimum convex polygons (MCPs) have also been widely used to describe home ranges in the past (Southwood 1966, Worton 1995), I calculated MCPs in addition to the kernel home ranges for comparison. Few studies have attempted to describe home ranges using the sample size of locations I had available, thus it was important to get a visual description of elk home ranges using several home range estimator techniques. These graphics facilitated comparisons of how each home range estimator performed with locations taken at 30-min intervals that in sum represent a nearly complete description of individual elk movement patterns.

Calculation of 30-Minute Movement Rates

I calculated the mean daytime and nighttime movement rates for each collared elk during summer, general archery, and general rifle seasons, as well as during the spring and fall migrations. Rates were defined as the average Euclidian distance (m) moved at 30-min intervals for each season per individual. Movement rates during the summer, archery, and general rifle season were the response variables in multiple regression analyses evaluating effects of motorized and total (combined motorized and non-motorized) access networks on elk movement. I hypothesized that access levels would have a larger impact on elk movement during the diurnal and crepuscular time periods, thus, daytime was defined as beginning one hour before sunrise and ending one hour after sunset for each season. I calculated summer movement rates during the same time period used to estimate summer home range size. Movement rates during the hunting seasons

were calculated beginning two days before the start of each respective season (archery and general rifle) and extending for the duration of that season. I included the data from two days prior to hunting seasons in order to account for the increase in human activity associated with hunting camp preparation. If an animal began its fall migration before a particular hunting season ended, the movement data were censored at that time to eliminate obvious bias. I censored any distances calculated from consecutive locations >30 minutes apart (e.g., in instances where a GPS location attempt failed or was eliminated due to a PDOP value >10).

Spring and Fall Migration Rates and Duration

Timing of spring migration in large herbivore populations is largely a function of climate characteristics such as snowmelt and subsequent green-up of forage vegetation and, for breeding females, the need to find a suitable area for calving (Festa-Bianchet 1988, Mysterud et al. 2001, Irwin 2002). Also, the spring migration does not include the predation threat of human hunting present during the fall migration. Because of this, the movement behavior, routes, and duration of an animal's spring and fall migrations may vary considerably (Irwin 2002). I measured differences in duration (days) and 30-min movement rates during spring and fall migration for each instrumented animal. I further provided a description of differences in travel routes (corridors) used during the spring and fall migrations. I expected that elk would display anti-predator behavior during the fall migration by moving more quickly to minimize the amount of time at risk from human hunters. Thus, I hypothesized duration of the fall migration would be shorter than

the spring migration and mean 30-min movement rates would increase during the fall migration. However, it would also be plausible to hypothesize that elk would play a "hide and seek" game with hunters during the fall migration as they travel to safer winter ranges, only moving short distances at a time, hiding for long periods of time in large patches of protective cover, and thus increasing duration of migration and decreasing mean movement rates.

Covariate and Model Development

Five covariates were considered in multiple linear regression (MLR) models to evaluate hypotheses about effects on five response variables: adult female elk summer home range size (Appendix A), initiation (Julian date) of fall migration (Appendix B), and 30-min movement rates during the summer, archery, and general rifle seasons (Appendix C). Covariates included exposure to motorized (MOT) and the combination of motorized and non-motorized (ACCESS) human access networks and the proportion of forested canopy coverage (CAN) within each summer home range. I also derived an index of the accumulation of snow on elk summer ranges from daily measurements of snow water equivalent (SWE), recorded at automated SNOTEL stations (http://www.wcc.nrcs.usda.gov/snotel/) located on the elk summer ranges. SWE is a measure of the mass of water in a column of snow and provides a metric that integrates both snow depth and density. Daily measurements from the Madison Plateau (elev 2583m), Beaver Creek (elev 2617m), and Carrot Basin (elev 3000m) stations (Appendix I) were obtained from the first snowfall of the year through Jan 31 (Appendix K), when

the last elk arrived on winter range following fall migration (Figure 7). However, SWE measurements had a 94% (year 2005) and 97% (year 2006) colinearity with Julian date, the response variable for timing of fall migration, and so could not be added into MLR models as an explanatory covariate. As a surrogate for differences in snow pack, I used the elevation (ELEV) of each elk summer home range centroid, as snow pack was correlated with elevation (see elevation of SNOTEL sites, Appendix K). Though neither winter had substantial snowpack, snowpack the second year was particularly mild and was only about one-half the level of the first year (Appendix K). Thus, I also considered a categorical covariate indexing each year of the study as an index of annual variation in snowpack (YEAR). I developed and compared competing *a priori* hypotheses, expressed as MLR models (Appendices D-F) using the R statistical software (R Development Core Team 2004), to evaluate the relative influence of each covariate to the response variables. Hypotheses were stated as candidate MLR models and included the expected direction of each coefficient. After testing for normality and multicollinearity, I fit all candidate models and evaluated goodness-of-fit using R^2_{adj} values. I used Akaike's Information Criterion, corrected for sample size (AIC_c), to compare the relative ability of each model to explain variation in the data and Akaike model weights (w_i) provided a measure of model-selection uncertainty (Burnham and Anderson 2002).

To evaluate the potential effects of human recreation and hunting pressure on elk movement and distribution, I developed an index of exposure to human access for each elk summer home range using a U.S. Forest Service GIS database of roads and trails. Roads and trails were categorized as allowing motorized or non-motorized travel,

representing two potential levels of disturbance to elk (Rost and Bailey 1979, Wisdom et al. 2005). These categorizations provided an index of both motorized access and total combined (motorized and non-motorized) access for evaluation in MLR models. Lyon and Burcham (1998) found 97% of hunters remained within 1 km of a road, thus I considered human activity corridors to extend 1 km from either side of a road or trail. This provided an area of potential human disturbance that I overlaid with elk summer ranges to obtain a percentage of motorized and total access overlap for each elk summer home range polygon.

Heterogeneous landscapes interact with perceived threats to affect wildlife responses to risky situations. Given a certain exposure level to human activities, availability of nearby hiding cover may influence an elk's decision to flee from recreationists and hunters using nearby roads and trails (Lyon 1979, Ager et al. 2003). Further, forest canopy likely influences available forage and thus may influence elk movements and home range size. As an index of hiding cover, I calculated the proportion of each summer home range polygon that was forested using 30m resolution LANDSAT images of forested canopy cover.

Proximity to urban areas is correlated with usage rates and thus the levels and types of human hunting and recreational use they sustain (Ewart 1993, Hammitt and Cole 1998, De Vries and Goosen 2002). Thus, I further developed a categorical *post-priori* covariate to evaluate regional effects (REG) derived after the first year of GPS-collar data indicated the East Madison winter elk herd was primarily summering in 4 generally distinct areas. These regions were discernable based on differing migration corridors

used by elk, geographically distinct sub-basins, and watersheds differing substantially in their proximity to human urban areas. The 4 regions where elk generally summered included the Taylor Fork of the Gallatin Canyon (TF), the Cabin Creek Wildlife Management area and its surroundings (CC), the Henry's Mountains south into Idaho (ID/Henry's), and Yellowstone National Park (YNP). YNP and the adjacent Bacon Rind portion of the Lee Metcalf Wilderness were both closed to human hunting activity, thus animals summering in those 2 locales were grouped into one region. Elk wintering on the east Madison Study area and summering in the Taylor's Fork and YNP regions shared similar migration corridors and summered in sub-basins draining into the Gallatin River. Cabin Creek animals tended to use migration corridors further south and east and summered in sub-basins draining south into the Madison River, while elk summering in the Henry's Mountains and south into Idaho migrated south across the Madison River and summered in areas near the continental divide and Montana-Idaho border (Figures 2 and 5). The YNP region was used as the reference region in MLR analyses because I expected human activity to have the least amount of influence on elk movement and distribution in this region.

In combination with the regional covariate I also included 2 other covariates, straight-line distance of summer home range centroids from the East Madison winter range (DIST) and age of the animal (AGE), to the most supported *a priori* models in some exploratory *post priori* analyses. I used the distance covariate only in timing of fall migration exploratory analyses to evaluate whether elk whose summer ranges were closest to winter ranges were more likely to migrate earlier. Because the region and

distance covariates were nested within each-other, they were not included in the same models. Age of each elk was estimated at capture based on tooth replacement and wear (Hamlin et al. 2000) and was included in exploratory analyses to evaluate whether younger animals were more likely to make long, exploratory movements, potentially resulting in larger summer home ranges and increased movement rates (Lindstedt et al. 1986, Johnson and Gaines 1990, Cederlund and Sand 1994).

I hypothesized elk summer home range size, date of departure from summer range, and movement rates would be positively correlated with motorized and total access networks, as both of these covariates represent relative access of humans, which can result in varying levels of potential disturbance during the summer time period and/or predation risk during the hunting seasons (Lyon 1979, Rost and Bailey 1979, Rowland et al. 2000, Wisdom et al. 2005). I expected increased access would present elk with a risky environment and thus increase movement rates on summer ranges and stimulate earlier fall migration to safer areas on winter ranges. I further hypothesized that motorized access would result in a stronger relative effect than total access due to increases in noise and usage rates associated with motorized-use areas. I hypothesized forest canopy cover would have a buffering effect on these disturbances by potentially providing refuge areas for elk, and would thus would be negatively correlated to summer home range size, initiation of fall migration, and movement rates. I expected regional differences to occur because of the inability to directly account for differences in usage rates among roads and trails and because some collared elk summered in drainages and sub-basins closer to metropolitan areas that are likely more frequently used by recreationists and hunters

(pers. comm., MTFWP, U.S. Forest Service). Based on this, I expected the Taylor Fork region to receive the highest use rates, followed by the Cabin Creek region, then the ID/Henry's region and the YNP region. Further I expected regional effects in the timing of fall migration due to the exclusion of human hunting pressure in the YNP region and the limited number of licenses allocated for the ID/Henry's region.

RESULTS

Of the 49 GPS radio collars placed on adult female elk on the East Madison winter range from 2005-2007, 42 were recovered after recording a full year of data and were used in final analyses. The other 7 were not used in analyses for various reasons: 1 elk died shortly after capture of apparent capture myopathy; 1 elk died of unknown causes during the spring following capture; a faulty release mechanism released 1 collar after only 2 months of deployment; 2 collars were not retrieved due to failed release mechanisms; and 2 collars either suffered failures or the elk dispersed from the area and did not return to the Madison Valley the winter following capture. Successful GPS fix attempts exceeded 95% for 40 of the 42 retrieved collars. The remaining 2 units were successful on 80% and 36% of GPS fix attempts. Total successful fix attempts numbered 674,940 and ranged from 6,181 to 17,112 recorded locations per elk ($\bar{x}$ = 16,070, SD = 1,851) annually.

Summer Distribution of the East Madison Wintering Elk Herd

Elk wintering on the East Madison winter range had summer ranges that extended to the mountainous areas primarily to the south and east of the winter range, with a relatively small proportion whose summer ranges include Yellowstone National Park (Figure 2). Elk arrival on summer ranges ranged from 12 May to 12 July ($\bar{x}$ = 4 June; SD = 15.79 days). Five (2 in 2005 and 3 in 2006) of 42 elk summer home ranges occurred primarily within YNP (12%). An additional 3 animals summered primarily in

the adjacent Bacon Rind portion of the Lee Metcalf Wilderness closed to hunting (7%). Seventeen elk summered in the Taylor Fork region of the Gallatin River drainage (40%) and 1 elk summered in the Jack Creek drainage above Ennis Lake. Eleven elk summered in or near the Cabin Creek Wildlife Management Area north of Hebgen Lake (26%) and 1 elk summered along the Madison Face, just above the East Madison winter range. Four elk summered in the Henry's Mountains along the Montana/Idaho border or crossed into the Henry's Lake and Island Park portions of southeast Idaho (10%).

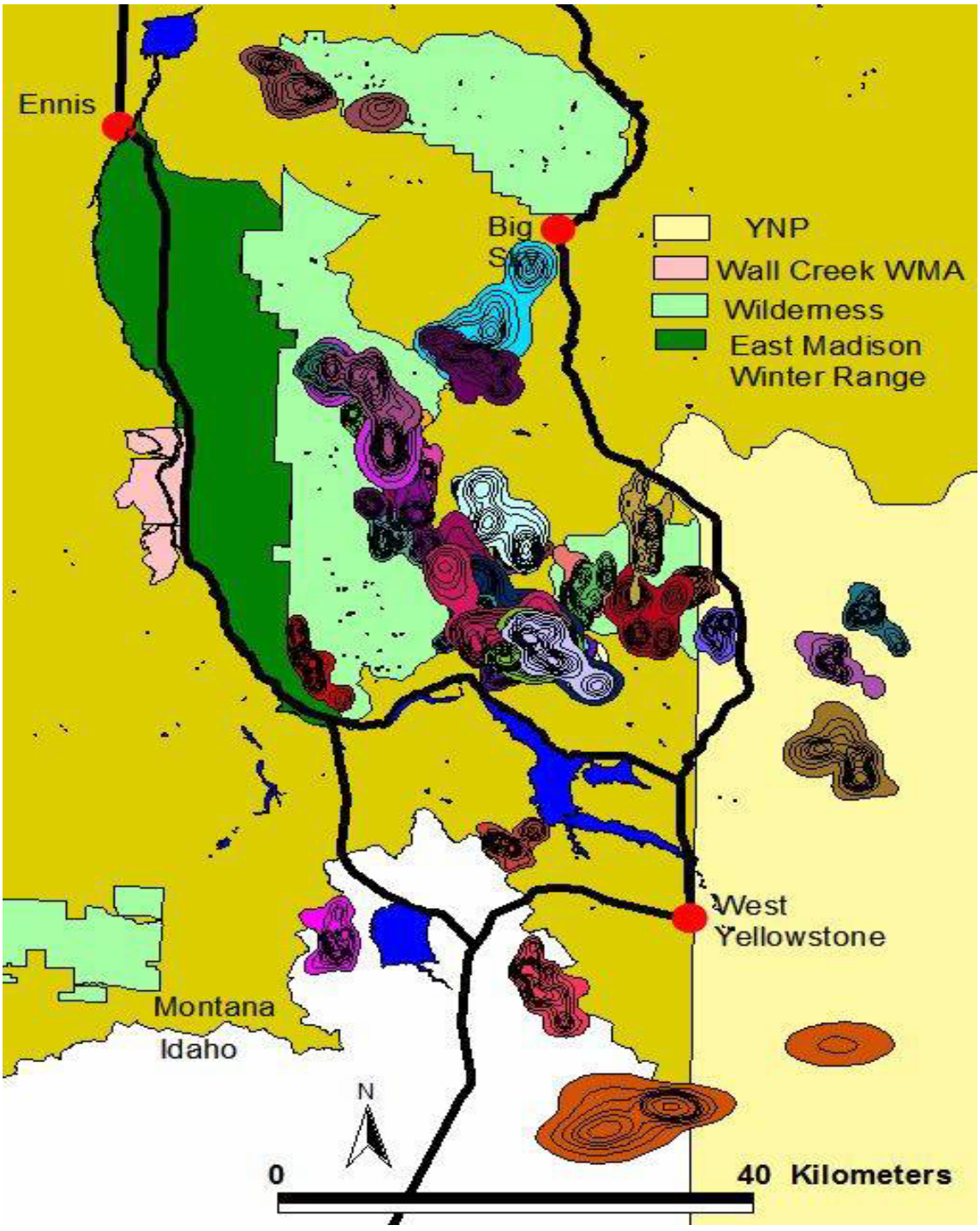


Figure 2. Summer distributions of 42 adult female elk fitted with GPS radio collars on the East Madison Valley winter range during the winters of 2005 and 2006. Summer home ranges were calculated from GPS collar locations recorded at 30-minute intervals from 15 July through 30 August and are represented as 90% adaptive kernel polygons.

Summer Home Range Size

Adaptive kernel techniques appeared to best fit the data for elk summer home ranges, resulting in contiguous polygons that tightly fit the distribution of summer locations recorded at 30-minute intervals (Appendix H). Fixed kernel techniques, using the reference smoothing parameter (h_{ref}) also generally performed well. However, for some summer data sets, the fixed kernel technique appeared to under-smooth and produced multiple disjunctive polygons that appeared to underestimate the home range (Appendix I). For many of the GPS collar datasets, minimum convex polygons tended to include large areas within the home range estimate that did not appear to be used by the animal (Appendix I). Adaptive kernel adult female elk summer home range (n = 42) sizes ranged from 14.9 km^2 to 128.0 km^2 ($\bar{x}$ = 43.8, SD = 24.8). Summer home range overlap with the motorized access variable ranged from 0 to 94% ($\bar{x}$ = 22.8, SD = 24.0) and overlap with the total access variable (combined motorized access and non-motorized trails) ranged from 1 to 96% ($\bar{x}$ = 64.9, SD = 23.4). Elevation of summer home range centroids ranged from 2250 to 2800 m ($\bar{x}$ = 2551.7, SD = 137.3).

Motorized access, total access, and canopy cover all correlated with elk summer home range size (Table 1) in the hypothesized direction. Home range size did not vary annually, as CIs for coefficient estimates overlapped zero (Table 2). Equally supported top *a priori* models included combinations of the motorized access, total access, and canopy coverage covariates. Coefficient estimates for these covariates were in the hypothesized directions with CIs that did not overlap zero (Table 2; $\hat{\beta}_{Mot} = 0.40$, 95% CI

= [0.69, 0.11] $\hat{\beta}_{Access} = 0.47$, 95% CI = [0.78, 0.16], $\hat{\beta}_{Can} = -0.68$, 95% CI = [-1.29, -0.07]). Though unexplained variation was substantial (Mot $R^2_{adj} = 0.13$, Access $R^2_{adj} = 0.10$), a general trend indicated summer home ranges 2 times as large in areas with relatively high levels of motorized access compared to elk summer home ranges occurring in areas with little or no motorized access and 3 times as large in areas with relatively high total access compared to areas with lower amounts of total access (Figure 3). Further, because canopy cover had a negative correlation with summer home range size (Table 2), model results provided support for my *a priori* prediction that canopy coverage within summer home ranges may have a buffering effect on disturbance associated with human access. As expected, age was negatively correlated with home range size (Figure 4 and Table 2; $\hat{\beta}_{Age} = -2.14$, 95% C.I. = -3.94, -0.34). Adding age of the elk to the top *a priori* models in *post priori* analyses (Table 1) increased the R^2_{adj} from 0.18 for the most supported *a priori* model to 0.24, but reduced the AIC_c by less than 2 units and thus did not significantly improve the top *a priori* models. Further, there was no evidence of regional effects on elk summer home range size when this covariate was evaluated in post priori analyses (Table 1).

Model (~Summer HR Size)	R^2_{adj}	*K*	AIC_c	ΔAIC_c	w_i
a priori					
Access + Can	0.18	4	386.75	**0**	0.36
Mot	0.13	3	387.89	**1.14**	0.2
Mot + Can	0.14	4	388.47	**1.71**	0.15
Access	0.10	3	389.07	2.31	0.11
Access + Can + Year	0.16	5	389.16	2.40	0.11
Mot + Can + Year	0.14	5	390.34	3.58	0.06
post priori					
Mot + Age	0.22	4	384.83	**0**	0.34
Access + Can + Age	0.24	5	385.09	**0.26**	0.3
Mot + Can + Age	0.23	5	385.78	**0.95**	0.21
Access + Can	0.18	4	386.75	**1.92**	0.13
Access + Can + Reg + Age	0.20	8	392.34	7.51	0.01
Access + Can + Reg	0.16	7	392.69	7.86	0.01

Table 1. Summary of model selection results from *a priori* candidate models explaining variation in adult female elk summer home range size (n = 42). Covariates evaluated included degree of motorized (Mot) and the combination of motorized and non-motorized (Access) access, canopy coverage (Can) on summer ranges, and yearly variation (Year) between 2005 and 2006. Number of parameters (*K*) contained in each model and Akaike weights (w_i) are also shown. Competitive models ($\Delta AIC_c < 2$) are outlined in bold text. Results from exploratory *post priori* models are shown below. Covariates evaluated included the region (Reg) in which an animal's summer home range occurred and the age (Age) of the animal.

Model (~Summer HR Size)	$\hat{\beta}_{Mot}$	$\hat{\beta}_{Access}$	$\hat{\beta}_{Can}$	$\hat{\beta}_{Year}$
a priori				
Access + Can	--	**0.47 [0.78, 0.16]**	**-0.68 [-1.29, -0.07]**	--
Mot	**0.40 [0.69, 0.11]**	--	--	--
Mot + Can	**0.40 [0.69, 0.11]**	--	-0.41 [-1.02, 0.20]	**--**
Access	--	**0.37 [0.68, 0.06]**	--	--
Access + Can + Year	--	**0.46 [0.77, 0.15]**	**-0.65 [-1.30, -0.01]**	2.99 [17.47, -11.49]
Mot + Can + Year	**0.40 [0.69, 0.11]**	**--**	-0.36 [-0.97, 0.25]	5.98 [20.50, -8.54]
	$\hat{\beta}_{Mot}$	$\hat{\beta}_{Access}$	$\hat{\beta}_{Can}$	$\hat{\beta}_{Age}$
post priori				
Mot + Age	**0.29 [0.58, 0.01]**	--	**--**	**-2.14 [-3.94, -0.34]**
Access + Can + Age	**--**	**0.35 [0.66, 0.04]**	-0.57 [-1.18, 0.04]	**-1.87 [-3.69, -0.05]**
Mot + Can + Age	**0.30 [0.59, 0.02]**	--	-0.36 [-0.93, 0.21]	**-2.06 [-3.84, -0.28]**
Access + Can	**--**	**0.47 [0.78, 0.16]**	**-0.68 [-1.29, -0.07]**	--

Table 2. Coefficient values and 95% confidence intervals for *a priori* covariates representing the effects of motorized (Mot) and the combination of motorized and non-motorized (Access) access, canopy coverage (Can), and yearly variation (Year) between 2005 and 2006 on adult female elk summer home range size (km^2). Coefficient values and 95% confidence intervals for *post priori* covariates representing the effects of age (AGE) of the animal when added to the top *a priori* models are shown below. Coefficient values for regional effects (Reg) are not shown because this variable did not improve the top *a priori* models (Table 1). Coefficient estimates whose 95% confidence interval does not overlap zero are shown in bold.

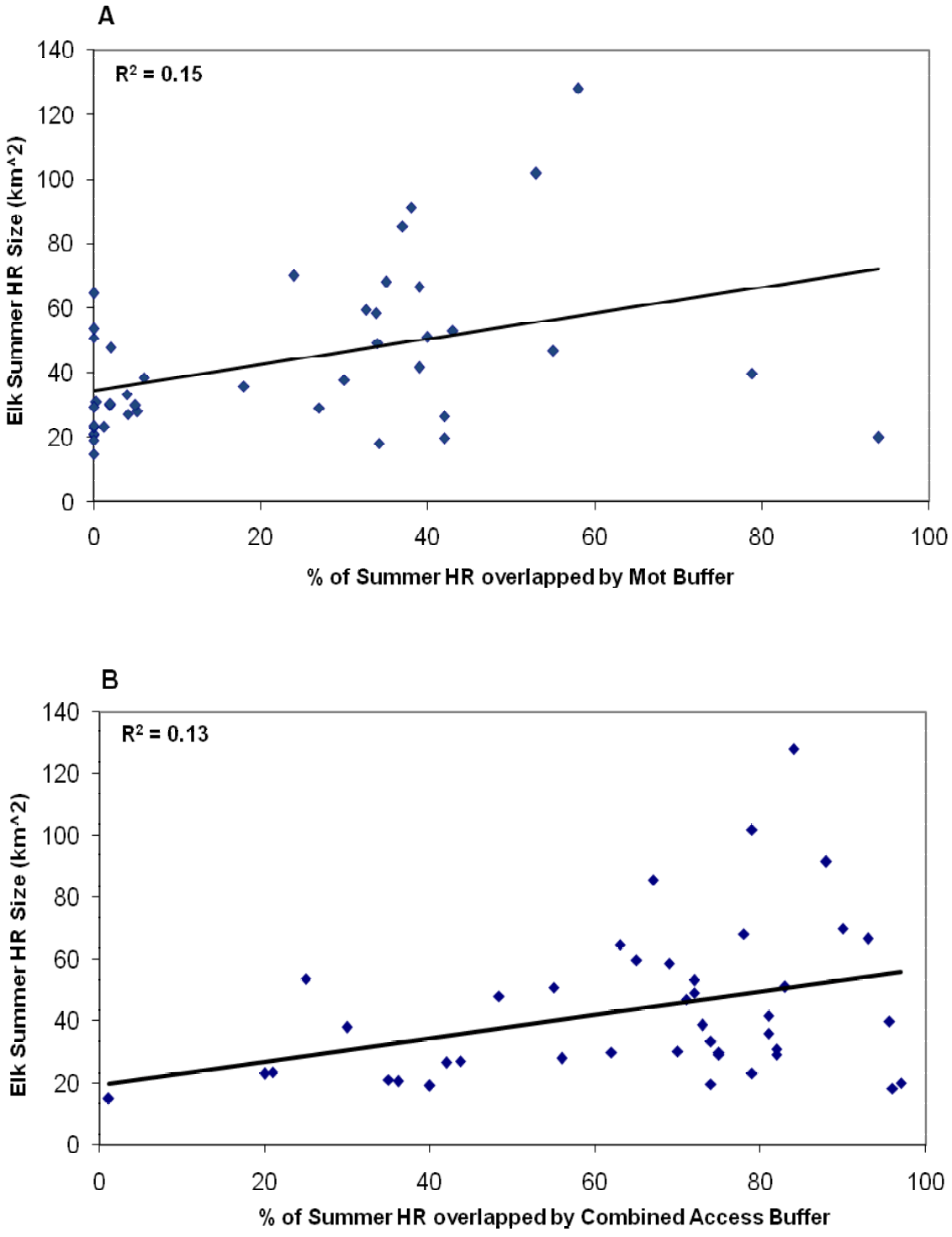


Figure 3. Correlation between adult female elk summer home range size (90% adaptive kernel estimators) and percentage of summer home range overlap with (A) motorized access and (B) total combined motorized and non-motorized access.

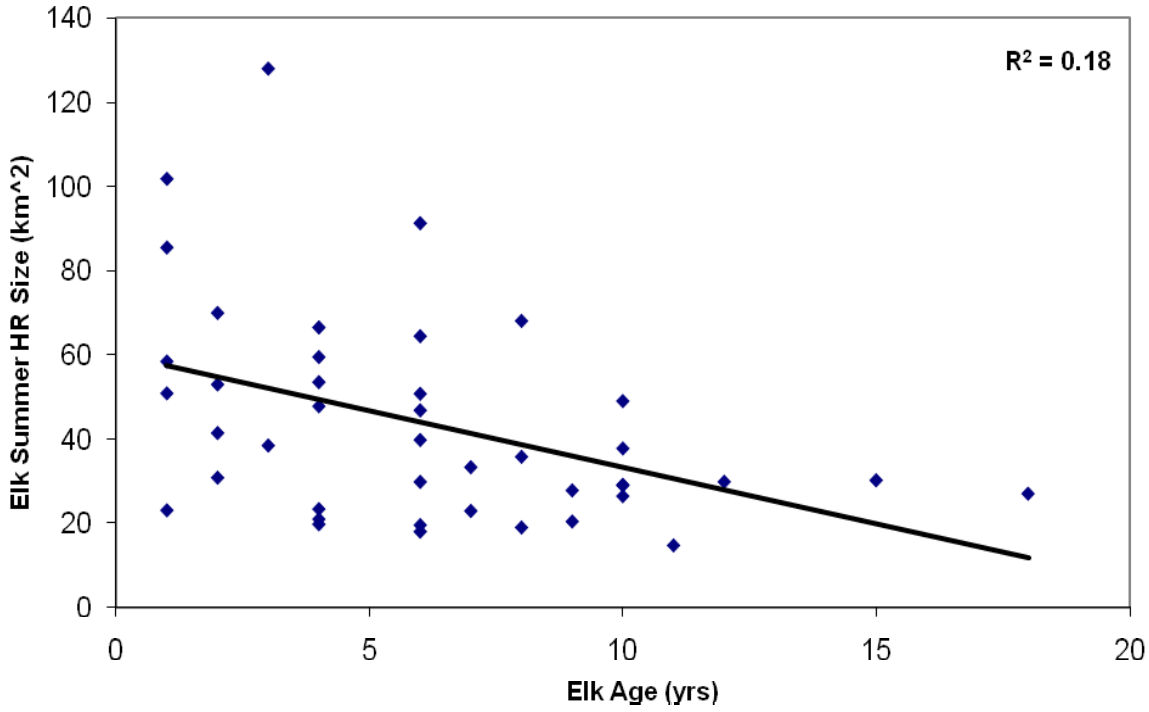


Figure 4. Correlation between elk summer home range size (90% adaptive kernel estimators) and age.

Timing of Fall Migration

Elk GPS collars generally provided clear migration vectors to summer ranges and back again to the East Madison winter range (Figures 5, 6). Only 1 summer home range had overlap with the winter range and thus exhibited no discernable migration between summer and winter range. Data from this elk, who summered primarily along the Madison face above the winter range (Figure 2), were censored for timing of migration analyses (thus, n = 41). Thirty (73%) of 41 elk used the same corridor for both their spring and fall migrations (Figure 7 and Table 3). Durations of spring migrations ($\bar{x}$ = 7.7 days, SD = 9.8 days) were generally shorter than the duration of fall migrations ($\bar{x}$ = 9.2 days, SD = 14.0 days) and displayed less variation. Initiation of departure from the East Madison winter range (i.e., the start of spring migration) ranged from 6 May to 12 July ($\bar{x}$ = 30 May, SD = 16.1 days). Arrival on summer range (i.e., the end of spring migration) ranged from 12 May to 12 July ($\bar{x}$ = 6 June, SD = 16.6 days). Initiation of departure from summer home ranges (i.e., the start of fall migration) ranged from 2 September to 25 January ($\bar{x}$ = 23 October 23, SD = 27.3 days). Arrival on the East Madison winter range (i.e., the end of fall migration) ranged from 18 September to 31 January ($\bar{x}$ = 1 November, SD = 33.0 days). Elk arriving to winter ranges during the general hunting seasons tended to migrate more quickly ($\bar{x}$ = 4.3 days, average straight-line distance = 17.3 km, n = 32) than elk arriving on winter range after the end of the general rifle season ($\bar{x}$ = 26.4 days, average straight-line distance = 36.6 km, n = 9). No differences were detected in 30-min movement rates or total migration vector distance

between the spring and fall migrations, as individual behavior tended to vary dramatically.

Migration Path	Fall	Spring
Bear Creek	5	1
Deadman Creek	0	1
Indian Creek	13	15
Jack Creek	1	0
Madison Face	0	4
Moose Creek	11	15
Papoose Creek	1	0
Raynolds Pass	5	4
Wolf Creek	5	1
Total	41	41

Table 3. Migration corridors used by 41 elk fitted with GPS radio-collars on the East Madison winter range, 2005 and 2006.

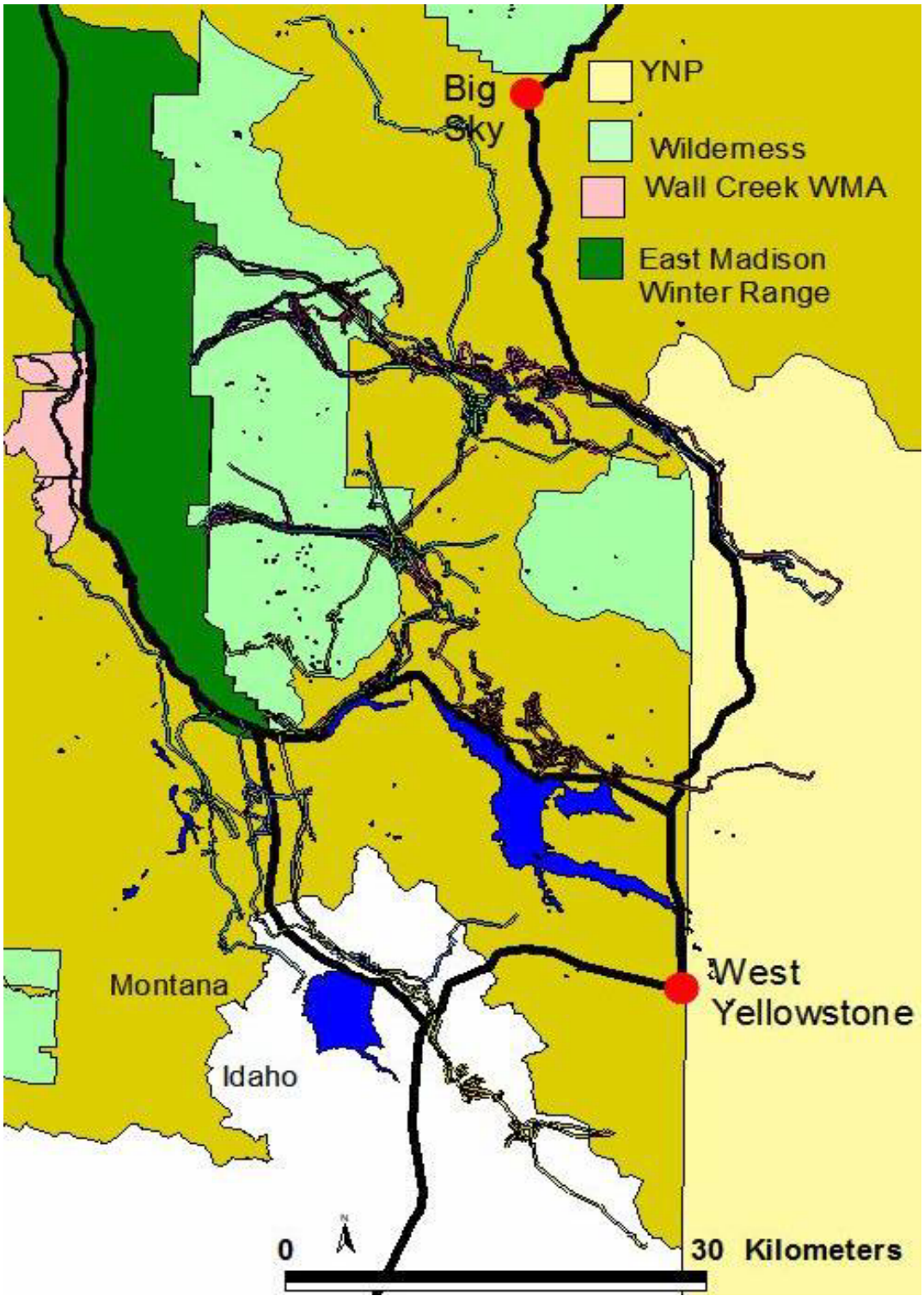


Figure 5. GPS spring migration vectors from winter to summer ranges for 41 elk collared on the East Madison winter range, 2005 and 2006.

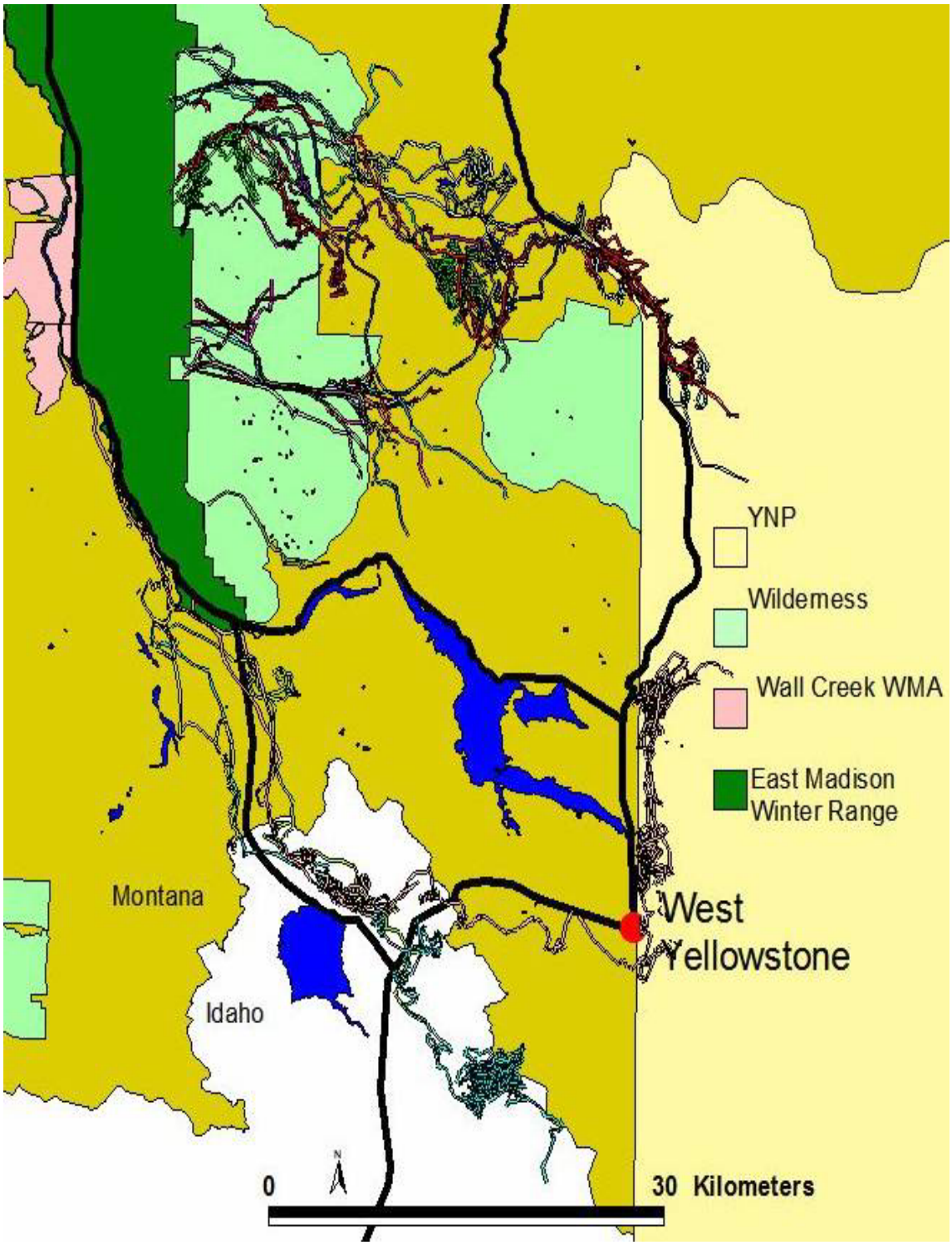


Figure 6. GPS fall migration vectors from summer to winter ranges for 41 elk collared on the East Madison winter range, 2005 and 2006.

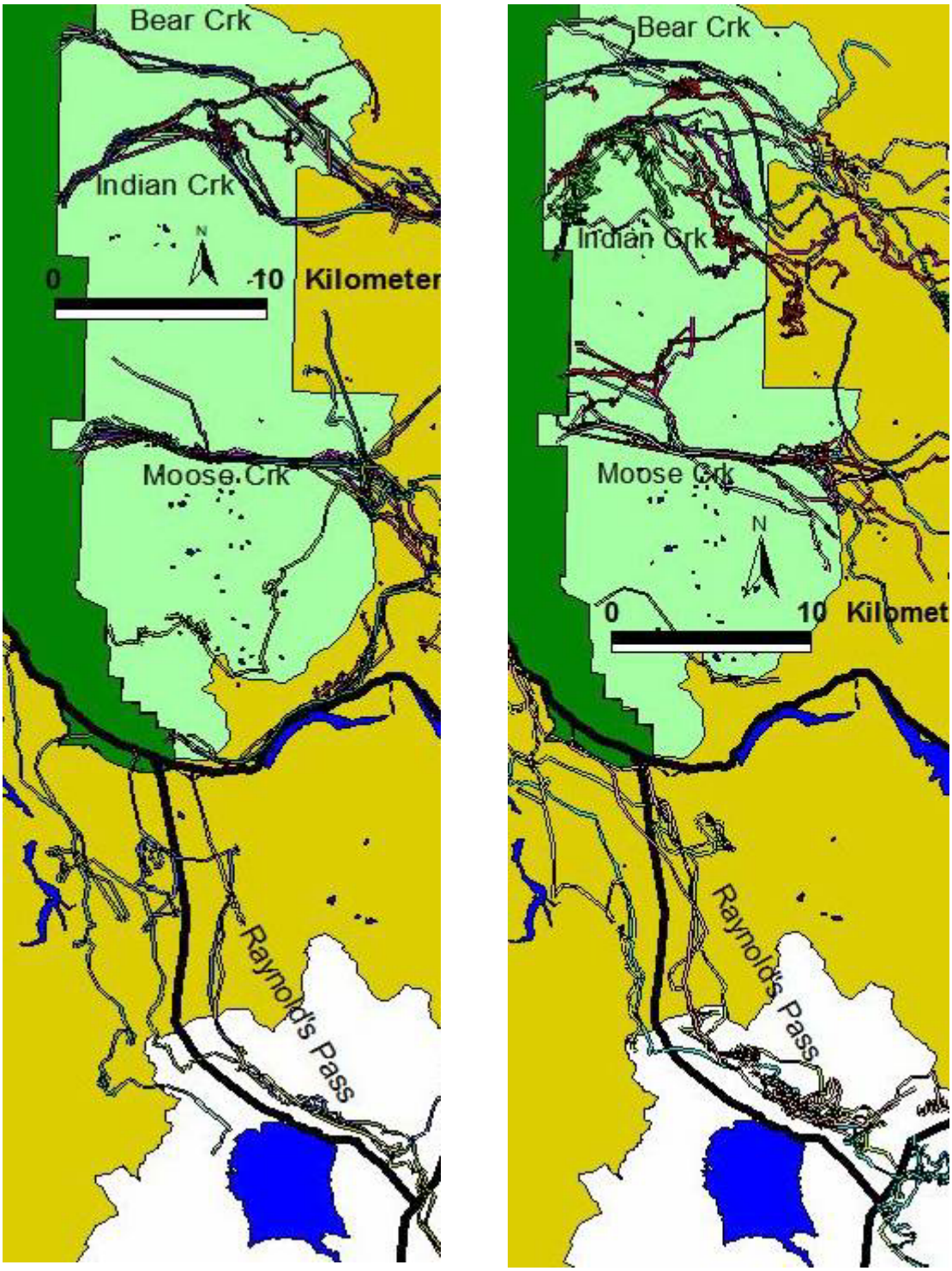


Figure 7. Spring (left) and fall (right) migration corridors used by 41 elk fitted with GPS radio-collars on the East Madison winter range, 2005 and 2006.

I found little evidence from *a priori* model results that the predictor variables influenced timing of elk fall migration in the hypothesized directions. The top *a priori* models (Table 4) indicated that both motorized access (Table 5; $\hat{\beta}_{Mot} = 0.49$, 95% C.I. = 0.80, 0.18) and canopy coverage (Table 5; $\hat{\beta}_{Can} = -0.77$, 95% C.I. = -0.14, -1.40) were influential; however coefficient estimates were opposite of predicted direction. Coefficient values for the total access (combined motorized and non-motorized access) covariate were in the hypothesized direction (Table 5); however this variable was not included in the top-ranked models. *Post priori* exploratory analyses indicated that regional effects strongly influenced timing of fall migration. The region covariate increased the R^2_{adj} value of the top *a priori* model from 0.25 to 0.70 and decreased its AIC_c value by nearly 33 units (Table 4), thus indicating that timing of elk fall migration was strongly influenced by regional attributes not captured in our *a priori* covariates. Distance of elk summer home range centroid from the East Madison winter range also improved the top *a priori* model when added in exploratory analyses, but was not as influential as the regional covariate (Table 4) when evaluated separately.

I was unable to detect a response in timing of elk fall migration related to snow pack (Table 5; see coefficient values for $\hat{\beta}_{Elev}$ and $\hat{\beta}_{Year}$). However, elk demonstrated large variation in timing of fall migration that appeared to parallel regional predation risk from human hunters (Table 5; see coefficient values for $\hat{\beta}_{\mathrm{Re}g_{ID}}$, $\hat{\beta}_{\mathrm{Re}g_{CC}}$, and $\hat{\beta}_{\mathrm{Re}g_{TF}}$). Mean SWE values (Appendices F and G) at initiation of fall migration (Figure 8) were generally much lower for Taylor Fork ($\bar{x}$ = 2.3 cm; range 0 – 15.8 cm) and Cabin Creek

WMA ($\bar{x}$ = 4.1 cm; range 0 – 10.1 cm) elk than for elk summering in YNP ($\bar{x}$ = 11.2 cm; range 5.2 – 15.2 cm) or the Henry's Mountains and Idaho ($\bar{x}$ = 14.2 cm; range 8.4 – 26.7 cm). Although photoperiod and snow are likely influential in timing of elk fall migration to winter ranges (Irwin 2002), strong differential timing of migration in this study that is not explainable by snow pack suggests elk are behaviorally responding to regional predation risk during the hunting seasons by altering timing of fall migration.

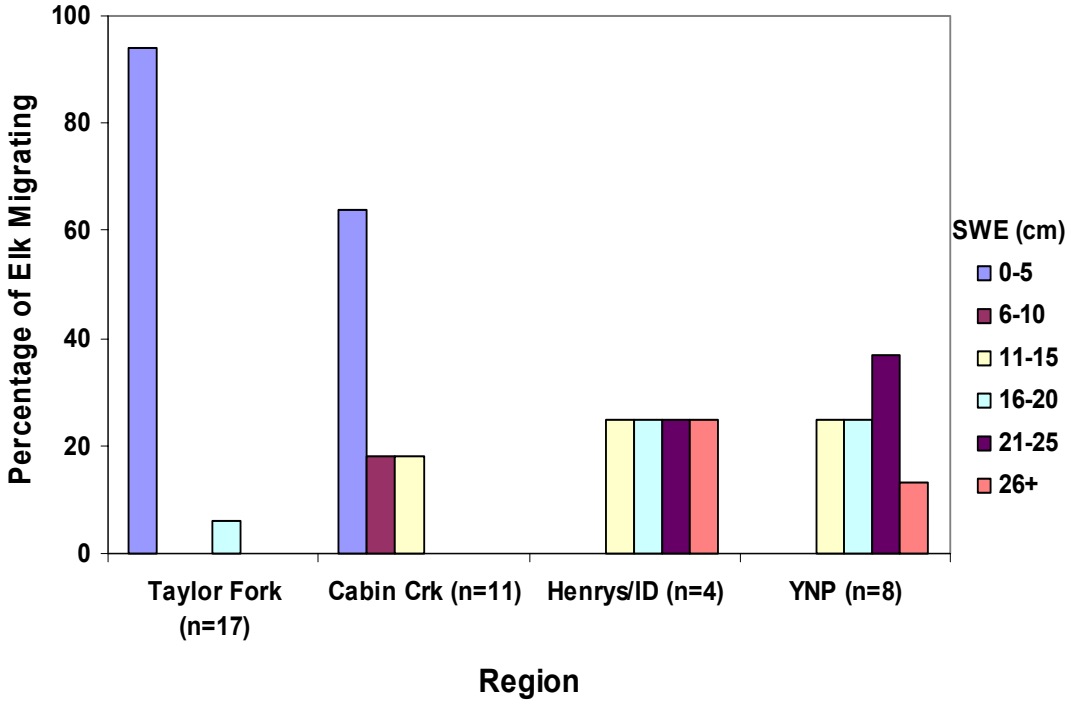


Figure 8. Snow-water equivalent (SWE) values at initiation of elk migration from summer to winter ranges, categorized by region.

Elk summering in the Taylor Fork region tended to initiate migration to winter ranges with the onset of the hunting seasons (Figure 9), earlier than elk summering in other regions (Table 5; see coefficient values for $\hat{\beta}_{\mathrm{Re}g_{ID}}$, $\hat{\beta}_{\mathrm{Re}g_{CC}}$, and $\hat{\beta}_{\mathrm{Re}g_{TF}}$). Only 4 of 17 elk summering in the Taylor Fork region over the course of the two-year study still remained on summer ranges when the general rifle season opened, the majority of animals having migrated during the archery season (Figure 9). Of the 4 remaining, 3 migrated within 2 days of opening day of the general rifle season. In comparison, 7 of 11 elk summering in the Cabin Creek region and all elk summering in the ID/Henry's Mountains (4/4) and YNP (including the Bacon Rind portion of the Lee Metcalf Wilderness closed to hunting; 8/8) regions were still on summer home ranges when the general rifle season opened. All elk summering in the Taylor Fork and Cabin Creek regions had arrived on the East Madison winter range by the end of the general rifle season, while 3 of 4 elk summering in the ID/Henry's Mountains and 6 of 8 elk summering in the YNP region did not arrive on winter range until after the end of the general rifle season.

Although the Taylor Fork region is accessible via approximately 30 km of arterial roads open to passenger vehicles and has high levels of overall access, elk summer home ranges in the Taylor Fork region had less overlap with motorized access than for elk summering in the ID/Henry's region and the Cabin Creek region (Figure 10). Elk summering in the Cabin Creek region had slightly higher levels of overlap with motorized access than elk summering in the Taylor Fork region, but similar levels of total access and tended to migrate slightly later ($\bar{x}$ = 23 October; range 17 September – 19

November) than the Taylor Fork elk ($\bar{x}$ = 4 October; range 2 September – 19 November) but earlier than YNP elk ($\bar{x}$ = 13 November; range 8 November – 18 November) and elk summering in the ID/Henry's region ($\bar{x}$ = 4 December; range 10 November – 25 January). Elk summer home ranges in the YNP region had the lowest levels of overlap with motorized and total access compared to the other 3 regions. Elk summer home ranges in the ID/Henry's region had the highest levels of overlap with motorized access, yet tended to migrate later than the Taylor Fork and Cabin Creek animals and had similar migration dates as elk summering in the YNP region (Table 5; $\hat{\beta}_{\mathrm{Re}g_{ID}} = -15.36$, 95% C.I. = 8.55, -39.27). These results suggest that other variables, such as recreation and hunter usage rates that I was unable to directly account for, but indirectly are captured in the regional covariate, are likely interacting with access corridors to influence the onset of fall migration.

Model (~Timing Fall Migration)	R^2_{adj}	*K*	AIC_c	ΔAIC_c	w_i
a priori					
Mot + Can	0.25	4	382.84	**0.00**	0.53
Mot + Can + Elev + Year	0.28	6	384.56	**1.72**	0.30
Mot	0.16	3	386.11	3.27	0.13
Mot + Elev + Year	0.14	5	389.98	7.14	0.01
Access + Can	0.11	4	390.08	7.24	0.01
Access + Can + Elev + Year	0.16	6	390.57	7.73	0.01
Access	0.06	3	390.62	7.78	0.01
Access + Elev + Year	0.07	5	393.37	10.53	0.00
Elev + Year	0.01	4	394.35	11.51	0.00
post priori					
Mot + Can + Reg	0.70	7	350.05	**0.00**	1.00
Mot + Can + Dist	0.53	5	365.29	15.24	0.00
Mot + Can	0.25	4	382.84	32.79	0.00

Table 4. Summary of model selection results from *a priori* candidate models explaining variation in initiation of adult female elk fall migration to winter ranges (n = 41). Covariates evaluated included degree of motorized (Mot) and the combination of motorized and non-motorized (Access) access, canopy coverage (Can) on summer ranges, elevation (Elev) of summer home range centroid, and yearly variation (Year) between 2005 and 2006. Number of parameters (*K*) contained in each model and Akaike weights (w_i) are also shown. Competitive models ($\Delta AIC_c < 2$) are outlined in bold text. Results from exploratory *post priori* models are shown below. Covariates evaluated included the region (Reg) in which an animal's summer home range occurred and the distance (Dist) between its summer home range centroid and the East Madison winter ran

Model (~Timing Fall Migration)	$\hat{\beta}_{Mot}$	$\hat{\beta}_{Access}$	$\hat{\beta}_{Can}$	$\hat{\beta}_{Elev}$	$\hat{\beta}_{Year}$	
a priori						
Mot + Can	**0.49 [0.80, 0.18]**	--	**-0.77 [-0.14, -1.40]**	--	--	
Mot + Can + Elev + Year	**0.44 [0.75, 0.13]**	--	**-0.92 [-0.27, -1.57]**	-0.03 [0.03, -0.09]	-14.97 [1.32, -31.26]	
Mot	**0.49 [0.82, 0.16]**	--	**--**	**--**	**--**	
Mot + Elev + Year	**0.47 [0.82, 0.12]**	**--**	**--**	-0.02 [0.04, -0.08]	-9.16 [8.05, -26.37]	
Access + Can	--	-0.27 [0.10, -0.64]	-0.62 [0.11, -1.35]	**--**	**--**	
Access + Can + Elev + Year	--	-0.21 [-0.58, 0.16]	**-0.85 [-0.12, -1.58]**	-0.06 [0.00, -0.12]	-15.84 [1.85, -33.53]	
Access	--	**-0.37 [-0.01, -0.74]**	**--**	**--**	**--**	
	$\hat{\beta}_{Mot}$	$\hat{\beta}_{Can}$	$\hat{\beta}_{Dist}$	$\hat{\beta}_{\mathrm{Re}g_{ID}}$	$\hat{\beta}_{\mathrm{Re}g_{CC}}$	$\hat{\beta}_{\mathrm{Re}g_{TF}}$
post priori						
Mot + Can + Reg	**0.65 [0.92, 0.38]**	0.06 [0.51, -0.39]	**--**	-15.36 [8.55, -39.27]	**-46.19 [-27.61, -64.77]**	**-52.82 [-37.85, -67.79]**
Mot + Can + Dist	**0.51 [0.75, 0.27]**	0.16 [0.79, -0.47]	**1.59 [2.24, 0.94]**	--	**--**	--
Mot + Can	**0.49 [0.80, 0.18]**	**-0.77 [-0.14, -1.40]**	--	--	--	--

Table 5. Coefficient values and 95% confidence intervals for *a priori* covariates representing the effects of motorized (Mot) and the combination of motorized and non-motorized (Access) access, canopy coverage (Can), elevation (Elev) of summer home range centroid, and yearly variation (Year) between 2005 and 2006 on the timing of elk fall migration. Coefficient values and 95% confidence intervals for *post priori* covariates representing regional effects (Reg) and the distance (Dist) between an animal's summer home range centroid and the East Madison winter range when added to the top *a priori* model are shown below. Coefficient estimates with 95% confidence intervals not overlapping zero are shown in bold.

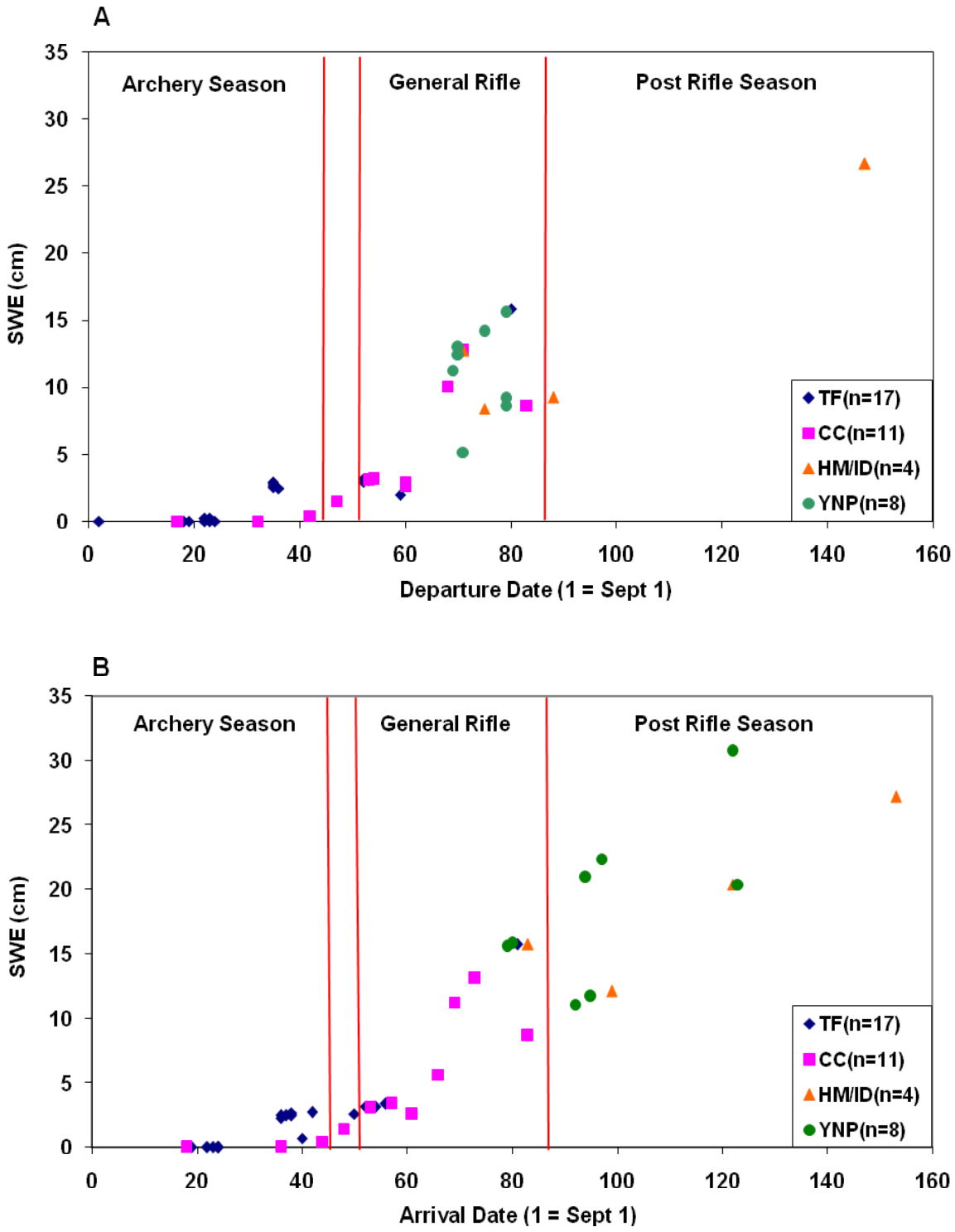


Figure 9. Regional elk departure from summer ranges (A) and arrival on winter ranges (B) plotted against snow-water equivalent (SWE) over the course of two years of fall migration (2005, 2006). Red lines indicate hunting season start and end dates.

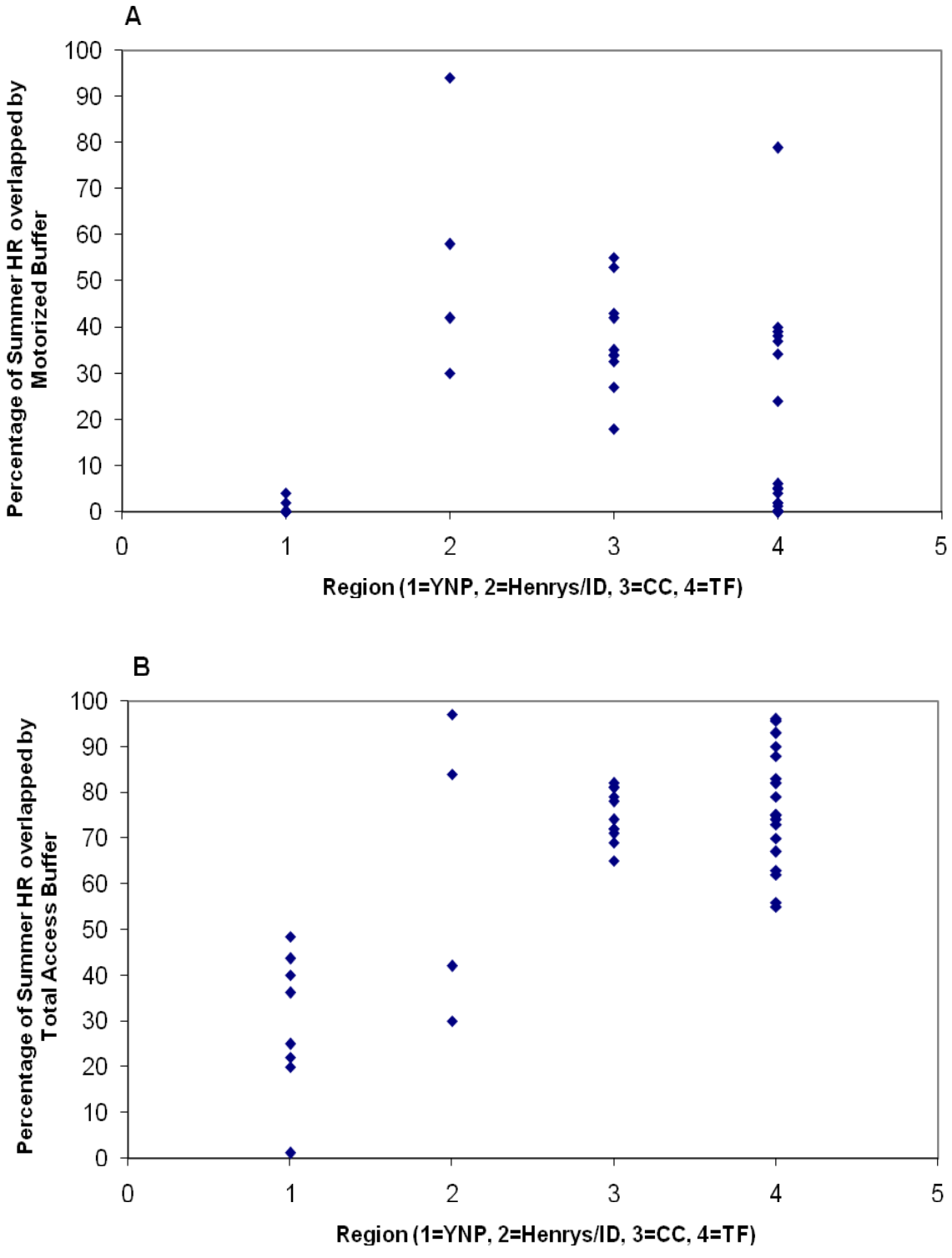


Figure 10. Motorized (A) and total combined motorized and non-motorized (B) access overlap with elk summer home ranges, categorized by region.

Elk Movement Rates during Summer, Archery, and Rifle Seasons

I calculated daytime and nighttime movement rates during summer, general archery season, and general rifle season for each of the 42 elk fitted with GPS radio collars. I censored 22 elk from the rifle season analyses because they initiated fall migration before the opening date of the season. During the first year of the study, elk movement rates (Euclidean distance moved (m) per 30-min interval) were positively correlated with motorized and total combined motorized and non-motorized access levels on summer ranges (Figure 11). Movement rates during summer ($R^2 = 0.34$) and during the archery season ($R^2 = 0.35$) increased in response to total combined access, while movement rates during the general rifle season of 2005 were positively correlated with motorized access ($R^2 = 0.63$). However, these patterns were not apparent in the second year of data from 2006 (Figure 11), resulting in ambiguous final models in which I was largely unable to detect movement rate responses relative to the motorized and total access covariates.

Summer daytime movement rates per 30-min interval ranged from 86.0 to 229.2 m ($\bar{x}$ = 119.6, SD = 28.9), while nighttime rates ranged from 41.0 to 201.0 m ($\bar{x}$ = 71.1, SD = 30.0). None of the final summer season *a priori* models had coefficient values that did not overlap zero. When I included age of the elk in *post priori* exploratory analyses of summer models it was significant in combination with canopy coverage ($R^2_{adj} = 0.22$; $\hat{\beta}_{Age} = -2.10$, 95% C.I. = -0.10, -4.10; $\hat{\beta}_{Can} = -0.99$, 95% C.I. = -0.32, -1.66). Daytime movement rates per 30-min interval during archery season ranged from 67.7 to 200.3 m

($\bar{x}$ = 106.1, SD = 22.9), while nighttime rates ranged from 37.4 to 127.0 m ($\bar{x}$ = 66.9, SD = 17.0). The top *a priori* archery season model (R^2_{adj} = 0.13) included only the total access covariate ($\hat{\beta}_{Access} = 0.38$, 95% C.I. = 0.65, 0.11) and this was the only covariate in any model for which the 95% CI for its coefficient value did not include zero. Age and region did not improve the archery season *a priori* model results when included in *post priori* exploratory analyses. General rifle season daytime movement rates per 30-min interval ranged from 54.0 to 225.8 m ($\bar{x}$ = 121.7, SD = 37.9), while nighttime rates ranged from 29.8 to 81.6 m ($\bar{x}$ = 59.4, SD = 14.0). None of the final general rifle season *a priori* models had coefficient values that did not overlap zero. However, there was support for regional differences when the region covariate was included *post priori.* Elk whose summer ranges occurred in the YNP region had lower movement rates during the general rifle season than elk whose summer ranges occurred in the other 3 regions (R^2_{adj} = 0.21; $\hat{\beta}_{\mathrm{Re}g_{ID}} = 5.89$, 95% C.I. = 46.42, -34.64; $\hat{\beta}_{\mathrm{Re}g_{CC}} = 45.93$, 95% C.I. = 80.17, 11.69; $\hat{\beta}_{\mathrm{Re}g_{TF}} = 38.71$, 95% C.I. = 108.90, -31.48). Daytime movement rates during the rifle season were generally higher for elk whose summer ranges were located in the Taylor Fork and Cabin Creek regions ($\hat{\beta}_{\mathrm{Re}g_{TF\&CC}} = 147.51$, 95% C.I. = 187.14, 107.88) than for elk whose summer ranges were located in the YNP and ID/Henry's regions ($\hat{\beta}_{\mathrm{Re}g_{YNP\&ID}} = 104.44$, 95% C.I. = 114.28, 94.60), though 95% CIs did overlap.

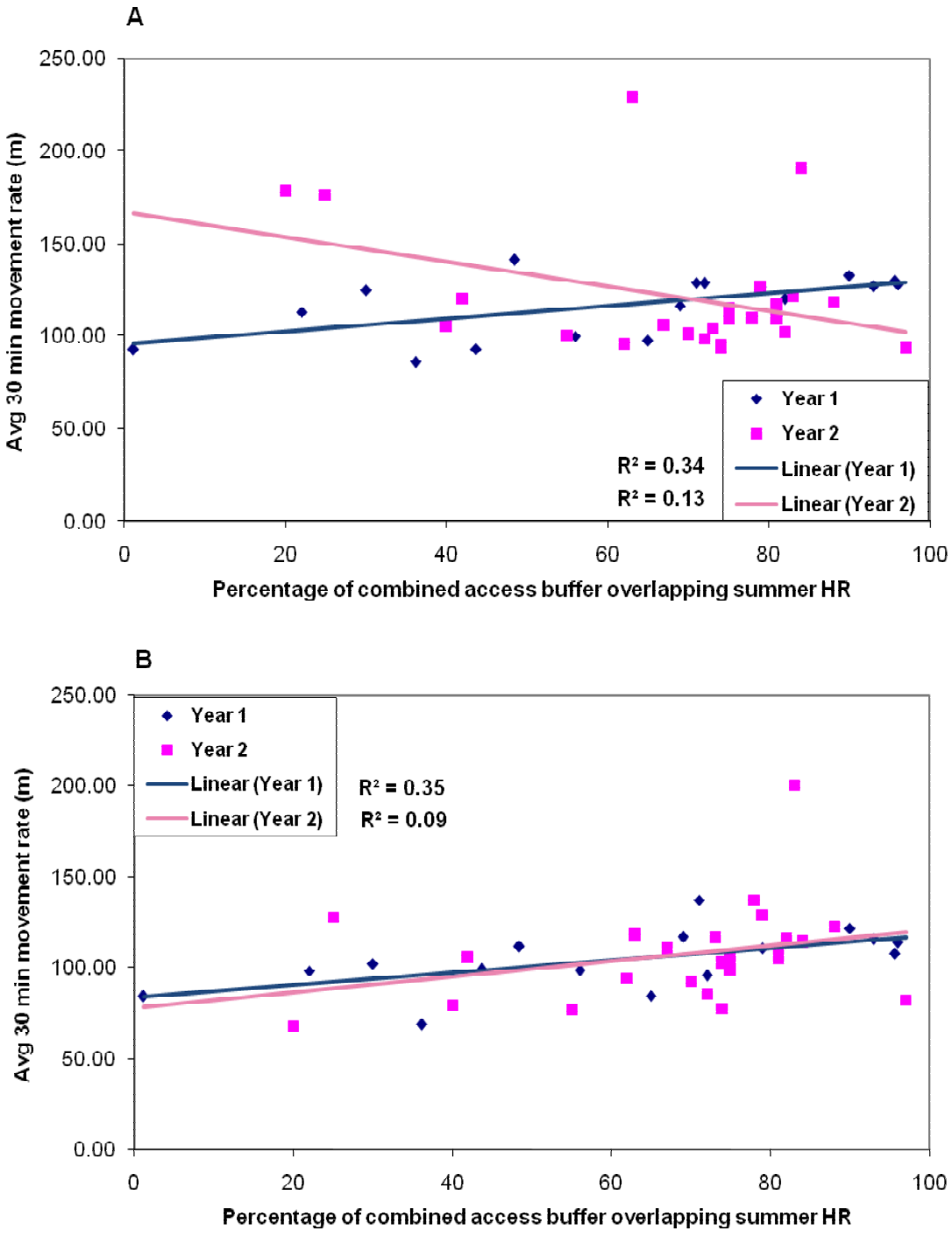


Figure 11. Correlations between adult female elk daytime movement rates (m/30-min) and motorized and total combined motorized and non-motorized access during the (A) summer, (B) archery, and (C) general rifle seasons over the period of two years (2005, 2006). R^2 values for each year are displayed adjacent to the legend for each year.

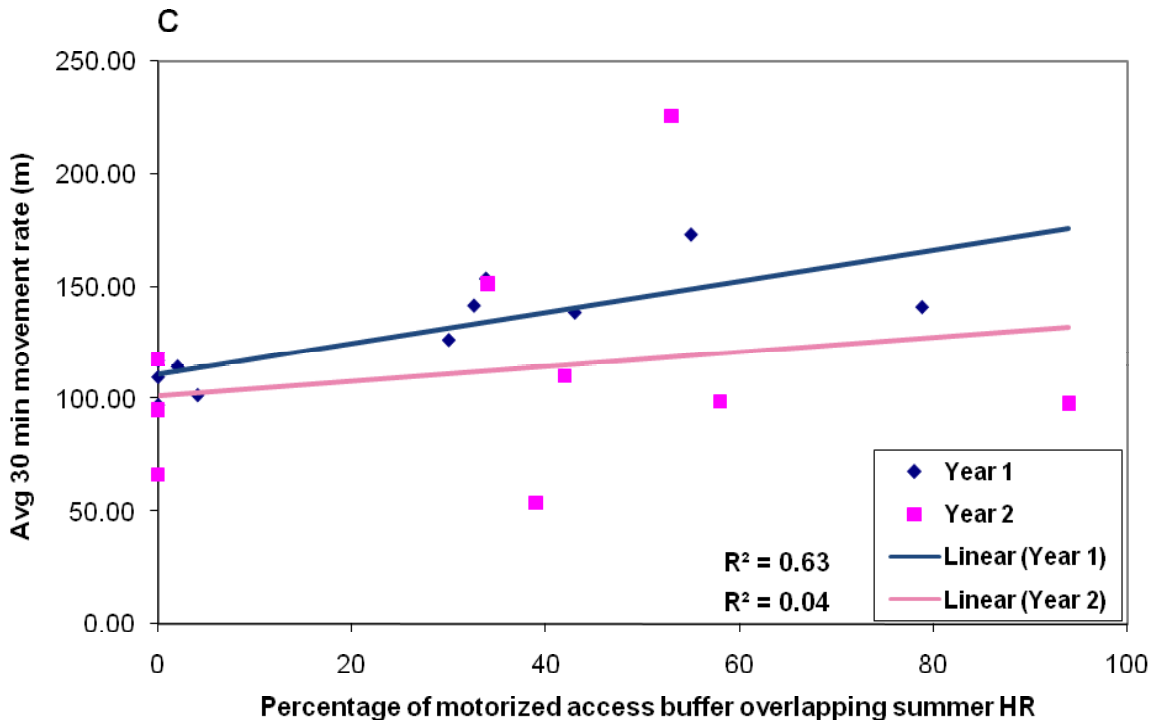


Figure 11, Continued. Correlations between adult female elk daytime movement rates (m/30-min) and motorized and total combined motorized and non-motorized access during the (A) summer, (B) archery, and (C) general rifle seasons over the period of two years (2005, 2006). R^2 values for each year are displayed adjacent to the legend for each year.

DISCUSSION

Few studies have considered wildlife responses to human disturbance and hunting pressure within the larger ecological context of predator-prey shell games (Mitchell and Lima 2002). Given that large herbivores respond behaviorally to the presence of wolves and other predators (Creel et al. 2005, Hebblewhite et al. 2005, Gude et al. 2006), we should expect similar adaptive behavioral shifts when large herbivores are presented with risk in the form of human disturbance and hunting pressure (Beale and Monaghan 2004). The results from this study appear to support such expectations and indicate that large herbivore responses to human disturbance and hunting pressure is easily framed within the wider discussion of general predator-prey theory (Houston and McNamara 1991, Mitchell and Lima 2002). I found support for *a priori* predictions that elk summer home range size is affected by summer recreational access and timing of the fall migration is strongly influenced by regional gradients in predation risk from human hunters associated with hunting license allocation, access to summer ranges, and proximity to urban areas. Further, it seems likely that elk movements and distribution were heavily influenced not merely by road and trail access networks, but also by usage rates of the access networks that we were unable to directly account for. Just as predators such as wolves may affect elk populations through both direct predation (direct effects) as well as behavioral shifts leading to indirect effects (Hebblewhite 2000, Jaffe 2001, Smith et al. 2004), humans appear to have similar effects on prey animals. Distributional shifts have potential impacts on animal physiological and nutritional condition if they are driven from areas of

preferred habitat. Further, distributional shifts of animals from publicly-owned lands to large tracts of privately-owned land acting as refuge areas can negatively impact hunting opportunities for sportsmen who hunt publicly-owned lands and complicate biologists' task of managing herd sizes at biological and societal objectives.

Large herbivores do not distribute themselves randomly on the landscape (Irwin and Peek 1983, Unsworth et al. 1998), they reduce habitat use of areas near roads (Lyon 1979, Rost and Bailey 1979, Rowland et al. 2000, Wisdom et al. 2005), and increasing road and trail access can make animals more vulnerable to hunting mortality (Hurley and Sargeant 1991, Unsworth and Kuck 1991, Hayes et al. 2002, McCorquodale et al. 2003). Given empirical evidence that large herbivores tend to reduce use of habitats near roads and trails, I examined how access to summer ranges influences elk summer home range size, movement rates, and timing of the fall migration. Results indicated that many elk summering on public lands were unavailable to public-land hunters, particularly during the general rifle season. The majority of elk summering in the Taylor Fork and Cabin Creek regions, two popular hunting areas, left public-land summer ranges and migrated to private-land winter ranges during the general archery season or around the opening weekend of the general rifle season. Although other studies found evidence that snow is the primary driver of elk migration (Rudd et al. 1983, Sweeney and Sweeney 1984), 28% of the elk summering in the Taylor Fork and Cabin Creek regions migrated to winter ranges before the first snowfall of the season, coinciding with the onset of the archery hunt. Further, 83% of elk summering in these 2 regions migrated to winter ranges when regional SWE accumulations were <5 cm. All elk summering in the Taylor Fork and

Cabin Creek regions (28/28) completed migration to winter ranges by the end of the general rifle season. This is in stark contrast to migration patterns of elk summering in YNP and the Bacon Rind portion of the Lee Metcalf Wilderness, both closed to hunting, and elk summering to the south along the Montana-Idaho border. Although the area surrounding the Montana-Idaho border receives some hunting pressure, allotted hunter licenses on the Idaho portion of this region are heavily restricted, particularly during the rifle hunts, and seasons are shorter than in Montana (pers. comm., Idaho Fish and Game). Thus, it is reasonable to assume that elk in this region receive considerably less hunting pressure than elk in the Taylor Fork and Cabin Creek regions. All collared elk in the YNP and Idaho/Henry's regions (12/12) remained on summer ranges until at least 8 November, well into the general rifle season in Montana. Further, 75% of these animals did not arrive on winter ranges until after the general rifle season had ended. SWE exceeded 10 cm (and was often >20 cm) upon initiation of migration for all elk summering in these 2 regions. The large variation in the timing of fall migration along regional gradients of hunting risk provided strong indication that fall migration of elk in the Taylor Fork and Cabin Creek regions was largely driven by response to predation risk from human hunters, while fall migration of elk summering in the YNP/Bacon Rind and Idaho/Henry's regions was likely driven primarily by plant phenology and snow pack.

There are several likely explanations for the result that timing of fall migration was not strongly influenced solely by motorized and total access covariates. It appears evident that usage rates and types of activities associated with use act in concert with road and trail densities to influence how elk respond to roads and trails. Roads and trails

receiving less use and relatively lower-impact types of use (e.g., hiking vs. motorized use and hunting vs. non-hunting pressure) likely have less impact on animal movements and distribution. Elk summering in the Henry's Mountains and south into Idaho had the highest levels of summer home range overlap with motorized access, yet tended to migrate late in the fall, similar to the migration timing of elk summering in YNP and the non-hunted Bacon Rind portion of the Lee Metcalf Wilderness. These elk summer home ranges all extended at least partially into Idaho, where hunting license allotments are limited, particularly during the rifle seasons, and hunting seasons are shorter (pers. comm. Idaho Fish and Game). It appears plausible that the relatively reduced hunting pressure associated with individual roads and trails bisecting elk summer ranges in this region had a substantial effect on the influence of road and trail densities on initiation of elk fall migration. Because elk summer home ranges in the Henry's/ID region had higher levels of overlap with motorized access routes than for elk summering in the Taylor Fork and Cabin Creek regions, the *a priori* models were unable to detect hypothesized effects of motorized access on the timing of fall migration. It appears likely this result manifests from the relatively lower levels of usage rates and hunting pressure apparently associated with roads and trails in this area. The Taylor Fork region lies in close proximity, relative to the other regions where elk in this study summered, to the metropolitan human population center of Bozeman (Figure 1) and likely receives higher use rates than other regions where elk summered (pers. comm., MTFWP, USFS; Ewart 1993, Hammitt and Cole 1998, De Vries and Goosen 2002). This region is accessible via approximately 30 km of gravel road open to passenger vehicles, receives heavy hunting pressure and is a

popular destination for horse camps and outfitters (pers. comm., MTFWP, USFS). Though limited in its accuracy, hunter check station data suggests the Taylor Fork region receives substantially higher numbers of hunters than other regions in this study (unpublished data, MTFWP). If hunters drive motorized access routes as far as possible, then travel non-motorized trails (which heavily overlapped elk summer home ranges in the Taylor Fork region) either by foot or horse-back from that point, elk summer ranges in the Taylor Fork region become accessible very readily (Figure 12). It is likely that the intensity of use of the roads and trails and type of risk associated with it (e.g., hunted vs. non-hunted areas) on elk summer ranges may have been an important influence on timing of fall migrations. Thus, the access covariates used may have been confounded by varying degrees and types of human use associated with the travel networks. Unfortunately, I was unable to directly account for usage rates along roads and trails leading to elk summer ranges. This would be a beneficial metric to add to models testing the effects of human access on wildlife spatial dynamics in the future (Beale and Monaghan 2004).

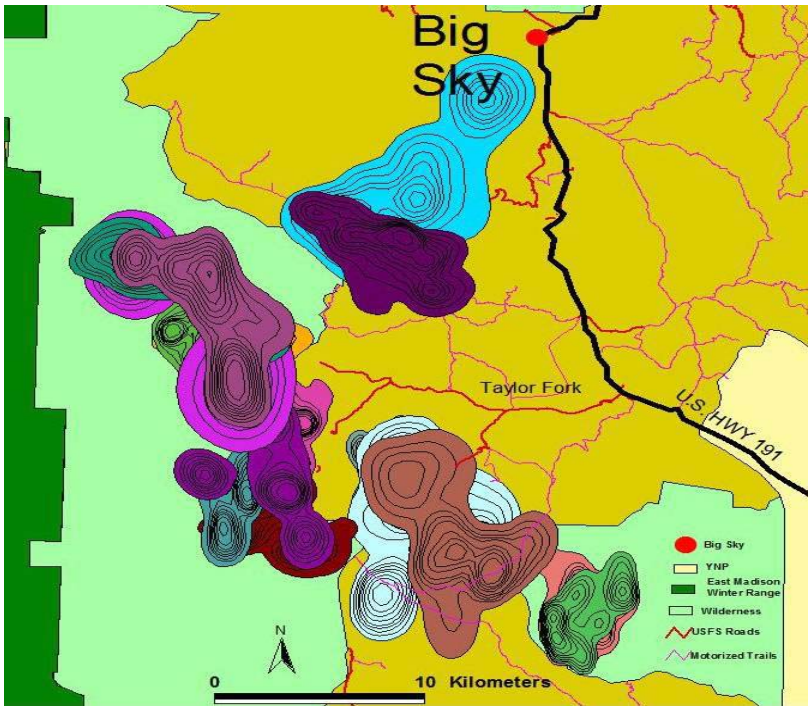


Figure 12. Appparent non-random distribution of elk summer home ranges (n=17) around the main arterial access road into the Taylor Fork region during the summers of 2005 and 2006.

In addition to altering distribution, habitat use, and migration patterns of wildlife, we might further expect that increases in human access to wildlife habitat would influence movement rates of animals. I attempted to examine this by measuring elk Euclidean distance moved at 30-min intervals, rationalizing that increased movement rates could impact habitat use and physiological condition of animals as they prepare for harsh winters when nutrition intake drops to a sub-maintenance level and animals enter a period of energy conservation (Delgiudice et al. 2001, Cook et al. 2004). Although data from the first year gave some indication that movement rates increased relative to access,

particularly during the hunting seasons, these effects were not evident in the second year of data and my final models were ambiguous, with confidence intervals for coefficients spanning zero. However, there was some indication that regional gradients of predation risk during the hunting seasons influenced movement rates, as animals whose summer ranges included the Taylor Fork and Cabin Creek regions moved an average of 7.1 km per day compared to YNP and ID/Henry's elk that moved an average of 5.0 km per day during the general rifle season.

Though the movement rate models were ambiguous and I was not able to detect trends related directly to access levels maintained over both years, the larger elk summer home ranges associated with motorized access may be an indicator that elk require larger areas to acquire necessary food reserves while avoiding human disturbance (Nicholson et al. 1997). I also found age of the elk to be influential in summer home range size, likely a result of younger animals increasing exploratory movements as they become familiar with new ranges and search for the best available habitat areas (Beckoff 1977). Most animals were pregnant when captured in February (2005 = 15/17, 88%; 2006 = 20/25, 80%) but because I could not monitor fetus or neonate survival, it was impossible to test the influence of calving on summer home range size, though it would make biological sense that these factors are influential.

Although the general trends associated with summer home range results were substantial, the large amount of unexplained variation indicated that individual elk differ substantially in how they perceive and respond to disturbance and risk. Interestingly, elk appeared to respond differently to access based on seasonal occurrence. For example,

motorized access correlated with larger summer home ranges, though no general regional effects were evident; yet elk appeared to respond strongest to general regional vulnerability to hunting pressure during the fall hunting seasons. This may relate to how elk perceive risk from human presence at different times of the year. For example, during summer, humans present elk with a disturbance but are not an imminent predation threat. In contrast, during hunting seasons, human access is not just associated with disturbance, but rather is associated with a direct predation threat and elk appeared to respond to this threat of varying regional intensities by initiating migration and completely leaving areas of high predation risk. On summer ranges, elk appeared to adjust to human disturbance on much smaller spatial scales by moving, but generally did not abandon the general summer range area. The threat of direct mortality, however, may be strong enough to push them entirely off summer ranges prematurely as they balance the trade-off of food acquisition and predation risk (Krebs and Davies 1993).

One potential advantage of GPS radio-collar technology over other methods used to monitor wildlife is that it provides biologists with detailed descriptions of paths used and behavioral traits demonstrated during migrations (Blake et al. 2001, Sawyer et al. 2006). I found strong evidence that many individuals within a population may use the same corridors and that these corridors are often very narrow in places. Migration vectors from our research provide descriptive evidence of anti-predator strategy in some elk fall migrations during the hunting seasons, as some animals appeared to circumnavigate areas of potential high hunter activity. For example, one elk followed the YNP boundary south for several weeks, staying just inside the park boundary, before

leaving the park and quickly proceeding to winter ranges in the Madison Valley (Figure 13). Her route back to winter range differed entirely from her spring migration path along the Madison River drainage, where hunting pressure is substantial during the fall. Examples this dramatic were uncommon, but they provided detailed insight into individual anti-predator strategy. Elk often used the same corridors for both spring and fall migrations, though behavior exhibited during these migrations often varied substantially and large individual variation in behavior was evident.

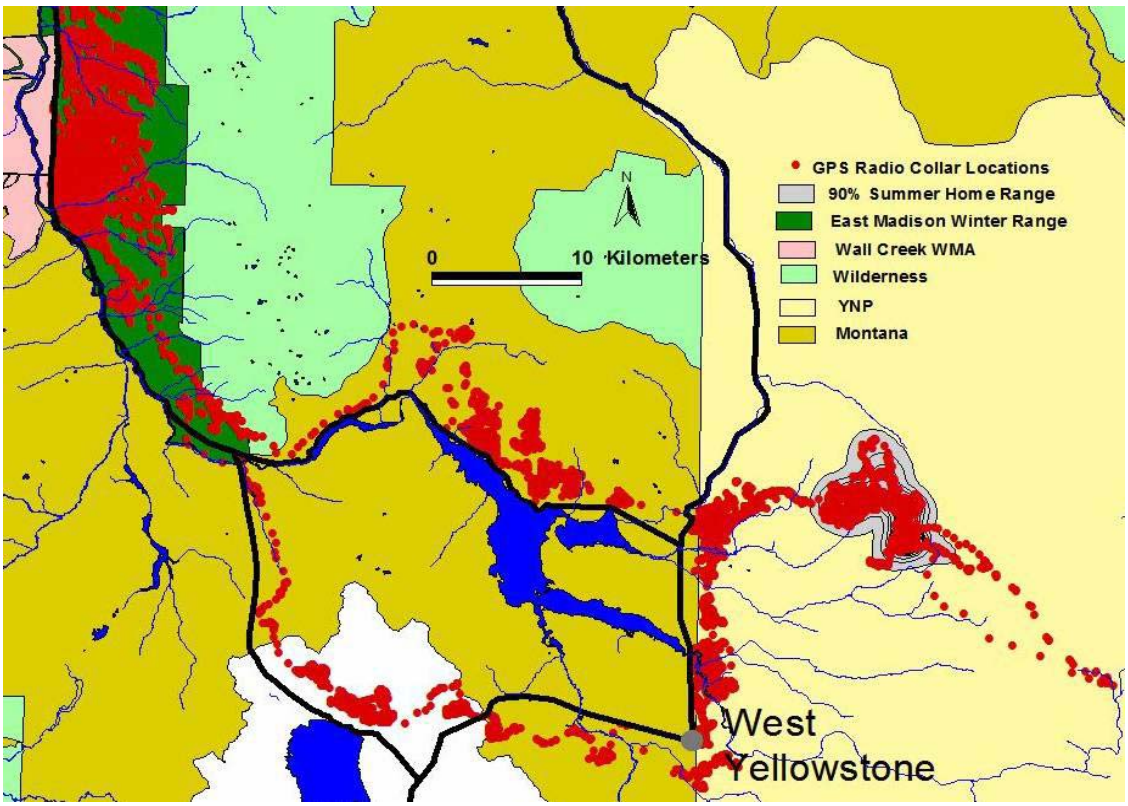


Figure 13. Apparent anti-predator strategy exhibited by a radio-collared elk during the fall migration. Locations stored on GPS radio collar indicate this elk followed the Yellowstone National Park boundary south during its fall migration, then traveled a low-risk route back to winter range, rather than the path used during its spring migration which is an area receiving relatively heavy hunting pressure during the fall.

Although increasing road and trail levels on public lands may increase access for more people, my results support previous research that increased access and usage rates also increases disturbance to wildlife (Rowland et al. 2000, Wisdom et al. 2005), presents wildlife with increased predation risk during hunting seasons (Hurley and Sargeant 1991, Unsworth and Kuck 1991, Hayes et al. 2002, McCorquodale et al. 2003), and that animals adapt behaviorally to these threats. Elk presented with the highest disturbance levels in this study had larger summer home ranges. Further, unequal gradients of risk during the hunting seasons initiated fall migration to less heavily-hunted winter ranges earlier for elk summering in relatively heavily hunted areas than elk summering in more secure areas. Elk summering in relatively protected areas, such as Yellowstone National Park, tended to migrate later in the winter, once snow pack became substantial. In contrast, elk summering in areas where access was high during the hunting seasons often migrated with the onset of the archery or general rifle seasons and were largely unavailable to public-land hunters for significant portions of the hunting seasons. This indicates a large behavioral response to predation risk, resulting in the altering of migration timing to winter ranges.

The East Madison wintering elk herd is similar to many large herbivore populations across the western United States that summer on public lands where management policies and objectives vary widely and winter primarily on privately-owned agricultural ranchlands (Knight and Landres 1998). If large herbivores migrate from public lands to privately owned winter ranges before or during the first few days of hunting seasons, management of herd sizes can become a tremendously difficult task for

biologists, and public opportunity to hunt these animals is diminished. Somewhat ironically, increasing road and trail access routes to summer ranges of large herbivores may actually decrease public access to these animals during the hunting seasons as animals respond by shifting to privately-owned refuge areas. Certainly this appears to be the case for the East Madison wintering elk herd, which remains above population objective and continues to grow despite liberalized hunting regulations (pers. comm., MTFWP). If managers want to provide incentive for large herbivores to remain on public land summer ranges through the hunting seasons, as elk in areas of low hunting risk did in this study, strategies may need to be devised that create a more even gradient of risk across the landscape (Lima 2002). Specifically, road and trail access to summer ranges may need to be limited to decrease regional hunting pressure and provide a more even gradient of risk across the landscape. Landowners who suffer hardship due to early elk arrivals on private winter ranges may help alleviate the problem by allowing access to public hunters during the general archery and rifle seasons to help balance the unequal gradient of hunting pressure between public and private lands. Further, public programs that give landowners incentive to allow public hunters access to private wintering areas that act as refuge from hunting risk may redistribute predation risk and discourage early fall migrations of large herbivores.

LITERATURE CITED

Ager, A.A., B.K. Johnson, J.W. Kern, and J.G. Kie. 2003. Daily and seasonal movements and habitat use by female rocky mountain elk and mule deer. Journal of Mammalogy **84**:1076-1088.

Barham, E. 2001. Ecoloical boundaries as community boundaries: the politics of watersheds. Society and Natural Resources **14**:181-191.

Beale, C.M., and P. Monaghan. 2004. Human disturbance: people as predation-free predators? Journal of Applied Ecology **41**:335-343.

Bekoff, M. 1977. Mammalian dispersal and the ontogeny of individual behavioral phenotypes. The American Naturalist **111**:715-732.

Berger, J. 2004. The last mile: how to sustain long-distance migration in mammals. Conservation Biology **18**:320-331.

Blake, S., I. Douglas-Hamilton, and W.B. Karesh. 2001. GPS telemetry of forest elephants in Central Africa: results of a preliminary study. African Journal of Ecology **39**:178-186.

Blundell, G.M., J.A.K. Maier, and E.M. Debevec. 2001. Linear home ranges: effects of smoothing, sample size, and autocorrelation on kernel estimates. Ecological Monographs **71**:469-489.

Burcham, M., W.D. Edge, and C.L. Marcum. 1999. Elk use of private land refuges. Wildlife Society Bulletin **27**:833-839.

Burnham, K.P., and D.R. Anderson. 2002. Model selection and multi-model inference. Springer-Verlag, New York, NY, USA.

Caro, T.M., editor. 1998. Behavioral Ecology And Conservation Biology. Oxford University Press, New York, NY, USA.

Cederlund, G., and H. Sand. 1994. Home range size in relation to age and sex in moose. Journal of Mammology **75**:1005-1012.

Cook, J.G., B.K. Johnson, R.C. Cook, R.A. Riggs, T. Delcurto, L.D. Bryant, and L.L. Irwin. 2004. Effects of summer-autumn nutrition and parturition date on reproduction and survival of elk. Wildlife Monographs **155**:1-61

Cook, R.C., J.G. Cook, and L.D. Mech. 2004. Nutritional condition of northern Yellowstone elk. Journal of Mammalogy **85**:714-722.

Connor, M.M., G.C. White, and D.J. Freddy. 2001. Elk movement in response to early-season hunting in northwest Colorado. Journal of Wildlife Management **65**:926-940.

Creel, S., J. Winnie, Jr., B. Maxwell, K. Hamlin, and M. Creel. 2005. Elk alter habitat selection as an anti-predator response to wolves. Ecology **86**:3387-3397.

Delgiudice, G.D., R.A. Moen, F.J. Singer, and M.R. Riggs. 2001. Winter nutritional restriction and simulated body condition of Yellowstone elk and bison before and after the fires of 1988. Wildlife Monographs **147**:1-60.

D'eon, R.G., and D. Delparte 2005. Effects of radio-collar position and orientation on GPS radio-collar performance, and the implications of PDOP in data screening. Journal of Applied Ecology **42**:383-388.

Despain, D.G. 1990. Yellowstone Vegetation. Robert Rhinehart, Boulder, CO, USA.

De Vries, S., and M. Goossen. 2002. Modelling recreational visits to forests and nature areas. Urban Forestry and Urban Greening **1**:5-14.

Ewart, A.W. 1993. The wildland-urban interface: introduction and overview. Journal of Leisure Research **25**:1-5.

Festa-Bianchet, M. 1988. Seasonal range selection in bighorn sheep: conflicts between forage quality, forage quantity, and predator avoidance. Oecologia **75**:580-586.

Festa-Bianchet, M., and M. Apollonio, editors. 2003. Animal Behavior and Wildlife Conservation. Island Press, Washington, D.C., USA.

Geist, V. 2002. Adaptive behavioral strategies. Pages 389-433 *in* D. E. Toweill and J. W. Thomas, editors. North American Elk: ecology and management. Wildlife Management Institute, Washington, D.C., USA.

Gude, J.A. 2004. Applying risk allocation theory in a large mammal predator-prey system: elk-wolf behavioral interactions. Thesis. Montana State University, Bozeman, MT, USA.

Gude, J.A., R.A. Garrott, J.J. Borkowski, and F. King. 2006. Prey risk allocation in a grazing ecosystem. Ecological Applications **16**:285-298.

Hamlin, K.L., D.F. Pac, C.A. Sime, R.M. DeSimone, and G.L. Dusek. 2000. Evaluating the accuracy of ages obtained by two methods for Montana ungulates. Journal of Wildlife Management **64**:441-449.

Hammit, W.E., and D.N. Cole. 1998. Wildland Recreation: Ecology and Management. Wiley, New York, NY, USA.

Hansen, A.J., R. Rasker, B. Maxwell, J.J. Rotella, J.D. Johnson, A.W. Parmenter, U. Langner, W.B. Cohen, R.L. Lawrence, M.P.V. Kraska. 2002. Ecological causes and consequences of demographic change in the new west. BioScience **52**:151-162.

Hayes, S. G., D. J. Leptich, and P. Zager. 2002. Proximate factors affecting male elk hunting mortality in northern Idaho. Journal of Wildlife Management **66**:491-499.

Hebblewhite, M. 2000. Wolf and elk predator-prey dynamics in Banff National Park. Thesis. University of Montana. Missoula, MT, USA.

Hebblewhite, M., C.A. White, C.G. Nietvelt, J.A. McKenzie, T.E. Hurd, J.M. Fryxell, S.E. Bayley, and P.C. Paquet. 2005. Human activity mediates a trophic cascade caused by wolves. Ecology **86**:2135-2144.

Horne, J.S., and E.O. Garton. 2006. Selecting the best home range model: an information-theoretic approach. Ecology **87**:1146-1152.

Houston, A.I., and J.M. McNamara. 1999. Models Of Adaptive Behavior. Cambridge University Press, Cambridge, England.

Hurley, M.A., and G.A. Sargeant. 1991. Effects of hunting and land management on elk habitat use, movement patterns, and mortality in western Montana. Pages 94-98 *in* A.G. Christensen, L.J. Lyon, and T.N. Lonner, editors. Proceedings of elk vulnerability symposium, Montana State University, Bozeman, USA.

Irwin, L.L., and J.M. Peek. 1983. Elk habitat use relative to forest succession in Idaho. Journal of Wildlife Management **47**:664-672.

Irwin, L.L. 2002. Migration. Pages 493-513 *in* D. E. Toweill and J. W. Thomas, editors. North American Elk: ecology and management. Wildlife Management Institute, Washington, D.C., USA.

Jaffe, R. 2001. Winter wolf predation in an elk-bison system in Yellowstone National Park, Wyoming. Thesis. Montana State University, Bozeman, MT, USA.

Johnson, M.L., and M.S. Gaines. 1990. Evolution of dispersal: theoretical models and empirical tests using birds and mammals. Annual Reviews in Ecology and Systematics **21**:449-480.

Kerley, G.I.H, R.L. Pressey, R.M. Cowling, A.F. Boshoff, and R. Sims-Castley. 2003. Options for the conservation of large and medium-sized mammals in the Cape Floristic Region. Biological Conservation **112**:169-190.

Knight, R.L., and P.B. Landres, editors. 1998. Stewardship Across Boundaries. Island Press, Washington, D.C., USA.

Krebs, J.R., and N.B. Davies. 1993. An Introduction To Behavioral Ecology. Blackwell Scientific Publications, San Diego, CA, USA.

Lima, S.L. 2002. Putting predators back into behavioral predator-prey interactions. Trends in Ecology and Evolution **17**:70-75.

Lindstedt, S.L., B.J. Miller, and S.W. Buskirk. 1986. Home range, time, and body size in mammals. Ecology **97**:413-418.

Lyon, J. 1979. Habitat effectiveness for elk as influenced by roads and cover. Journal of Forestry **77**:658-660.

Lyon, L.J., and M.G. Burcham. 1998. Tracking elk hunters with the Global Positioning System. Res. Pap. RMRS-RP-3. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. Ogden, UT, USA.

Lyon, L.J., and A.G. Christensen. 2002. Adaptive behavioral strategies. Pages 557-581 *in* D.E. Toweill and J.W. Thomas, editors. North American Elk: ecology and management. Wildlife Management Institute, Washington, D.C., USA.

McCorquodale, S.M., R. Wiseman, and C.L. Marcum. 2003. Survival and harvest vulnerability in the Cascade Range of Washington. Journal of Wildlife Management **67**:248-257.

Mitchell, W., and S.L. Lima. 2002. Predator-prey shell games: large-scale movement and its implications for decision making prey. Oikos **99**:249-259.

Mysterud, A., R. Langvatn, N.G. Yoccoz, and N.C. Stenseth. 2001. Plant phenology, migration, and geographic variation in body weight of a large herbivore: the effect of a variable topography. Journal of Animal Ecology **70**:915-923.

Nicholson, M.C., R.T. Bowyer, and J.G. Kie. 1997. Habitat selection and survival of mule deer: tradeoffs associated with migration. Journal of Mammalogy **78**:483-504.

R Development Core Team. 2004. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-00-3, URL http://www.R-project.org.

Rodgers, A.R., and A.P. Carr. 1998. HRE: The home range extension for ArcView. Ontario Ministry of Natural Resources, Centre for Northern Forest Ecosystem Research, Thunder Bay, Ontario, Canada.

Rost, G., and J. Bailey. 1979. Distribution of mule deer and elk in relation to roads. Journal of Wildlife Management **43**:634-641.

Rowland, M.M., M.J. Wisdom, B.K. Johnson, and J.G. Kie. 2000. Elk distribution and modeling in relation to roads. Journal of Wildlife Management **64**:672-684.

Rudd, W.J., A.L. Ward, and L.L. Irwin. 1983. Do split hunting seasons influence elk migrations from Yellowstone National Park? Wildlife Society Bulletin **11**:328-331.

Sawyer H., R.M. Nielson, F. Lindzey, and L.L. McDonald. 2006. Winter habitat selection of mule deer before and during development of a natural gas field. Journal of Wildlife Management **70**:396–403.

Seaman, D.E., and R.A. Powell. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. Ecology **77:**2075-2085.

Silverman, B.W. 1986. Density estimation for statistics and data analysis. Chapman and Hall, London, England.

Skovlin, J.M., P. Zager, and B.K. Johnson. 2002. Elk habitat selection and evaluation. Pages 531-556 *in* D. E. Toweill and J. W. Thomas, editors. North American Elk: ecology and management. Wildlife Management Institute, Washington, D.C., USA.

Smith, D.W., T.D. Drummer, K.M. Murphy, D.S. Guernsey, and S.B. Evans. 2004. Winter prey selection and estimation of kill rates in Yellowstone National Park, 1995-2000. Journal of Wildlife Management **68**:153-166.

Soule, M.E., and J. Terborgh. 1999. Conserving nature at regional and continental scales: a scientific program for North America. BioScience **49**:809-817.

Southwood, T.R.E. 1966. Ecological Methods. Methuen, London, England.

Sweeney, J.M., and J.R. Sweeney. 1984. Snow depths influencing winter movements of elk. Journal of Mammalogy **65**:524-526.

Unsworth, J.W., and L. Kuck. 1991. Bull elk vulnerability in the Clearwater drainage of north-central Idaho. Pages 85-88 *in* A. G. Christensen, L. J. Lyon, and T. N. Lonner, editors. Proceedings of elk vulnerability symposium, Montana State University, Bozeman, USA.

Unsworth, J.W., L. Kuck., E.O. Garton, and B.R. Butterfield. 1998. Elk habitat selection on the Clearwater National Forest, Idaho. Journal of Wildlife Management **62**:1255-1263.

Vieira, M.E.P., M.M. Connor, G.C. White, and D.J. Freddy. 2003. Effects of archery hunter numbers and opening dates on elk movement. Journal of Wildlife Management **67**:717-728.

White, G.C., and R.A. Garrott. 1990. Analysis Of Wildlife Radio-Tracking Data. Academic Press, San Diego, CA, USA.

Wisdom, M.J., N.J. Cimon, B.K. Johnson, E.O. Garton, and J.W. Thomas. 2005. Spatial partitioning by mule deer and elk in relation to traffic. Pages 53-66 *in* M. J. Wisdom, editor. The Starkey Project: a synthesis of long-term studies of elk and mule deer. Alliance Communications Group, Lawrence, KS, USA.

Worton, B.J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology **70**:164-168.

Worton, B.J. 1995. A convex hull estimator of home-range size. Biometrics **51:**1206-1215.

APPENDICES

APPENDIX A

FOUR *A PRIORI* AND TWO *POST PRIORI* COVARIATES USED IN MODELS OF ADULT FEMALE ELK SUMMER HOME RANGE SIZE (90% ADAPTIVE KERNEL, km^2)

Dependent Variable: Adult Female Summer Home Range Size (km^2)

***a priori* covariates:**
Mot: % of motorized trails buffer overlapping summer HR
Access: % of combined motorized and non-motorized trail buffer overlapping summer HR
Can: % forest canopy cover overlapping summer HR
Year: categorical (2005, 2006)

exploratory covariates:
Age: estimated age of the elk at capture
Reg: categorical (YNP, Henry's/ID, CC, TF)

APPENDIX B

FIVE *A PRIORI* AND TWO *POST PRIORI* COVARIATES USED IN MODELS OF TIMING OF INITIATION OF ELK FALL MIGRATION

Dependent Variable: Date Elk Departs Summer HR en route to Winter Ranges in the Madison Valley (Departure)

***a priori* covariates:**
Mot: % of motorized trails buffer overlapping summer HR
Access: % of combined motorized and non-motorized trail buffer overlapping summer HR
Can: % forest canopy cover overlapping summer HR
Elev: Elevation of summer HR centroid
Year: categorical (2005, 2006)

exploratory covariates:
Reg: categorical (YNP, Henry's/ID, CC, TF)
Dist: Straight-line distance from summer HR centroid to winter range

APPENDIX C

FOUR *A PRIORI* AND TWO *POST PRIORI* COVARIATES USED IN MODELS OF ADULT FEMALE ELK 30-MIN MOVEMENT RATES DURING THE SUMMER, ARCHERY, AND GENERAL RIFLE SEASONS (m/30-MIN)

Dependent Variable: Adult Female Elk Movement Rates during Summer, Archery, and General Rifle Seasons

***a priori* covariates:**
Mot: % of motorized trail buffer overlapping summer HR
Access: % of combined motorized and non-motorized trail buffer overlapping summer HR
Can: % forest canopy cover overlapping summer HR
Year: categorical (2005, 2006)

exploratory covariates:
Age: estimated age of the elk at capture
Reg: categorical (YNP, Henry's/ID, CC, TF)

APPENDIX D

A PRIORI AND *POST PRIORI* MODEL LIST FOR ANALYSES OF FACTORS AFFECTING ELK SUMMER HOME RANGE SIZE

Model (~Summer HR Size)
a priori
Mot
Access
Mot + Can
Access + Can
Mot + Can + Year
Access + Can + Year
post priori
Mot + Age
Access + Age
Mot + Can + Age
Access + Can + Age
Mot + Can + Reg
Access + Can +Reg
Mot + Can + Reg + Age
Access + Can + Reg + Age

APPENDIX E

A PRIORI AND *POST PRIORI* MODEL LIST FOR ANALYSES OF FACTORS AFFECTING TIMING OF ELK FALL MIGRATION

Model (~Timing of Fall Migration)
a priori
Mot
Access
Mot + Can
Access + Can
Elev + Year
Mot + Elev + Year
Access + Elev + Year
Mot + Can + Elev + Year
Access + Can + Elev + Year
post priori
Mot + Can + Reg
Mot + Can + Dist

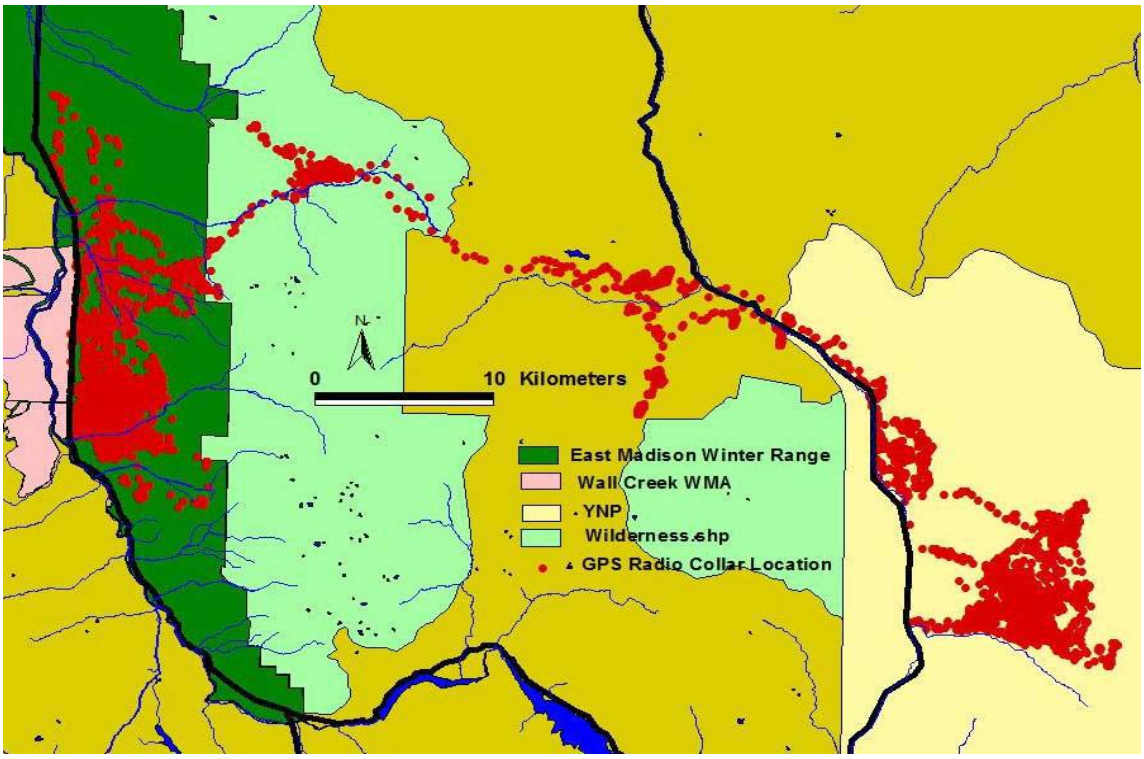
APPENDIX F

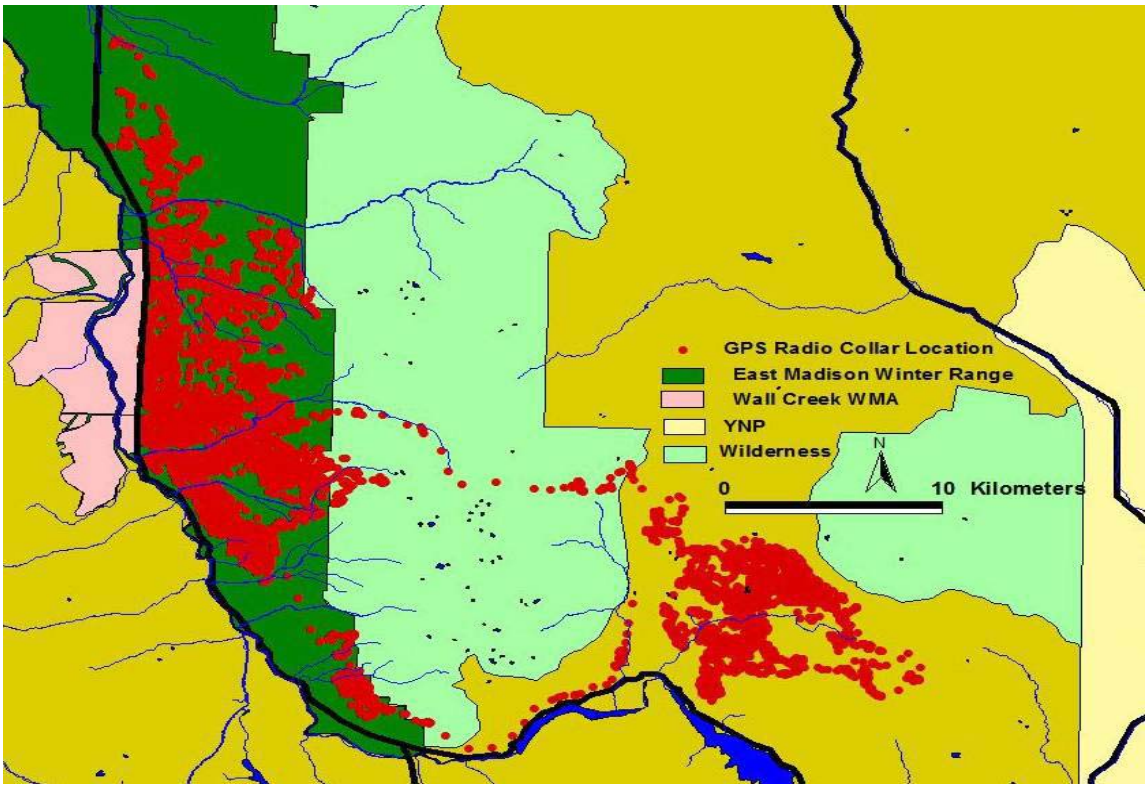
A PRIORI AND *POST PRIORI* MODEL LIST FOR ANALYSES OF FACTORS AFFECTING ELK MOVEMENT RATES ON 30-MIN INTERVALS DURING THE SUMMER, ARCHERY, AND GENERAL RIFLE SEASONS

Model (~Elk Movement Rates)
a priori
Mot
Access
Mot + Can
Access + Can
Mot + Can + Year
Access + Can + Year
post priori
Age
Region
Mot + Age
Access + Age
Mot + Can + Age
Access + Can + Age
Mot + Can + Reg
Access + Can +Reg
Mot + Can + Reg + Age
Access + Can + Reg + Age

APPENDIX G

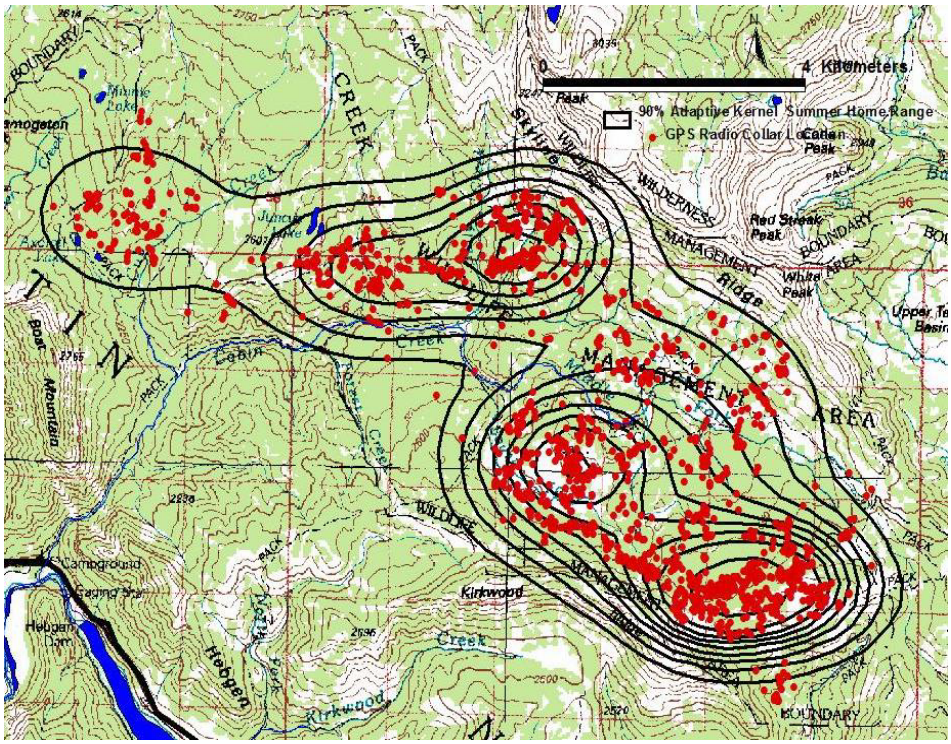
EXAMPLES OF ELK MOVEMENTS THROUGHOUT THE PERIOD OF A FULL YEAR FROM LOCATIONS RECORDED USING GPS RADIO COLLARS WITH 30-MIN FIX INTERVALS

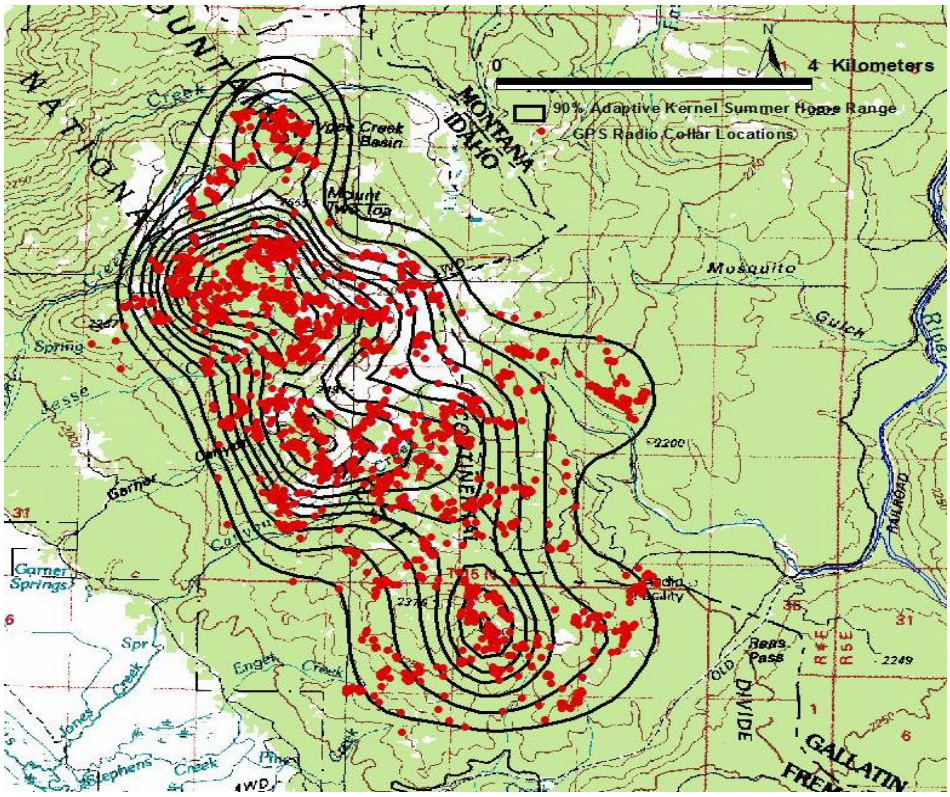

N
0
10 Kilometers
East Madison Winter Range
Wall Creek WMA
YNP
Wilderness.shp
GPS Radio Collar Location


GPS Radio Collar Location
East Madison Winter Range
Wall Creek WMA
YNP
Wilderness
N
0
10 Kilometers

APPENDIX H

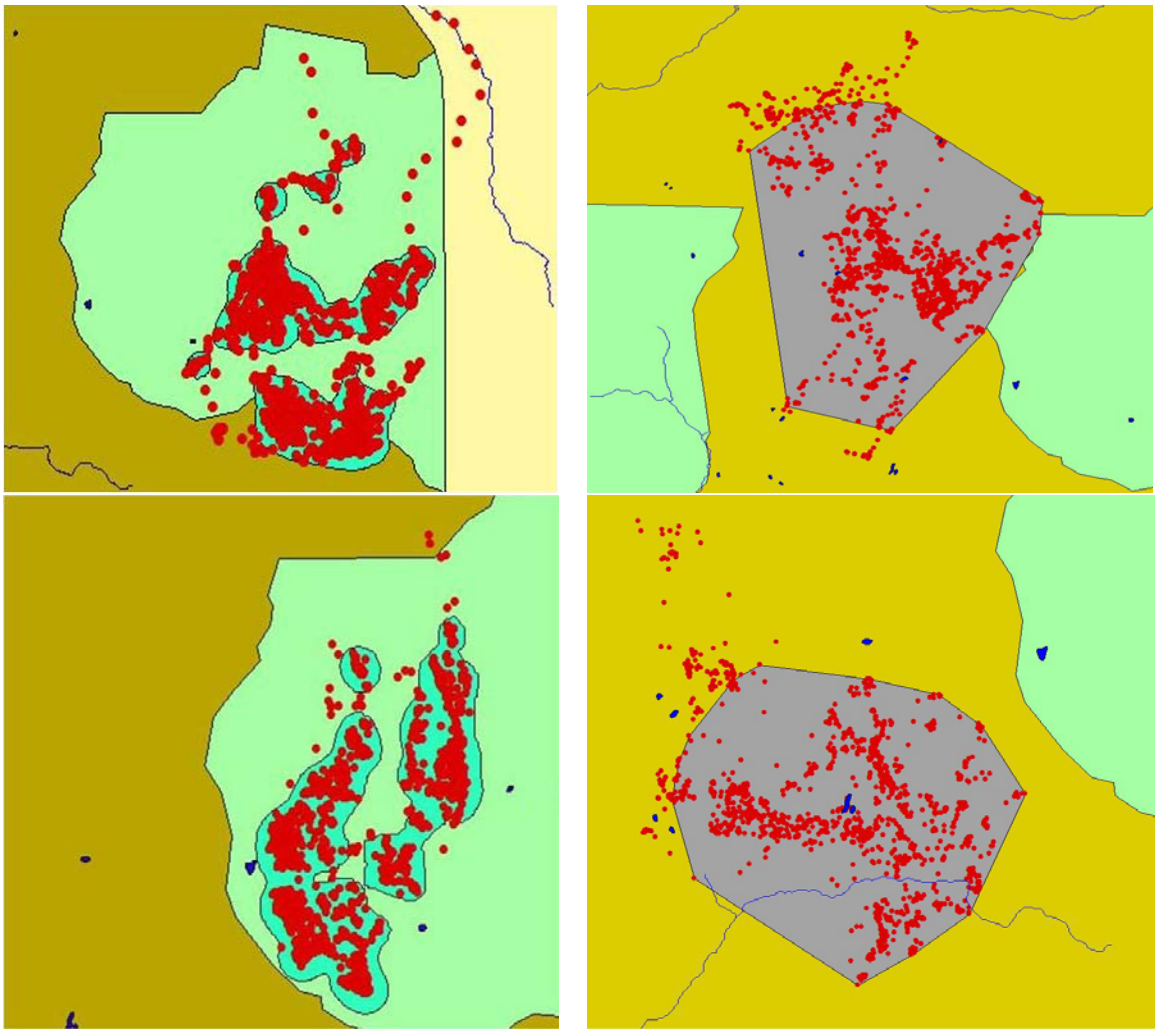
EXAMPLES OF ELK SUMMER HOME RANGES CALCULATED USING 90% ADAPTIVE KERNEL ESTIMATORS. RED DOTS REPRESENT GPS RADIO COLLAR LOCATIONS RECORDED AT 30-MIN INTERVALS


0
4 Kilometers
90% Adaptive Kernel Summer Home Range
GPS Radio Collar Locations
WILDERNESS
MANAGEMENT
AREA
BOUNDARY
Ridge
Creek
Kirkwood
Campground
Hebgen Dam
Red Streak Peak
Cabin
Mountain


0
4 Kilometers
90% Adaptive Kernel Summer Home Range
GPS Radio Collar Locations
MONTANA
IDAHO
Mount Two Top
Mosquito
Gulch
Spring
Garnet
Garnet Springs
Engen Creek
Jones Creek
Stephens Creek
Reas Pass
DIVIDE
GALLATIN

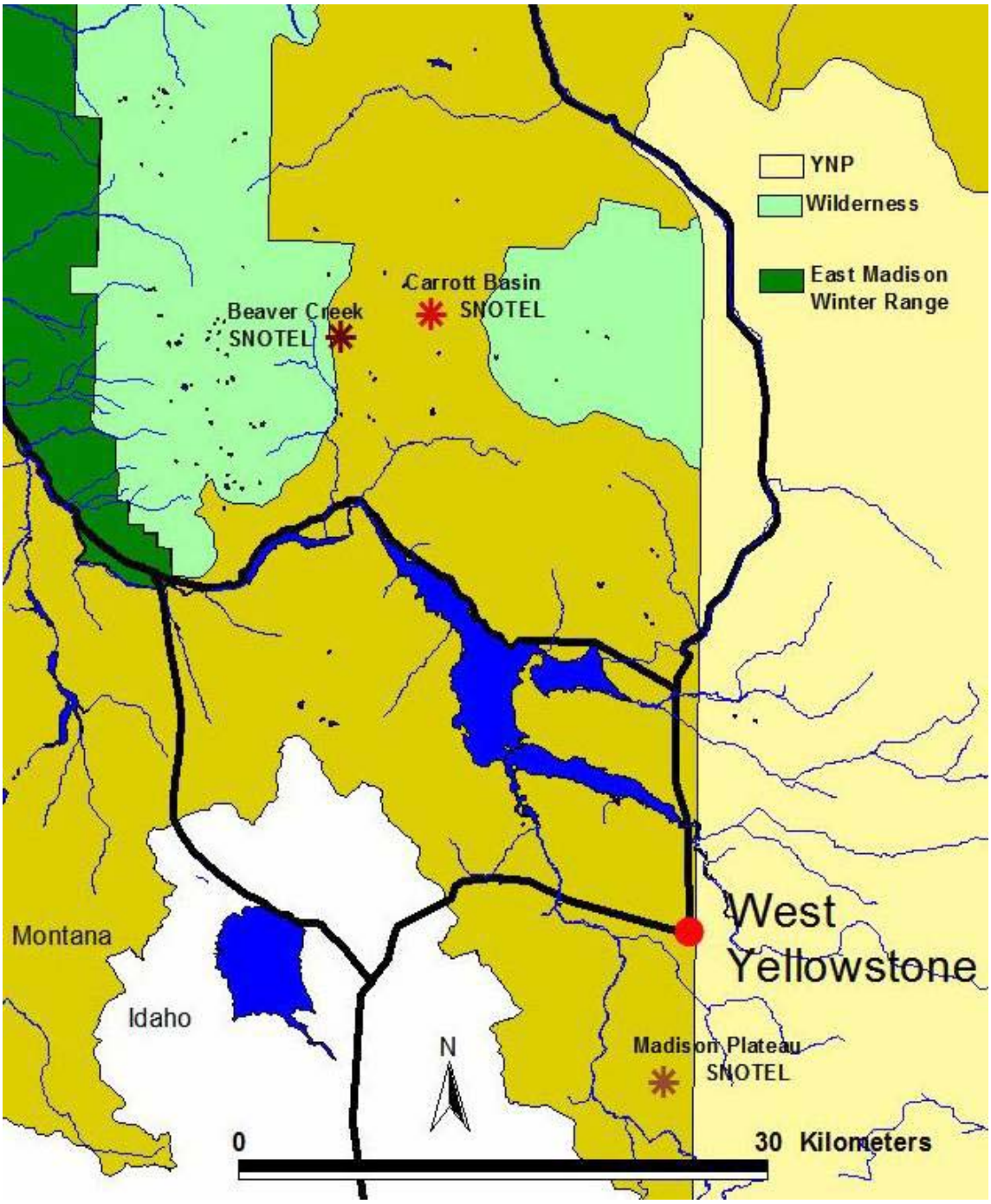
APPENDIX I

EXAMPLES OF TWO SUMMER HOME RANGES PRODUCED USING 90% FIXED KERNEL ESTIMATORS THAT RESULTED IN FRAGMENTED AND POORLY-ESTIMATED HOME RANGE POLYGONS (LEFT) AND EXAMPLES OF TWO SUMMER HOME RANGES PRODUCED USING 90% MINIMUM CONVEX POLYGONS THAT INCLUDED LARGE AREAS THAT APPEARED NOT TO BE USED BY THE ANIMAL (RIGHT)



APPENDIX J

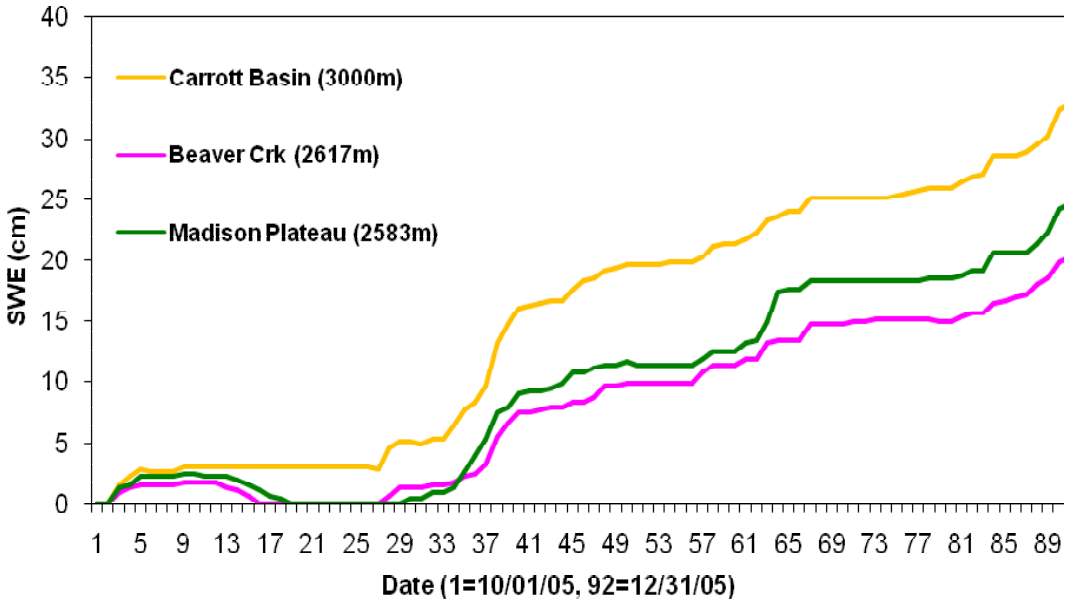
BEAVER CREEK, CARROTT BASIN, AND MADISON PLATEAU SNOTEL SITES USED TO MEASURE SNOW-WATER EQUIVALENT (SWE) VALUES ACROSS ELK SUMMER RANGES


YNP
Wilderness
East Madison
Winter Range
Carrott Basin
SNOTEL
Beaver Creek
SNOTEL
West
Yellowstone
Montana
Idaho
N
Madison Plateau
SNOTEL
0
30 Kilometers

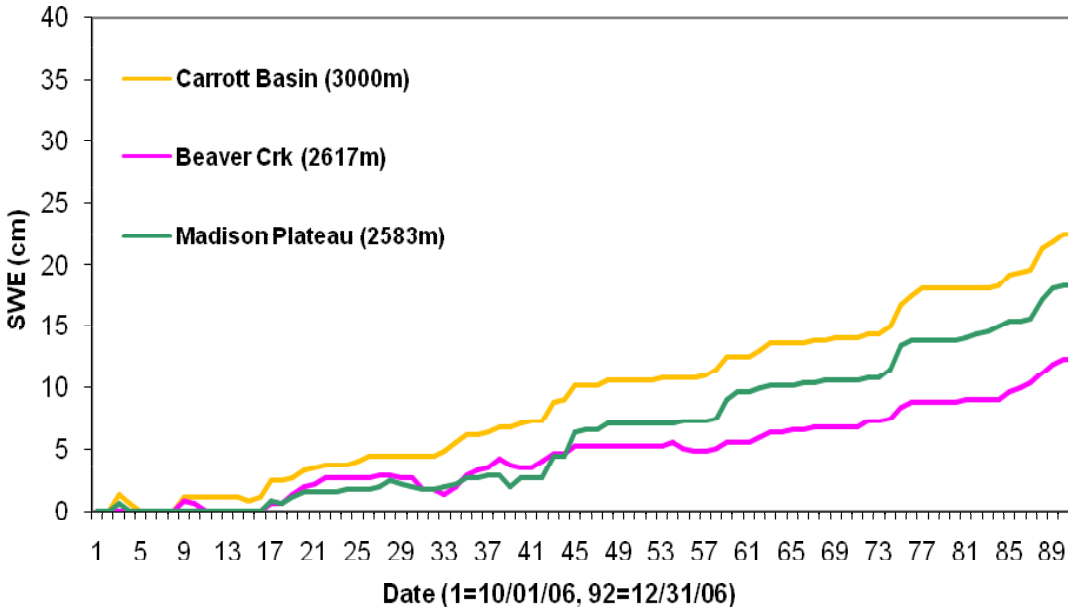
APPENDIX K

SNOW-WATER EQUIVALENT (SWE) VALUES OBTAINED FROM THREE SNOTEL STATIONS DISTRIBUTED ACROSS GPS-COLLARED ELK SUMMER RANGES FOR THE FALL OF 2005 (A) AND 2006 (B)

A


Carrott Basin (3000m)
Beaver Crk (2617m)
Madison Plateau (2583m)
SWE (cm)
0
5
10
15
20
25
30
35
40
1 5 9 13 17 21 25 29 33 37 41 45 49 53 57 61 65 69 73 77 81 85 89
Date (1=10/01/05, 92=12/31/05)

B


Carrott Basin (3000m)
Beaver Crk (2617m)
Madison Plateau (2583m)
SWE (cm)
0
5
10
15
20
25
30
35
40
1 5 9 13 17 21 25 29 33 37 41 45 49 53 57 61 65 69 73 77 81 85 89
Date (1=10/01/06, 92=12/31/06)

APPENDIX L

SUMMER RANGES AND SPRING AND FALL MIGRATION DATES FOR GPS RADIO-COLLARED ELK WINTERING ON THE EAST MADISON WINTER RANGE, 2005 (n = 17)

Animal ID	Summer Range	Leave Winter Range	Arrive Summer Range	Duration Spring Migration (days)	Leave Summer Range	Arrive Winter Range	Duration Fall Migration (days)
150280	Taylor Fork	05/22/05	05/25/05	3	10/05/05	10/06/05	1
150420	Mt Two Top, ID	05/18/05	05/22/05	4	11/10/05	11/22/05	12
150450	YNP	05/07/05	05/28/05	21	11/18/05	12/06/05	21
150470	Taylor Fork/Lee Metcalf Wilderness	06/30/05	06/30/05	1	10/05/05	10/12/05	7
150480	Cabin Crk WMA	06/15/05	06/16/05	1	11/07/05	11/08/05	1
150490	Cabin Crk WMA	07/06/05	07/07/05	1	11/10/05	11/12/05	2
150740	Cabin Crk WMA	06/21/05	06/22/05	1	10/30/05	11/05/05	6
151030	YNP/Lee Metcalf Wilderness	05/22/05	05/29/05	7	11/09/05	12/31/05	52
151140	YNP/Lee Metcalf Wilderness	06/17/05	06/21/05	4	11/09/05	11/18/05	9
151150	Taylor Fork	06/25/05	06/27/05	2	10/06/05	10/08/05	2
151550	Buck Crk	05/17/05	05/18/05	1	11/19/05	11/20/05	1
151560	YNP/Lee Metcalf Wilderness	05/23/05	05/30/05	7	11/08/05	11/19/05	11
151620	Taylor Fork	05/22/05	06/05/05	14	10/05/05	10/06/05	1
151640	YNP/Lee Metcalf Wilderness	06/21/05	06/27/05	6	11/14/05	12/03/05	19
151660	Cache Crk/Lee Metcalf Wilderness	05/22/05	05/22/05	1	10/05/05	10/07/05	2
151670	Taylor Fork	05/17/05	05/18/05	1	09/19/05	10/08/05	20
151730	Cabin Crk WMA	05/25/05	05/31/05	6	10/30/05	10/31/05	1

APPENDIX M

SUMMER RANGES AND SPRING AND FALL MIGRATION DATES FOR GPS RADIO-COLLARED ELK WINTERING ON THE EAST MADISON WINTER RANGE, 2006 (n = 25)

Animal ID	Summer Range	Leave Winter Range	Arrive Summer Range	Duration Spring Migration (days)	Leave Summer Range	Arrive Winter Range	Duration Fall Migration (days)
150280	Taylor Fork/Lee Metcalf Wilderness	05/22/06	05/27/06	5	10/19/06	10/20/06	1
150420	Island Park, ID	05/13/06	06/02/06	20	11/14/06	12/31/06	46
150450	YNP	05/13/06	05/21/06	8	11/18/06	12/01/06	13
150470	Cabin Crk WMA	05/18/06	06/03/06	16	10/24/06	10/26/06	2
150480	Henry's Lake, ID	05/14/06	05/18/06	4	11/27/06	12/08/06	11
150490	Taylor Fork/Lee Metcalf Wilderness	05/12/06	05/12/06	1	09/23/06	09/23/06	1
150740	Cabin Crk WMA	07/01/06	07/10/06	9	09/17/06	09/18/06	1
150950	YNP	05/21/06	07/12/06	52	11/10/06	01/01/07	52
151030	Cabin Crk WMA	06/06/06	06/08/06	2	10/12/06	10/14/06	2
151140	Cabin Crk WMA	05/25/06	05/25/06	1	11/19/06	11/19/06	1
151150	Taylor Fork/Lee Metcalf Wilderness	05/13/06	05/13/06	1	09/22/06	09/22/06	1
151240	Taylor Fork/Lee Metcalf Wilderness	06/15/06	06/16/06	1	09/23/06	09/24/06	1
151279	Taylor Fork/Lee Metcalf Wilderness	05/24/06	05/25/06	1	09/22/06	09/24/06	2
151510	Buck Crk/Taylor Fork	06/08/06	06/23/06	15	10/22/06	10/24/06	2
151530	Jack Crk	05/11/06	06/02/06	22	10/22/06	10/22/06	1
151550	Taylor Fork	05/12/06	05/31/06	18	10/23/06	10/26/06	3
151560	Cabin Crk WMA	05/26/06	06/02/06	7	10/23/06	10/23/06	1
151588	Taylor Fork/Lee Metcalf Wilderness	06/06/06	06/06/06	1	09/02/06	10/10/06	39
151620	Madison Face/Olliffe Ranch	No migration	N/A	N/A	N/A	N/A	N/A
151640	Taylor Fork	06/19/06	06/23/06	4	09/18/06	09/19/06	1
151660	Taylor Fork/Lee Metcalf Wilderness	06/13/06	06/25/06	12	09/24/06	09/24/06	1
151670	SW of Hebgen Lake/Lionhead	05/06/06	05/16/06	10	01/25/07	01/31/07	6
152390	Cabin Crk WMA	07/08/06	07/09/06	1	10/17/06	10/18/06	1
152490	Cabin Crk WMA	05/19/06	05/22/06	3	10/02/06	10/06/06	4
152530	YNP	05/18/06	06/09/06	22	11/18/06	12/04/06	16

APPENDIX N

AGE, SUMMER HOME RANGE SIZE, MOTORIZED ACCESS OVERLAP WITH SUMMER HR, TOTAL COMBINED MOTORIZED AND NON-MOTORIZED ACCESS OVERLAP WITH SUMMER HR, CANOPY OVERLAP WITH SUMMER HR, DISTANCE OF SUMMER HR CENTROID FROM WINTER RANGE, AND ELEVATION OF SUMMER HR CENTROID FOR GPS RADIO-COLLARED ELK WINTERING ON THE EAST MADISON WINTER RANGE, 2005 (n = 17)

Animal ID	Age (yrs)	Summer HR Size (km^2)	Motorized Access (%)	Total Access (%)	Canopy Coverage (%)	Distance to Winter Range (km)	Summer HR Elevation (m)
150280	04	66.6	39	93	59	19.0	2500
150420	10	38.0	30	30	55	33.9	2750
150450	11	14.9	00	01	73	36.3	2300
150470	09	28.0	05	56	37	10.4	2800
150480	01	58.6	34	69	52	21.3	2500
150490	02	53.1	43	72	51	22.2	2580
150740	04	59.6	33	65	60	20.1	2500
151030	09	20.6	00	36	49	25.2	2700
151140	18	27.2	04	44	52	24.9	2700
151150	02	70.1	24	90	62	16.9	2600
151550	06	40.0	79	96	43	17.8	2750
151560	04	47.9	02	48	41	30.8	2750
151620	06	18.2	34	96	62	19.2	2650
151640	04	21.2	00	35	51	34.3	2500
151660	02	31.0	00	82	64	09.2	2500
151670	01	23.3	01	79	58	15.8	2700
151730	06	47.0	59	81	54	24.3	2600

APPENDIX O

AGE, SUMMER HR SIZE, MOTORIZED ACCESS OVERLAP WITH SUMMER HR, TOTAL COMBINED MOTORIZED AND NON-MOTORIZED ACCESS OVERLAP WITH SUMMER HR, CANOPY OVERLAP WITH SUMMER HR, DISTANCE OF SUMMER HR CENTROID FROM WINTER RANGE, AND ELEVATION OF SUMMER HR CENTROID FOR GPS RADIO-COLLARED ELK WINTERING ON THE EAST MADISON WINTER RANGE, 2006 (n = 25)

Animal ID	Age (yrs)	Summer HR Size (km^2)	Motorized Access (%)	Total Access (%)	Canopy Coverage (%)	Distance to Winter Range (km)	Summer HR Elevation (m)
150280	06	50.9	00	55	66	08.3	2550
150420	03	128.0	58	84	26	49.3	2250
150450	07	23.1	00	20	31	44.6	2700
150470	10	49.2	34	72	63	20.5	2500
150480	10	26.6	42	42	48	22.8	2250
150490	03	38.6	06	73	61	07.5	2500
150740	08	68.2	35	78	53	16.8	2500
150950	04	53.7	00	25	13	46.9	2400
151030	06	19.8	42	74	57	15.8	2400
151140	02	41.6	39	81	54	22.5	2500
151150	06	64.6	00	63	55	07.2	2500
151240	07	33.5	04	74	50	09.8	2500
151279	06	30.0	05	75	62	10.7	2700
151510	01	85.6	37	67	44	17.8	2500
151530	01	51.0	40	83	51	11.5	2400
151550	15	30.4	02	70	56	30.3	2600
151560	01	101.9	53	79	51	19.7	2600
151588	10	29.3	00	75	67	08.4	2600
151620	04	23.6	00	21	45	No Migration	N/A
151640	06	91.4	38	88	53	13.0	2600
151660	12	30.0	02	62	43	09.0	2500
151670	04	20.0	94	97	55	20.5	2400
152390	10	29.2	27	82	52	19.8	2500
152490	08	36.0	18	81	55	19.9	2500
152530	08	19.2	00	40	28	49.7	2800