Factors affecting elk (*Cervus elaphus*) encounter rate by gray wolves (*Canis lupus*) in Yellowstone National Park

A Thesis
SUBMITTED TO THE FACULTY OF
UNIVERSITY OF MINNESOTA
BY

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IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF
MASTER OF SCIENCE

Dr. L. David Mech

May, 2016

Acknowledgements

This project would not have been possible without the help and support of my mentors, colleagues, friends, and family, and I would like to thank all who have made this endeavor possible.

I would first like to acknowledge the Yellowstone Wolf Project and the technicians, volunteers, and donors who have contributed their time, expertise, and money to advance the study of wolves in Yellowstone National Park. I would especially like to thank Doug Smith, Dan Stahler, Erin Stahler, Kira Cassidy, Dan MacNulty, and Matt Metz for sharing their time and knowledge with me while working on the Yellowstone Wolf Project and my Master's Degree. This project would not have been possible without their trust, support, and guidance.

I would like to express my gratitude to Valerie Gates for supporting and appreciating the science of carnivore conservation. Her passion for scientific development and her inquisitive nature have led her to be a keystone supporter of young, up-and-coming scientists. I thank her for entrusting me with this position and assisting me in pursuing my career.

Dr. L. David Mech has been a great advisor, mentor, and friend throughout my Master's project. After over 55 years of studying wolves, his enthusiasm for science is unwavering and his thirst for knowledge unquenchable. I appreciate not only his guidance, but also his support and encouragement. Dr. Mech treated me not as a student, but as a colleague and friend, for which I am very grateful. I would also like to thank my committee members, John Fieberg and Glenn DelGuidice for their assistance with this project. I would especially like to thank John for allowing me to be part of his lab and for sharing his knowledge of statistics and his advice on the successful navigation of graduate school.

My parents, Max and Deanna, and my sister Andrea share my passion of science and have fostered my love for the natural world. The life experiences they exposed me to have shaped my life and my love of adventure and I thank them for encouraging me to follow my dreams. Without their encouragement and advice I would not be where I am today.

Finally, I would like to thank my partner Anna Berberet for her unwavering support throughout the duration of this project. She has supported me from 1,000 miles away when I was in Yellowstone, listened to countless presentations, read countless drafts, and pushed me to be my best. I would like to thank her for all of the pep talks, weekend getaways, walks, and fishing excursions that were essential to my well being. I am extremely lucky to spend my life with such an amazing and supportive woman.

Dedication

I would like to dedicate this thesis to Roy and Charlotte Lukes and Lincoln and Florence McGurk, four people who have contributed greatly to my development as a scientist, naturalist, story-teller, and human. Roy and Charlotte Lukes have dedicated their lives to understanding the natural world and sharing that knowledge and their experiences with the public. One of my first interactions with Roy and Charlotte involved searching for short-eared owls and ended in a bag full of owl pellets in my freezer for further investigation. Their youthful exuberance upon finding a new fungus in the woods or observing the first migratory woodcock of the season made me fully appreciate every plant, animal, and fungus. Roy and Charlotte have sent me countless articles on wolves throughout my research and have followed my progress as a scientist and naturalist. I want to thank them for their support and instilling in me an excitement and passion for nature.

Lincoln and Florence McGurk have been an important part of my life and have taught me that life is about adventure, love, friendship, and the stories that come from it. They have shared so many amazing experiences with me and I am forever grateful for each walk in the woods and sailing adventure. Lincoln and Florence's enthusiasm for science and learning kept me captivated as a young child, as my mind swirled with thoughts of galaxies, trade-winds, and fossilized cephalopods. I will never forget calling owls in their backyard, seeing the Hale-Bopp comet, and watching coral spawn from the deck of their boat. Lincoln and Florence's outlook on life and their relationship has been an inspiration to me and I am forever grateful that we are in each other's lives and stories.

Abstract

Few studies of wolf predation have quantified wolf encounter rates of prey and the factors that influence them. Elk population decline, variable weather, and changing wolf-pack dynamics on the Northern Range (NR) of Yellowstone National Park (YNP) provide an opportunity to examine factors affecting wolf-elk encounter rates and their role in wolf hunting success. Wolf kill rate is influenced by several factors but not by elk density. However, I found that elk density seems to be the only factor that drives wolf-elk encounter rates, and encounter rates are somewhat correlated with hunting success at least during early winter. Thus the factors affecting wolf hunting success of elk on the NR of YNP do not explain variation in encounter rates. Wolves appear to be able to adjust their hunting behavior to compensate for all the factors predicted to affect encounter rates except for elk density.

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INTRODUCTION

Predation in its most basic form can be defined as the act of one animal killing another. The probability of a predator killing a prey animal is the product of the probability of an encounter between a predator and a prey and the probability of a successful attack (Holling 1959). The first step in any predator-prey interaction is an encounter, making encounters an important component of predation. Spatial ecologists define an encounter as the spatial intersection of a predator and its prey (Lima and Zollner 1996, Hebblewhite et al. 2005), and behavioral ecologists define an encounter as a predator's awareness of the presence of a prey animal and vice versa (Peckarsky 1980, Scheel 1993, MacKenzie and Kiørboe 1995, MacNulty et al. 2007). Theoretical studies have described encounter rates as a function of the effective search area of a predator and the distribution and density of prey on the landscape (Fryxell et al. 2007). We can gain unique insights into predation and how predator and prey decisions are made by examining encounters from these different perspectives and linking spatial, behavioral, and theoretical ecology.

Despite numerous studies on wolf (*Canis lupus*) predation, few have quantified encounter rates and the factors that influence them (Hebblewhite and Pletscher 2002, Whittington et al. 2011, Middleton et al. 2013). Nevertheless, many models of predator-prey dynamics assume that the encounter rate of prey by a predator is proportional to prey density (Lotka 1925, Nicholson 1933, Pyke et al. 1977, Stephens and Krebs 1986). Not only are encounter rates a vital part of predation rate, but some studies suggest that wolf-prey encounters influence prey pregnancy rates (Creel et al. 2007, White et al. 2011a, Middleton et al. 2013), prey displacement (Middleton et al. 2013), prey movement

(Fortin et al. 2005), and behaviorally-mediated trophic cascades (Fortin et al. 2005, Kauffman et al. 2010).

The reintroduction of wolves to Yellowstone National Park (YNP), and the extensive monitoring program that has followed, presents a unique and rare opportunity to observe predator-prey dynamics in a wolf-elk (*Cervus elaphus*) system. Previous long term studies of wolf-prey dynamics have focused on wolf-moose (*Alces americanus*) (Vucetich et al. 2002) and wolf-deer (*Odocoileus virginianus*) (Mech 2009) systems making the Yellowstone Wolf Project unique.

A recent decline in the Northern Yellowstone Elk Herd presents an ideal opportunity to examine the effect of prey density as well as other biotic and abiotic factors on wolf-elk encounter rates and how encounter rate affects wolf hunting success. The Northern Yellowstone Elk Herd is the largest elk herd in the park, and its wintering range, referred to as the Northern Range (NR), extends west from the Lamar Valley to Gardiner, Montana (total area=1,526 km^2) (Houston 1982, Cook et al. 2004). From 1995 to 2013, the winter count of this herd declined from 17,000 to 3,915 elk (Wyman 2015). Researchers debate the causes of the decline, suggesting competing theories of human harvest and severe climate (drought and harsh winters) (Vucetich et al. 2005); winter weather, harvest, and wolves (Varley and Boyce 2006); and wolves and bears (White and Garrott, 2013). The long-term study of wolf-elk interactions and wolf movement in YNP has provided the opportunity to pose the following questions: (1) How are encounter rates affected by factors shown to influence kill rates in YNP and encounter rates in other wolf-ungulate systems? (2) What is the relationship between wolf hunting success and encounter rate? To answer these questions, I studied wolf-elk interactions and wolf hunting success in YNP from 2003-2013.

Mech and Peterson (2003) suggested that wolf kill rates (kg/wolf/day) depend more on pack size and prey vulnerability than on prey density. This is supported by evidence from YNP where kill rates are correlated with pack size, winter severity, and season (Mech et al. 2001, Smith et al. 2004, Metz et al. 2012). However, the predation response to prey density is highly variable in wolf-ungulate systems, with some studies finding that killing rates (prey animals killed/wolf/unit time) increase proportionally with prey density (Dale et al. 1994, Messier 1994, Hayes et al. 2000, Messier and Joly 2000) and others finding no such relationship (Eberhardt 1997, Eberhardt and Peterson 1999, Smith et al. 2004). The amount of control that predators exert on a prey population depends partly on how the predators respond to changes in prey density.

To better understand the relationship between prey density and hunting success we must study encounter rates and how wolf predation changes in response to declines in the prey population. For this study, I focused on the following factors shown to affect wolf-ungulate encounter rates and wolf pack kill rates (number of prey killed/pack/unit time) in other studies. These factors fall into three characteristic groupings based on those that affect (1) elk availability and elk predictability (elk density in a pack's territory; average elk group size in pack's territory; snow depth; winter severity), (2) elk grouping (elk group density in a pack's territory; average elk group size in pack's territory), and (3) wolf-pack space use and prey detection (wolf-pack size; wolf-pack-territory size).

Elk availability and elk predictability

The availability of prey within a wolf's territory and the predictability of the prey's location may influence wolf-prey encounters and ultimately kill rate. Prey availability is affected by the size of the prey population and the distribution of the population. Prey distribution and local density are affected by snow depth which limits resource availability and restricts movement. This concentrates elk at lower elevations and in areas of less snow, making their locations more predictable (Sweeney and Sweeney 1984, Eriksen et al. 2009). Snow depth and elevation across the NR of YNP influence the spatial and demographic distribution of elk within wolf territories (Coughenour and Singer 1996). Snow depth and winter severity also influence elk migration and movement, and cow elk with calves migrate farther to avoid deep snow (Sweeney and Sweeney 1984, Boyce 1991, Schaefer 2000). While snow depth and winter severity affect local elk density and predictability, they also reduces elk nutritional condition by limiting food availability and increasing thermoregulatory demands (DelGiudice et al. 1991).

Elk grouping

Theoretical models suggest that prey can reduce encounters by forming groups (Cosner et al. 1999). Empirical data from multiple predator-prey systems support these findings. Fryxell et al. (2007) found that lion (*Panthera leo*) predation of wildebeest (*Connochaetes taurinus*) in the Serengeti is driven by the density of prey groups and encounters of these groups and not by total prey density. Similarly, the predation rate of mountain caribou (*Rangifer tarandus*) by wolves in British Columbia is driven by group density rather than population size (McLellan et al. 2010). Huggard (1993) argued that for wolves hunting elk, encounter rate is dependent on the number of groups and not the number of individuals, because wolves rarely make more than one kill per encounter. In Banff National Park, the relative risk of encounter was highest for elk in group sizes of 13-30. Wolves encountered fewer small elk groups (<6 elk) and more large elk groups (6-30 elk) based on availability, but wolves encountered very large elk groups (>30 elk) equal to availability (Hebblewhite and Pletscher 2002). Larger elk groups are more predictable to locate in mountainous habitats, because they associate with meadows or avalanche slopes, and wolves travel between these locations to encounter them (Huggard 1993). This finding suggests that the influence of group size on encounter rate depends on habitat features, prey species, and study area, rather than group size only being a reflection of prey density.

Wolf-pack space use and prey detection

The search area of a predator is a variable often included in theoretical predation models (Hassell and Varley 1969, Cosner et al. 1999). Search area can be defined as the two-dimensional product of detection radius and path of travel (Cosner et al. 1999). The detection radius can be influenced by spatial organization of a predator group (Cosner et al. 1999), sensory ability to detect prey (Mech et al. 2016), and motivation (Kuzyk et al. 2005).

Wolves hunting on Isle Royale used olfactory cues to detect moose on 43 of 51 hunts and usually detected moose upwind when within 300 meters and in one case, when a moose was up to 2.4 km away (Mech 1966). Thus, factors that affect scent will cause changes in the search radius during a hunting bout.

The spatial organization and size of predatory groups affect the search radius and predatory behavior of individuals within the group. Schools of bluefin tuna (*Thunnus* *thynnus*) form a line transverse to the direction of travel, aggregating once a school of prey is encountered (Partridge et al. 1983). This cooperative-hunting strategy increases the search area of the school and the individual-encounter rates (Cosner et al. 1999). Similarly, wolves in larger hunting groups can increase their search radius by traveling in smaller hunting groups (Murie 1944, Mech 1966, Barber-Meyer and Mech 2015) or spreading out across the landscape when traveling (Stenlund 1955, Mech et al. 2015). This increases their detection rate by having more individuals over a larger area to detect olfactory and visual cues of prey (MacNulty et al. 2012). While traveling through deep snow, wolves travel in single file; however, when there is no trail to break, wolves sometimes pick individual trails (Burkholder 1959).

An underappreciated characteristic of wolf packs is the tendency for some large packs to split temporarily (usually for a couple of days) and hunt and move independently (Mech 1966). Metz et al. (2012) accounted for pack separation when assessing kill rate (kg/wolf/day) by using a double-count method involving pairs of GPS-collared wolves and their presence at kill sites. This method accounted for wolves' tendencies during summer to only be present at a proportion of the total kills made by a pack.

The amount of time required to process a prey animal after it has been killed is called *handling time* or *period of satiation* (Holling 1959). This period includes the time spent consuming and digesting prey and depends on the size of prey (MacNulty et al. 2009), the pack size (Hayes et al. 2000), and the amount consumed by scavengers (Stahler et al. 2002, Vucetich et al. 2004). Satiation reduces motivation for encountering prey as wolves will remain at a kill from 1-4 days depending on prey size, and travel 4.2 times less distance when near a kill (Kuzyk et al. 2005).

Wolf-pack-territory size could also influence encounter rate. Variation in wolf-pack-territory size is related to prey biomass and abundance (Fuller et al. 2003, Kittle et al. 2015). However, wolf density also influences territory size because individual territories are bounded by other defended territories, and wolves risk intraspecific strife if they trespass into neighboring territories (Mech 1994b, Cassidy et al. 2015). A larger territory could provide more prey to encounter, but a larger territory could also be a function of dispersed prey and the need to defend resources spread out on the landscape.

Objectives

The objectives of this study are to: (1) determine how wolf-pack encounter rates of elk are affected by elk density, elk group density, average elk group size, and snowpack severity in a pack's territory; wolf-pack size; wolf-pack territory size; and season; and (2) understand how encounter rates affect wolf hunting success.

STUDY AREA

The study area includes the NR of YNP, Wyoming (Fig. 1). Elevations across the study site range from 1,500 to 2,400 m with the lower and upper elevations characterized by wide river valleys and open slopes, mountain tops, valleys, and plateaus, respectively. Plant communities on the NR consist of coniferous forests at higher elevations (lodgepole pine [*Pinus contorta*], spruce [*Picea* spp.], fir [*Abies* spp.], douglas fir [*Pseudotsuga menziesii*], and whitebark pine [*Pinus albicaulis*]) and grasslands and sagebrush (*Artemisia tridentate*) at lower elevations. Winters on the NR are long and cold, and snow depth varies significantly (0-0.7m) with elevation and location (Houston 1982). This area's large expanses of open slopes, valleys, and plateaus provide researchers the opportunity to observe wolves daily.

YNP is inhabited by a diverse suite of ungulates, including elk, moose, bison (*Bison bison*), mule deer (*Odocoileus hemionus*), whitetail deer, and pronghorn (*Antilocapra americana*). These ungulates are preyed upon by a predator community recently returned to its endemic state by the reintroduction of wolves in 1995 (Fritts et al. 1997). Predators include wolves, grizzly bears (*Ursus arctos*), cougars (*Puma concolor*), coyotes (*Canis latrans*), and black bears (*Ursus americanus*). Wolves' primary prey is elk, comprising over 89% of kills in spring, 85% in summer, and 96% during winter (Metz et al. 2012). Adult elk constitute the majority of kills during winter and neonates during spring and summer (Metz et al. 2012).

METHODS

Data collection

The Yellowstone Wolf Project maintains collars on approximately 20% of the total wolf population inside the park. These wolves are captured using aerial darting following the capture and handling protocols recommended by the American Society of Mammalogists (Sikes et al. 2011). The Yellowstone Wolf Project's ground crews annually monitored movements of 2-3 wolf packs daily on the NR from November 15th to December 15th and March 1 to March 30th. Since 1996, these packs have been located via aerial and ground radio telemetry and monitored from sunrise to sundown to collect data on wolf travel behavior, wolf-prey interaction, and kill rate.

Wolf-prey interactions were observed from 200-3,000m via spotting scopes, and data were recorded on voice-recorders so field crews could observe and record data simultaneously. Accounts of behavior and interactions were then transcribed onto data forms including the following specific information: date, time, duration of encounter, prey-group size, prey-group demographics, prey-group response, encounter location, wolf-pack name, individual wolves present, individual wolf-hunting behavior, and whether or not the interaction resulted in a kill (Appendix A). These data, along with daily-activity summaries and maps of wolf movement (Appendix B), contain a wealth of information on wolf movement, hunting activity, and wolf-prey encounters.

Park biologists estimated wolf-pack kill rates and prey-acquisition rate for wolf packs observed during the biannual study using the methods of Metz et al. (2012). Per-capita kill rate was defined as the number or biomass of prey killed per wolf per day, and the prey-acquisition rate was the number or biomass of prey killed or scavenged per day (Metz et al. 2012). Wolf-pack hunting success rate was the number of observed kills divided by the number of observed attempts during the biannual study. Mech et al. (2001) estimated hunting success rates during the 1997 and 1998 biannual studies as 26 and 15 percent, respectively.

I obtained the total number of wolf-elk encounters observed for individual packs during each field season from the wolf-prey interaction forms (Appendix A). An encounter was defined for this study by the wolf pack being observed in any one of the following foraging states specified by MacNulty et al. (2007): (1) approach (fixating on and traveling toward prey), (2) watch (Fixating on prey while not traveling), or (3) attack (Running after a fleeing group or lunging at a standing group or individual).

Daily-activity summaries (DAS) are time budgets of observed behaviors exhibited by each wolf pack and were recorded from 1999 to 2013(Appendix B). These behaviors included time spent traveling, resting/sleeping, hunting, feeding, howling, and other, and a pack was assigned a particular behavior based on how the majority of the pack was behaving. I cleaned the DAS database using a protocol to detect any errors. The data-cleaning protocol combined the DAS and ground-tracking data to record the number of wolves observed, which then prepared the database to be digitized. Field crews recorded the locations of daily activities on USGS 7.5-minute, quadrangle, topographic maps, and depicted travel routes creating daily-activity maps which matched the DAS (Appendix B.). I digitized the daily-activity maps for 78 study-packs using ArcGIS to increase the efficiency of obtaining information from the maps and to facilitate spatial analysis of the data. I obtained distance and time wolves were observed traveling from these maps by linking the DAS and daily-activity maps using Linear Referencing in ArcGIS (Appendix C) (Scarponcini 2002). Total time wolves were observed traveling was considered searching behavior, and I excluded all travel associated with kill sites in accordance with the searching state defined by MacNulty et al. (2007). In the digitizing process, I cross-referenced the wolf-kill dataset, DAS, and daily-activity maps to identify kill site locations, record the number of wolves within the group, and determine if the wolves were at a kill site during recorded activities (Appendix D.).

To create an index of winter territory size for the wolf packs observed, I used observations from ground and fixed-wing aerial surveys from November 1 to March 31. Aerial locations were used on days when packs were seen both from the air and ground. If wolf packs were split during a day, locations of both groups were kept in the analysis to account for the total area occupied by the pack. I used the package *adehabitats* in R to create 90% isopleths of Kernel Density Estimates using the *ad hoc* method to estimate smoothing parameters for winter territory size (Börger et al. 2006, Calenge 2006). I considered the areas associated with these isopleths as a relative index of space use, rather than as an absolute estimate of home-range size (Fieberg and Börger 2012, Signer et al. 2015).

Annual winter (November-March) elk counts were conducted by the Northern Yellowstone Cooperative Wildlife Working Group with the methods of White et al. (2011b). I calculated average group size, median group size, and 70th quantile of group size, elk group density, and elk density in each wolf pack's territory by intersecting 90% isopleths of Kernel Density with the locations of elk groups seen in the corresponding winter-year. Winter elk migration occurs before the annual winter elk count, so a single count can provide an index of average group size and relative elk abundance in each pack's territory (White et al. 2010).

As an index of snow depth and winter severity (or snow-pack severity), I used average snow water equivalent (SWE), which I calculated for each wolf-pack territory using modeled SWE from the National Weather Service's Snow Data Assimilation System with 1-km spatial resolution and 24-hour temporal resolution from 2003 to 2013 (National Operational Hydrologic Remote Sensing Center 2004). Snow-pack severity for each season and wolf-pack territory was calculated by taking the daily mean SWE across time (during the study period) and space (within a wolf-pack territory).

Data Analysis

I used Bayesian Generalized Linear Mixed Effects models to explore relationships between encounter rates and SWE, elk density, elk group density, elk group size, territory size, and pack size (Appendix D). I assumed, conditional on the random effects, that the number of encounters followed a negative binomial distribution. This allowed for the fact that the count data were overdispersed relative to a Poisson distribution. I included random effects for pack and winter year. I centered and scaled all of the variables so I could directly compare the effect size of variables (Schielzeth 2010) and to improve mixing of the Monte Carlo Markov Chains (MCMC) (Kery 2010). I initially explored including the log of time observed traveling as a fixed effect to account for the amount of time wolves were observed searching for elk. The estimated regression coefficient was close to one (0.95, 95% CI=0.64, 1.30). Because the confidence interval included 1, I chose to model log of time observed traveling as an offset, effectively modeling encounter rates as the response variable (McCullagh and Nelder 1989).

I evaluated a series of generalized linear mixed-effect models that modeled elk encounters using variables to explain (1) elk distribution and predictability (elk density, elk group density, average elk group size, and SWE) (Sweeney and Sweeney 1984, Boyce 1991, Huggard 1993, Cosner et al. 1999, Schaefer 2000, Hebblewhite and Pletscher 2002, Fryxell et al. 2007) and (2) wolf-pack space use (winter territory size) and prey detection (pack size) (Hassell and Varley 1969, Cosner et al. 1999, Hayes et al. 2000, Kuzyk et al. 2005). Due to correlation between measures of elk abundance (elk density, elk group density, and average elk group size), I evaluated two models, one that included elk density to describe elk abundance and another that used elk group density and average elk group size. The elk-density model (Elk Density + Season+ Territory Size

+ SWE + Wolf Pack Size) used the elk density within a pack's territory to model encounter rates. The elk group density and size model used elk group density within a pack's territory and the average elk group size to model encounter rates (Elk Group Density + Average Elk Group Size +Wolf Pack Territory Size + Season + SWE + Wolf Pack Size). The estimated coefficients represent the effect of the variables on encounter rates.

In addition, I examined the posterior distributions of the random year effects to explore year-to-year variability in encounter rates not explained by the fixed effects. These year effects measure annual deviations from the overall mean log encounter rate during the study.

I also tested for a non-linear relationship between elk (and group) density and encounter rate by adding a quadratic term for elk (and group) density. In addition, I considered alternative measures of elk group size as a sensitivity analysis to determine the importance of group size to encounter rates, using the median and 70th percentile instead of mean group size to account for the often right-skewed distribution of ungulate group sizes (Brennan et al. 2015).

I used data from 46 pack-observation sessions over 9 years (2004-2012), 24 from early winter and 22 from late winter (Table 1). On average, 2.56 packs (range 1 to 3) were observed for two 30-day periods each year for an average of 108.40 hours (SD=43.45) within each of the two 30-day observation periods, and spent an average of 13.47 hours traveling (range 2.85 to 27.82, SD=6.20). I used estimates of elk density ($\bar{x}$ =3.88 elk/km^2, SD=2.75), group density ($\bar{x}$ =0.21 groups/km^2, SD=0.11), average elk group size ($\bar{x}$ =16.52, SD=5.83), and SWE ($\bar{x}$ =11.89 cm, SD=9.28) to characterize elk distribution and predictability within a pack territory. I used winter pack territory size ($\bar{x}$ =310.34 km^2, SD=162.54), and pack size ($\bar{x}$ =11.87, SD=4.77) to characterize wolf-pack space use and prey detection.

RESULTS

Average wolf-elk encounter rates in early winter ($\bar{x}$ =0.79 encounters/hr traveling, SD=0.46) were lower than encounter rates in late winter ($\bar{x}$ =0.94 encounters/hr traveling, SD=0.33) for packs on the NR, although not significantly different ($\bar{x}$ diff= -0.15, 95% CI= -0.36, 0.06) (Table 2).

The sign of the estimated coefficients agreed with the hypothesized effects except for SWE. Coefficients associated with elk density, elk group density, group size, and pack size were all positive; regression coefficients associated with territory size and SWE were negative (Fig. 2). However, the 95% credible intervals for all coefficients were fairly wide and included zero, most likely due to weak effects and my small sample (n=46 pack observation years). Despite the limited support for the hypothesized effects, season, pack size, SWE, and territory size were all robust to how elk abundance was modeled (elk density, group density; linear or nonlinear relationship with encounter rate) (Fig. 2). The effect of elk group size was also robust to the method used to describe them (average, median, 70th percentile), but measuring group size using the median and 70th percentile reduced the effect of group density in the models (Table 3).

I found evidence for a significant nonlinear relationship between elk density and encounter rate but no evidence for a significant nonlinear relationship between elk group density and encounter rate (Fig. 3). Unexplained year-to-year variability in encounter rates was minimal, and all credible intervals of the posterior distributions of the random effect of year overlapped 0, suggesting these effects were not statistically significant (Fig. 4).

I found evidence for a linear relationship between wolf-pack encounter rates (elk groups encountered/ hr observed traveling) and the number of elk killed in early winter (adjusted r^2=0.26, P<0.01) but not in late winter (adjusted r^2=-0.02, P=0.47) (Fig. 5).

DISCUSSION

I hypothesized that the biotic and abiotic factors shown to affect kill rates and encounter rates in other wolf-ungulate systems would influence wolf-elk encounter rates on the NR of YNP. By comparing factors that affect kill rates to those that affect encounter rates, I might be better able to understand the importance of prey encounters to wolf predation. However, I did not find convincing evidence to support my hypothesis that those factors affecting pack kill rates in this system (wolf-pack size, snow, and season) are also influencing encounter rate (Fig. 2).

SWE

I hypothesized that snow-pack severity (indexed by SWE) would reduce elk movement, increase elk concentration, and therefore make elk more predictable to locate and increase encounter rates. The data did not support this hypothesis despite winter severity and snow depth being the primary driver of wolf kill rate in YNP and other wolf-ungulate systems (Mech et al. 2001, Smith et al. 2004). Elk avoid deep snow, causing them to concentrate at lower elevations and in areas with less snow (Sweeney and Sweeney 1984, Eriksen et al. 2009). However, in our study area, snow depths within wolf territories rarely reached the levels shown to inhibit mature elk movement, so that may account for why I did not see the hypothesized effect (Sweeney and Sweeney 1984). Additionally, one study has shown a positive relationship between winter home range sizes of elk across North America and mean SWE (Anderson et al. 2005), suggesting that individual elk locations in areas with more snow may be less predictable. However, this is in contrast to the affect of snowdepth on monthly home-range size of red deer (*Cervus elaphus)* in Norway which is negatively correlated with snow depth (Rivrud et al. 2010).

A reduction in the amount of habitat available to elk caused by increased snow depth may not affect encounter rates because wolves often use olfaction to locate prey (Mech 1966), and small differences in concentration may not affect wolves' ability to locate them. In accounts of wolf hunting success, snow depth most often influences the success or failure of an encounter when prey animals run into areas of deeper snow (Mech et al. 2015). This finding leads me to conclude that if snow-pack severity does limit elk movements in this system, it does not influence wolf-elk encounters and has a stronger effect on the outcome of encounters than on the occurrence of encounters. Further information regarding the effect of snow-pack severity on elk seasonal home ranges in mountainous habitats is needed to better understand this relationship.

Early vs. late winter

Although not statistically significant, elk encounter rates were lower in early winter than late winter, aligning with trends in kill rate (Smith et al. 2004, Metz et al. 2012). Increased kill rates in late winter have been attributed to a decline in elk condition throughout winter and thus better wolf hunting success. Decreased nutritional condition is caused by limited food supply, costs of thermoregulation, and gestation throughout winter that reduce fat reserves (DelGiudice et al. 1991, Metz et al. 2012). Thus, increased kill rates in late winter may be due to an increase in killing success rather than to increased encounters.

However, if encounter rates were significantly higher in late winter that might suggest that elk in poorer condition move less and might actually be contributing to increased wolf encounters. White-tailed deer in poor nutritional condition and pregnant show a similar decrease in activity (Rongstad and Tester 1969, Moen 1976). Additionally, yearly changes in habitat suitability and snow depth alter elk locations, forcing wolves to repeatedly re-learn how elk are distributed on the landscape. Wolves might remember the location of debilitated animals (Mech and Peterson 2003) and frequent areas where prey are more vulnerable to predation (McPhee et al. 2012) leading to higher encounter rates in late winter. Lower encounter rates in early winter might reflect the benefit of migration in the Northern Yellowstone Elk Herd, because it may take time for wolves to develop a search image for elk locations and rebuild their cognitive map of these locations.

Wolf-pack size

Wolf-pack size was nearly significant in all models and had a positive effect on encounter rate as hypothesized (Fig. 2). MacNulty et al. (2012) found that the probability of an individual wolf killing an elk during an encounter did not increase in hunting groups with more than four members and that additional individuals withheld effort during the hunting process. My results suggest wolf packs may benefit from having more members to encounter prey animals even though individuals may be withholding effort during the later stages of the hunt. These larger packs might have a larger search radius or more motivation to encounter prey and therefore encounter more animals. A larger search radius reduces the freeloading burden of a larger pack which could partly explain larger packs. Furthermore, wolf packs have been known to split, hunting as smaller groups to form more efficient hunting parties (Mech 1966, Metz et al. 2012). By splitting, a large pack increases the amount of area it can search and still maintain high success rates (MacNulty et al. 2012). These smaller hunting groups within large packs and with larger search radii may explain the higher encounter rates in larger packs. Pack size is highly dependent on the dispersal of maturing members, triggered by competition for food and mates (Mech and Boitani 2003). Packs experience increased dispersal and reduced sizes in years of low food availability (Messier 1985, Peterson and Page 1988). When encounter rates are high, that might reflect a food surplus, so individual wolves postpone dispersal, leading to larger packs (Mech et al. 1998). This relationship suggests it may be difficult to sort out cause and effect if there is a positive association between food surplus and encounter rates.

Elk density and elk group density

Although there seems to be no evidence for an elk density-dependent effect on kill rate (Smith et al. 2004), my results suggest that elk density might influence wolf-elk encounter rates. I found evidence for a nonlinear relationship between encounter rate and elk density that suggests encounter rates are limited by elk group formation and the handling time associated with an encounter (Figure 3).

Prey grouping reduces encounters by creating interstitial space void of prey that would be filled if individuals were randomly or evenly distributed on the landscape. Elk group size is correlated with elk density which means that despite increases in population, the number and distance between groups might remain the same leading a lower encounter rate than expected by a random distribution.

The nonlinear relationship between elk density and encounter rate might also be caused by handling time limiting the number of encounters that a pack can have. The decreasing rate of increase in Holling's (1959) Type II functional response results from the handling time, or amount of time a predator takes to capture, eat, and digest a prey animal, or, in the case of encounter rate, to evaluate and target elk within a group (MacNulty et al. 2007). The functional response of kill rate to prey density in wolf-ungulate systems is a highly debated concept, as are the factors that affect the asymptote of the functional response (Mech and Peterson 2003). My finding suggests that the mechanisms causing a Type II functional response may include both the encounter phase of the hunt and the handling time of killed prey.

Given the nonlinear relationship I found between elk density and encounter rate and the definition of an encounter for this study being the encounter of an elk or elk group, I expected to find a significant linear relationship between elk group density and encounter rate. However, I did not, although I did find trends indicating a non-linear relationship.

For other studies of predators hunting grouped prey, group density was a better predictor of kill rate and encounter rate than total density because only one prey animal is usually taken from a group (Huggard 1993, Fryxell et al. 2007, McLellan et al. 2010).

The coarseness of the elk group density data I used in this analysis may have dampened the effect of elk group density on encounter rates because constancy in elk group composition is low, and individuals change grouping strategies depending on habitat type, predation risk, snow depth, and season, leading to plasticity in elk groups not captured in a single count (Knight 1970, White et al. 2011b). Another potential reason that I did not see a linear effect of elk group density is that elk group density may be describing variance in elk density because elk group size and elk group density are correlated with elk density (r=0.90, P<0.001 and r=0.75, P<0.001, respectively).

Wolf-pack territory size

I hypothesized that packs with larger territories would have fewer encounters than packs with smaller territories because territory size has been negatively correlated with human encounter rates of prey (Schmidt et al. 2007). However, I did not find a significant relationship between territory size and wolf encounter rate of elk. Territory size may depend on the arrangement of prey on the landscape and landscape features but may not accurately describe resource availability or distribution especially when comparing territory size during different periods of use. Territory size is often correlated with prey biomass (Fuller et al. 2003), as it was in this study (r=-0.35, P=0.02), but is also constrained by competition with neighboring packs. Due to the limited sample of locations defining pack territory size, winter territory sizes may not have accurately represented the space use of wolves during the 30-day study sessions.

CONCLUSION

This study shows that the factors affecting wolf hunting success of elk on the NR of YNP do not significantly explain variation in prey encounter rates, which raises the question of the importance of encounter rates in wolf-ungulate hunting success. The influence of encounter rates on hunting success depends on season. In early winter they were correlated with the number of elk killed, suggesting that hunting success in early winter is dependent on encounter rates. However, in late winter, the number of elk killed was not correlated with encounter rates indicating that they had little effect on hunting success.

Huggard (1993) proposed that a pack's search time between kills would not decline as significantly as predicted at high kill rates because most kills occur in distinct, predictable areas, and the distances between these kill locations remain the same regardless of wolves encountering prey in other unpredictable locations. Similarly, variations in encounter rate in my study may not be contributing to hunting success if most kills are made from encounters in specific locations and random encounters do not contribute to predation.

The lack of a significant effect of SWE, territory size, and season suggests that wolves behaviorally compensate in response to changes in these factors to maintain encounter rates. Wolves may change the speed of travel, directional persistence, and amount of time spent searching for prey to compensate for changes in prey abundance, predictability, and movement. Additionally, wolves may adapt hunting strategies to take advantage of elk in poor condition or near vulnerable landscape features, i.e. terrain traps (Mech et al. 2015). This study assumed that all observed search behavior contributed equally to the probability of an encounter and that all encounters contributed equally to hunting success; however, this may not be the case.

Other predators change searching behavior and rate when experiencing low encounter rates to locate prey more efficiently. When ladybird beetle (*Coccinella septempunctata*) encounter rates with pea aphids (*Acyrthosiphon pisum*) are low, the beetles conduct extensive [longer distance with fewer turns] search behavior, but when encounter rates are high, the beetles' search pattern was intensive [shorter distance with more turns] (Biesinger and Haefner 2005). Similarly, wolves with lower encounter rates may make longer more extensive movements to detect prey.

Predators can increase search distance and the time spent searching for prey to increase encounters. Three-spine sticklebacks (*Gasterosteus aculeatus*) and great tits (*Parus major*) increase their search rate at low prey densities, leading to a shorter time to encounter than predicted by prey density (Travis and Palmer 2005, Ioannou et al. 2008). The speed at which wolves travel depends on their activity, and normal travel speeds are between 8-9 km/hr when hunting (Burkholder 1959, Mech 1966, 1994a, Shelton 1966), but travel at a rate of 10 km/hr when returning to the den (on Ellesmere Island) (Mech 1994a). I am not aware of any studies that compare daily travel rates and prey density or prey type, but these factors might affect both the rate at which wolves travel and the distance they cover. This behavior modification may compensate for low prey abundance and predictability, reducing the observable effects within this study.

Wolves might be able to maintain high hunting success despite lower encounter rates by increasing the distance they cover searching for prey. The distance they cover may reflect the distribution of food resources on the landscape as well as the search patterns required to most effectively find these resources. For example, wolves in winter on Isle Royale traveled an average of 14.4 km/day (Mech 1966); in Poland, 22.8 km/day

(Jedrzejewski et al. 2001); and in Italy, 27.4 km/day (Ciucci et al. 1997). The wolves in these studies utilized different food resources (moose, red deer [*Cervus elaphus*]) and wild boar (*Sus scrofa*), and garbage dumps respectively) which exhibited different levels of predictability and distribution. If prey locations are unpredictable but abundant, wolves might search haphazardly to try to locate them, exhibiting movement patterns similar to Brownian motion (Bartumeus et al. 2002). When prey are unpredictable and less abundant, Levy flights characterized by long movements followed by shorter step lengths may be adopted to maximize efficiency (Viswanathan et al. 2008). Movement characteristics of Levy flights often best describe wolf movement when wolves travel extensively, using linear routes to cover their territory in a short period of time (Burkholder 1959, Mech 1966, McKenzie et al. 2012). Wolves may employ different methods of searching behavior; the first is extensive traveling to locate new forage patches, and the second is intensive movement within a forage patch.

Finally, wolves might change hunting strategies to take advantage of different factors influencing prey vulnerability. For example, neonate predation demonstrates wolves' ability to learn about novel food sources and vulnerability in young of the year (Murie 1944, Mech 1966, Pimlott 1967, Carbyn and Trottier 1988, Kunkel and Mech 1994). Wolves also utilize different hunting strategies to capitalize on vulnerability caused by poor condition (Murie 1944, Mech and Frenzel 1971, DelGiudice 1998, Mech et al. 1998, 2001) or by landscape characteristics (Kauffman et al. 2007). Targeting predictable, larger groups increases the probability of encountering a physically vulnerable individual. However, if elk are in good condition and their vulnerability then depends on landscape features, wolves might target more elk groups or hunt where there are known terrain traps (Mech et al. 2015) to increase the likelihood of encountering an elk close to a habitat or terrain feature that increases the elk's vulnerability. These various strategies suggest that not all encounters contribute equally to hunting success.

Despite the possible factors that would seem to affect encounter rates on the NR, wolves appear to be able to adjust their hunting behavior to compensate for all of these factors, except elk density. Studies of wolf hunting behavior and effort might further our understanding of how wolves compensate for these factors to maintain encounter rates and for changes in elk density to maintain hunting success.

Fig. 1. Yellowstone National Park, the wintering area of the Northern Yellowstone Elk (*Cervus elaphus*) Herd or Northern Range, and the study area.

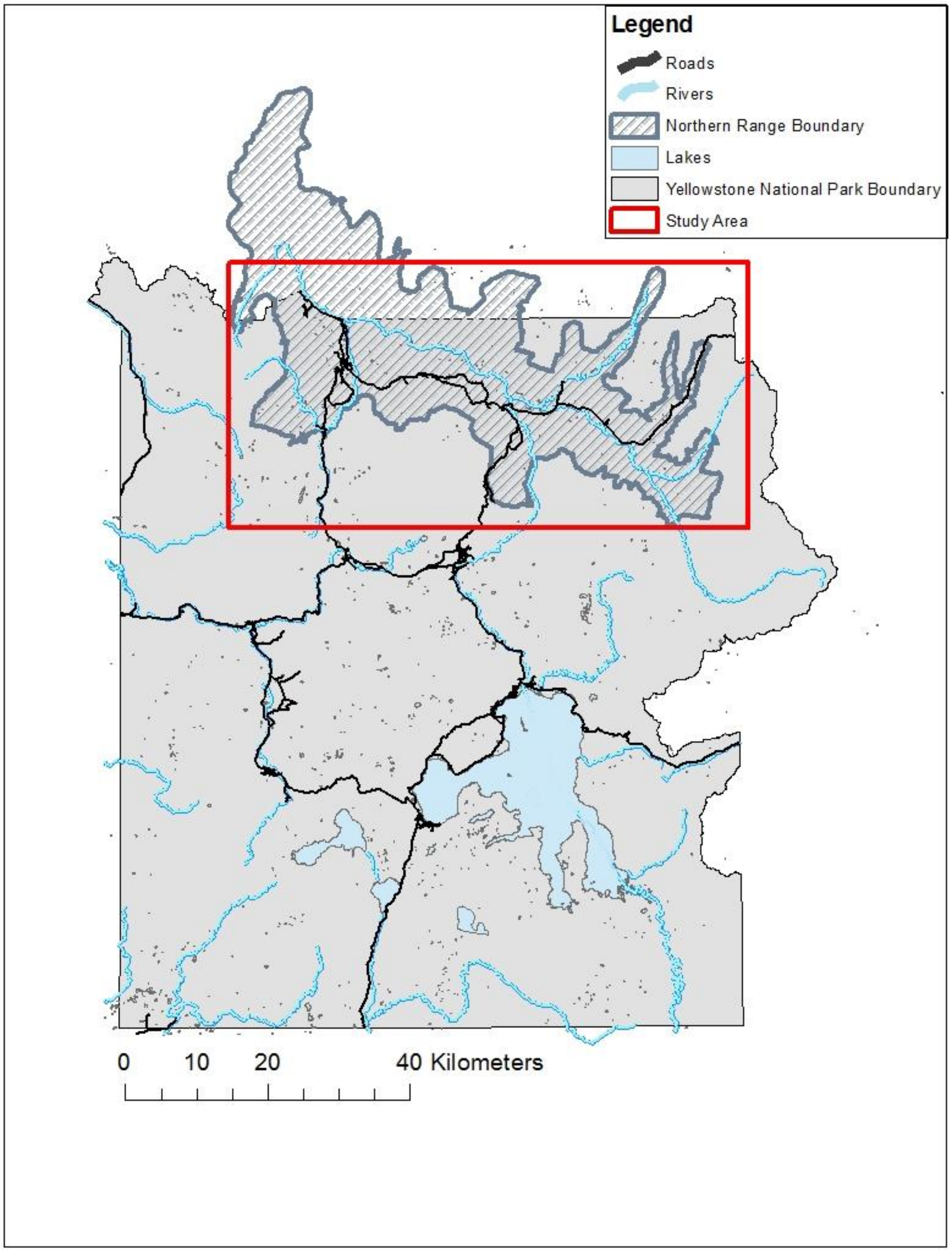

Fig. 2. Estimated coefficients and 95% credible intervals of the models hypothesized to predict wolf (*Canis* lupus)-elk (*Cervus elaphus*) encounter rates on the Northern Range of Yellowstone National Park (winter-years 2004-2012).

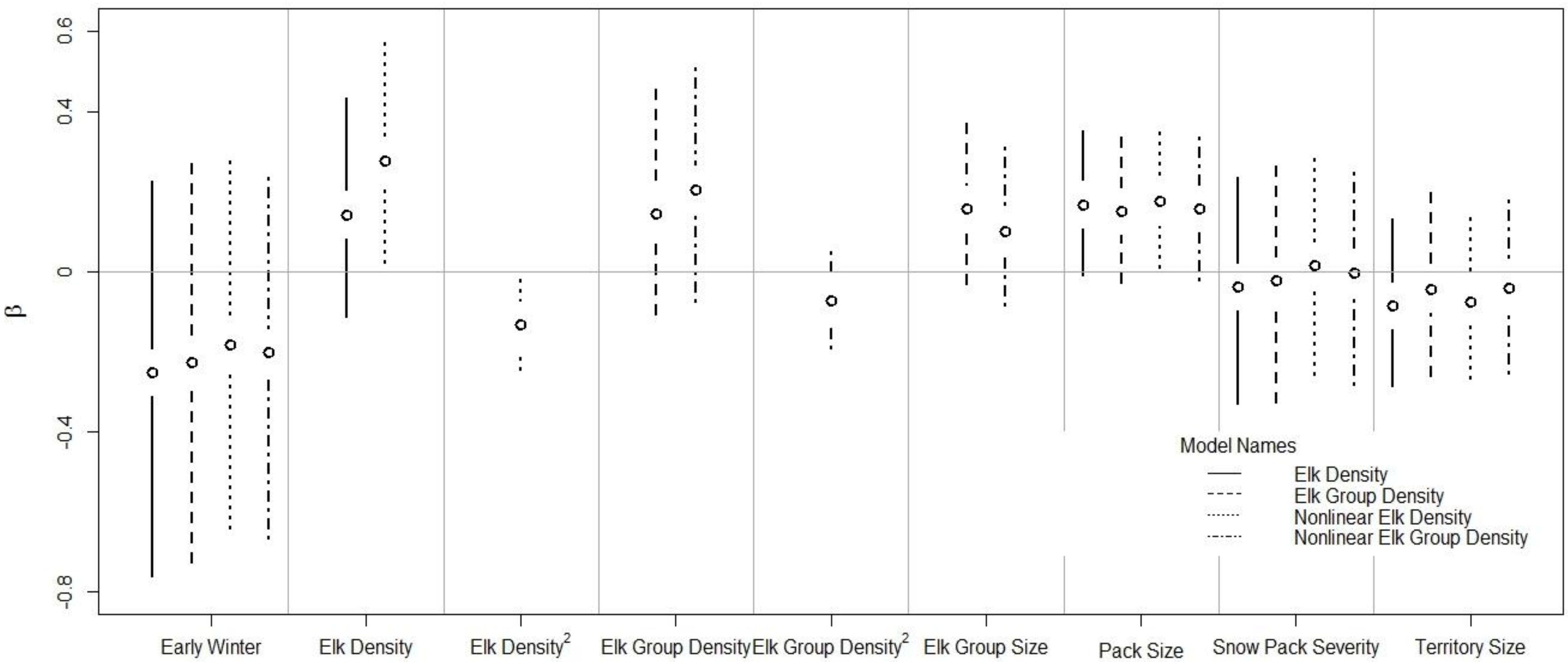

Fig. 3. Prediction curve and 95% credible intervals of the Nonlinear Elk Density Model on wolf (*Canis lupus*)-elk (*Cervus elaphus*) encounter rates at varying levels of elk density on the Northern Range of Yellowstone National Park (winter-years 2004-2012).

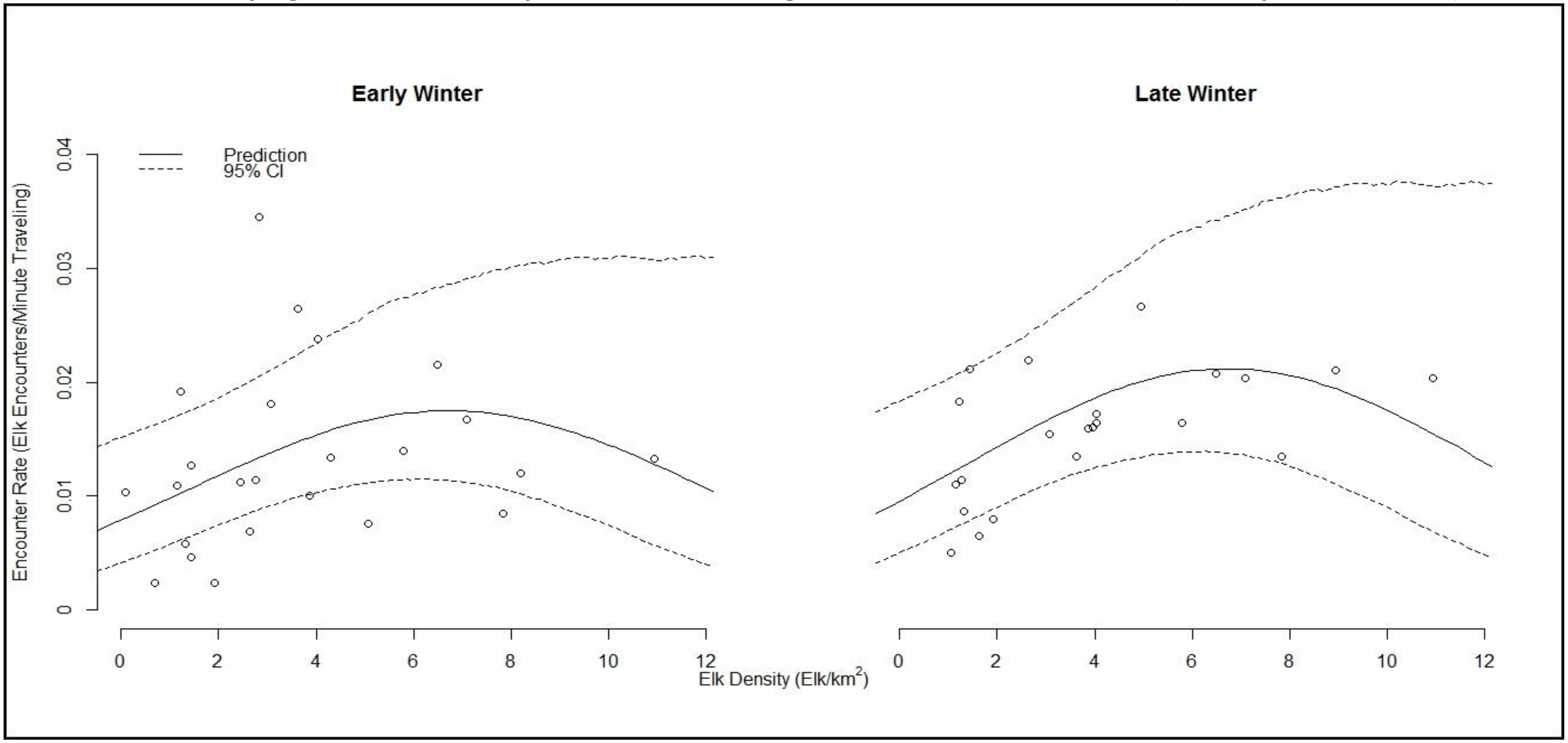

Fig. 4. The mean and 95% credible intervals of the posterior distribution of the random year effect describing year-to-year variation of wolf (*Canis lupus*)-elk (*Cervus elaphus*) encounter rates on the Northern Range of Yellowstone National Park (winter-years 2004-2012) not accounted for by the other parameters within the Nonlinear Elk Density Model.

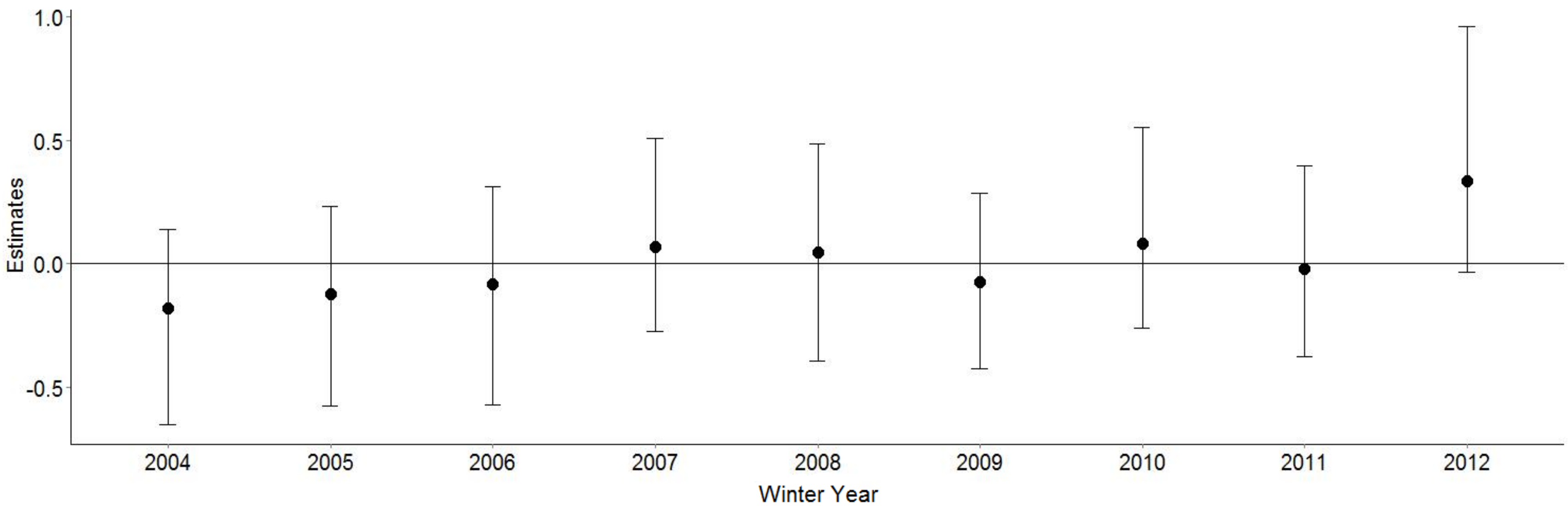

Fig. 5. The linear regression line and 95% confidence intervals of the effect of hourly wolf (*Canis lupus*)-elk (*Cervus elaphus*) encounter rates when searching for prey on the number of elk killed during early (November 15 –December 15) and late (March 1-30) winter on the Northern Range of Yellowstone National Park, winter-years 2004-2012.

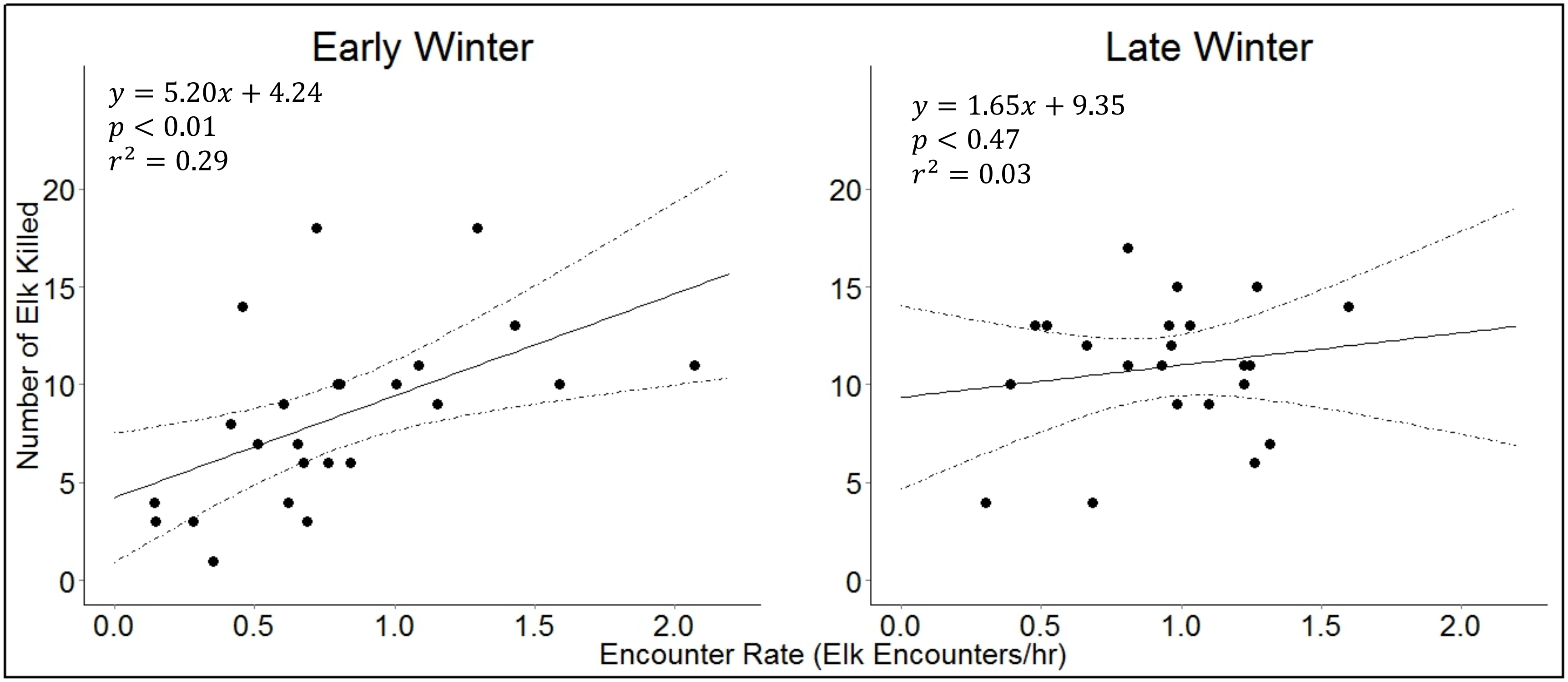

Table 1. Wolf (*Canis lupus*) pack encounters and kills of elk (*Cervus elaphus*) and the biotic and abiotic factors hypothesized to affect them on the Northern Range of Yellowstone National Park, winter-years 2004-2012.

Pack Name	Study[a]	Winter Year	Elk Encounters	TIV Travel[b]	Territory Size(km^2)[c]	Average Elk Group Size	Median Elk Group Size	70th Percentile of Elk Group Size	Mean SWE(cm)[d]	Elk Group Density	Encounters/Minute	Elk Density	Elk Kills	Pack Size	Elk Kills/Day
DRUID PEAK	March	2004	17	820	291.13	31.48	10.50	17.00	151.12	0.21	0.02	6.49	11	13	0.37
GEODE CREEK	March	2004	6	446	186.02	24.73	16.00	29.20	133.16	0.32	0.01	7.84	11	6	0.38
LEOPOLD	March	2004	19	933	196.21	22.15	8.00	22.20	122.07	0.49	0.02	10.95	11	17	0.39
DRUID PEAK	Nov_Dec	2004	36	1669	291.13	31.48	10.50	17.00	44.00	0.21	0.02	6.49	18	17	0.64
GEODE CREEK	Nov_Dec	2004	3	353	186.02	24.73	16.00	29.20	36.57	0.32	0.01	7.84	7	8	0.39
LEOPOLD	Nov_Dec	2004	10	753	196.21	22.15	8.00	22.20	29.15	0.49	0.01	10.95	10	19	0.44
GEODE CREEK	March	2005	11	692	249.51	15.58	10.00	16.00	114.46	0.25	0.02	3.87	13	11	0.48
LEOPOLD	March	2005	24	1179	264.50	20.40	10.00	17.00	116.35	0.35	0.02	7.10	10	25	0.36
SLOUGH CREEK	March	2005	22	1370	253.21	17.02	10.00	16.60	111.81	0.23	0.02	3.97	12	15	0.41
DRUID PEAK	Nov_Dec	2005	16	1427	452.86	17.87	10.00	17.70	40.54	0.14	0.01	2.45	6	11	0.22
GEODE CREEK	Nov_Dec	2005	3	299	249.51	15.58	10.00	16.00	36.20	0.25	0.01	3.87	9	13	0.39
LEOPOLD	Nov_Dec	2005	14	836	264.50	20.40	10.00	17.00	34.50	0.35	0.02	7.10	10	24	0.40
HELLROARING	March	2006	13	793	328.12	20.05	10.00	18.50	197.01	0.20	0.02	4.03	9	7	0.32
LEOPOLD	March	2006	17	990	126.71	15.52	9.00	17.40	160.17	0.26	0.02	4.04	13	7	0.45
SLOUGH CREEK	March	2006	24	1312	346.28	12.06	7.00	13.40	209.84	0.10	0.02	1.22	9	12	0.32
LEOPOLD	Nov_Dec	2006	22	923	126.71	15.52	9.00	17.40	56.53	0.26	0.02	4.04	13	15	0.46
SLOUGH CREEK	Nov_Dec	2006	20	1043	346.28	12.06	7.00	13.40	67.76	0.10	0.02	1.22	9	13	0.32
AGATE CREEK	March	2007	16	601	291.69	20.07	10.00	18.70	109.41	0.25	0.03	4.95	14	12	0.56
DRUID PEAK	March	2007	7	1074	351.93	17.27	6.00	12.20	220.66	0.09	0.01	1.62	10	11	0.37

(Cont'd) Table 1 Wolf (*Canis lupus*) pack encounters and kills of elk (*Cervus elaphus*) and the biotic and abiotic factors hypothesized to affect them on the Northern Range of Yellowstone National Park, winter-years 2004-2012.

Pack Name	Study	Winter Year	Elk Encounters	TIV Travel	Territory Size	Average Elk Group Size	Median Elk Group Size	70th Percentile of Elk Group Size	Mean SWE	Elk Group Density	Encounters/ Minute	Elk Density	Elk Kills	Pack Size	Elk Kills/Day
HELLROARING	Nov_Dec	2007	3	262	887.39	18.94	8.00	19.00	38.82	0.15	0.01	2.75	3	8	0.18
LEOPOLD	Nov_Dec	2007	17	1419	119.75	32.70	19.00	38.00	22.51	0.25	0.01	8.19	18	19	0.64
SLOUGH CREEK	Nov_Dec	2007	4	524	155.55	17.91	4.00	9.20	26.08	0.28	0.01	5.07	14	8	0.58
DRUID PEAK	March	2008	13	1177	236.99	8.30	5.00	8.00	178.14	0.14	0.01	1.16	12	16	0.43
DRUID PEAK	Nov_Dec	2008	17	1556	236.99	8.30	5.00	8.00	49.83	0.14	0.01	1.16	7	16	0.29
LEOPOLD	Nov_Dec	2008	11	822	270.99	12.63	6.00	14.00	29.80	0.34	0.01	4.29	10	16	0.40
OXBOW CREEK	Nov_Dec	2008	29	840	162.27	10.48	5.50	14.20	32.94	0.27	0.03	2.84	11	17	0.38
BLACKTAIL	March	2009	7	426	318.72	14.41	9.00	15.00	232.30	0.40	0.02	5.79	15	6	0.60
DRUID PEAK	March	2009	5	630	590.06	11.72	6.50	12.50	332.77	0.16	0.01	1.91	13	13	0.50
EVERTS	March	2009	11	523	88.71	19.85	10.50	17.30	179.11	0.45	0.02	8.95	6	6	0.22
BLACKTAIL	Nov_Dec	2009	9	642	318.72	14.41	9.00	15.00	32.94	0.40	0.01	5.79	6	10	0.24
DRUID PEAK	Nov_Dec	2009	3	1235	590.06	11.72	6.50	12.50	56.27	0.16	0.00	1.91	3	13	0.13
BLACKTAIL	March	2010	7	452	300.54	14.68	7.00	13.00	125.34	0.21	0.02	3.08	11	9	0.41
LAMAR CANYON	March	2010	3	263	99.15	8.33	7.00	8.80	134.08	0.15	0.01	1.26	4	3	0.14
SILVER	March	2010	5	998	471.14	11.32	6.50	10.10	162.02	0.09	0.01	1.06	4	5	0.14
BLACKTAIL	Nov_Dec	2010	10	553	300.54	14.68	7.00	13.00	43.76	0.21	0.02	3.08	11	10	0.42
DRUID PEAK	Nov_Dec	2010	3	643	444.79	12.09	6.00	10.40	62.52	0.12	0.00	1.44	3	11	0.12
AGATE CREEK	March	2011	7	808	146.46	13.71	10.00	19.60	349.03	0.10	0.01	1.31	13	8	0.59
BLACKTAIL	March	2011	6	446	538.31	16.68	12.00	23.20	329.28	0.22	0.01	3.62	17	12	0.74

(Cont'd) Table 1 Wolf (*Canis lupus*) pack encounters and kills of elk (*Cervus elaphus*) and the biotic and abiotic factors hypothesized to affect them on the Northern Range of Yellowstone National Park, winter-years 2004-2012.

Pack Name	Study	Winter Year	Elk Encounters	TIV Travel	Territory Size	Average Elk Group Size	Median Elk Group Size	70th Percentile of Elk Group Size	Mean SWE	Elk Group Density	Encounters/ Minute	Elk Density	Elk Kills	Pack Size	Elk Kills/Day
LAMAR CANYON	March	2011	24	1133	264.04	12.70	11.50	14.00	359.61	0.11	0.02	1.44	15	7	0.56
AGATE CREEK	Nov_Dec	2011	1	171	146.46	13.71	10.00	19.60	104.20	0.10	0.01	1.31	1	9	0.11
BLACKTAIL	Nov_Dec	2011	19	718	538.31	16.68	12.00	23.20	101.32	0.22	0.03	3.62	10	15	0.50
LAMAR CANYON	Nov_Dec	2011	6	471	264.04	12.70	11.50	14.00	79.39	0.11	0.01	1.44	6	7	0.29
BLACKTAIL	March	2012	14	638	560.37	17.68	8.50	15.00	232.54	0.15	0.02	2.65	7	12	0.28
AGATE CREEK	Nov_Dec	2012	1	418	250.99	8.55	4.50	8.30	62.41	0.08	0.00	0.68	4	8	0.21
BLACKTAIL	Nov_Dec	2012	5	722	560.37	17.68	8.50	15.00	61.27	0.15	0.01	2.65	8	15	0.29
LAMAR CANYON	Nov_Dec	2012	12	1165	415.57	11.33	9.00	14.60	60.13	0.01	0.01	0.08	4	11	0.19

a Study represents the observation session with Nov-Dec representing early winter and March representing late winter.
b TIV Travel is the total amount of time the pack was observed traveling not associated with a kill.
c Territory Size was calculated using 90% Isopleths of Kernel Density
d Mean SWE is the average snow water equivalent within a pack's territory.

Table 2. Mean seasonal yearly wolf (*Canis lupus*) pack encounter rates with elk (*Cervus elaphus*) on the Northern Range of Yellowstone National Park, winter-years 2004-2012, using the total number of observed wolf-elk encounters and total amount of time wolves were observed searching for prey.

	Early Winter [a]					Late Winter [a]				
Winter Year [b]	Elk Encounters	Hours	Encounter Rate	LCI [c]	UCI	Elk Encounters	Hours	Encounter Rate	LCI	UCI
2004	49	46.3	1.1	0.8	1.4	42	36.7	1.1	0.8	1.5
2005	33	42.7	0.8	0.5	1.1	57	54.0	1.1	0.8	1.4
2006	42	32.8	1.3	0.9	1.7	54	51.6	1.0	0.8	1.4
2007	24	36.8	0.7	0.4	1.0	23	27.9	0.8	0.5	1.2
2008	57	53.6	1.1	0.8	1.4	13	19.6	0.7	0.4	1.1
2009	12	31.3	0.4	0.2	0.7	23	26.3	0.9	0.6	1.3
2010	13	19.9	0.7	0.3	1.1	15	28.6	0.5	0.3	0.9
2011	26	22.7	1.1	0.7	1.7	37	39.8	0.9	0.7	1.3
2012	18	38.4	0.5	0.3	0.7	14	10.6	1.3	0.7	2.2

a Winter year starts in October and ends the following September, taking the name of the year in which the majority of the months fall within. For example, the calendar year November 2010 is in the winter year 2011.
b Encounter rate is calculated in this table as the number of wolf-elk encounter per hour observed traveling.
c Confidence intervals were calculated using exact Poisson confidence intervals (Cohen and Yang 1994).

Table 3. Coefficient estimates and 95% credible intervals of parameters from the Bayesian models of wolf (*Canis lupus*)-elk (*Cervus elaphus*) encounter rates on the Northern Range of Yellowstone National Park, winter-years 2004-2012.

MODEL	Elk Density Model			Elk group Density Model			Nonlinear Elk Group Density Model			Nonlinear Elk Density Model			Nonlinear Elk Group Density Median Group Size Model[a]			Nonlinear Elk Group Density 70^{th} Percentile Group Size Model[a]		
Parameter[b]	**Estimate**	**LCI**	**UCI**	**Estimate**	**LCI**	**UCI**	**Estimate**	**LCI**	**UCI**	**Estimate**	**LCI**	**UCI**	**Estimate**	**LCI**	**UCI**	**Estimate**	**LCI**	**UCI**
Pack Size	0.17	-0.01	0.35	0.15	-0.03	0.34	0.16	-0.02	0.34	0.17	0.01	0.35	0.17	0.00	0.36	0.17	0.00	0.35
Elk Density	0.14	-0.12	0.43	---	---	---	---	---	---	0.27	0.02	0.57	---	---	---	---	---	---
Elk Density^2	---	---	---	---	---	---	---	---	---	-0.13	-0.25	-0.02	---	---	---	---	---	---
Elk Group Size Avrg	---	---	---	0.16	-0.03	0.37	0.10	-0.09	0.31	---	---	---	---	---	---	---	---	---
Elk Group SizeMedian	---	---	---	---	---	---	---	---	---	---	---	---	0.23	-0.04	0.52	---	---	---
Elk Group Size 70^{th} Percentile	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	0.23	-0.04	0.49
Elk Group Density	---	---	---	0.14	-0.11	0.45	0.20	-0.08	0.51	---	---	---	-0.05	-0.26	0.16	0.01	-0.15	0.18
Elk Group Density^2	---	---	---	---	---	---	-0.07	-0.19	0.05	---	---	---	-0.09	-0.21	0.03	-0.10	-0.21	0.01
Territory Size	-0.09	-0.29	0.13	-0.05	-0.26	0.20	-0.04	-0.26	0.18	-0.08	-0.27	0.13	-0.01	-0.28	0.28	-0.07	-0.27	0.14
SWE[c]	-0.04	-0.33	0.23	-0.02	-0.33	0.26	-0.01	-0.28	0.25	0.01	-0.26	0.28	0.04	-0.12	0.22	0.01	-0.27	0.29
Early Winter[d]	-0.25	-0.76	0.22	-0.23	-0.73	0.27	-0.20	-0.67	0.24	-0.18	-0.64	0.28	-0.22	-0.68	0.27	-0.18	-0.67	0.32
Intercept	-4.11	-4.54	-3.68	-4.13	-4.57	-3.67	-4.07	-4.51	-3.63	-4.02	-4.43	-3.60	-4.05	-4.49	-3.61	-4.06	-4.48	-3.64

a Models used to assess the sensitivity of different measure of elk herd size on encounter rate.
b Parameter estimates are from variables centered and scaled using mean and standard deviation.
c SWE variable is the average daily snow-water equivalent during the study.
d Early winter parameter estimates represent the difference in encounter rates between early winter (Nov-Dec) and late winter (March).

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APPENDICES

Appendix A. An example of the wolf-prey interaction form (side 1) used to determine wolf-elk encounter rates on the Northern Range (NR) of Yellowstone National Park (YNP) (Smith et al. 2011).

EXAMPLE 3:

Page 2 of 2

Data entered into database: ______ (initials)
Data in database double checked:

YELLOWSTONE WOLF-PREY FORM
(Wolf and Elk, Deer, Bison, Moose, Bighorn sheep, Mt. Goat, Pronghorn)

Date: 3 / 24 / 02 **Observers:** First initial, Last name of observers. (circle) Air (Ground)

Pack: Leopold **Encounter #:** 1 **Attempt #:** 2 **Is this Attempt simultaneous:** Y (N) UNK

# of Attempts in Encounter: 2 **Encounter Time (Begin/End):** 100510 / 101410 **Duration:** 9 min ϕ sec

General Location: ______

UTM (at first point of encounter) **Easting** ______ **Northing** ______ **NAD 27 / 83**

Topography: *(circle one)* Flat, Slope, Ridge, Rolling hills, Ravine

Cover: *(Circle one)* Upland grass, Wet meadow, Riparian brush, Thermal area, Sagebrush, Conifer, Aspen, Unvegetated, Burn, Creek, Lake

Interaction Initiated By: (wolf) prey species unknown

Snow Depth (meters): ______ **Crust on Snow:** Yes No Unknown

WOLF INFO: *(Circle all that apply for each category and provide # of each age type when applicable – if number of wolves is unknown for particular interaction type, circle* **unk** *below category type)*
# of wolves: 6

							WOLF ID'S AM	AF	A-A	PUP
Alpha Male Present?: (Yes) No Unk		**Alpha Female Present?** (Yes) No Unk								
Individuals involved Approach:	**unk**	AM	AF	__Aux-Adult	__Pup	__Unk				
Individuals involved Watch:	**unk**	(AM)	(AF)	(1 Aux-Adult)	(3 Pup)	__Unk	2M	7F	259F	
Individuals involved Attack:	**unk**	(AM)	(AF)	(1 Aux-Adult)	(3 Pup)	__Unk	2M	7F	259F	
Attack point of wolves:		Neck	Hind end	Nose Flank	Front leg	Unknown				
Individuals involved Target:	**unk**	(AM)	(AF)	(1 Aux-Adult)	(3 Pup)	__Unk	2M	7F	259F	
Attack point of wolves:		Neck	Hind end	Nose Flank	Front leg	Unknown				
Individuals Capture Attempt:	**unk**	AM	AF	__Aux-Adult	__Pup	__Unk				
Attack point of wolves:		Neck	Hind end	Nose Flank	Front leg	Unknown				
Who initiated travel?	(**unk**)	AM	AF	__Aux-Adult	__Pup	__Unk				
Who initiated approach?	**unk**	AM	AF	__Aux-Adult	__Pup	__Unk				
Who initiated watch?	(**unk**)	AM	AF	__Aux-Adult	__Pup	__Unk				
Who initiated attack?	**unk**	(AM)	AF	__Aux-Adult	__Pup	__Unk	2M			
Who initiated target?	(**unk**)	AM	AF	__Aux-Adult	__Pup	__Unk				
Who initiated capture attempt?	**unk**	AM	AF	__Aux-Adult	__Pup	__Unk				

(OVER)

(cont'd) Appendix A. An example of one wolf-prey interaction form (side 2) used to determine encounter rate of wolf-packs on the Northern Range (NR) of Yellowstone National Park (YNP) (Smith et al. 2011).

PREY INFO: *(Circle all that apply for each category and provide # of each age type when applicable)*

Species: Elk

Encounter Group Size: _____ *or* UNKNOWN **Encounter Group Comp.:** __ MA __ FA __ YY __ UNK MIXED

Attempt Group Size: 10 *or* UNKNOWN **Attempt Group Comp.:** (10 MA) __ FA __ YY __ UNK MIXED

Prey Response during: *(Applies to portion of group that wolves are engaging with)*

Approach: GT SG MG RN ST CH KI TP FS MW EY AH MC OS U

Watch: (GT) SG MG RN (ST) CH KI TP FS MW EY AH MC OS U

Attack: (GT) SG MG RN (ST) (CH) KI TP FS MW EY AH MC OS U

Target: GT SG MG (RN) (ST) CH KI TP FS MW EY AH MC OS U

If wolves target, individual prey info: (MA) FA YY UNK

Capture Attempt: GT SG MG RN ST CH KI TP FS MW EY AH MC OS U

If capture attempt, individual prey info: MA FA YY UNK

If prey initiate encounter: **Prey Behavior:** approach chase attack

Wolf Response: travel away stand ground attack reposition

If prey attempt to injure wolves at any point, what happened to the wolf?

No injury Kicked Antlered/Horned Tripped Unknown

DID PREDATION ATTEMPT RESULT IN A KILL? Yes (No) Unknown **MORT #:** __________

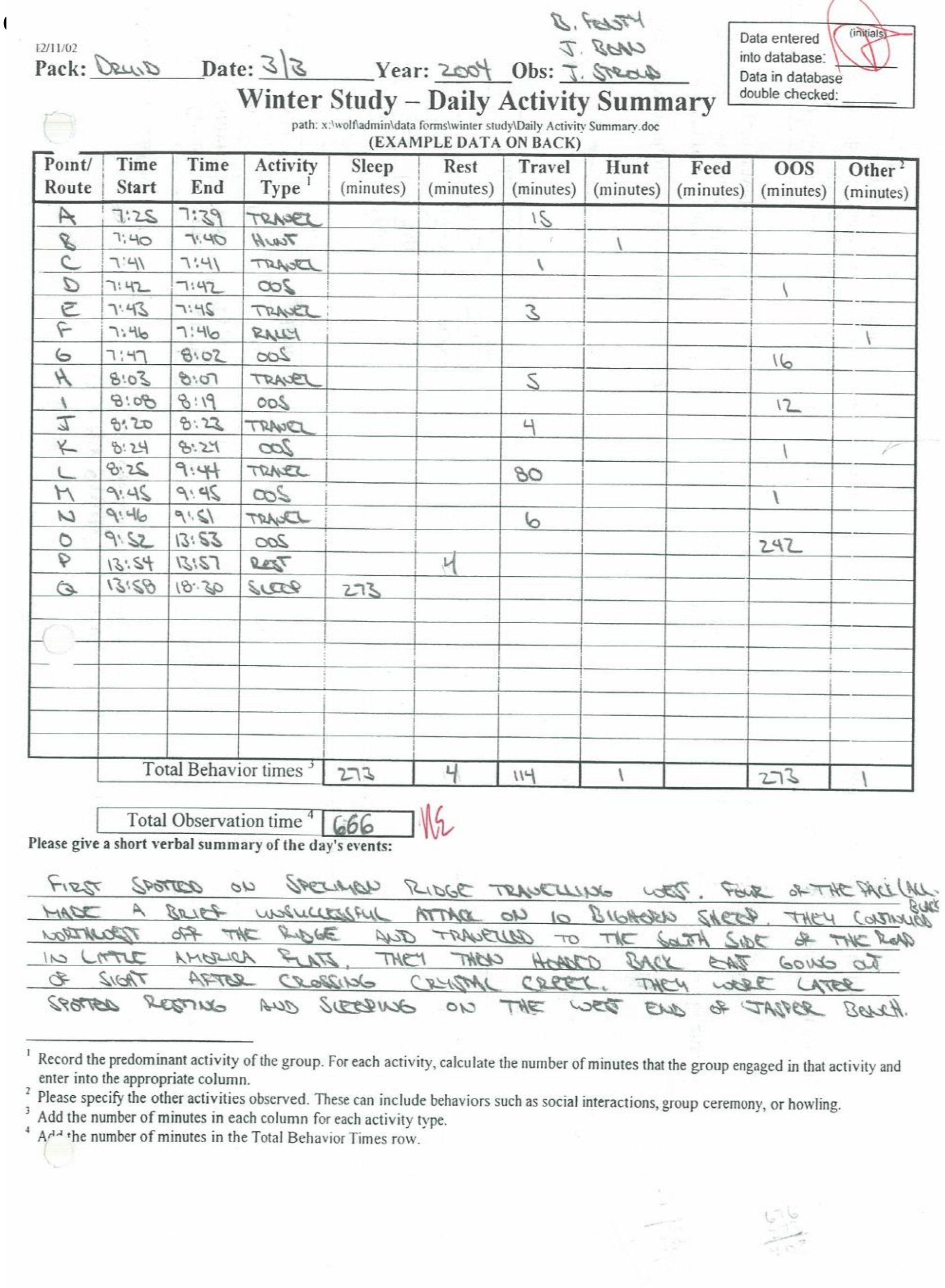
COMMENTS: Comments are extremely important. Describe what is seen in as much detail as possible.

EXAMPLE 3:

Six wolves (2M, 7F, 259F, 3 uncollared pups) are traveling when first seen. They encounter a group of 16 bull elk. 2M initiates a watch at 100510 of the elk. The elk stand. All wolves watch. 2M then initiates an approach of the 16 bulls. The bulls group together and stand their ground. 7F, 259F, and 2 pups approach with 2M. 7F initiates an attack of the elk. The elk separate (into groups of 10 and 6) and run. 259F and 1 pup are also involved. The 3 wolves chase the group of 6 before giving up pursuit and regrouping (all 6 wolves) at 100830 – these wolves watch the sub-group of 10 elk and 2M initiates an attack of these elk. The elk stay grouped and stand their ground. All 6 wolves hold at bay this group of 10 elk. One of the elk charges at the wolves at this point. The wolves then run it and begin pursuing this elk (target). Unknown which wolf initiated target. The elk runs with all 6 wolves in pursuit before standing its ground. The wolves then test the elk until 101410 before traveling off. The wolves travel until bedding for the afternoon.

Continue comments on additional pages if necessary. Did you? (circle one): Y (N)

Appendix B. An example of one daily-activity summary and daily-activity map from the … d distance


12/11/02

Pack: DRUID Date: 3/3 Year: 2004 Obs: J. STROUD, B. FENSTY, J. BOND

Data entered into database: (initials)
Data in database double checked: ______

Winter Study – Daily Activity Summary

path: x:\wolf\admin\data forms\winter study\Daily Activity Summary.doc
(EXAMPLE DATA ON BACK)

Point/ Route	Time Start	Time End	Activity Type [1]	Sleep (minutes)	Rest (minutes)	Travel (minutes)	Hunt (minutes)	Feed (minutes)	OOS (minutes)	Other [2] (minutes)
A	7:25	7:39	TRAVEL			15				
B	7:40	7:40	HUNT				1			
C	7:41	7:41	TRAVEL			1				
D	7:42	7:42	OOS						1	
E	7:43	7:45	TRAVEL			3				
F	7:46	7:46	RALLY							1
G	7:47	8:02	OOS						16	
H	8:03	8:07	TRAVEL			5				
I	8:08	8:19	OOS						12	
J	8:20	8:23	TRAVEL			4				
K	8:24	8:24	OOS						1	
L	8:25	9:44	TRAVEL			80				
M	9:45	9:45	OOS						1	
N	9:46	9:51	TRAVEL			6				
O	9:52	13:53	OOS						242	
P	13:54	13:57	REST		4					
Q	13:58	18:30	SLEEP	273						
	Total Behavior times [3]			273	4	114	1		273	1

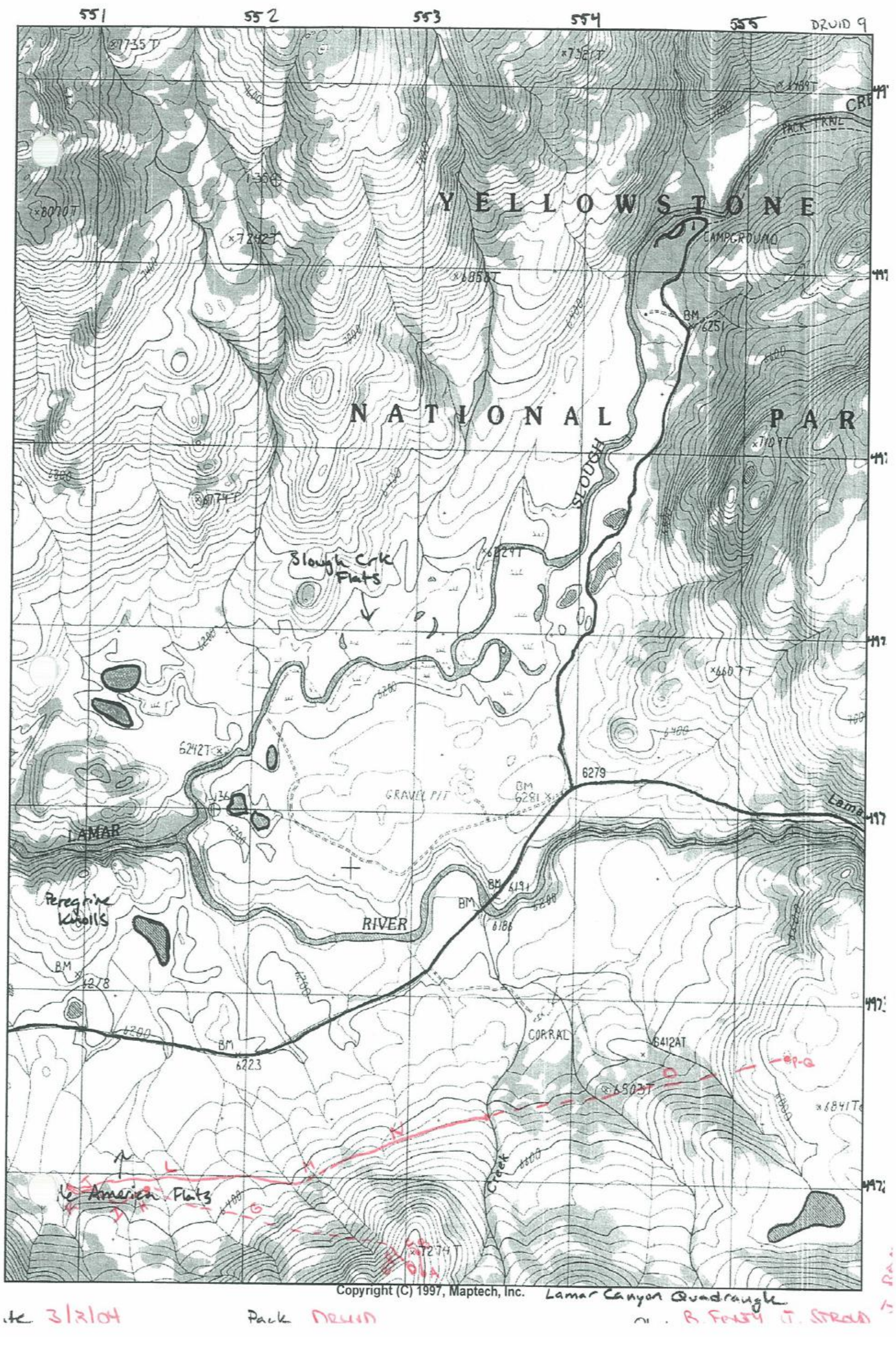
Total Observation time [4] 666

Please give a short verbal summary of the day's events:

FIRST SPOTTED ON SPECIMEN RIDGE TRAVELLING WEST. FOUR OF THE PACK (ALL BLACKS) MADE A BRIEF UNSUCCESSFUL ATTACK ON 10 BIGHORN SHEEP. THEY CONTINUED NORTHWEST OFF THE RIDGE AND TRAVELLED TO THE SOUTH SIDE OF THE ROAD IN LITTLE AMERICA FLATS. THEY THEN HEADED BACK EAST GOING OUT OF SIGHT AFTER CROSSING CRYSTAL CREEK. THEY WERE LATER SPOTTED RESTING AND SLEEPING ON THE WEST END OF JASPER BENCH.

[1] Record the predominant activity of the group. For each activity, calculate the number of minutes that the group engaged in that activity and enter into the appropriate column.
[2] Please specify the other activities observed. These can include behaviors such as social interactions, group ceremony, or howling.
[3] Add the number of minutes in each column for each activity type.
[4] Add the number of minutes in the Total Behavior Times row.

(cont'd) Appendix B. An example of one daily-activity summary and daily-activity map from the Druid Peak Pack in March 2004 which were digitized to determine time and distance observed traveling resulting in the data in Appendix C.



Appendix C. Procedure used to digitize and link the daily-activity summaries, daily-activity maps, and kill dataset to create a dataset from which the time observed traveling not associated with a kill was derived.

Linear Referencing in ArcMap
Linear Referencing is typically used in traffic or utility data modeling to record road or pipe attributes over space with directional capabilities. This process is also capable of associating behavior with the distance and direction of daily actives. Written by Charlene Arney and Hans Martin.

PROJECT SUMMARY:
The objective of this project is to digitize the Daily-Activity Maps and spatially reference the corresponding activities which are found in the Daily-Activity Summary database to facilitate in the analysis of wolf behavior, activity, and movement. These data has been collected by wolf-project ground crews on the Northern Range of Yellowstone National Park since 2000 during the biannual winter studies during which wolf packs are observed from the ground using spotting scopes and binoculars. Pack activities are recorded and mapped in the Daily-Activity Maps and Daily-Activity Summaries each day the wolves are observed. This database links these two forms with the Ground Tracking database which monitors individual wolves observed and pack size and the kill database which identifies kills based on unique kill numbers.

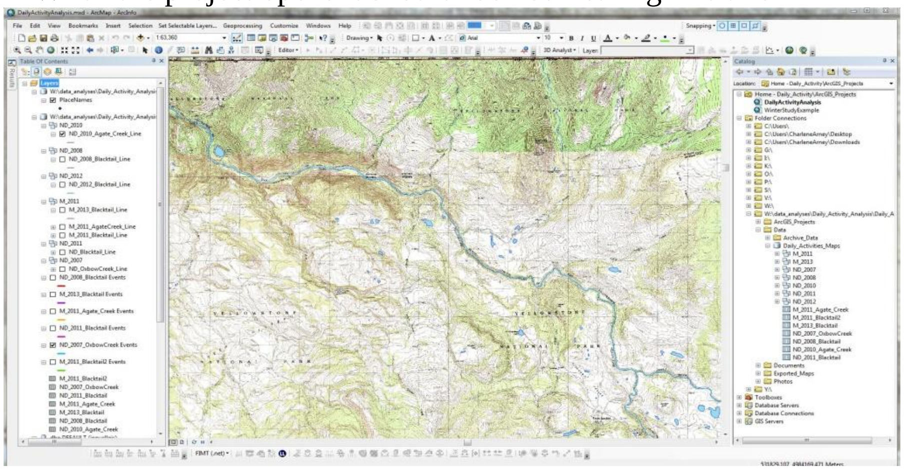
The Daily Activity map document can be found at W:\data_analyses\Daily_Activity_Analysis\Daily_Activity\ArcGIS_Projects\DailyActivityAnalysis.mxd
Double click on this .mxd to open the project. An .mxd is a map document that stores connections to spatial data for display and analysis. It does not actually store any of the data. This can cause "links" or the paths for the data to be broken when files are renamed or moved.

Map Scores

As you are editing various issues will arise from how the technician created the hard copy map. These include spatial activities like travels being only a point on the map, the map lines getting confused, OOS with no lines showing assumed travel past, and many more exciting acts of stupidity. Consult a wolf project staff if they are around and if not Flag the map in the excel file located at W:\data_analyses\Daily_Activity_Analysis\Daily_Activity\Documents\Flagged Maps.

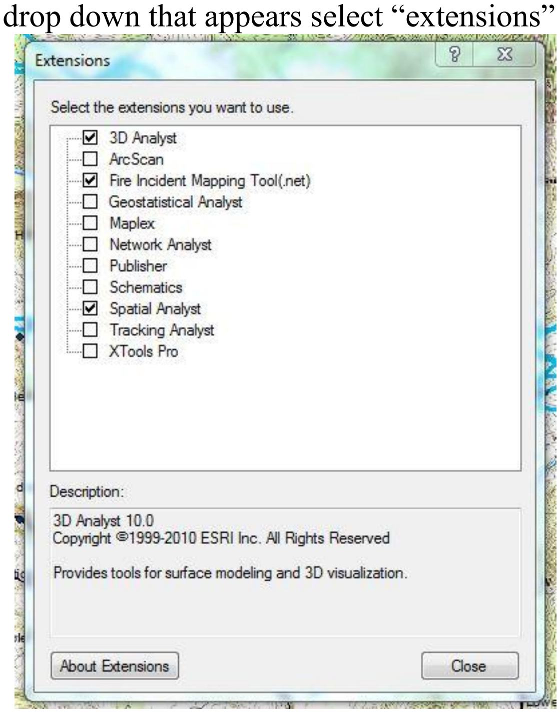
For each of these errors enter a 1 in the MapScore column. This will eventually be used to create map scores that will represent the quality of the data.

1. Follow the file path above and double click on this .mxd to open the project. When the project opens it should look something like this



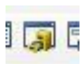
On the left is the Table of Contents where the features of the map are displayed. On the right is the Catalog. This is where data can be added to the maps and new shape files are created or deleted. Above are the tool bars that contain the tools you will use to manipulate your daily activity data. First the linear referencing extension and tool bar need to be added to you GIS home screen.

2. On the top most toolbar on your ArcGIS home screen click on the "Customize" drop down that appears select "extensions" make sure Spatial Analyst is selected

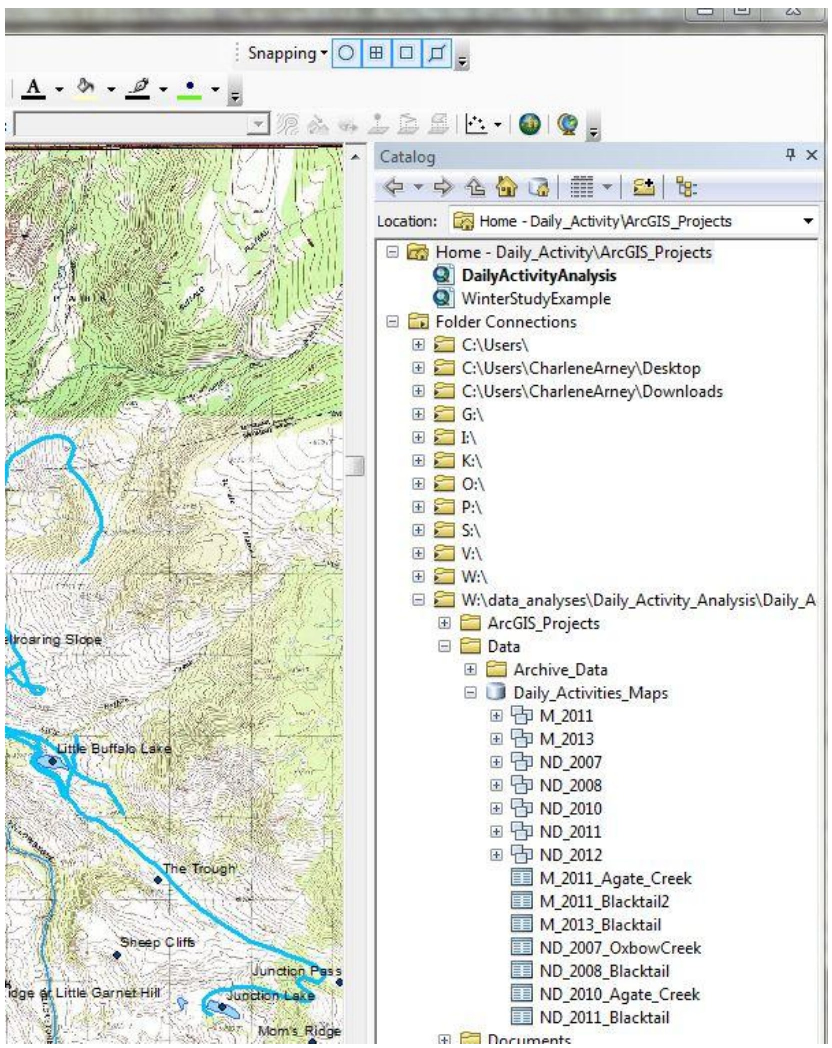


3. Select the Customize drop down again and select toolbars. Enable “Route Editing” by selecting it.

4. If your Catalog menu is not docked to the right side of your GIS home screen do that now. In the Standard toolbar on your home screen select the ArcCatalog button.

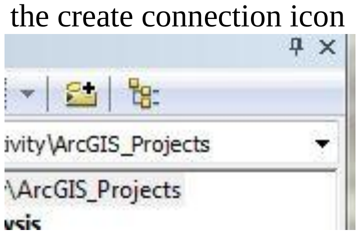


When the ArcCatalog menu appears drag it to the right side of the home screen and small blue arrows will appear on the sides of your home screen. Pull the catalog menu to the far right blue arrow. This should doc your catalog menu.



You can close and open this window using the push pin icon on the upper right hand corner of the window.

5. Expand your ArcCatolog window pinned to the right side of your screen. You will need to add a folder connection to the O:drive where the wolf data is stored and the G:drive where the base data is stored. At the top of the catalog window is the create connection icon

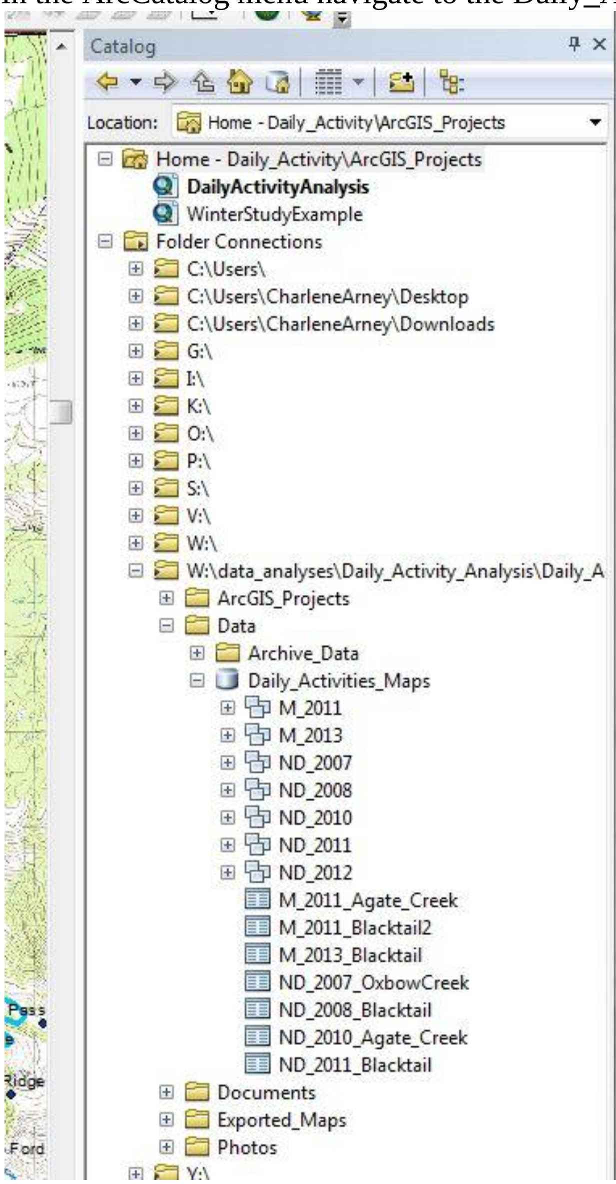


Select this icon and in the pop up window navigate to W:\data_analyses\Daily_Activity_Analysis\Daily_Activity

and select ok. Repeat this process for G:\ArcGIS_Layers.
You are now ready to begin the digitizing process. Things you will need to get started are.

1. An excel file for an individual pack's winter study
2. The hard copy maps and observations for that pack

6. In the ArcCatalog menu navigate to the Daily_Activities_Maps.gdb

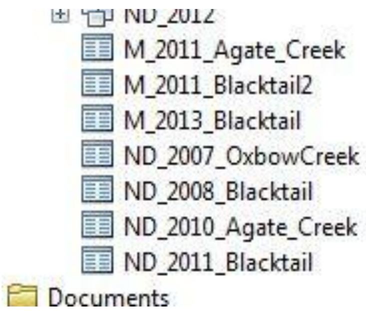


Right click on the Daily_Activities_Maps geodatabase which is the grey cylinder icon. In the pop up that appears select

Import →Table (single)

Navigate to where the winter study excel data files are stored. (W:\data_analyses\Daily_Activity_Analysis\Daily_Activity\Documents\For_Charly) and select the pack you want to digitize by double clicking it. Name the file WinterStudyType_Year_PackName (M for March or ND for November/December and be sure to use the full pack name I.E. Oxbow Creek vs Oxbow) EXAMPLE: ND_2007_Oxbow_Creek

7. The new table is now in your geodatabase in your ArcCatalog window next to a geodatabase table icon



8. Select the new table from the catalog menu and drag it into the Table of Contents on the opposite side of your home screen. Right click the new table and select → Open

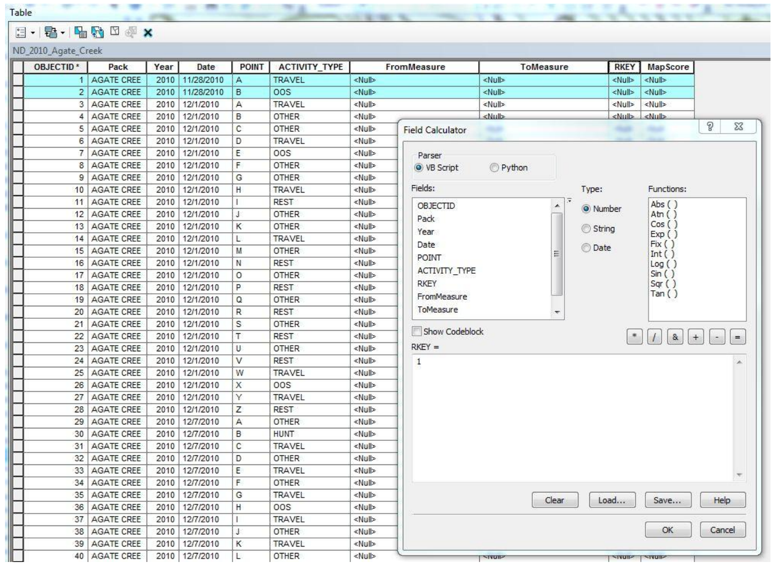
9. In the top right hand corner of the table select the table options icon and choose → Add Field

   In the pop up box name the field “RKEY” select type as “short integer” and select → OK

   Repeat these steps to create a field called FromMeasure with type as double and another called ToMeasure with type as double
   And MapScore with type as short integer
   Also add field called SPLITYES with type as short integer,
   SPLITGROUP as Short integer
   ATKILL as short integer
   MORTNUM as text

   An RKEY number must be assigned to each day. Select all of the first day’s activities. Right click the RKEY column title and select Field Calculator →

   In the menu that appears enter 1 or the next number in the series (2,3,4,5..) until each day has a unique RKEY



In the table of contents right click the table you added the fields to and select properties. Select the tab at the top called Fields. In this window you can turn fields on and off by checking and un-checking them. You only need the columns associated with behaviors and space (RKEY ect) so turn off the ones you do not need. Save your edits

10. Next you will create the line that the route will be based on. In the catalog menu right click the feature class that is the appropriate year and winter study (i.e. ND_2012) → New Feature Class. If you are digitizing a pack and year that have never been done before you will need to create a new feature dataset to hold your new feature class. To do this, right click on the geodatabase in the catalog window. And select New → Feature Dataset. Name the data set the WinterStudySeason_Year. Then create a feature class with in it.

    Name the new Feature class WinterStudy_Year_Pack_Line(M or ND). Example: M_2001_Druid_Peak_Line

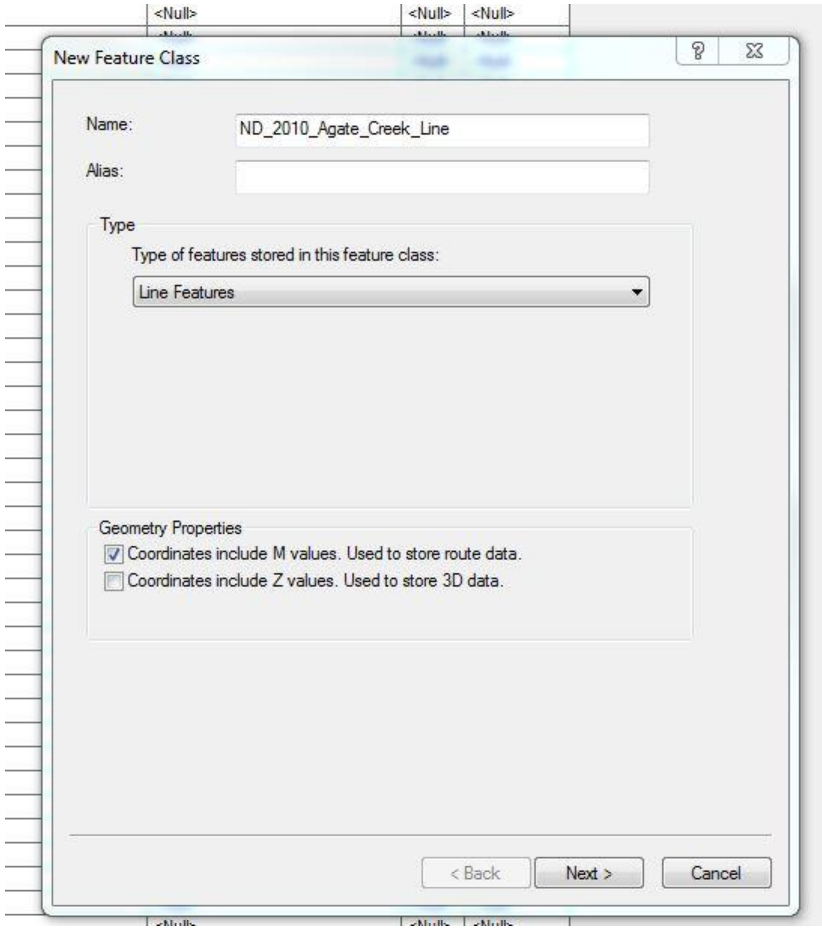
    Select Line feature for Type

    Select the box for Coordinates include M values and select continue

    Accept the default setting for the next two prompts

    Add a field called RKEY and set the type to short integer. This is how linear referencing will connect the table and the line spatially. Now select finish

The line should be automatically added to the Table of Contents(TOC) if it is not drag it into the TOC as you did the table



11. Right click on the table for the winter study/pack you are digitizing and select → Display Route Events. This is where you create the connection between the table and the line to create a route event.

Set the Route Reference to be the line you created.
Set the Route Identifier as RKEY
Select Line Events for the type of event the table contains
Select FromMeasure for From Measure
Select ToMeasure for To Measure
Leave the offset as none
Select OK

A new "Event Layer" Has been added to your Table of Contents. This is not a table you will use or edit but if it is removed from the map document the connection between the non-spatial table and the spatial line feature will be lost and the daily activity distances cannot be measured.

12. (If the editor tool bar is not installed use the Customize drop down menu to add it.) On the editor tool bar select the editor drop down menu and
    → Start Editing

    →(Select the line feature you created that the route is to be based on) You will receive a warning that some layers are not editable which is fine. Accept this warning

You will now begin to digitize the daily activities from the hard copy maps into routes with measures. When you select the line you will edit the Create menu will appear. You can dock this on the side of your screen as you did the Catalog window.

13. Create a template for the line you are digitizing. Select the Organize Templates icon.

Select New Template from the menu bar and select the line you want to edit and then select finish. The line is now in your Create Features menu.

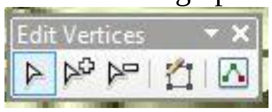
14. Using the hard copy map find the corresponding area on the topo and digitize the daily activity. When you have finished creating the line double click to finish the sketch. Digitize the entire day's activity. You will split it by behaviors later.

    Sometimes a day will have behaviors that are associated with distance. If they are at a kill they might eat and sleep all day. For this instance you would create a VERY small line that will give each behavior .01 of space. If you had 24 behaviors for a day your line would be only .24 meters long.

    To do this, locate the area where the point/line will be and create a very tiny line. Double click the line with the editor arrow and the vertices will appear. Pull the red vertice toward the green one until the SHAPE_Length in the lines attribute table matches the length you need to cover your behaviors (or close to it being a little over is better than being under) As usual copy the SHAPE_Length field into the final ToMeasure.

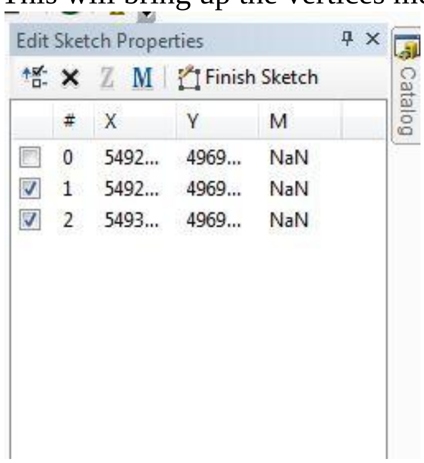
15. Select the editor selection tool and double click the route you just created

This will bring up the edit vertices toolbar.

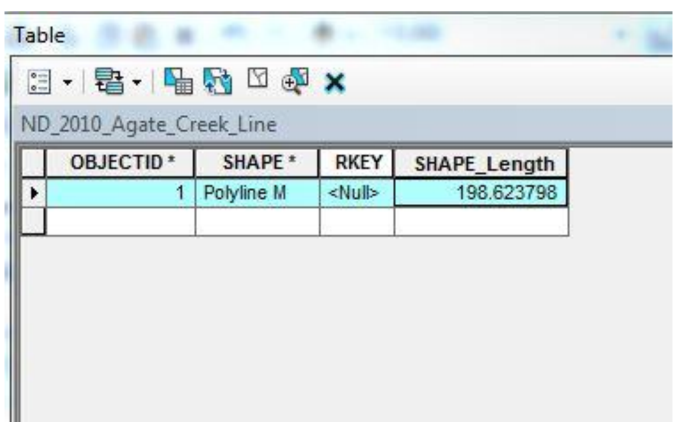


Next select the Sketch properties icon

This will bring up the vertices menu



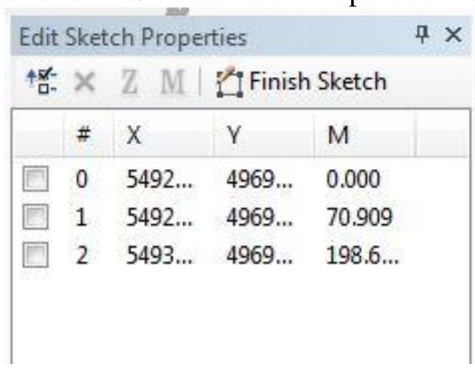
The M column is where the measures for the route will be calculated you will use the attribute table of the line feature you are editing to create this. Open that attribute table now.



OBJECTID *	SHAPE *	RKEY	SHAPE_Length
1	Polyline M	<Null>	198.623798

Right Click and copy the SHAPE_Length number and paste it into the last M value in the sketch properties menu. Enter a 0 for the M values of the first vertice.

On the route you created right click on any green vertice and select → Route Measure Editing → Calculate NaN this will update the Measures for all the vertices on the line. The Sketch Properties menu is now updated.



From the editor drop down Menu save your edits.

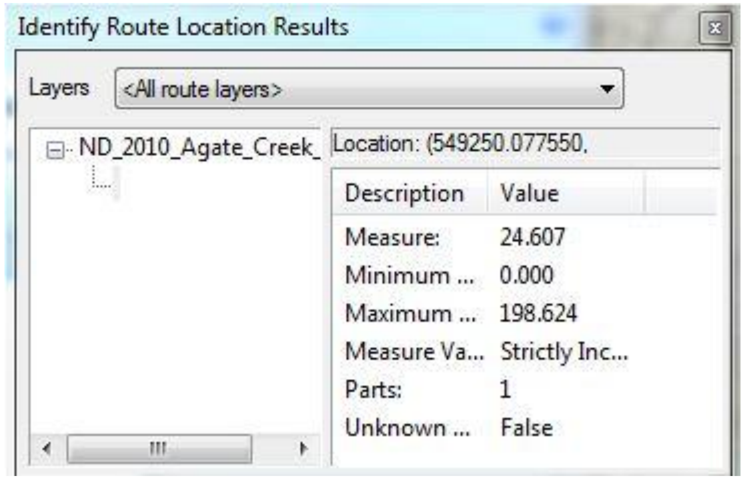
16. In the attribute table for the line feature update the RKEY to correspond with the correct daily activity RKEY that you created in the Table earlier and save your edits.

The RKEY is not linking the Route Events, Line Feature, and Daily activity table. You will never need to update the event layer because it is dynamically linked with the daily activity table and will update automatically. All three of these features are necessary to measure the routes. If the route event is deleted or lost it will have to be rebuilt using the Display Route x,y as you did earlier. This is why saving your edits frequently is important.

Certain behaviors have space associated with them and others do not but because this is a line feature space must be assigned to every row/ behavior. These non spatial behaviors are assigned an increment of .01 If, for example, the wolves traveled from 0 meters to 187.124 meters and stopped to howl the whole would take place from 187.124 meters to 187.134 meters.

17. You will now use the Route Measure tool to completely fill in the From and To Measures in the table. Select the route measures identifier tool from the Route measure tool bar.

The first behavior of each day will start at 0. So in the FromMeasure Column for the first behavior enter a 0. Using the hard copy map locate where the behavior ended and click that place on the route. This will cause the route measure pop up to appear showing the measure from the beginning of that line to the spot you selected.



Copy the measure field by right clicking it and then paste it into the ToMeasure Field for that behavior. You will need to use back space or delete to be able to see the information you just pasted because of formatting. You will also need to delete the word measure. This is a numerical field and will only allow for numbers. You may get a few errors when you are first attempting to paste in the measure but be patient and make sure you are in the cell when you paste not just selecting it.

The route event will now be superimposed over the line feature which will allow you to keep track of your progress along the line (I prefer to symbolize my route even as the same color as the line event but at a thicker line width). The line must be continuous so the end of one behavior is the beginning of the next behavior.

Use this method to spatially link the behaviors to the route based on the hard copy maps. When you reach the last ToMeasure copy the SHAPE_Length field from the corresponding line and paste it into the last field to ensure that the entire daily activity distance is accounted for.

NOTE! If the Identify Route Locations Results does not pop up try this fix! The window probably ended up off your screen. This happened to me when I went from using two smaller monitors one big monitor.

The only solution I found to fix it was to edit the registry. Make sure ArcMap is not running. Go to your start menu > click run > type in regedit > click OK.

Go to
HKEY_CURRENT_USER\Software\ESRI\ArcMap\DynSeg\IdentifyToolPos

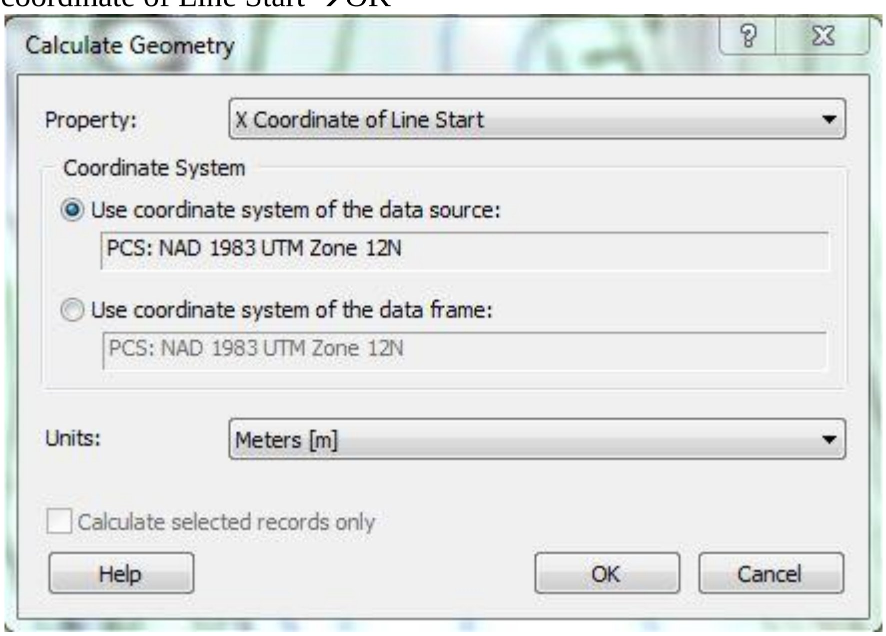
In the Value data box, replace the values that are in there with 0,0,500,300

Save your edits!!

Map Scores
As you are editing various issues will arise from how the technician created the hard copy map. These include spatial activities like travels being only a point on the map, the map lines getting confused, OOS with no lines showing assumed travel past, etc. Consult a wolf project staff member if they are around and if not Flag the map in the excel spreadsheet located at W:\data_analyses\Daily_Activity_Analysis\Daily_Activity\Documents\Flagged Maps.
For each of these errors enter a 1 in the MapScore column. This will eventually be used to create proportional map scores that will represent the quality of the data.

Calculate beginning ending x and y

When you have fully completed a data set and have all the measures completed you will add 4 Data fields columns BeginningX, BeginningY, EndingX, and EndingY with type as double. Open the Route event attribute table and right click BeginningX column → Calculate Geometry (if you are not in an edit session a warning will appear accept it and move on) From the drop down menu select X coordinate of Line Start →OK



Do these for each of the following columns. It should update in the data table as well because these are linked by the RKEY. You CANNOT calculate the geometry in the original table because it has does not spatial data to pull it from. If it does not update automatically you can link the tables by the Unique ID and use calculate field to add the UTMs to the original table. For the behaviors that have only .01 of spatial data the calculation 'errors out' and you will need to fill in these missing values with the coordinates of the end of line from before it. At this data scale there increments are not a concern.

It is important that you back up the geodatabase in the Archive folder (located in the data folder) regularly. If you delete something major or mess something up this will be your reset button.
Exporting the data:
Before you export the table, make sure to turn all fields on for the table. Then Export. A box will come up and you want to export all records. The output table should be saved in the documents folder under Completed_ws_pack. This should be saved as a dBASE Table and should be named using the same naming system as the table i.e. Winterstudyperiod_Year_Pack_Name (M_2009_Druid_Peak) This dBASE file must then be opened in EXCEL and saved as an EXCEL file.

Special situations:

1) Daily activity summaries where wolves are bedded near a carcass and feed throughout the day:

   The daily activities are designed to represent the behavior/activity of the majority of the pack. This can lead to scenarios where behavior switches occur as different numbers of wolves switch behavior or move and join other wolves in a behavior. One of the most common examples of this is when wolves are resting near a carcass and feed throughout the day. Wolves move between the carcass and bedding area but because the movement of individual wolves is not recorded as the majority of the pack's activity this movement is not recorded. Because of this, resting behavior can have a spatial component where movement occurs while wolves are resting. If one wolf goes to a carcass to feed then is joined by another wolf, and another, the activity switches from rest to feed once the majority of the pack is feeding on the carcass. Even though the majority of the pack did move from the resting/bedding area to the carcass this information is not portrayed by the daily activities because the majority of the pack was never moving at the same time. Because linear referencing requires activities to be linked by a line and a majority movement did occur in these scenarios the movement between carcasses and bedding areas will be captured under the resting behavior. To account for this movement being associated with a carcass we will add two columns to the table [CARCASS] and [MORTNUM]. The first indicates if the activity was associated with a carcass. <Null> indicates that the activity wasn't associated with a carcass and 1 indicates that it is. The next column [MORTNUM] identifies the mortality number(s) associated with the activity and is a text string.

Handling Procedure:
When activities are associated with a carcass with no information regarding distance traveled between activities
1) FLAG the activity [YES]
2) In comments write AT KILL
3) Digitize a line from the carcass location to the location of the other activities
3) To account for this movement being associated with a carcass we will add two columns to the table [CARCASS] and [MORTNUMS]. The first indicates if the activity was associated with a carcass. <Null> indicates that the activity wasn't associated with a carcass and 1 indicates that it is. The next column [MORTNUMS] identifies the mortality number(s) associated with the activity as a text string. To determine the carcass numbers associated with a daily activity, reference either the carcass numbers on the DAS sheet or use the table Query_FULL_WS_Kills_Ground_Fed_On_IE.xlsx found under the Documents folder of the Daily_Activity folder.
(Bedding, wolf-nonprey interactions, short travels to and from the carcass)
*travel activity and bedding which extends further than 1 km from the kill site is treated as behavior independent of the kill location.
4) Once you have done this for the activities associated with a carcass begin to digitize the data. When there is a jump in activities from one point location to another, (i.e. Rest to feed) these two locations are joined by a line with the Rest activity FromMeasurement beginning at the resting location and ToMeasurement ending at feeding location. If there was a pre-existing path (identified as travel) to and from the carcass follow this path as wolves usually take similar paths to and from carcasses.

2) Daily activity summaries where packs split into multiple groups.
   For scenarios when a pack splits into 2 or more groups during the day and these splits are recorded you must first add these splits into the pack_split_table.xlsx found in the Daily_Activity folder under Documents. The pack_split_table.xlsx is used to identify individual wolves that are present in the split groups as well as the number of wolves present. The pack_split_table will be used for this purpose instead of the wolf locations database when a split is indicated. This table is set up in the same fashion as the wolf locations database and should be filled out similarly. Each collared or wolf uniquely identified in the split group is recorded on a single line in the table. The total group size/composition is

also filled out if available. Each split group receives a SPLITGROUPID that corresponds to that group's daily activities. If the pack splits into 2 different groups the initial group receives a SPLITGROUP ID of 0 or <NULL> indicating that the wolf locations database correctly identifies the individuals present in this group. The groups formed by the split receive a SPLITGROUPID of 1 and 2. If these groups come together at the end of the day and form a group with the same number of individuals as they started with, the SPLITGROUPID for the activity returns to 0. If however the groups come together at the end of the day and more wolves are present then this new group would get a SPLITGROUPID of 3 and this group would have corresponding lines in the pack_split_table. For activities where a pack is split enter a 1 into the SPLITYES column for that activity. This identifies that the pack_split_table must be used to obtain the correct group size for this activity.

When mapping these scenarios the two groups obtain a new RKEY which corresponds to the line representing movement and activity locations. The ACT_ID should remain the same.

NOTE: if activities of two separate groups from the same pack are recorded and have different initial locations this information should be identified in the wolf locations database and these independent groups should be assigned a separate Act_ID as well as separate point locations.

Appendix D. Example of the wolf (*Canis lupus*) pack activity dataset resulting from digitizing and combining the daily-activity summaries (Appendix B), daily-activity maps (Appendix B), kill dataset, and wolf locations dataset for one day of observations.

OBJECTID[a]	Unique_ID[a]	ActID[a]	PACK_TYPE[b]	FLAG	Pack	OBS[b]	GROUP[b]	Year	Date	POINT	START	END	ACTIVITY_TYPE[c]	TIME
37	7774	656	GROUND	NO	DRUID PEAK	1	A	2004	3/3/2004	A	07:25	07:39	TRAVEL	15
38	7775	656	GROUND	NO	DRUID PEAK	1	A	2004	3/3/2004	B	07:40	07:40	HUNT	1
39	7776	656	GROUND	NO	DRUID PEAK	1	A	2004	3/3/2004	C	07:41	07:41	TRAVEL	1
40	7777	656	GROUND	NO	DRUID PEAK	1	A	2004	3/3/2004	D	07:42	07:42	OOS	1
41	7778	656	GROUND	NO	DRUID PEAK	1	A	2004	3/3/2004	E	07:43	07:45	TRAVEL	3
42	7779	656	GROUND	NO	DRUID PEAK	1	A	2004	3/3/2004	F	07:46	07:46	OTHER	1
43	7780	656	GROUND	NO	DRUID PEAK	1	A	2004	3/3/2004	G	07:47	08:02	OOS	16
44	7781	656	GROUND	NO	DRUID PEAK	1	A	2004	3/3/2004	H	08:03	08:07	TRAVEL	5
45	7782	656	GROUND	NO	DRUID PEAK	1	A	2004	3/3/2004	I	08:08	08:19	OOS	12
46	7783	656	GROUND	NO	DRUID PEAK	1	A	2004	3/3/2004	J	08:20	08:23	TRAVEL	4
47	7784	656	GROUND	NO	DRUID PEAK	1	A	2004	3/3/2004	K	08:24	08:24	OOS	1
48	7785	656	GROUND	NO	DRUID PEAK	1	A	2004	3/3/2004	L	08:25	09:44	TRAVEL	80
49	7786	656	GROUND	NO	DRUID PEAK	1	A	2004	3/3/2004	M	09:45	09:45	OOS	1
50	7787	656	GROUND	NO	DRUID PEAK	1	A	2004	3/3/2004	N	09:46	09:51	TRAVEL	6
51	7788	656	GROUND	NO	DRUID PEAK	1	A	2004	3/3/2004	O	09:52	13:53	OOS	242
52	7789	656	GROUND	NO	DRUID PEAK	1	A	2004	3/3/2004	P	13:54	13:57	REST	4
53	7790	656	GROUND	NO	DRUID PEAK	1	A	2004	3/3/2004	Q	13:58	18:30	REST	273

a These categories are defined in Appendix E and are used in the linear referencing process.
bThese categories link this data set to the Yellowstone Wolf Project's Wolf Locations Dataset.3 Definitions for activity codes can be found in Smith et al. 2011.

(cont'd) Appendix D. Example of the wolf (*Canis lupus*) pack activity dataset resulting from digitizing and combining the daily-activity summaries (Appendix B), daily-activity maps (Appendix B), kill dataset, and wolf locations dataset for one day of observations.

OBJECTID	OTHER_DESC[d]	COMMENTS	RKEY	FromMeasure[d]	ToMeasure[d]	MapScore[e]	SPLITYES[f]	SPLITGROUPf	ATKILL[g]
37			2	0.0	105.8	0	0	0	0
38			2	105.8	114.0	0	0	0	0
39			2	114.0	161.5	0	0	0	0
40			2	161.5	278.2	0	0	0	0
41			2	278.2	348.8	0	0	0	0
42	SOCIALIZE		2	348.8	348.8	0	0	0	0
43			2	348.8	1890.7	0	0	0	0
44			2	1890.7	1999.9	0	0	0	0
45			2	1999.9	2258.8	0	0	0	0
46			2	2258.8	2350.2	0	0	0	0
47			2	2350.2	2436.3	0	0	0	0
48			2	2436.3	3878.0	0	0	0	0
49			2	3878.0	4082.9	0	0	0	0
50			2	4082.9	5087.3	0	0	0	0
51			2	5087.3	6968.9	0	0	0	0
52			2	6968.9	6968.9	0	0	0	0
53			2	6968.9	6968.9	0	0	0	0

c OTHER_DESC indicates what the behavior classified as OTHER was interpreted as by the field crew.
d From(To)Measure indicates what distance along the daily map the activity began (From) and ended (To)
e MapScore indicates if this activity was clearly identified on the map (0) or if it was not (1)
f SPITYES and SPLITGROUP link this dataset with a dataset which indicates the number and ID of wolves that were observed in this activity if the pack was split.
g ATKILL indicates if this activity was associated with a kill.

(cont'd) Appendix D. Example of the wolf (*Canis lupus*) pack activity dataset resulting from digitizing and combining the daily-activity summaries (Appendix B), daily-activity maps (Appendix B), kill dataset, and wolf locations dataset for one day of observations.

OBJECTID	MORTNUM[h]	BeginningX[i]	BeginningY[i]	EndingX[i]	EndingY[i]
37		553054.1	4971705.0	553024.5	4971806.6
38		553024.5	4971806.6	553017.0	4971809.9
39		553017.0	4971809.9	552971.6	4971821.5
40		552971.6	4971821.5	552920.3	4971759.6
41		552920.3	4971759.6	552867.9	4971806.6
42		552867.9	4971806.6	552867.9	4971806.7
43		552867.9	4971806.7	551373.4	4972113.1
44		551373.4	4972113.1	551271.3	4972092.8
45		551271.3	4972092.8	551038.9	4972100.9
46		551038.9	4972100.9	550947.6	4972103.2
47		550947.6	4972103.2	550876.5	4972137.8
48		550876.5	4972137.8	552297.3	4972173.7
49		552297.3	4972173.7	552474.6	4972275.1
50		552474.6	4972275.1	553431.8	4972556.6
51		553431.8	4972556.6	555272.9	4972910.8
52		555272.9	4972910.8	555272.9	4972910.8
53		555272.9	4972910.8	555272.9	4972910.8

h MORTNUM indicates the unique kill number assigned by the kill database that the wolves are associated with during this activity.
i Beginning X(Y) and Ending X(Y) are the UTM Coordinates where activity began and ended.

Appendix E. R code and output for the nonlinear elk (*Cervus elaphus*) density Bayesian model of wolf (*Canis lupus*)-elk encounter rate.

Encounter Rate Model

Hans Martin

Saturday, April 16, 2016

Load libraries and set working directory

```
library(ggplot2)
library(R2jags)
library(R2WinBUGS)
library(mcmcplots)
```

Read in Encounter Rate Data

```
encounter_data_set<-read.csv("thesis_wolf_elk encounter_data_set.csv")
```

JAGS random intercept model:

family-Negative Binomial
Fixed effects:elk_density.sc,elk_density.sc2, mean_SWE.sc, study, kde.area.90.sc, Pack.Size.sc
Random effects: pack, winter.year
Offset: Log.time.in.view.travel
model names: jags.ri.negbin.mode

```
jags.ri.negbin.model<-function(){

  # Priors for the intercepts
    for (j in 1:n.winter.year){
      alpha.year[j]~dnorm(0,  tau.int.year)  # Assigns random intercepts for each winter year
    }
  tau.int.year<-1/(sigma.int.year*sigma.int.year)
  sigma.int.year~dunif(0,50) #Standard deviation hyperparameter for random intercepts.

       # Priors for the intercepts
    for (i in 1:n.pack){
      alpha.pack[i]~dnorm(0, tau.int.pack)  # Assigns random intercepts for each unique pack
    }
  tau.int.pack<-1/(sigma.int.pack*sigma.int.pack)
  sigma.int.pack~dunif(0,50) #Standard deviation hyperparameter for random intercepts for pack.

    # Priors for regression parameters
    bo~dnorm(0, 0.001)  #Intercept
    beta.elk_density_in_territory.sc~dnorm(0, 0.001) #Prior for the effect of elk density
    beta2.elk_density_in_territory.sc~dnorm(0, 0.001) #Prior for the effect of elk density squared
    beta.mean_SWE.sc~dnorm(0, 0.001) #Prior for mean SWE
    beta.kde.area.90.sc~dnorm(0, 0.001) #Prior for Territory size
    beta.Pack.Size.sc~dnorm(0, 0.001) #Prior for pack size
    beta.study~dnorm(0, 0.001) # Prior for the difference in encounter rate between late winter and early
winter
    theta~dunif(0,50) # Prior for the theta Value for the negative binomial distribution
    # Likelihood
    for (k in 1:nobs) {
     elk.encounters[k]~dnegbin(p[k],theta)  #The observed value comes from a negative binomial distribution
     p[k] <- theta/(theta+mu[k])
      log(mu[k]) <- bo+alpha.pack[pack[k]]+alpha.year[winter.year[k]]+
```

```
beta.elk_density_in_territory.sc*elk_density_in_territory.sc[k]+beta2.elk_density_in_territory.sc*elk_densi
ty_in_territory.sc[k]^2+beta.study*study[k]+
beta.mean_SWE.sc*mean_SWE.sc[k]+beta.kde.area.90.sc*kde.area.90.sc[k]+beta.Pack.Size.sc*Pack.Size.sc[k]+1*l
og(Time.in.view.travel.no.kill[k]) #Expected value with time in view travel added as an offset so that this
is a model of encounter rate.
    #added to make prediction curves and to calculate Bayesian p-values
    Presi[k] <- (elk.encounters[k] - mu[k]) / sqrt(mu[k]+mu[k]*mu[k]/theta) # Pearson residuals
    elk.encounters.new[k] ~ dnegbin(p[k],theta)    # Replicate data set
    Presi.new[k] <- (elk.encounters.new[k] - mu[k]) / sqrt(mu[k]+mu[k]*mu[k]/theta) # Pearson residuals
    D[k] <- pow(Presi[k], 2)
    D.new[k] <- pow(Presi.new[k], 2)
    }
  #Sum discrepancy measures
  fit<-sum(D[])
  fit.new<-sum(D.new[])
  }
   # Bundle data
  jags.data <- list(elk.encounters=encounter_data_set$elk.encounters,
elk_density_in_territory.sc=as.numeric(encounter_data_set$elk_density_in_territory.sc),
mean_SWE.sc=as.numeric(encounter_data_set$mean_SWE.sc),
kde.area.90.sc=as.numeric(encounter_data_set$kde.area.90.sc),
winter.year=as.numeric(as.factor(encounter_data_set$winter.year)), study=encounter_data_set$study.num,
Pack.Size.sc=as.numeric(encounter_data_set$Pack.Size.sc), pack=as.numeric(encounter_data_set$pack),
Time.in.view.travel.no.kill=as.numeric(encounter_data_set$Time.in.view.travel.no.kill),
n.pack=length(unique(encounter_data_set$pack)),
n.winter.year=length(unique(encounter_data_set$winter.year)), nobs = nrow(encounter_data_set))

  # Parameters to estimate
  parameters <- c("bo","alpha.pack", "alpha.year", "beta.elk_density_in_territory.sc",
"beta2.elk_density_in_territory.sc", "beta.mean_SWE.sc", "beta.kde.area.90.sc",
"beta.Pack.Size.sc","beta.study","sigma.int.pack","sigma.int.year", "Presi", "fit", "fit.new",
```

```r
"mu","theta","elk.encounters.new")

  # MCMC settings
  ni <- 10000
  nb <- 5000
  nt <- 3
  nc <- 3

  # Start Gibbs sampling
  out.jags.ri.negbin.model <- jags(data=jags.data, parameters.to.save=parameters, model=
jags.ri.negbin.model, n.thin=nt, n.chains=nc, n.burnin=nb, n.iter=ni, progress.bar="gui")

## module glm loaded

## Compiling model graph
##    Resolving undeclared variables
##    Allocating nodes
##    Graph Size: 1428
##
## Initializing model
```

Bayesian p-value outside winbugs in r
H_o: The data were generated by the specified negative binomial model.
H_A: The data were not generated by the specified negative binomial model.

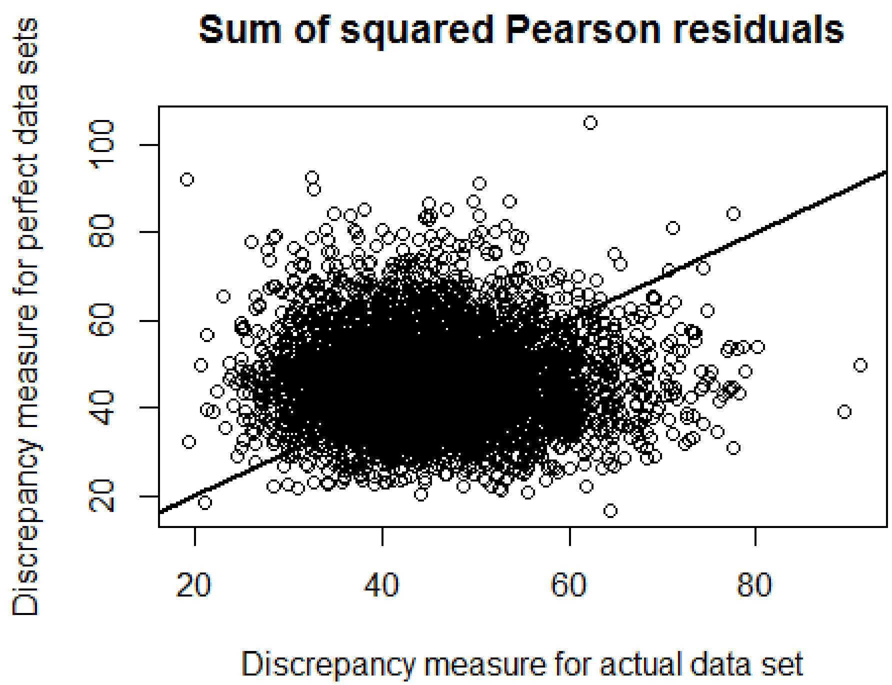
```r
#bayesian p-value goodness of fit test
mean(out.jags.ri.negbin.model$BUGSoutput$sims.list$fit.new>out.jags.ri.negbin.model$BUGSoutput$sims.list$fi
t)

## [1] 0.5182963
```

We fail to reject the null hypothesis in favor of the alternative.

Posterior Predictive Check

```
plot(out.jags.ri.negbin.model$BUGSoutput$sims.list$fit,
out.jags.ri.negbin.model$BUGSoutput$sims.list$fit.new, main =
"Sum of squared Pearson residuals",
xlab = "Discrepancy measure for actual data set",
ylab = "Discrepancy measure for perfect data sets")
abline(0,1, lwd = 2, col = "black")
```



Beta Coefficients and 95% Credible Intervals

```
CI<-
data.frame(out.jags.ri.negbin.model$BUGSoutput$summary[67:73,1],out.jags.ri.negbin.model$BUGSoutput$summary
[67:73,3],out.jags.ri.negbin.model$BUGSoutput$summary[67:73,7])
```

```r
colnames(CI)<-c("Estimate","low.ci","upper.ci")
CI

##                                         Estimate       low.ci    upper.ci
## beta.Pack.Size.sc                     0.17864658  0.007907983  0.35753070
## beta.elk_density_in_territory.sc   0.27132009  0.006586473  0.54824418
## beta.kde.area.90.sc                  -0.07046216 -0.266825681  0.13800075
## beta.mean_SWE.sc                      0.01125848 -0.261323064  0.27548069
## beta.study                           -0.18851867 -0.659395481  0.28923483
## beta2.elk_density_in_territory.sc -0.13193944 -0.245313922 -0.02299281
## bo                                   -4.01159820 -4.420426735 -3.53202662
```