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The Demography and Comparative Ethology of Top Predators in a Multi-Carnivore System

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THE DEMOGRAPHY AND COMPARATIVE ETHOLOGY OF TOP PREDATORS IN A MULTI-CARNIVORE SYSTEM

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by

Colby B. Anton

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ABSTRACT

THE DEMOGRAPHY AND COMPARATIVE ETHOLOGY OF TOP PREDATORS IN A MULTI-CARNIVORE SYSTEM

Colby B. Anton

Widespread habitat loss and overharvest have been identified as major drivers of population declines and range contractions for terrestrial mammalian species. Protected areas, like national parks, are increasingly important as refuges for rare and exploited species, as well as critical natural laboratories that serve as baseline examples of ecological processes largely free from human intervention. Yellowstone National Park (YNP) sits at the center of a 22-million-acre mosaic of federal, state, and privately managed land in northwest Wyoming known as the Greater Yellowstone Ecosystem. The region boasts one of the last nearly intact temperate-zone ecosystems on Earth, providing vital habitat for seven species of native ungulate and seven large predators. We sought to answer fundamental wildlife conservation and management questions pertaining to large predator distributions and behavior. We snow-tracked cougars (*Puma concolor*) for four consecutive winters to gather noninvasive genetic samples. We applied Bayesian spatial capture-recapture models to estimate abundance, density, apparent survival and recruitment for this cryptic, low-density species. In addition to these noninvasive studies, we captured and GPS-collared cougars and wolves (*Canis lupus*), a subset of which contained tri-axial accelerometers to monitor instantaneous movement signatures. Using GPS locations from these animals we searched and identified predation events, allowing us to directly link known predatory behavior to accelerometer readings. We compared patterns in seasonal predatory behavior for these sympatric species that utilize divergent social strategies. Finally, we examined nearly twenty years of wolf GPS locations to understand the impact of growing visitation (>4 million human visitors/year) on habitat selection patterns. We identified behavioral shifts away from the road during peak visitation but found increased tolerance by wolf packs exposed to more human visitation. Findings from our work give managers information to effectively monitor population trends for cryptic species, remotely gain insights on fine scale behavioral patterns and circumvent visitor use management issues that may be modifying wildlife behavior.

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I never thought I would go to graduate school, let alone get a PhD. I think my family was equally perplexed when I stated my intentions to go back to school six years ago. My sole motivation for choosing ecology as my primary field, was the desire to make a positive impact in conservation of wild animals and landscapes. After years of field work throughout the West, it became apparent that to be a successful conservationist, I needed to go back to school and gain the proper skills.

This dissertation was the hardest endeavor I have undertaken, and it's because of my family, friends, and collaborators that it was (finally) finished. First and foremost, I want to thank Dan Stahler who made the project a reality through spearheading its inception and following through to make sure the project was successful. It has been an honor to work with you and I truly value your mentorship and our friendship that has been strengthened through this process. I want to thank Chris Wilmers for accepting me into the program even though I did not possess much prior quantitative experience and no master's degree. Our discussions on Yellowstone ecology were helpful and I appreciated your insight from your experience there. Tim Duane was wonderful to work with and I thoroughly enjoyed talking about mountain biking, camping out the back of our trucks, and the nuances of U.S. environmental policy. Justin Suraci and Doug Niven were always willing to lend a helping hand, or some helping code.

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CHAPTER 1

INTRODUCTION

Widespread habitat loss and overharvest have been identified as major drivers of population declines and range contractions for terrestrial mammalian species (Schipper et al. 2008). Moreover, human development of natural areas increases the effects of fragmentation, particularly for carnivores that often require large areas and exist in low densities (Mattson 2004, Crooks et al. 2011). Given large carnivore's relatively slow life histories that contribute to low population growth rates, carnivore species' can be markedly vulnerable to ecosystem change (Crooks et al. 2011). As a result, members of the order Carnivora have experienced unrivaled declines and range contractions in many areas (Chapin III et al. 2000, Ripple et al. 2014). This is especially troubling given the comprehensive evidence demonstrating the fundamental role of predation in shaping ecosystem health and function (Ripple et al. 2014). Not unlike most areas within the western United States (US), predators in Yellowstone National Park (YNP), suffered from federally extirpation efforts at the turn of the 20th century (Schullery and Whittlesey 1999). Nonetheless, more recent changes to predator management policy have led to predator population restorations (Treves et al. 2017), but this can generate conflict with humans (Treves and Karanth 2003). Accordingly, research of carnivore survival, distribution, population density, habitat use, and of their varying relationships within trophic webs in areas like YNP, where predators have been increasing, may shed light on the intrinsic and extrinsic factors allowing their proliferation.

In 1872, the US government made an unprecedented decision, to designate over 1.2 million acres of land in northwestern Wyoming as a national park. An additional 1 million acres has been added since its inception. YNP became the world's first designation of this kind and sought to keep a truly wild landscape safe from the future misuse that was rapidly consuming much of America (Lowry 2010). Over the years, YNP has become an icon among protected areas and is redefining how we think about ecosystem management and large landscape conservation (Clark and Milloy 2014). It sits at the center of the 22 million-acre Greater Yellowstone Ecosystem (GYE), which is comprised of a patchwork of federal, state, and privately managed land. Due to its historically central position, both politically and within the environmental conservation movement, the GYE must continue to take the lead in developing innovative and effective management policies (Keiter 2013).

Estimating predator abundance and density can be critical to understanding relative impacts of carnivores to ecosystems. Typically, such assessments have relied on the physical capture and tagging of individual animals (Ruth et al. 2019); however, studies involving marked animals have been met with increased resistance from the public who are concerned with animal welfare (Murray and Fuller 2000, Mech and Barber 2002). In response, noninvasive methods coupled with spatial capture-recapture analytics have been developed to study the distribution and abundance of low-density species, like the cougar (Sawaya et al. 2011, Royle et al. 2013). In the case of noninvasive genetic sampling, “molecular tags”, or individual genotypes, replace traditional marking methods to individual animals (Schwartz et al. 2007).

While noninvasive methods are viable alternatives to answering certain ecological questions, there are subjects that still require animal tagging techniques. New technologies in animal borne sensors have opened doors to answering critical ecological questions (Wilmers et al. 2015). Specifically, GPS-enabled collars coupled with onboard accelerometers can be used to estimate behavior allocation (Watanabe et al. 2005, Wang et al. 2015), build energetic landscapes (Wilson et al. 2012, Shepard et al. 2013, Mosser et al. 2014, Scharf et al. 2016), measure foraging efficiency (Shepard et al. 2011, Wilson et al. 2013, Williams et al. 2014, Hubel et al. 2016a), and identify predation or den site locations (Blecha and Alldredge 2015, Mahoney and Young 2017). Species’ evolutionary adaptations and natural histories contribute to varying energetic efficiency across habitat types, climatic zones, and levels of human intervention. For large predators, prey acquisition and composition, reproductive state, and habitat selection may be primary drivers in energetic changes daily, seasonally, and annually. Further, an animal’s energy expenditure increases during movement, referred to as cost of transport (COT), which can comprise a significant amount of its daily energy budget, excluding the superlative costs of reproduction (Garland 1983, Halsey et al. 2015). Felids and canids are adapted for cursorial locomotion but differ in morphological attributes. Efficient and reliable locomotion that allows minimization of COT drives evolutionary adaptation in organisms (Dickinson et al. 2000). Moreover, efficient energy acquisition, attributable to social, morphological, and temporal covariates, can determine individual fitness and impact population productivity.

In addition, collar technologies afford the ability to quantify the effect of environmental change on wildlife conservation indicators. Worldwide, tourism is emerging as one of the biggest industries generating billions of dollars annually (Das and Chatterjee 2015). In some areas, tourism constitutes a vast majority of local income and economic generation (Das and Chatterjee 2015). Due to the usual rural geographic location of national parks and harsh, mountainous climates, the surrounding communities tend to rely heavily on tourism for incomes ranging from nature guiding companies to hotel and restaurant services. Fifty-seven parks set recreation visit records in 2015 leading to $16.9 billion spent in gateway regions, delineated as communities within 60 miles of park boundaries (Thomas and Koontz 2016). Many perceive protected areas like YNP to be pristine landscapes free of human influence; however, marked effects to non-consumptive recreational use have been documented, primarily in winter (e.g. Creel et al. 2002). Interestingly, non-winter months are characterized by significant human use through tourism, but little research has been conducted on the effects of visitor use within YNP during these seasons. Findings from other studies suggest wildlife responses to tourism could manifest through alterations in habitat selection, diel activity, or physiological performance (Whittington et al. 2005, Barnett et al. 2016, Bateman and Fleming 2017). Paved roads bisect much of the gray wolf habitat within YNP and a majority of tourists seek personal encounters with these wild canids (Resource Systems Group

2017). It is unknown to what degree variation in human activity has fitness consequences for gray wolves.

The overall objectives of this research are to not only to illuminate gaps in knowledge on cougar (*Puma concolor*) population dynamics and physiological performance, but to also incorporate anthropogenic influences, largely overlooked in previous YNP summer research, to gray wolf (*Canis lupus*) fitness dynamics. Chapter 1 utilizes noninvasive genetic sampling coupled with open-population spatial capture recapture models to provide robust cougar density estimates and population growth rates in northern YNP. Further, management of wolves within the GYE is contentious and this research takes an innovative approach to measuring the effect of human use on wolf habitat selection in a protected area. Chapter 2 builds step selection functions for wolves in northern YNP and relates habitat selection to landscape, diel and seasonal variability in human visitation to the park. Moreover, this research will improve our understanding of how carnivores coexist by looking to energetic efficiency and external competitive processes that affect fitness. Chapter 3 synthesizes the evolutionary life histories of cougars and wolves and incorporates measurements form tri-accelerometer radio collars to remotely calculate behavior allocation associated with predator foraging behavior. These research goals fit into larger scientific objectives in YNP to properly outline the effects of multiple predators on their prey species and growing tourism crucial to improving conservation both within YNP and beyond its boundaries in the GYE.

CHAPTER 2

Applying Open-Population Noninvasive Genetic Spatial Capture-Recapture to Estimate Density of a Large Carnivore

Abstract

Understanding population demography is imperative for effective wildlife conservation and management in order to link population changes over time and space to ecosystem function and processes. Many population monitoring programs focus on estimates gained from snapshots of short-term efforts that get pieced together to make inferences on population trends. Given the emergence of noninvasive data collection methods (genetic sampling, remote cameras, etc.) coupled with spatial capture-recapture (SCR) analysis, multi-year population monitoring efforts can be implemented to monitor population changes. We conducted noninvasive genetic sampling by snow-tracking cougars in Yellowstone National Park during winters 2014-2017. We successfully genotyped 39 individual cougars and estimated density and abundance using demographically closed- and open-population Bayesian SCR models. Given the low detection probability that led to low individual recapture rates, we found cougar density estimates with open-population SCR (OSCR) models that were able to effectively pool captures across all four years. OSCR models estimated between 1.72 and 2.33 cougars/100 km^2. In addition, we estimated individual (sex) and spatio-temporal (sampling effort and snow cover) covariate impacts on baseline detection probability and found a significant positive relationship between sampling effort and detection. The addition of trap- and occasion-specific snow cover increased precision of detection probability estimates. We included individual sex to estimate sex-specific differences in detection function scaling parameter (σ), baseline detection probability (*p0*) and overall abundance (N). OSCR models estimated similar scaling parameters for both sexes but calculated larger baseline detection probability for male cougars than for females. Further, OSCR estimated 21-23 female and 12-19 male cougars within our study area. Our results highlight that noninvasive genetic sampling coupled with open-population spatial capture-recapture can be effective when surveying cryptic, low-density species that produce sparse capture histories.

Introduction

Many wildlife management and conservation agencies lack robust vital rates of carnivore populations due to low detectability or inadequate funding to conduct large-scale monitoring programs. In response, noninvasive genetic sampling (NGS) has been used for over two decades as a cost-effective method to detect rare species, estimate population vital rates, evaluate landscape connectivity, measure disease dynamics, assess dietary niche, and plot spatial organization (Waits and Paetkau 2005, Long et al. 2008, Beja-Pereira et al. 2009). Traditional capture-mark recapture statistical methods have been applied to NGS samples of individually identifiable animals to obtain some of these critical population measures (Otis et al. 1978, Lukacs and Burnham 2005). Most population studies of this kind repeatedly sample the same area over a relatively short time period and apply closed population models that account for imperfect detection but assume demographic closure. As an alternative, open population models can be applied to data collected over several time steps to estimate both population density and vital rates like population growth, survival and recruitment (Gardner et al. 2010a, Royle et al. 2013, Whittington and Sawaya 2015, Gardner et al. 2018).

Recent statistical advances have also incorporated the spatial information of detections to estimate density from individual activity centers (Efford 2004, Royle et al. 2013). These spatial capture recapture (SCR) models use these individual activity centers and approximations of space use to assign a finite number of activity centers within the study area to yield an estimate of abundance. Moreover, the incorporation of spatial information allows for direct estimation of the study area location and size, leading to the ability to calculate density (Royle et al. 2013). In addition, spatially referenced detections are used to assign an individual's exposure to a trap and estimate detection probability as a decreasing function of the distance between a trap and an animal's activity center (Royle et al. 2013). The most precise abundance estimates are obtained when encounter probability is high, which can be difficult to attain when surveying low-density species (Lukacs and Burnham 2005). Further, SCR models allow researchers to explicitly incorporate ecological processes like movement, spatial organization, and space usage into the model, which properly addresses the heterogeneous capture probabilities and abundance distributions inherent in most populations (Royle et al. 2013). SCR methods can be used in conjunction with traditional marking techniques that involve the physical capture and tagging of animals or with noninvasive sampling techniques like NGS, remote cameras, or acoustic sampling (Efford 2004, Royle et al. 2013). Further, SCR methods may provide more robust density estimates with fewer biases and assumption violations compared to non-spatial capture-recapture (Sollmann et al. 2011, Gerber et al. 2012, Blanc et al. 2013).

SCR models provide flexibility to account for spatial variation in density and detectability, but most applications thus far lack inference on temporal processes leading to changes in abundance trends, information that is critical to conservation and management decisions. For example, identifying factors impacting population regulation processes, both natural and anthropogenic, can be essential to reaching goals for endangered or regulated populations (Cougar Management Guidelines Working Group 2005, Logan 2019). This can be achieved by estimating demographic parameters like mortality, fecundity, immigration, and emigration (Caswell 1989). If sampling is discontinuous and extends across multiple primary periods, like years, an open-population framework can be applied to account for the lack of demographic closure. Most open population models estimate "apparent survival", a combination of survival and emigration probability, given population abundance estimates treat dead and dispersed individuals similarly (Jolly 1965, Seber 1965).

Accounting for demographic processes is likely even more important in areas that see relatively high emigration rates or mortality between sampling events, patterns observed in source-sink populations (Cooley et al. 2009, Ruth et al. 2011). Previous studies have identified the cougar (*Puma concolor*) population of northern Yellowstone National Park (YNP) as a potential source population with relatively higher adult and kitten survival relative to the surrounding area (Ruth et al. 2011). Moreover, on landscapes where regulated harvest or other human-related mortalities are prevalent, it is imperative that managers' decisions are determined by systematic monitoring that can detect population shifts over time (Treves and Karanth 2003). In response, open-population SCR (OSCR) models have been implemented to estimate population trends and to address closure assumption violations in capture-recapture studies.

Here we apply OSCR models to estimate population parameters using a four-year NGS dataset for cougars on the northern range of YNP. Our objectives were to estimate sex-specific population abundance and density from this cryptic, low-density species, while evaluating the relative impacts of individual and spatio-temporal covariates on detection processes.

Methods

Study Area

We conducted winter track surveys within a 963 km^2 area within YNP's Northern Range (Figure 2.1). Surveys spanned elevations from 1,500 to 2,600m, positioned around the Yellowstone River corridor and its sub drainages. Eight different ungulates inhabit the area: elk (*Cervus elaphus*), bison (*Bison bison*), mule deer (*Odocoileus hemionus*), white-tailed deer (*Odocoileus virgianus*), moose (*Alces alces*), pronghorn antelope (*Antilocarpa americana*), bighorn sheep (*Ovis canadensis*), and introduced mountain goats (*Oreamnos americanus*; Lemke 2004). This area of YNP provides critical winter habitat due to its relatively low snow depth compared to the surrounding areas (Houston 1982). Cougars compete for ungulates with four other large carnivores, wolves (*Canis lupus*), grizzly bears (*Ursus arctos*), black bears (*Ursus americanus*), and coyotes (*Canis latrans;* Ruth et al. 2003).

Two 8-year cougar studies have taken place in YNP since the late 1980s with the primary focus to document cougar population dynamics, habitat use, and prey selection before and during wolf reestablishment, which occurred in the mid-1990s (Murphy 1998, Ruth et al. 2019). Both of these studies used intensive radio collaring as a primary method for marking and monitoring individuals, which was time intensive and costly. Population size was estimated across the entire northern range within and beyond YNP's boundary, 15-22 cougars during the first phase and 26-42 cougars during the second phase of research (Murphy 1998, Ruth et al. 2019).

Field Sampling

Sawaya et al. (2011) previously used NGS by snow tracking to identify individual pumas. They were able to accurately identify over 80% of known collared cougars from 2003-2005 in a portion of our study area (Sawaya et al. 2011, Ruth et al. 2019). We conducted cougar snow tracking surveys during January to March from 2014-2017 following protocols outlined by Sawaya et al. (2011). Twenty-two snow track sampling routes were designated based on a 3.2 km x 3.2 km grid positioned within the study area (Figure 2.1). Sixteen of these routes were originally designated by Sawaya et al. (2011), upon which we created and searched 6 additional routes to fill in gaps in the study area that could increase the probability of encountering cougar sign. The grid cell size was chosen based on the minimum winter home range size for female cougars in the study area (Ruth et al. 2019) and methods outlined for lynx (*Lynx canadensis*) in the Lynx Detection Protocol (McKelvey et al. 1999, Sawaya et al. 2011). Specifically, 3.2 km represents the mean radius of a female home range (Sawaya et al. 2011, Ruth et al. 2019 and this trap spacing ensures that all individuals that exist within the trap grid are exposed to at least one trap (Karanth and Nichols 1998). We attempted to encompass the full gamut of cougar habitat quality with these 22 transects and we travelled them weekly or bi-weekly based on availability of field personnel. Further, these spatial searches along transects were unstructured allowing field personnel to increase detection probability based on topography, climatic characteristics, and logistical constraints (Russell et al. 2012, Thompson et al. 2012). The unstructured nature of the sampling design specifically allows field personnel to deviate from the transect in order to search areas that are more likely to hold cougar sign and maximize identification of individuals rather than simply finishing the transect. As a result, transects in consecutive weeks were seldom spatially identical. Each cougar track detected was followed until noninvasive genetic samples like hair, scat, and/or blood were discovered, or personnel were unable to continue due to terrain, tracking conditions, or time constraints. Field personnel carried Garmin Map62s GPS unit to determine the location of cougar tracks and genetic samples, and to take detailed track logs for recording snow tracking effort. Hair and blood samples were collected primarily from bed sites or natural snags (e.g. branches, thorns, rocks) and identified to species in order to minimize bycatch. Scat samples were collected at scrape sites, latrines associated with carcasses, or opportunistically in the snow. Genetic samples were placed in paper bags or envelopes and stored in a cool, dry location in an enclosed container filled with industrial desiccant.

Laboratory Analysis

Following each sampling season, we sent all genetic samples to the United States Forest Service Rocky Mountain Research Station (Missoula, MT, USA) to identify individuals. Initially, samples were prepared for DNA extraction and some samples were screened from further analysis due to insufficient amounts of DNA. Given that some samples could be from sympatric species, the lab performed a species test to exclude samples from non-target animals. Using polymerase chain reaction analysis with 11 microsatellites, multi-locus genotypes were produced from samples that tested positively for cougar DNA using loci identified in Biek et al. (2006). All samples were run twice at each locus and programs DROPOUT (McKelvey and Schwartz 2005) and MICROCHECKER (Van Oosterhout et al. 2004) were used to identify genotyping errors. These two programs can help identify errors due to poor quality samples, multiple individuals mixed into one sample, or database entry.

Spatial Capture-Recapture Analysis

Typically, NGS studies operate across several time-steps and some individuals may be captured in multiple sampling occasions or secondary sampling periods. Given that our sampling occurred over four successive years, we applied open population models that incorporate individual, spatial and temporal covariates.

SCR analysis begins by building encounter histories, which outline, for each individual detected during sampling, the time and location of capture. Since our sampling did not occur at static detector sites like remote cameras or hair snares, we assigned captures to the center of the 3.2km^2 grid cell in which the DNA sample was collected (Russell et al. 2012, Thompson et al. 2012, Proffitt et al. 2015). Our sampling regime took place over successive winters, resulting in a binary encounter history, y_{ijkt}, where individual, i, was detected and genotyped at grid cell (trap), j, during sampling occasion (week) k, in year, t (Royle et al. 2013). These captures occurred within the limits of the state-space, S, which included the trapping area plus a 10 km buffer. With the buffer, the model estimated cougar population density over a total of 1,802km^2. Previous research has demonstrated that density estimates display low sensitivity to buffer size (Russell et al. 2012), so we only focused on a buffer of 10km.

SCR models estimate trap-, occasion-, and individual- specific encounter probabilities, p_{ijkt} (Figure 2.2). We represent encounter probability as a decaying function of the distance between individual activity centers and trap locations (Efford 2004, Royle et al. 2013) using the general power model (Russell et al. 2012) given by,

$$p_{ijkt} = 1 - \exp\left(-p0_{ijkt} \times g_{ij}\right) \times Trapuse_{jkt} \tag{1}$$

where $p0_{ijkt}$ signifies the baseline detection probability when the trap is located right at the activity center of the individual's home range and $Trapuse_{jkt}$ provides a binary matrix signifying if the grid cell (trap) was searched during the occasion, effectively constraining p_{ijkt} to zero when it was unsearched. Further, g_{ij} represents the effect of distance on detection probability and is given by,

$$g_{ij} = \exp(-\frac{d_{ij}^2}{\sigma_{Sex}^2}) \tag{2}$$

Here, d_{ij} is the Euclidean distance between the activity center for individual i and grid cell j, and σ is the scale parameter represented in km (Gardner et al. 2010b, Russell et al. 2012). The scale parameter (σ) dictates the rate of the decaying function of detection probability as the activity centers is distributed farther from the trap. In addition, σ is a sex-specific approximation of space use of home range size (Sollmann et al. 2012). All of our models estimated σ separately for males and females with an uninformed uniform (2,15) prior based on minimum (2 km radius) and maximum (15 km radius) home range size data from GPS collared cougars in YNP from 1998-2006 (Ruth et al. 2019).

We focused on three covariates we believed to have important influences on baseline cougar detection probability: individual sex, trap- and occasion-specific snow-tracking survey effort and snow cover. Due to heterogeneity in space use by male and female cougars (Ruth et al. 2019), individual sex was used to estimate variability in detection, space use, and abundance. To model its influence on detection probability, we assigned known individuals binary sex classes (0 = Female, 1 = Male) based on the results of the Amelogenin test. The sex of undetected individuals was modeled as a random variable, $SEX_i \sim Bernoulli(\psi_{sex})$, where ψ_{sex} corresponds to the probability that an individual is male. We used a prior for ψ_{sex} using population sex ratio data from sixteen years of cougar research in YNP from Ruth et al. (2019), resulting in $\psi_{sex} \sim Uniform(0.1, 0.5)$. To account for the inherent heterogeneity in search effort from the unstructured spatial sampling, we took the log-transformed km travelled per grid cell (trap) during each occasion obtained from GPS units tracking observer movements during snow-tracking surveys (Russell et al. 2012). Over the course of four years of sampling, we observed considerable variation in winter snow cover, with parts of the study area absent of snow for some of the winter. When snow cover was absent, we struggled to find cougar tracks and genetic samples. To account for this variation in snow conditions, we obtained daily Normalized Difference Snow Index values from Moderate

Resolution Imaging Spectroradiometer (MODIS) satellite imagery at 500m resolution using the MODIStsp package in R (Busetto and Ranghetti 2016, Hall and Riggs 2016). We took the average of daily MODIS snow cover estimates at each trap for each week-long occasion. Snow cover values ranged from 0-100 and included observation quality algorithms (Hall and Riggs 2016). Poor quality observations can occur when imagery is taken during thick cloud cover, night hours, or other possible errors (Hall and Riggs 2016). Since we had seven days to get a high-quality observation during each occasion, we recorded at least one usable snow cover observation for each weekly occasion in this study. We used the natural log of snow cover and log-transformed snow-tracking effort as well as cougar sex to model baseline detection probability, $p0_{ijkt}$, as follows:

$$Logit(p0_{ijkt}) = \alpha_{0_{Sex}} + \beta_1 \times SEX_i + \beta_2 \times \log(EFFORT_{jkt})$$
$$+\beta_3 \times \ln(SNOWCOVER_{jkt}) \tag{3}$$

All β parameters were given flat priors, $\beta \sim Uniform(-4,4)$. Additionally, $\alpha_{0_{Sex}}$ was estimated separately for males and females (Royle et al. 2013).

We modeled observed capture histories, y_{ijk}, as a Bernoulli observation model,

$$y_{ijkt} \sim Bernoulli(\, p_{ijkt} \times z_{it}). \tag{4}$$

Implementation of the Jolly-Seber SCR model deviates from closed population model primarily in how the data augmentation variable, *z,* is estimated. Instead of zi being dependent on only ψ (see Equation 5), we allow z_{it} to vary by year, *t*, and is now estimated from μ_{it}, which is a deterministic node calculated from estimates of apparent survival, ϕ, and a recruitment parameter, γ (Royle et al. 2013, Whittington and Sawaya 2015, Gardner et al. 2018):

$$z_{it} \sim Bernoulli(\mu_{it}) \tag{5}$$

where

$$\mu_{it} = \phi \times z_{it-1} + \gamma_t \times R_{t-1}. \tag{6}$$

Here, z_{it-1} indicates if the individual was included in the true population during the previous sampling year and R_{t-1} indicates the number of individuals available to be recruited into the population. Thus, μ_{it} is the probability that individual, *i*, existed in the population during year, *t*, within state-space, *S*. Therefore, inclusion of each individual into a year's true population, N_t, is determined by summing over all zit,

$$N_t = \sum_{i=1}^{M} \sum_{t=1}^{T} z_{it}. \tag{7}$$

Density can then be obtained by dividing the population size by the area of the state-space, S,

$$D_t = {}^{N_t}/_{S}. \tag{8}$$

Both ϕ and γ were assigned flat priors with $Beta(1,1)$ distributions. We calculated annual population growth rate, λ, as the ratio of total abundance in year *t + 1* to the total abundance in year *t*.

We assume that a finite number of individual activity centers, or home range centers, s_i, exist within the state-space during each year of sampling. Further, we imagine this collection of activity centers within the state-space is a realization of a homogenous point process with a uniform prior,

$$s_{i.x} \sim uniform\ (Sx_{min}, Sx_{max}) \tag{9}$$

$$s_{i.y} \sim uniform\ (Sy_{min}, Sy_{max}) \tag{10}$$

Here, S.x and S.y represent a rectangular coordinate matrix with the minimum and maximum Universal Transverse Mercator (UTM) coordinates that overlays the irregularly shaped true statespace (Figure 2.1). The location of each s_i is latent and estimated based on the average of all NGS genotype UTM coordinate locations for each individual. In order to restrict the location of activity centers to within our irregularly shaped state-space, we used the "ones trick" which entails determining if s_i falls within the boundary of the state-space using an indicator variable, pOK_i (Meredith 2016, Milleret et al. 2019). If s_i falls within the irregularly shaped state-space, $pOK_i = 1$, and $pOK_i = 0$ if s_i lies beyond this boundary. We can then reject the proposed s_i if it falls outside the boundary using:

$$OK_i \sim Bernoulli(pOK_i) \tag{11}$$

where OK is a vector of ones.

Building on the single-year closed population structure outlined above, we combined the four-year dataset and estimated population density, survival, and recruitment using the Jolly-Seber framework (Jolly 1965, Seber 1965).

We estimated a single activity center for each individual for the entire four-year sampling effort, instead of estimating each year separately (Gardner et al. 2010b, Whittington and Sawaya 2015). The initial value for activity centers was calculated by taking the mean UTM coordinate from pooled captures for each individual across all years.

Implementation.-We used data augmentation and Bayesian analytical methods in the R package nimble (Royle et al. 2013, NIMBLE Development Team 2019). Models were run with 3 chains of 20,000 iterations and 5,000 iteration burn-in. Nimble allows for flexible assignment of different samplers to model nodes to improve parameter estimation (de Valpine et al. 2017). We assigned slice samplers for model nodes $s_i, \sigma, \alpha_0, \psi_{sex}$, and all β parameters, which helped reduce auto-correlation within chains. In addition, we assigned binary samplers to z_{it} and y_{ijkt} and a conjugate sampler for ϕ and γ. We assessed model convergence using the Gelman-Rubin statistic in the R package coda (Gelman and Rubin 1992, Plummer et al. 2006). We implemented a conventional approach to variable selection by inspecting 95% credible intervals of posteriors of coefficient estimates (Royle et al. 2013). We discarded covariates if 95% CI's significantly overlapped zero. The exception to this was for the sex-specific variable, which is biologically relevant to any cougar population estimate (Logan and Sweanor 2001, Royle et al. 2013, Ruth et al. 2019).

Results

Field Sampling and Laboratory Analysis

We conducted snow-tracking surveys along 8,850km (Mean: 2,212.5 km /year, SD: 702.12 km/year) and collected 833 genetic samples (Mean: 208.25 samples/year, SD: 31.77 samples/year) during winters 2014-2017 (Table S2.1). A majority of the samples (68%) were hair from bed sites, natural hair snags or tracks (Figure S2.2-S2.4). In addition, 5 blood samples were extracted directly from captured individuals.

In total, 206 samples (24%) yielded genotypes that identified 40 individuals (20 Females, 20 Males). Some samples were discarded due to insufficient amounts of DNA material or being identified from a species other than cougar and others were culled after failing to amplify. Due to many samples being collected in close proximity to one another, many successful genotyped samples for an individual were positioned within the same cell and sampling occasion (Figure S2.1). As a result, we were able to use 145 of these genotypes as captures and recaptures (Mean: 36.25 captures/year, SD: 2.87 captures/year) for 39 individuals (Table 2.1). Twelve individuals were captured in >1 years, 14 individuals were captured only once during the entire study, and 13 individual were captured multiple times within a year (Table S2.2).

Open-Population Models

We estimated total average cougar density between 1.88 and 2.33 cougars/100km2 for all years, which includes both dependent and independent cougars. The lowest density occurred in the first year of sampling in 2014 and it increased slightly in subsequent winters, but then decreased in 2017 (Figure 2.3). In addition, 95% CI estimates for densities were smaller in the open population results, compared to those from closed population models (Figure 2.3). We estimated sex-specific abundances and the full model estimated 22 females in both 2014 and 2015 and 23 females in both 2016 and 2017 (Figure 2.3). Male abundances fluctuated more with estimates of 12 ± 4 (95% CI: 6-22) and 13 ± 4 (95% CI: 7-21) in 2014 and 2015, respectively. In 2016, the male abundance increased to 19 ± 4 (95% CI: 13-28) then dropped in 2017 to 14 ± 3 (95% CI: 8-22; Table 2.2). ψ_{Sex}, probability an individual is male, was consistent across models with an estimate of 0.41 ± 0.06 (95% CI: 0.27-0.49). Initially, we allowed ϕ to vary by year, but the results indicated similar estimates, so our final models include a single estimate of apparent survival for all years. Regardless of model formulation, the estimate of apparent survival, ϕ, for all individuals was identical at 0.59 ± 0.08 (95% CI: 0.44-0.74).

We tested the impact of three covariates on baseline detection probability: sex, sampling effort, and snow cover. Sex had a negligible impact on detection probability and the 95% CI for the β_{Sex} parameter crossed zero in all models (Table 2.3); however, we left it in the models due to its intrinsic importance to sex-specific detection, space use, and population sex ratios (Logan and Sweanor 2001, Ruth et al. 2019). Occasion- and trap-specific snow-tracking effort displayed a strong, positive relationship with baseline detection with β_{Effort}'s 95% CI well above zero (3.83 ± 0.16, 95% CI:3.40-4.00; Table 2.3). Further, snow cover exhibited a positive relationship with minimal overlap with zero ($\beta_{SnowCover}$: 0.26 ± 0.22, 95% CI: -0.07-0.77; Table 2.3). Sigma estimates were similar for both sexes estimating 8.16 ± 0.88 (95% CI: 6.52-9.81) for females and 7.48 ± 0.84 (95% CI: 6.09-9.38) for males (Table 3). The larger sigma for females indicates a slower decline in detection at larger distances from activity centers and larger space use estimates (Russell et al. 2012). Gelman-Rubin convergence diagnostics indicated $\hat{R}$ values <1.2 for $\sigma, \alpha_0, \gamma, \phi, \psi_{Sex}$ and β parameters, confirming convergence of MCMC chains.

Discussion

Although the true cougar population in northern YNP is unknown, we believe the OSCR estimates represent the most accurate density results considering they are more congruent with estimates previously obtained from six years of intensive collaring efforts (Ruth et al. 2019) and they do not violate assumptions we have about cougar biology, population growth and population regulation (Quigley and Hornocker 2010, Logan 2019). Moreover, cougar populations are never truly closed to demographic changes which is especially true in YNP where cougars freely disperse, travel large distances, and are actively hunted during the winter just outside the park boundary (Newby 2011, Ruth et al. 2011, 2019). The OSCR models overcome this shortcoming by estimating apparent survival (combination of survival and emigration). Further, OSCR models are able to pool capture information across years, which was especially advantageous for cougar studies like ours where single-year capture histories are likely sparse with low recapture rates.

Noninvasive snow-tracking for cougar genetic samples over four consecutive winters in 2014-2017 yielded ample DNA to genetically identify 39 individual cougars, which led to annual density estimates of 1.88-2.33 cougars/100km^2. These estimates are comparable to previous cougar population study results when Murphy (1998) estimated density as 1.05-2.11 cougars/100km^2 from 1988-1993 and Ruth et al. (2019) estimated 1.52-2.46 cougars/100km^2 from 1998-2004 (See Ruth et al. 2019 for more information on methods and results). While these densities provide important benchmarks for interpreting recent density estimates in this study, the spatial extents used were not equivalent between all three studies, which makes comparisons harder (Quigley and Hornocker 2010, Beausoleil et al. 2013). Further, cougars were largely absent from YNP following predator extirpation in YNP during the early 1900s until recolonization of the area in the 1980s with population growth that continued into the early 2000s (Ruth et al. 2019).

Most genetic captures were located along the Yellowstone River, which provides easier travel in the winter months due to lower snow depths that also draw ungulates down from their higher elevation habitat in the summer and fall (Seidensticker et al. 1973, Singer and Norland 1994). Deeper snow at the higher elevations outside of this area was hard to access due to logistical constraints and our density estimates on the periphery of the study area, where effort was less, is likely biased low. Possible remedies for this issue would be to set trap grid spacing smaller to increase individual captures and spatial heterogeneity in the encounter history or enlarge the trapping area to increase sampling coverage. Due to the sharp increase in the number of traps this would create, we would suggest creating clusters of traps for computation efficiency (Sun et al. 2014, Clark 2019, Murphy et al. 2019).

We observed stable female abundance estimates, while male estimates fluctuated from year to year, contributing more to overall density changes. Male cougars are more likely to disperse farther distances beyond the study area and can die due to intra-specific competition for access to mates, contributing to higher rates of male turnover (Logan and Sweanor 2001, Biek et al. 2006, Newby 2011, Ruth et al. 2019). In addition, the northern boundary of the study area shifts to a mosaic of private and U.S. Forest Service land where cougars are legally hunted and male survival declines (Ruth et al. 2011). The combination of dispersal and harvest may explain why most males were not repeatedly detected. In addition, low recapture rates, of both males and females, may be due to the number of dependent young represented in the dataset that have a relatively low survival rate and a higher probability of dispersal beyond the study area (Quigley and Hornocker 2010, Ruth et al. 2019).

We recognize that there may be errors introduced in our study which is well documented across many studies and emanates from the laboratory genotyping analysis (Bonin et al. 2004, Beja-Pereira et al. 2009, Giangregorio et al. 2019). Given the low-quality of genetic material in samples collected through NGS, genotyping success rates were low, leading to low recapture rates. Consecutive years of sampling should yield a decreasing trend in new individual detection (Lukacs and Burnham 2005); however, our yearly capture histories displayed a similar number of new individuals in all years (Table 2.1). Single nucleotide polymorphisms (SNPs) have the potential to overcome the sparse detection histories that arises from microsatellite analyses and increase capture rates through higher genotyping success (Seddon et al. 2005, Fitak et al. 2015, Kraus et al. 2015, Eriksson et al. 2019, Giangregorio et al. 2019, Khan et al. 2020).

Further, we acknowledge some possible shortcomings of our OSCR model design given results from other SCR studies. The first occurs in our formulation for the estimation of animal activity centers. We assumed a cougar's activity center did not change between years, an assumption that has performed well in other studies (Gardner et al. 2010a, Whittington and Sawaya 2015). For low-density species that display low recapture rates like cougars, this approach allowed us to take advantage of the full capture dataset since many cougars were only captured once or not at all in a given year. However, this approach assumes that the spatial distribution of activity does not vary (even before initial capture), which may be unrealistic for large mammals that can move large distances in a lifetime (Gardner et al. 2018). Nonetheless, a simulation study by Gardner et al. (2018) demonstrated this method introduced relatively little bias to density estimates when estimating a single activity center for individuals across multiple sampling sessions, but may introduce bias in the estimates of apparent survival and population growth.

We were unable to include this more accurate movement process due to sparse capture data and lack of computing power. Alternatively, Gardner et al. (2018) suggests incorporating telemetry data, but this also was hampered by computing limitations (even when using a super-computer with 256gb RAM and 88 cores). Given the more recent deployment of GPS collars on cougars in YNP, future work may incorporate this data to not only inform inter-annual movement, but also aid in the estimation of σ and p_0. In addition, our data does not include known information on dispersal or mortality since much of these data were not available. We expect apparent survival estimates to be more accurate through an expanded and coordinated cross-jurisdictional effort with nearby states to collect DNA from all known cougar mortalities (eg., harvest, depredation, etc.; Proffitt et al. 2015). This may shed light on the fate of individuals who were only captured in a subset of years or once during the whole study.

Our results demonstrate the importance of conducting consecutive years of sampling and the advantages of combining data into an OSCR model when monitoring cryptic, low-density species like the cougar. Moreover, the cougar density estimates we produced hold greater importance to furthering our understanding of the complex trophic relationships within the Yellowstone ecosystem. Thus far, Yellowstone predator densities have been used to explain predator-prey dynamics (Vucetich et al. 2005, 2011, White et al. 2010, Tallian et al. 2017), intra-specific interactions (Cubaynes et al. 2014, Ruth et al. 2019), inter-specific interactions (Tallian et al. 2017, Ruth et al. 2019), space-use (Bjornlie et al. 2014, Uboni et al. 2015b), and population dynamics (Ruth et al. 2019).

Management Implications

Noninvasive genetic spatial capture-recapture holds promise for providing a cost-effective alternative to conventional capture and marking techniques to monitor populations of elusive carnivores. Snow tracking has been used to collect DNA to assess rare species presence and distributions (McKelvey et al. 2006, Ulizio et al. 2006, Franklin et al. 2019). In areas similar to YNP, with poor road access or prohibited motorized travel, we suggest coupling snow-tracking with another method that can produce superior quality DNA samples (e.g. biopsy darting; Russell et al. 2012, Proffitt et al. 2015, Beausoleil et al. 2016) and/or higher recapture rates (remote cameras, scat detection dogs; Davidson et al. 2014, Murphy et al. 2019). Noninvasive genetic snow-tracking could be even more effective in areas with good road access allowing field personnel to utilize motorized travel, which would increase overall search effort likely leading to more genetic samples and capture rates. Moreover, these methods give managers an important tool to not only enumerate cougar populations, but also build positive relationships with a variety of stakeholders through dissemination and discussion of results (Riley and Decker 2000, Sjölander-Lindqvist et al. 2015, Mitchell et al. 2018).

Acknowledgements

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Table 2.1. Genotype analysis results from cougar noninvasive genetic samples were obtained through PCR of 11 microsatellites. We were able to identify individuals and track encounter histories over the four consecutive years. Genetic samples were sexed using the Amelogenin region (Pilgrim et al. 2005).

Year	All Genotypes	# Female	# Male	Unique Individuals	Captured in Previous Year(s)?	New Individuals	Captures per Individual
2014	32	7	4	11	NA	11	2.91
2015	37	7	5	12	3	8	3.08
2016	38	6	10	16	6	10	2.38
2017	38	11	7	17	9	8	2.11
Mean	36.25	7.75	6.5	14	6.00	9.25	2.54
Total	145	20	19	39	-	-	-

Table 2.2. SCR models were used to estimate yearly cougar abundance. The models that included individual cougar sex, estimated sex-specific abundances. Models also estimated apparent survival, ϕ, and year-specific recruitment, γ. Using abundance estimates, we calculated yearly population growth rates, λ, as well.

Model	N_{Female}	N_{Male}	N	ϕ	γ	λ
Null						
2014	-	-	31 ± 8	0.59 ± 0.08	0.16 ± 0.05	-
95% CI			18-49	0.44-0.74	0.08-0.26	
2015	-	-	33 ± 7	0.59 ± 0.08	0.09 ± 0.04	1.11 ± 0.28
95% CI			22-48	0.44-0.74	0.02-0.18	0.70-1.78
2016	-	-	39 ± 7	0.59 ± 0.08	0.13 ± 0.05	1.21 ± 0.23
95% CI			27-55	0.44-0.74	0.05-023	0.83-1.74
2017	-	-	36 ± 7	0.59 ± 0.08	0.11 ± 0.05	0.93 ± 0.16
95% CI			25-51	0.44-0.74	0.03-0.22	0.66-1.29
Sex						
2014	21 ± 6	12 ± 4	33 ± 9	0.59 ± 0.08	0.17 ± 0.05	-
95% CI	11-37	6-22	20-54	0.44-0.74	0.09-0.29	
2015	21 ± 5	13 ± 3	34 ± 7	0.59 ± 0.08	0.09 ± 0.04	1.07 ± 0.28
95% CI	13-34	7-21	23-50	0.44-0.74	0.01-0.19	0.66-1.73
2016	22 ± 6	19 ± 4	41 ± 8	0.59 ± 0.08	0.14 ± 0.05	1.24 ± 0.24
95% CI	13-36	13-28	29-59	0.44-0.74	0.06-0.26	0.85-1.79
2017	23 ± 5	14 ± 4	37 ± 7	0.59 ± 0.08	0.11 ± 0.05	0.91 ± 0.16
95% CI	15-36	9-22	26-53	0.44-0.74	0.03-0.23	0.65-1.27
Sex + Effort						
2014	22 ± 7	13 ± 4	35 ± 9	0.59 ± 0.08	0.18 ± 0.05	-
95% CI	12-37	6-22	20-55	0.44-0.74	0.09-0.29	
2015	22 ± 5	13 ± 3	35 ± 7	0.59 ± 0.08	0.08 ± 0.04	1.05 ± 0.27
95% CI	14-34	7-21	23-50	0.44-0.74	0.01-0.18	0.65-1.69
2016	23 ± 6	19 ± 4	42 ± 8	0.59 ± 0.08	0.14 ± 0.05	1.24 ± 0.24
95% CI	13-36	13-28	29-60	0.44-0.74	0.06-0.26	0.85-1.79

2017	23 ± 5	14 ± 4	37 ± 7	0.59 ± 0.08	0.11 ± 0.05	0.90 ± 0.16
95% CI	15-36	9-22	26-53	0.44-0.74	0.03-0.23	0.63-1.24
Sex + Effort + Snow Cover						
2014	22 ± 6	12 ± 4	34 ± 9	0.59 ± 0.08	0.17 ± 0.05	-
95% CI	12-37	6-22	20-55	0.44-0.75	0.09-0.29	
2015	22 ± 5	13 ± 4	35 ± 7	0.59 ± 0.08	0.09 ± 0.05	1.08 ± 0.28
95% CI	14-34	7-21	23-50	0.44-0.75	0.01-0.19	0.67-1.76
2016	23 ± 6	19 ± 4	42 ± 8	0.59 ± 0.08	0.14 ± 0.05	1.22 ± 0.24
95% CI	13-37	13-28	29-60	0.44-0.75	0.06-0.26	0.84-1.78
2017	23 ± 5	14 ± 3	37 ± 7	0.59 ± 0.08	0.11 ± 0.05	0.89 ± 0.16
95% CI	15-36	8-22	26-53	0.44-0.75	0.03-0.23	0.63-1.24

Table 2.3. Open-population models used information from individual capture histories to estimate sex-specific σ, the scaling parameter for the detection function. We used an individual sex-specific covariate to model differences in baseline detection probability. In addition, we used trap and occasion-specific sampling effort and snow cover to better understand landscape differences in baseline detection probability. Calculated baseline detection probabilities can be seen in Figure S2.6.

Model		σ_{Female}	σ_{Male}	β_{Sex}	β_{Effort}	$\beta_{SnowCover}$
Null						
	Estimate	7.74 ± 0.67	7.74 ± 0.67	-	-	-
	95% CI	6.59-9.22	6.59-9.22			
Sex						
	Estimate	8.10 ± 0.89	7.29 ± 0.80	-1.24 ± 1.95		-
	95% CI	6.46-9.78	5.96-9.06	-3.87-3.15		
Sex + Effort						
	Estimate	8.19 ± 0.88	7.40 ± 0.81	-2.41 ± 1.54	3.82 ± 0.17	-
	95% CI	6.50-9.83	6.04-9.18	-3.96-1.86	3.35-4.00	
Sex + Effort + Snow						
	Estimate	8.16 ± 0.88	7.48 ± 0.84	-2.41 ± 1.34	3.83 ± 0.16	0.26 ± 0.22
	95% CI	6.52-9.81	6.09-9.38	-3.95-0.88	3.40-4.00	-0.07-0.77

Figure 2.1. Study area overview map that displays the 963km^2 trapping grid (black squares) that was buffered by 10 km to give the 1,802 km^2 state-space (blue outlined area) within which we estimated cougar density. We conducted noninvasive genetic sampling through unstructured spatial snow tracking (brown lines) for four consecutive winters from 2014-2017.

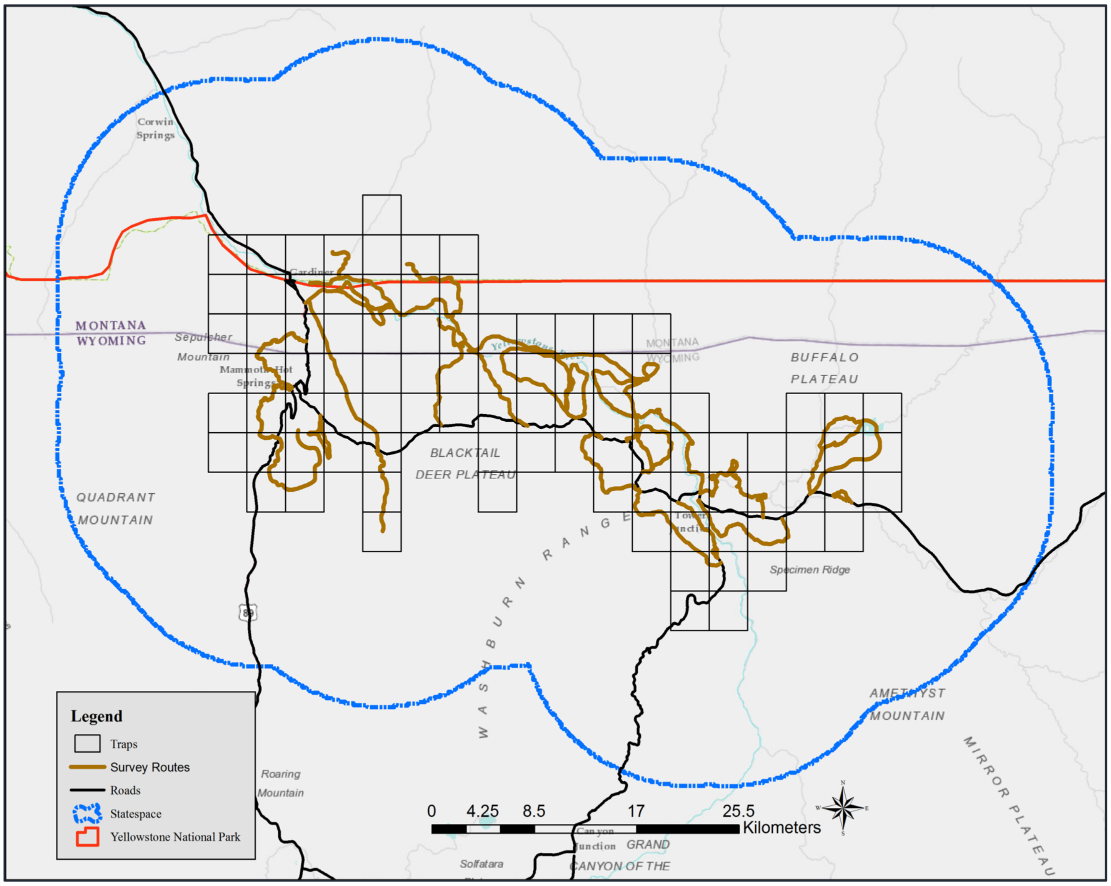
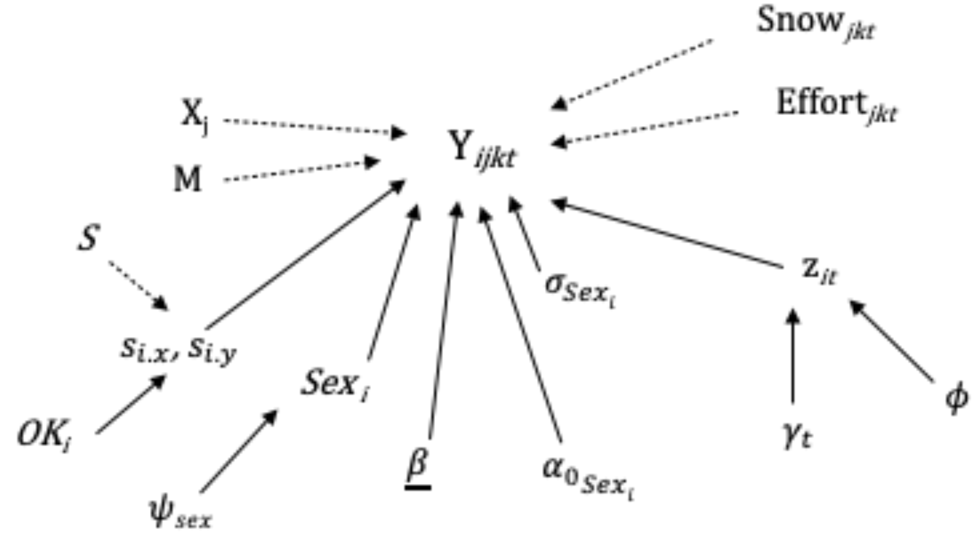


Figure 2.2. Directed Acyclic Graph (DAG; following Hobbs and Hooten 2015) and joint distribution for open-population SCR (OSCR) model. Distributions for model nodes and JAGS code for running model can be found in supplemental materials.



$$[Sex_i, \psi_{Sex}, \sigma_{Sex_i}, \alpha_{0_{Sex_i}}, \beta_1, \beta_2, \beta_3, s_{i.x}, s_{i.y}, OK_i, z_{it}, \gamma_t, \phi \mid y_{ijkt}] \sim \prod_{i=1}^{100} * \prod_{j=1}^{94} * \prod_{k=1}^{10} * \prod_{t=1}^{4} \text{ Bernoulli } (y_{ijkt} \mid z_{it}, P_{ijkt})$$

$$x \text{ Bernoulli } (z_i \mid \mu(\gamma_t, \phi))\ x \text{ Beta } (\phi \mid 1, 1)\ x \text{ Beta } (\gamma_t \mid 1, 1) \text{ x Bernoulli } (Sex_i \mid \psi_{Sex}) \text{ x uniform } (\psi_{Sex} \mid 0.1, 0.5)$$

$$x \text{ uniform } (s_{i.x} \mid Sx_{min}, Sx_{max}) \text{ x uniform } \left(s_{i.y} \mid Sy_{min}, Sy_{max}\right) \text{ x Bernoulli } (\text{Ok}_i \mid \text{pOK}_i)$$

$$x \text{ uniform } (\sigma_{Sex_i} \mid 2, 15) \text{ x normal}\left(\alpha_{0_{Sex_i}} \mid -2.5, 3\right) \text{ x uniform } \left(\underline{\beta} \mid -4, 4\right)$$

$$\mu(\gamma_t, \phi) = \phi \times z_{it-1} + \gamma_t \times R_{t-1}$$

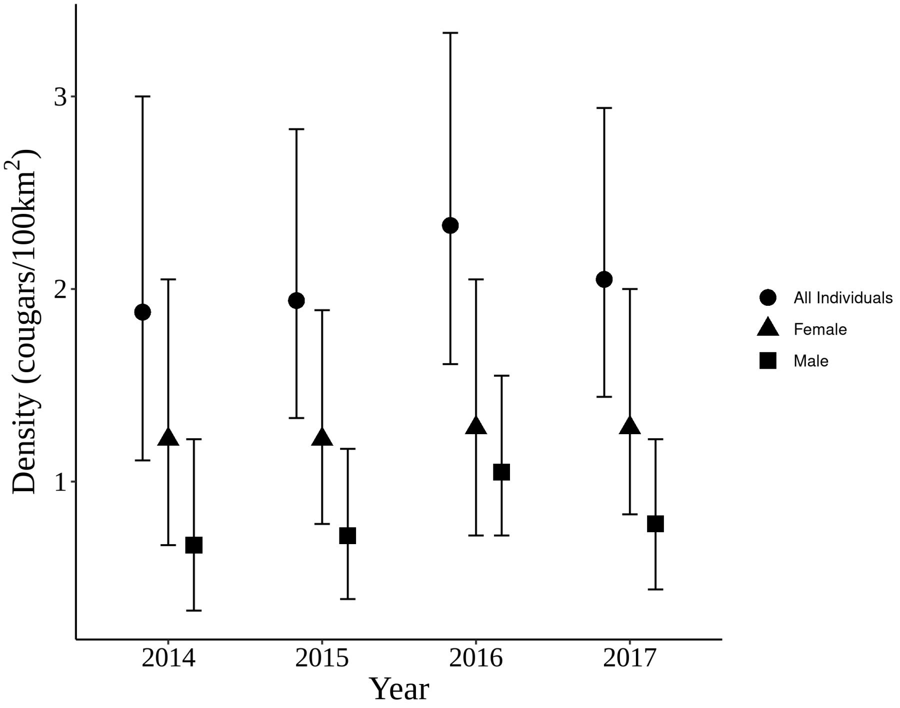
$$p_{ijkt} = 1 - \exp\left(-p0_{ijkt} \times g_{ij}\right) \times \text{trapuse}_{jkt}$$

$$g_{ij} = \exp(-\frac{d_{ij}^2}{\sigma_{Sex_i}^2})$$

$$\text{d}_{ij} = \| si - Xj \|$$

$$\text{Logit}(p0_{ijkt}) = \alpha_{0_{Sex_i}} + \beta_1 * \log(\text{Effort}_{jkt}) + \beta_2 * \ln(\text{SnowCover}_{jkt}) + \beta_3 * \text{Sex}_i$$

Figure 2.3. Sex-specific cougar density estimates using noninvasive genetic open-population spatial capture recapture (OSCR) for winters 2014-2017. Yearly OSCR model results are displayed, showing female (triangle), male (square), and summed total density for all individuals (circle) with 95% credible intervals.



Chapter 2: Supplementary Information

Figure S2.1. Study area overview map on the northern range of YNP where cougar snow-tracking surveys were collected during winters 2014-2017. The black gridded polygons denote 3.2 km2 traps where field personnel searched for cougar tracks and noninvasive genetic samples. Subsequently, density was estimated within 1,802 km2 statespace (blue polygon), which was created by adding a 10 km buffer around the trapping grid. Genotype analysis using 11 microsattelites was conducted on all noninvasive genetic samples, producing individual identification for 39 cougars. Genotypically identified females (triangles) and males (squares) are shown for each of the four sampling years (2014: dark green, 2015: light green, 2016: yellows, 2017: red).

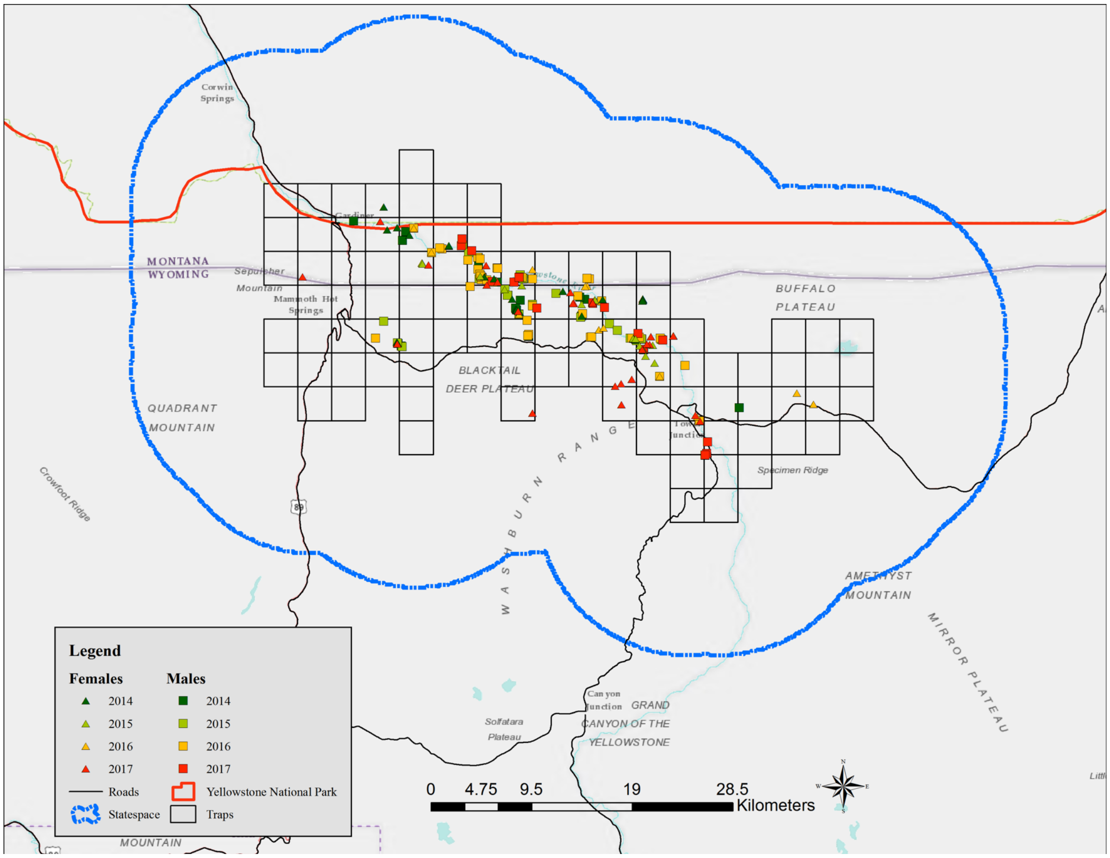


Table S2.1. Summary of snow tracking survey effort and noninvasive genetic sampling.

Year	# Surveys	Distance Surveyed (km)	Average Distance per Survey (km)	DNA Samples Collected	Track Detection	DNA Sample
2014	104	1,350	12.98	207	0.50	0.54
2015	134	2,200	16.42	163	0.49	0.59
2016	174	2,000	11.49	221	0.52	0.49
2017	223	3,300	14.80	242	0.40	0.34
Totals	635	8,850	13.92	833	0.48	0.49

Figure S2.2. Types of noninvasive genetic samples collected during snow-tracking efforts during winters 2014-2017.

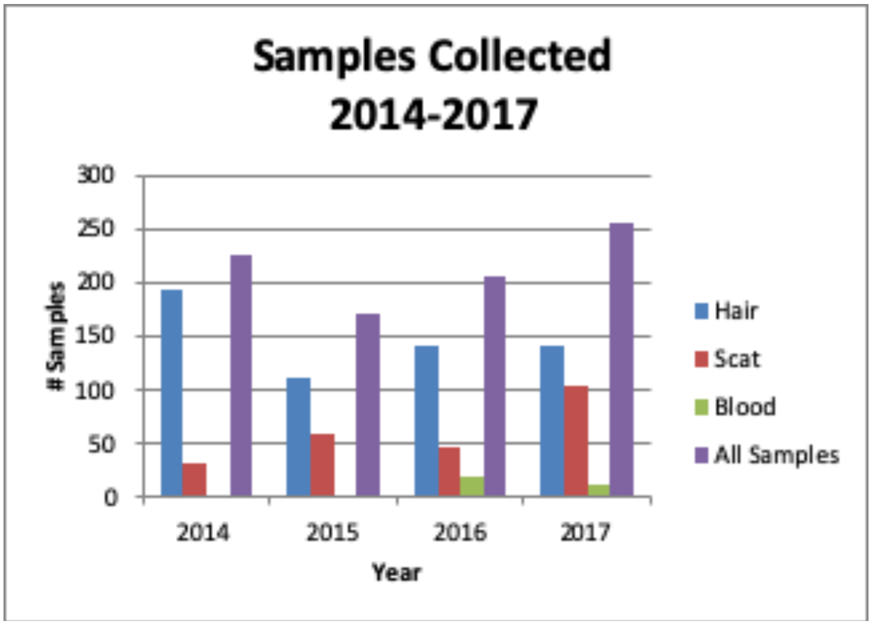


Figure S2.3. Genotyping success within each sample type category.

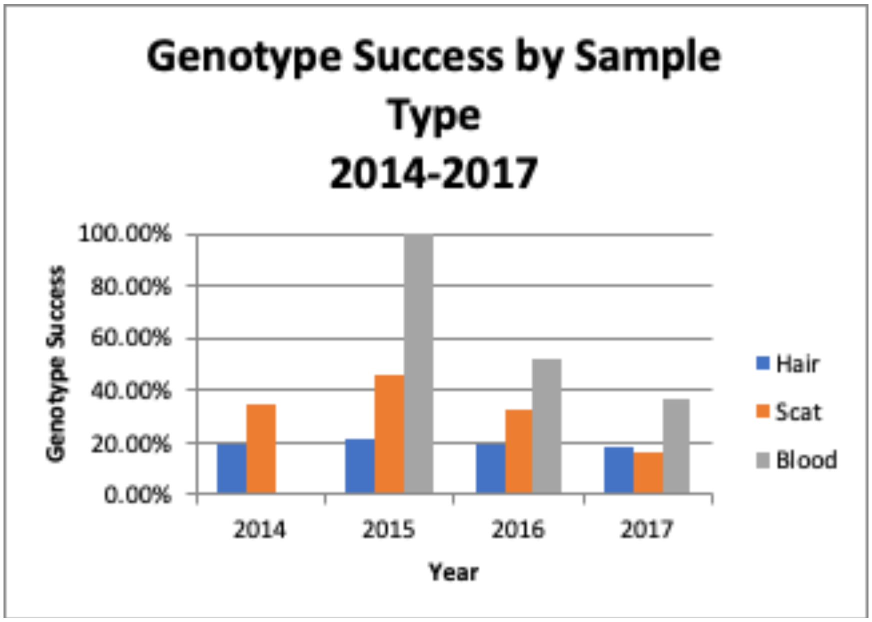


Figure S2.4. Genotyping success for cougar hair samples.

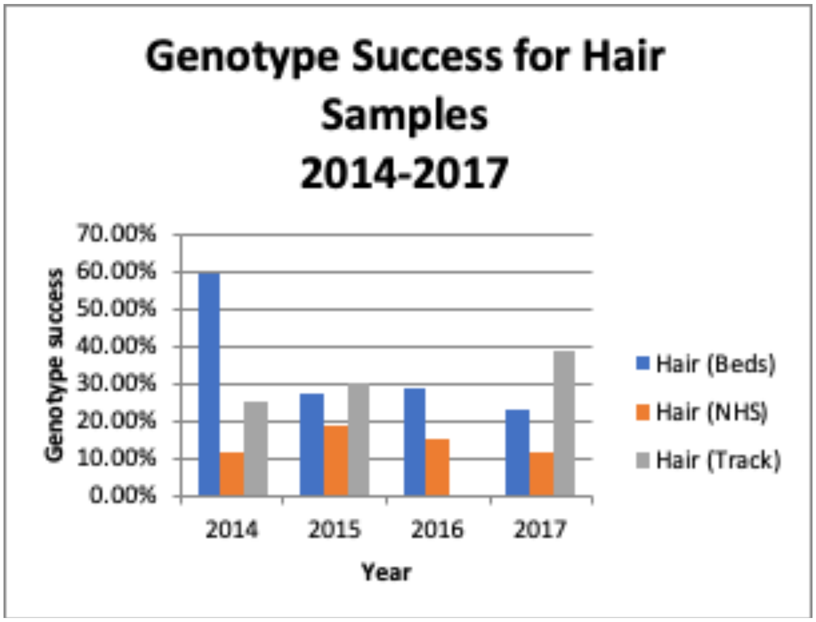


Table S2.2. Numbers of captures per individual within each year.

Individual	Sex	2014	2015	2016	2017
1	Female	7			3
2	Female	2			
3	Female	3	4		
4	Female	1			
5	Female	3			
6	Female	1		2	
7	Female	3		2	2
8	Male	1			1
9	Male	3			
10	Male		1		
11	Male	1	17	5	5
12	Male	7	3	3	
13	Female		3	1	2
14	Female		3	2	2
15	Female		1		3
16	Female		1		
17	Female		1		
18	Female		1		
19	Male		1		
20	Male		1		
21	Male			1	2
22	Female			1	
23	Female			1	1
24	Female				1
25	Female				1
26	Female				4
27	Female				1
28	Female				4
29	Male			2	
30	Male			3	
31	Male			4	
32	Male			5	
33	Male			1	
34	Male			2	
35	Male				2

36	Male			3	
37	Male				2
38	Male				1
39	Male				1
	Average	2.91	3.08	2.38	2.11

Figure S2.5. Snow-tracking effort for each winter of noninvasive genetic sampling for cougars in Yellowstone National Park during winters 2014-2017. Crosses indicate unsearched traps and circles display searched traps.

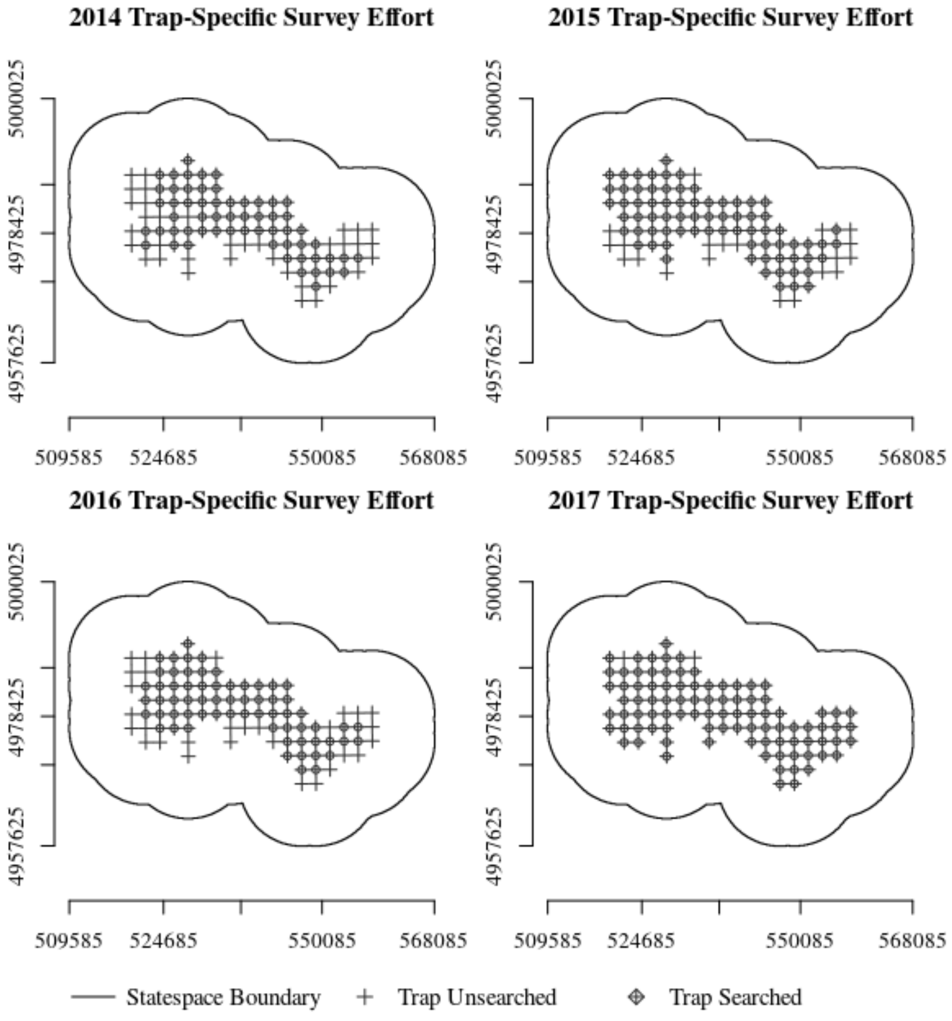
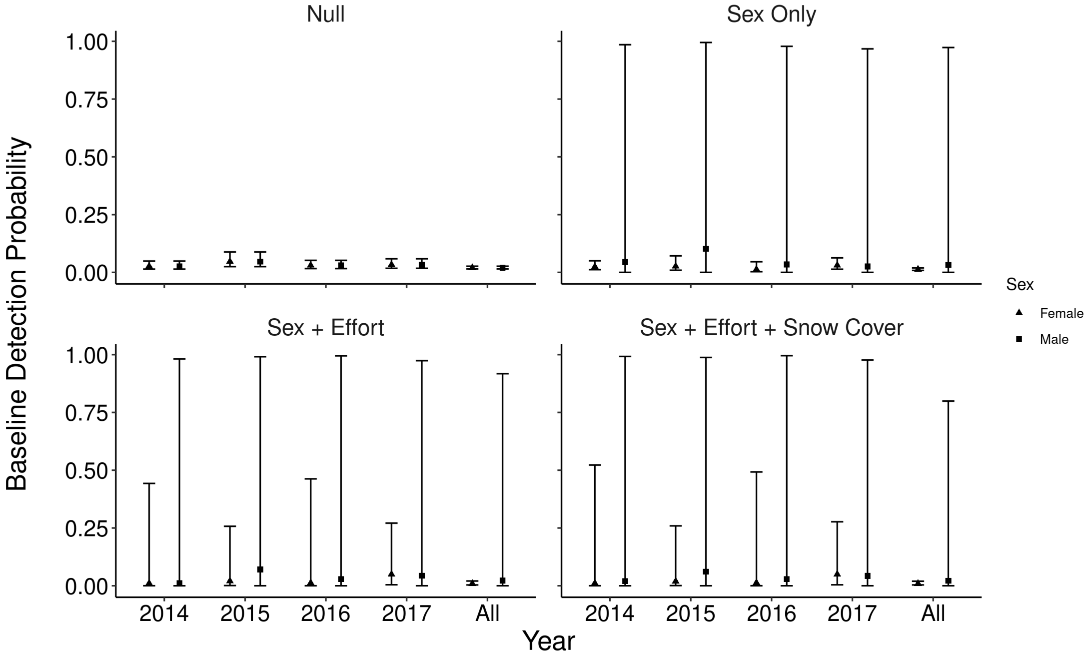


Figure S2.6. Sex-specific baseline detection probability, *p0*, estimated from open-population spatial capture-recapture models. Detection probability for females (triangles) and males (squares) was computed separately.



nimble code using JAGS language for open-population spatial capture-recapture models.

Open-population model

```
FullModel_OpenPop <- nimbleCode({
  #priors
  phi ~ dbeta(1,1)                    # Apparent survival
  psi.sex ~ dunif(.1,.5)                      #Prob of being male
  B.sex ~ dunif(-4,4)
  B.eff ~ dunif(-4,4)
  B.snow ~ dunif(-4,4)
  for(h in 1:2){
    alpha0[h] ~ dnorm(0,0.1)                  #Prior for baseline global detection
    sigma[h] ~ dunif(2,15)            # Prior specification for sigma,
  }
  for(t in 1:Year){
    gamma[t] ~ dbeta(1, 1)            # Prior for recruitment
    N[t] <- sum(z[1:M,t])             #calculate abundance each year
    N.male[t] <- sum(Sex[1:M] * z[1:M,t]) #Sex-specific abundance
    N.female[t] <- N[t]-N.male[t]
```

```
    D[t] <- N[t]/area  #calculate Density each year         #Density
    R.new[t] <- sum(R[1:M,t]) # Calculate the recruits for each year
  }
  for(i in 1:M){
    Sex[i] ~ dbern(psi.sex)   #assign Sex to each individuals
    Sex2[i] <- Sex[i] + 1       #Transfers 1 and 2's for indexing below
    # independent activity centers
    S[i,1] ~ dunif(1, upperLimit[1])                    # priors for the activity centers
    S[i,2] ~ dunif(1, upperLimit[2])                    # for each individual
    pOK[i] <- habMat[trunc(S[i,1])+1, trunc(S[i,2])+1] # Prior specification for
sigma,
    OK[i] ~ dbern(pOK[i])                          # OK[i] = 1, the ones trick
    z[i,1] ~ dbern(gamma[1])                            # Probability of inclusion in
year 1.
    avail[i, 1] <- (1 - z[i,1])
    R[i,1] <- z[i,1]                               # New individuals in Year 1

    for (t in 2:Year){
      mu[i,t] <- (phi * z[i, t-1]) + (gamma[t] * avail[i, t-1])
      z[i,t] ~ dbern(mu[i,t])
      ncaps[i,t] <- sum(z[i,1:t])                       #Ever alive
      avail[i,t] <- 1 - step(ncaps[i,t] - 1)       #change to binary
      R[i, t] <- z[i,t] * avail[i,t-1]             # New individual in Year t
    }
    for(j in 1:ntraps){                            # traps = trap locations, s = activity
centers
      d[i,j] <- pow(S[i,1]-trapMat[j,1],2) + pow(S[i,2]- trapMat[j,2],2) #distance
from capture to
      g[i,j] <- exp(-d[i,j]/(sigma[Sex2[i]]*sigma[Sex2[i]]))            # activity center

      for(k in 1:K){
        for(t in 1:Year){
          logit(p0[i,j,k,t])<- alpha0[Sex2[i]] + B.sex*Sex[i] + B.eff*effort[j,k,t] +
B.snow*snow[j,k,t]
          p[i,j,k,t] <- (1 - exp(-p0[i,j,k,t]*g[i,j]))*trapuse[j,k,t]       #General power
model, trapuse
          y[i,j,k,t] ~ dbin(p[i,j,k,t]*z[i,t],1)       # ensures P=0 when trap
unsearched
        }#t
      }#k
    }#j
  }#M
}
)
```

CHAPTER 3

Gray wolf habitat use in response to visitor activity along roadways in Yellowstone National Park

Abstract

Understanding the behavioral responses of large carnivores to human activity in protected areas is important for conserving top predators. Roads and associated vehicle traffic have a range of impacts on wildlife, including mortality from vehicle collisions and behavioral changes from increasing traffic levels. Roads concentrate human activities and may be particularly impactful when located adjacent to high-quality habitat for wildlife. However, people often overlook road impacts in protected areas because of relatively low road densities. From 1979 to 2017, annual visits to Yellowstone National Park increased from 1.9 to 4.1 million, with many visitors in the last 25 years focusing on the opportunity to view wild wolves (*Canis lupus*) in their natural habitat from the roadway. To better understand how human activity interacts with landscape attributes and prey availability to shape wolf habitat use, we developed seasonal and diel-specific step selection functions (SSF) for wolves. Wolves responded to increased human activity by using areas farther from roadways during the day and during peak visitation in summer. Prey availability, as estimated by an elk SSF, did not significantly alter habitat selection patterns by wolves. The strength of habitat selection in relation to roads varied among wolf packs. The most heavily viewed wolf packs exhibited less road avoidance, suggesting increased tolerance, which could lead to increased vulnerability to human harvest if they leave

the park. Federal and state managers have implemented several measures to mitigate disturbance effects to wolves and curtail habituation. These results may inform adaptive management strategies that seek to continue to conserve natural wolf behavior.

Introduction

Road corridors can have significant impacts on terrestrial wildlife communities. Habitat fragmentation and increased road use cause individual mortality from vehicle collisions, population-level behavioral changes from increasing traffic levels, and genetic flow disruptions among populations of animals (Forman and Alexander 1998, Riley et al. 2006, Ament et al. 2008, Monz et al. 2016). Road impacts also stem from the increased access they provide for humans to undeveloped areas. In some areas, roads can facilitate access by hunters, increasing pressure on animal populations through legal hunting and illegal poaching (Trombulak and Frissell 2000, Noss et al. 2003, Zimmermann et al. 2014). On the other hand, roads can benefit local economies by improving access to scenic, protected areas through ecotourism infrastructure for wildlife viewing (Ament et al. 2008) and providing recreational hunting opportunities (Smith et al. 2016).

In addition to direct mortality from vehicle collisions, the impacts of roads may stem largely from concentrating human activity in wildlands. Changes in habitat selection through avoidance of areas of higher human use have been documented across taxa in terrestrial and marine ecosystems (Chruszcz et al. 2003, Berger 2007, Lesmerises et al. 2012, Northrup et al. 2012, D'Amico et al. 2016, Bateman and Fleming 2017, Penteriani et al. 2017). Such behavioral responses to humans can manifest in activity changes, whereby animals shift times of peak activity or use areas with higher landscape cover and concealment when closer to humans (Ordiz et al. 2011, Wilmers et al. 2013, Zimmermann et al. 2014, Llaneza et al. 2016, Gaynor et al. 2018, Suraci et al. 2019b). In some locales, animals subjected to higher rates of visitation have displayed higher field metabolic rates (Barnett et al. 2016) and lowered reproductive success and growth rates of dependent young (McClung et al. 2004, French et al. 2011). Further evidence demonstrated altered large carnivore behavior from the sound of human voices, leading to cascading community-level effects (Suraci et al. 2019a). These effects can be especially troubling for large carnivores given their relatively low population densities, restricted distributions, and significant roles as keystone predators (Hebblewhite et al. 2005, Ripple et al. 2014). For example, increased visitor activity and the removal of carcasses along roads for traffic or safety reasons has displaced gray wolves (*Canis lupus*) from feeding sites near roadsides in Yellowstone National Park (YNP; YNP unpublished data). Repeated removals of wolf-killed carcasses could lead to changes in trophic relationships and indirect effects on prey similar to those seen in response to kleptoparasitism by dominant scavengers (Krofel et al. 2012, Elbroch et al. 2015). For example, carcass removals by humans are analogous to carcass abandonment, which can precede increases in kill rates and energetic expenditures or loss of feeding opportunities to scavengers (Kerley et al. 2002, Smith et al. 2015). In addition, wolf travel routes can be blocked as they move to and from their den areas to feed pups during late spring and early summer (Smith et al. 2003b). In response, management personnel will often close areas or institute “no stopping” zones along roadways to allow wolves to freely travel or feed without disturbance (Smith et al. 2003b). However, repeated displacements over time could lead to long-term behavioral changes through avoidance, tolerance, or habituation (Knight and Cole 1991, Sirot 2010). In other systems, behavioral changes have led to alterations in individual fitness and disruptions to trophic relationships (Knight and Cole 1991, Hebblewhite et al. 2005, Berger 2007).

The National Park Service (NPS) protects nearly one-quarter of the threatened and endangered species in the United States (Ament et al. 2008) through habitat protection and native species restoration. It also provides critical socio-ecological information for understanding the impacts of regulatory protections under different management jurisdictions (Pressey et al. 2015). Furthermore, national parks can serve as important ecological baselines that help scientists understand and predict changes in other ecosystems, especially those experiencing increased anthropogenic influences (Sinclair 1998, Berger 2007). The NPS's mission is to "conserve the scenery and the natural and historic objects and the wildlife therein and to provide for the enjoyment of the same in such manner and by such means as will leave them unimpaired for the enjoyment of future generations" (*NPS Organic Act of 1916*). This mandate distinguishes the NPS from most other land management agencies and guides its current wildlife policies. However, this mission statement contains objectives of conserving nature unimpaired and providing for enjoyment by people that may conflict at times (Clark and McCool 1985, Wright 1992, Keiter 2013). Understanding how to implement this dual mandate by simultaneously protecting wildlife and facilitating visitation in YNP requires monitoring and research on the impacts of roads and visitation on wildlife behavior, which is broadly applicable for wildlife managers in most protected areas.

Ecotourism provides enjoyment for millions of people and can boost surrounding community economies, but it can also result in some negative impacts to natural resources (Lilieholm and Romney 2000). From 1979 to 2017, visitation to national parks in the United States increased 70% from 50.4 to 85.5 million visitors annually (NPS 2018). The rise in visitation was even more dramatic in YNP during this time, with a nearly 120% increase from 1.9 to 4.1 million annual visitors, mostly occurring from June-August (Figure S3.1; NPS 2018). For example in 2017, average monthly visitation from November-April was approximately 4% (27,102/month) of that recorded during May-October (658,985/month; NPS 2018; see Figure S3.1, for monthly visitation examples). Although traffic is restricted to a 500-km road system that dates back to the 1930s and 1940s, the road corridor intersects several prime river valleys and landscape features, providing wildlife viewing opportunities to greater areas of the park (Keiter 2013). Previous research has indicated winter motorized travel can alter the behavior of animals, and possibly affect their physiological condition (e.g., Creel et al. 2002, Fortin and Andruskiw 2003). However, many animals appeared to habituate to this travel, and there was no evidence it affected their demography, population dynamics, or resource use (Fortin and Andruskiw 2003, Borkowski et al. 2006). It is possible that summer motorized travel could have similar or more substantial impacts on large carnivores like wolves in YNP since visitation is greater during this time. In recent years, wildlife watching has emerged as a popular recreational pursuit that is thought to be a low-impact activity (Knight 2009). From 1995 to 1997, gray wolves were reintroduced to YNP following a 70-year absence (Smith and Bangs 2009). In the years following the reintroduction, YNP became a world-class location to see wild wolves in their natural habitat because of their surprisingly high sightability from the roadway (Smith et al. 2016). Over the last two decades, the number of park visitors viewing wolves has increased substantially, which leads to large groups of people congregating at wolf viewing sites. This concentrated human activity could alter wolf behavior given that wolves in Scandinavia often fled when approached by humans and developed more cryptic behavior after interactions with humans (Wam et al. 2012, 2014).

We sought to quantify wolf behavioral changes to understand current patterns of responses to humans through the implementation of step selection functions (SSFs), which are common methods of estimating wildlife habitat selection from animal location data (Boyce et al. 2002, Manly et al. 2002). These methods have previously been used to show varying responses by wolves to roads and human activity (Hebblewhite and Merrill 2008). Studies in other systems have shown varying responses by wolves to roads depending on the level and type of human use. Selection for areas close to the road either increased (Courbin et al. 2013, Uboni et al. 2015a), decreased (Mladenoff et al. 1995, Latham et al. 2011), or displayed more context dependent responses (Thurber et al. 1994, Paquet et al. 1996, Whittington et al. 2005, 2011, Houle et al. 2010, Ehlers et al. 2014, Zimmermann et al. 2014). For example, Scandinavian wolves displayed an affinity for certain road types for their ease of travel, but exhibited adaptively cryptic behavior when travelling through areas of higher human activity (Zimmermann et al. 2014). Moreover, higher human activity levels have been related to decreased odds of selection and increased mortality in wolves, but can vary among wolf packs in an area due to relative exposure to human activity (Mladenoff et al. 1995, Hebblewhite and Merrill 2008). Legal wolf harvest is permitted in many areas, and, in these regions, road density has been linked to higher rates of human-caused mortality (Fuller et al. 1992, Person and Russell 2008). The absence of hunting within YNP would suggest that wolves would not associate the road and humans with risk (Baldwin and Bender 2008). However, 33 wolves have been killed by vehicle strikes in YNP since 1995 (YNP unpublished data), and some wolves that live primarily within YNP travel outside of the park, becoming exposed to potentially lethal consequences during hunting season in Montana, Idaho, and Wyoming (Smith et al. 2016, Borg et al. 2016). Since 2009, 44-46 wolves that spent at least 90% of their time inside the park have been harvested when they moved outside the park boundary (YNP unpublished data). The harvest of these wolves affected pack stability, which temporarily reduced denning and recruitment rates, as well as wolf sightings by visitors (Borg et al. 2016). However, harvest mortality and pack dissolution had no significant effects on the longer-term population dynamics of wolves (Borg et al. 2015, 2016, Smith et al. 2016).

In this study, our objective was to understand how increasing visitation and road use in YNP affected wolf habitat selection. Specifically, we evaluated whether visitor use associated with the roadway affected wolf resource selection patterns. We also evaluated whether these habitat selection patterns varied across wolf packs, diel periods, and season (spring-fall). We developed seasonal and diel-specific SSFs for wolves and their main prey (elk). We then tested the hypothesis that high human activity would cause wolves to avoid the road corridor more during the day when visitation is high. However, since elk have been known to use areas near human activity as refugia (Hebblewhite et al. 2005, Kauffman et al. 2007), we expected this avoidance would be mediated by possibly greater prey availability near the road, as well as landscape attributes that affect perceived risk from humans (Paquet et al. 1996, Uboni et al. 2015a).

Materials and Methods

Study area

Yellowstone National Park encompasses 8,991-km^2 of federally protected land in Wyoming, Montana, and Idaho. This study focuses on a 5,853-km^2 area that includes Yellowstone's northern range and extends south into the interior of the park and north beyond park boundaries into Custer Gallatin National Forest (Figure 3.1). Vegetation consists primarily of grasslands, sagebrush, and shrublands interspersed with varying sized patches of Douglas fir (*Pseudotsuga menziessi*), lodgepole pine (*Pinus contorta*), Engelmann spruce (*Picea engelmannii*) and juniper (*Juniperus occidentalis*). Higher elevations include areas of sagebrush steppe and whitebark pine (*Pinus albicaulis*). Eight different ungulates inhabit YNP: elk, bison, mule deer (*Odocoileus hemionus*), white-tailed deer (*Odocoileus virgianus*), moose (*Alces

alces), pronghorn (*Antilocapra americana*), bighorn sheep (*Ovis canadensis*), and nonnative mountain goats (*Oreamnos americanus*; Lemke 2004). Elk are the most abundant ungulate in summer, numbering 25,000 to 35,000 in eight different herds and are the primary prey for wolves, followed by bison and mule deer (White and Garrott 2005, Metz et al. 2012).

Wolf and elk spatial data

Following wolf reintroduction in 1995 through 1997, the number of wolves in YNP has ranged between 21 and 174 individuals in three to 16 packs (Fritts et al. 1997, 2001, Smith et al. 2017). We used GPS data from wolves captured annually during winter from 2001- 2016 using helicopter darting techniques following protocols approved by NPS Institutional Animal Care and Use Committee (IACUC; Permit: IMR_YELL_Smith_wolves_2012). During this time, various radio collar types were used including both Very High Frequency (VHF; Telonics, Mesa, Arizona, USA) and GPS-enabled (Televilt, Lindesberg, Sweden; Lotek, Newmarket, Ontario, Canada; Vectronic-Aerospace, Berlin, Germany). GPS collars were programmed to take fixes at 30-minute, 1-hour, or 6-hour intervals depending on the season. This study utilized 19,771 locations with 6-hour intervals between locations from 37 GPS-collared wolves (17 males, 20 females) from 2002-2016 (Mean: 2 packs/year, SD: 1.11 packs/year). These individuals represented 16 different packs (Table S3.1).

To understand the primary prey species for wolves, elk were captured across the northern range of Yellowstone from 2012-2016 under NPS IACUC 2011-47. Elk were fitted with GPS-enabled collars (Lotek, Newmarket, Ontario, Canada; Vectronic-Aerospace, Berlin, Germany). This study evaluated 74,615 GPS locations at a 5-hour fix rate during May-October from 33 adult female elk (Mean: 19.2 elk/year, SD: 5.85 elk/year).

Step selection function covariates

To test the effect of landscape attributes on wolf habitat use, we obtained various habitat and landscape layers that could influence wolf habitat selection based on findings from previous studies (e.g. Whittington et al. 2005, Fortin et al. 2005, Hebblewhite and Merrill 2008). We used a Digital Elevation Model with 30-m resolution to attain elevation data for the study area. We calculated slope and aspect using the *terrain* function in the *raster* package (v 2.8-19; Hijmans and van Etton 2012).

Land cover characteristics and fire boundaries were supplied by the YNP Spatial Analysis Center and used to identify the spatial distribution of vegetation types. The vegetation data was condensed into a categorical land cover type layer, which included herbaceous grassland, shrubland, unburned conifer forest, burned forest, and other land cover that included various wetland and cultivated land cover types. Barren ground was used as a reference category. Burned forest boundaries were identified using fire boundary layers dating back to the 1960s. These categorical land cover layers were used in both wolf and elk SSF models. Finally, we transformed the spatial distribution of perennial watercourses to a distance raster.

In addition to spatial heterogeneity in vegetation, forage quality changes temporally and has been shown to drive patterns in seasonal elk habitat selection (Hebblewhite and Merrill 2008, Merkle et al. 2016). We obtained normalized-difference vegetation index (NDVI), a measure of primary productivity, from Moderate Resolution Imaging Spectrometer (MODIS) satellites, which gives 500-m imagery resolution every 16 days (Didan 2015). NDVI imagery at 500-m resolution was downloaded for the entire study area using tools in the R package *MODIStsp* (v1.3.3.9; Busetto and Ranghetti 2016).

To test the effect of road use for visitation on wolf resource selection, we collected average daily traffic (ADT) estimates from the Transportation and Vehicle Mobility report (Otak 2017). The study placed automatic traffic counters along every major road segment of the park for 3 days in August of 2015 (Figure 3.1). These road counter data coupled with data on individual visitor driving habits were used to estimate the relative difference in use on each road segment in the park (Otak 2017). We combined this information with known visitation numbers from each park entrance to scale ADT estimates for the rest of the time period within this study following equation 1,

$$\frac{ADT_{x,t}}{\upsilon_t} = \frac{\alpha_{x,2015}}{\upsilon_{2015}}$$

where the ratio of ADT for road segment, x, during month, t, to park visitation estimate from entrance station vehicle counts, υ, during month, t, is proportional to the ratio between estimated vehicle volumes from road traffic counters, α, for road segment, x, in August of 2015 to the estimated total park visitation from entrance station vehicle counts, υ, in August 2015. Therefore, ADT was spatially assigned to each road segment in the study area and these estimates are temporally distinct by month and year. To estimate vehicle traffic at night, we examined hourly vehicle counts from entrance stations and found that average night traffic was approximately 5% of daytime traffic (NPS unpublished data). Thus, nighttime ADT was multiplied by 0.05 to reflect this temporal change. For each used and available wolf location, we identified the closest road segment and assigned the corresponding ADT values based on the month in which the GPS fix occurred.

We also included a road view metric that would account for the wolves' ability to see or hear the roadway. This also predicted locations where visitors were more likely to be positioned watching or looking for wolves. The road view metric was created by calculating the average openness value along a line identified by the Euclidean distance between each used or available location and the closest site on the road. Openness values ranged from 0 (deep forest) to 289 (open grassland) and were calculated from the sum of non-forested pixels within a $500m^2$ moving window centered on each pixel (see Kohl et al. 2018 for more information).

To control for the possible influence of prey availability on wolf habitat selection, we built an SSF for elk and used the output as a covariate in our wolf SSF model. We applied the same methodology to generate available locations as we did for wolf GPS locations (See Wolf Step Selection Function section; Forester et al. 2009, Thurfjell et al. 2014). We evaluated the effect of spatial and temporal variables on elk resource selection following similar methods described for wolves, using conditional logistic regression models via the *clogit* call in the *survival* package (Therneau 2015), and fitting generalized estimating equations (GEEs) to account for autocorrelation (Prima et al. 2017). Elk resource selection results, including model selection tables (Table S3.9-S3.12), beta parameter plots from top models (Figure S3.2), 5-fold cross validation results (Table S3.9-S3.12), and prediction surface maps (Figure S3.3-S3.11) can be found in supplemental information sections.

Wolf step selection function

Wolf resource selection can be predicted by topographic attributes, habitat type, prey availability, and anthropogenic influences (Thurber et al. 1994, Mladenoff et al. 1995, Whittington et al. 2005, Hebblewhite and Merrill 2008, Uboni et al. 2015). We applied a used-available framework common in SSF analyses, setting wolf GPS locations from collared wolves as used and matching each to four randomly generated available locations to form matched-case control sets (Thurfjell et al. 2014). Available points were generated using random sampling of step lengths and turning angles from the used GPS data set (Forester et al. 2009). This matched-case control method for generating available locations can minimize autocorrelation issues common in temporal and spatial data (Whittington et al. 2005, Craiu et al. 2008). Since Hebblewhite and Merrill (2008) displayed significant correlation among wolf resource selection between individuals within the same pack, we modeled random slopes and intercepts at the pack level using mixed effects conditional logistic regression (MCLR) models in the R package *coxme* (Hebblewhite and Merrill 2008, Duchesne et al. 2010, Therneau 2018). AIC was used to select the most parsimonious MCLR model and parameter estimates were averaged for models ≤Δ4 AIC of top models (Tables S3.3-S3.8).

We investigated wolf habitat selection during May-October because 96% of annual human visitation to YNP takes place during this time (NPS 2018). We partitioned our data and modelling procedure into nine temporal divisions (Hebblewhite and Merrill 2008, Kohl et al. 2018). Since elk are the primary prey for wolves (Metz et al. 2012) and ungulates display seasonal shifts in resource selection (Mao et al. 2005, Basille et al. 2013), we expected seasonal changes in predator and prey resource selection to correspond (Barnett and Semmens 2012). These included three diel periods (day, night, and crepuscular) in each of the three seasons we considered (spring, summer, and fall). The cut points for these seasons were identified by closely inspecting each individual elk's yearly movement to identify the day(s) of the year they migrated to and from their respective summer ranges. We then averaged these elk migration dates to identify the mean ordinal date that elk shifted to and from their summer ranges to subset the data into three seasons: spring, summer, and fall. Spring migration began on May 24. The summer season started on May 31 and ended on October 4. The fall season began on October 13 and extended through the end of our study period, November 1. We used these average elk migration dates to determine the break points for seasons in the wolf SSF. Diel periods were identified by assigning dawn and dusk times, based on astronomical twilight, for each GPS location using the *maptools* package in R (Bivand et al. 2016). For the crepuscular periods, we placed a 1-hour buffer before and after these dawn and dusk times. Day hours took place from dawn until dusk and night hours took place from dusk until dawn, accounting for those 1-hour buffers.

We investigated the relative probability of selection for landscape patches by wolves based on ecologically-informed combinations and interactions of covariates resulting in 17 distinct model formulations for the nine diel period and season combinations (Table S3.2). All models included a log-transformed distance to road covariate, along with different combinations of the covariates described in the following section. We also included interaction terms between the elk SSF and slope or habitat type to understand if wolf foraging behavior for elk is connected to terrain attributes (Kohl et al. 2018). In addition, we included an interaction between elk SSF values and distance to road to see if wolves were directly weighing foraging opportunities with potential risks associated with the roadway. In addition to the spatial variation in the use of areas close to the human-dominated roadway, we expected selection to vary based on the amount of vehicle and wildlife watching use. ADT (see SSF covariates section) was used in an interaction term with the log-transformed road distance to account for the conditional effect of varying road use. We tested for an interaction between road view (see SSF covariates section) and log-transformed road distance. Prior to fitting models, we standardized all continuous covariates (distance to road, ADT, slope, distance to water, probability of prey encounter [from elk SSF], and road view) to mean = 0 and standard deviation = 1 (Schielzeth 2010). We tested collinearity of model covariates by creating correlation matrices. We only used variables with correlation values less than 0.60. This was particularly important for the elk SSF layer, which was not collinear with any of the other covariates used in the wolf SSF.

Results

We found a significant effect of road attributes on wolf habitat selection. Wolves were more likely to select habitat closer to the road when there was low visibility to the road (road view was low) but avoided the road when bordering habitat was open (road view was high; Figure 2). However, the level of attraction or avoidance to the road given varying road view values exhibited significant variation among the diel periods and seasons. We found better model fit when taking the natural log transformation of the distance to road covariate, which adequately accounted for the nonlinear relationship. The most parsimonious MCLR model across all seasons and diel periods included an interaction term between log-transformed distance to road and road view (Table 3.1; Tables S3.3-S3.5).

We calculated odds ratios for selection coefficients at 50 m because current YNP regulations prohibit humans to approach or remain within 100 m of wolves, allowing direct insight on current protections against wolf habituation. During both summer and fall, wolves were more likely to select areas closer to the road when the road view was blocked during day and night when compared to crepuscular hours. During summer days, when the road view was blocked, wolves were 41.7 (95% CI: 40.6, 42.9) times more likely to use an area 50 m from the road than if the road view was open. When human activity lessened during crepuscular and night hours, the odds ratio changed to 6.0 (95% CI: 4.6, 7.5) and 10.6 (95% CI: 9.6, 11.6), respectively, for an area with the same distance to road and road view metrics. This trend persisted until odds ratios were equivalent for open and blocked road views at around 1 km, 750 m, and 850 m during day, crepuscular, and night hours, respectively (Figure 3.2). Further, when the road view was open, wolves were 3.5 (95% CI: 2.5, 4.4) times more likely to select for an area 1 km instead of 50 m from the roadway. Relative to spring, the differences were not as pronounced. In spring, the odds of an animal choosing a patch closer to the road with high vegetative cover blocking the view to the road were considerably lower during the day and increased during the night and into crepuscular times (Figure 3.2; Tables S3.6-S3.8). For example, during spring days, wolves were 67.3 (95% CI: 66.5, 68.1) times more likely to use an area 50 m from a road if the road view was blocked than if the road view was open. During crepuscular and night hours, odds of selection for this type of habitat changed to 19.9 (95% CI: 17.8, 22.0) and 29.0 (95% CI: 27.8, 30.2), respectively. This decline in the spring season odds ratios during crepuscular and night hours is due to the overall higher odds of selection for closer distances to the road, diminishing the differences between open and closed road views.

We found significant variation across wolf packs in their response to the road corridor. Two packs within the study area (Blacktail Plateau and Lamar Canyon) displayed significantly different selection, favoring areas closer to the road, while other packs avoided areas near the road (Figure 3.3). During the spring, the Blacktail

Plateau pack was 5.2 (95% CI: 4.8, 5.7) times more likely than the Junction Butte pack (representative of most of the other wolf packs besides Blacktail Plateau and Lamar Canyon) to be 50 m instead of 1 km from the road. While all wolf packs increased selection closer to the road in spring crepuscular and night hours (Figure 3.3), the Blacktail Plateau wolves displayed greater preference for these closer distances and were 2.4 (95% CI: 2.0, 2.8) and 3.9 (95% CI: 3.3, 4.5) times more likely to select these areas when compared to the Junction Butte pack. Compared to spring, summer selection displayed a considerable shift to farther distances from the roadway for all packs when visitation numbers are at their peak (Figure 3.3; NPS 2018). The Lamar Canyon pack displayed the most affinity for close distances to the road during summer where they were 4.2 (95% CI: 3.5, 4.9) and 4.2 (95% CI: 3.6, 4.8) times more likely than the Junction Butte pack to select an area 50 m from the road during day and night hours, respectively. Interestingly, there was no significant variation in distance to road selection during summer crepuscular hours, with wolf packs 1.6 (95% CI: 0.23, 3.0) times more likely to use an area 1 km than 50 m from the roadway (Figure 3). In the fall, the variation among packs in the effect of the road lessened and wolves were on average 4.9 (95% CI: 2.8, 7.0), 1.8 (95% CI: 0, 3.7), 1.1 (95% CI: 0, 2.5) more likely to select an area 1 km instead of 50 m from the road in day, crepuscular, and night hours, respectively (Figure 3.3). Further, neither ADT nor the elk SSF significantly influenced wolf resource selection.

Discussion

We found that wolves selected against habitat close to the road corridor in YNP when there was insufficient vegetative cover blocking their view of the roadway. Wolves selected areas closer to the road at night and crepuscular times when human activity decreased (Figures 3.2 and 3.3). In addition, wolves avoided the road more during the day than at night and crepuscular hours when road traffic decreased substantially. This pattern was most dramatic in spring when snow levels limit efficient wolf movement into the farther reaches of the study area, drawing them towards the low-cost movement path of the road corridor (Whittington et al. 2005). This season also takes place prior to elk spring migration and wolves may be able to maximize encounter rates with prey closer to the road since elk have been shown to select road corridors in other studies (Kauffman et al. 2007, Whittington et al. 2011, Courbin et al. 2013).

The impact of roads and their associated human activity on wildlife in protected areas is often overlooked because road densities are low compared to more human-dominated landscapes. However, the availability of high quality habitat adjacent to roads can lead to greater vulnerability of local wildlife to negative impacts of the road (Bernardino and Dalrymple 1992, Drews 1995, Kline and Swann 1998, Ament et al. 2008, Garriga et al. 2012, Bateman and Fleming 2017). In the Bow River Valley of Banff National Park, wolves began to change habitat use patterns when visitation exceeded 100 people per month, and wolves abandoned favorable habitat when visitation topped 10,000 people per month (Paquet et al. 1996). We expected ADT to be a reasonable approximation of human activity along the roadway that would help explain wolves' spatial and temporal relationship with the road corridor. However, ADT was not chosen through model selection routines in any seasonal and diel period combination. Though the inclusion of the ADT covariate did not provide significant adjustment on wolf selection coefficients for differing distances to the road, the inherent fluctuations in diel-specific visitor use (high during the day and low during the night) may be sufficient to draw conclusions on the impact of human activity along the road (Figure 3.2 and 3.3). Nevertheless, this pattern is not homogeneous across all wolf packs and our results show that two packs responded differently to human activity associated with the roadway.

The Lamar Canyon and Blacktail Plateau packs exhibited less avoidance of the road than other packs in the study area (Figure 3.3). The Lamar Canyon pack resides primarily in Lamar Valley, a famous wildlife watching area in the northeastern section of the park (Varley et al. In press). Historically, this area has received the most wolf watching use and the Lamar Canyon wolves have been exposed to substantial human presence at close distances to the road. In addition, this wolf pack often established natal den sites close to the roadway leading to frequent habitat selection close to the road. Similarly, the Blacktail Plateau pack received relatively high visitor viewing pressure compared to most packs used in this study. Moreover, the founding members of the Blacktail Plateau pack originated from packs that utilized areas similar to Lamar Canyon wolves, possibly carrying over some of these learned responses. These repeated human-wolf interactions without adverse consequences, sometimes with hundreds of people at a time, likely led to greater tolerance of humans at close distances to the road. This habituation may have contributed to greater harvest vulnerability because several individuals from these packs were harvested or illegally shot outside the park in 2011, 2012, and 2018 (Smith et al. 2016).

In addition to testing for anthropogenic influences, we wanted to understand if prey availability would be a driving force in determining wolf habitat use. Optimal foraging theory suggests individuals will select habitat that provides access to food resources (Pyke et al. 1977). Interestingly, the addition of the elk SSF did not significantly help explain wolf habitat use patterns. Future research will incorporate tri-axial accelerometer data to examine wolf behavior-specific SSF in relation to the elk SSF.

Conclusion

Wolves' reactions to human activity are shaped by the cumulative sum of repeated interactions with humans and the consequences of these interactions (Whittaker and Knight 1998, McNay 2002, Bejder et al. 2009). For some wolves in YNP, innocuous interactions with humans occur regularly as wolves traverse portions of the landscape along roadways where human use is concentrated and has increased. Nonetheless, an extensive study on YNP visitor values in 2016 found that 83% of respondents stated viewing wildlife in their natural habitat as a primary reason for visiting the park and half of all visitors surveyed rated wolves as "extremely important" to their experience in the park (Resource Systems Group 2017). In addition, wolf-centric ecotourism continues to increase in the Yellowstone area and generates tens of millions of dollars annually in the regional economy (Duffield et al. 2008, Varley et al. In press). However, our findings indicate human activity along roads in YNP can influence habitat selection decisions by wolves. Thus, visitor use, wolf management, and regional socioeconomics are inextricably entwined. In addition, our findings suggest high visitor use along roads in YNP may result in some wolves becoming less wary of people, which could increase their risk of being harvested if they leave the park during hunting seasons in surrounding states. Moreover, these patterns are broadly applicable beyond national parks and protected areas where roads may intersect high quality habitat, leading to alterations in wolf behavior.

Because most of YNP is managed as wilderness (92% of land area) with no public roads, relatively low and stable human backcountry use (Gunther et al. 2017), and designated campsites, many animals have limited exposure to people. For wolves living in YNP, some packs occupy territories largely in remote areas removed from human activity, while other packs' territories overlap extensively with the road corridor resulting in more frequent human encounters. We suggest that due to both variation in human exposure and individual wolves' tolerance to human activity, impacts on wolf behavior in YNP vary in significance.

Park managers have implemented several measures to mitigate specific disturbance effects to wolves, including closed areas around dens, no-stopping areas along roadways frequently crossed by wolves, and requiring people to stay at least

100 m from wolves. They have implemented a management plan to discourage excessive habituation and, in collaboration with Yellowstone Forever (an official non-profit education and fund-raising partner), supervised two employees to monitor wolves and manage visitor behavior in key wolf-watching areas. Park managers also coordinate regularly with state managers to discuss the trans-boundary management of wolves. These discussions have contributed to modest quotas and harvests of wolves in hunting areas along the boundary of YNP (Smith et al. 2016). Even though population-level impacts were not identified in our study, nor were individual-fitness impacts evaluated, our results provide new information on wolf responses to human activity along the roadways. This knowledge may aid both future research on visitor impacts, as well as guide adaptive management that seeks to continue conserving natural wolf behavior, while providing positive visitor experiences.

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Rick McIntyre for their knowledge and efforts to mitigate visitor impacts on wolves over the years.

Table 3.1. Model selection results for MCLR models demonstrating the relationship between wolf resource selection and seven spatial and/or temporal landscape metrics. This table shows only the top three models for each of the nine seasons and diel period combinations. Full model selection tables can be seen in Tables S3.2-S3.5). All models include a random intercept and slope for each wolf pack's habitat selection relationship to distance to road. The covariate combination used in each model's specification, AIC, and change in AIC from top model (ΔAIC) are shown for each season and diel period.

Model Rank	Model Specification	Season	Diel Period	AIC	ΔAIC
1	Distance To Road + Slope + Aspect + Habitat Type + Elk RSF + Elk RSF x Slope + Road View + Distance To Road x Road View	Spring	Day	4914.88	0
2	Distance To Road + Slope + Aspect + Habitat Type + Elk RSF + Elk RSF x Habitat Type + Road View + Distance To Road x Road View			4931.63	16.75
3	Distance To Road + Slope + Aspect + Habitat Type + Elk RSF + Road View + Distance To Road x Road View			4936.4	21.52
1	Distance To Road + Slope + Aspect + Habitat Type + Road View + Distance To Road x Road View	Spring	Crepuscular	911.17	0
2	Distance To Road + Slope + Aspect + Habitat Type + Elk RSF + Elk RSF x Slope + Road View + Distance To Road x Road View			911.95	0.78
3	Distance To Road + Slope + Aspect + Road View + Distance To Road x Road View			912.53	1.35
1	Distance To Road + Slope + Aspect + Habitat Type + Elk RSF + Elk RSF x Habitat Type + Road View + Distance To Road x Road View	Spring	Night	6040.36	23.41
2	Distance To Road + Slope + Aspect + Habitat Type + Elk RSF + Elk RSF x Slope + Road View + Distance To Road x Road View			6040.36	23.41
3	Distance To Road + Slope + Aspect + Habitat Type + Elk RSF + Road View + Distance To Road x Road View			6059.84	42.89
1	Distance To Road + Slope + Aspect + Habitat Type + Elk RSF + Elk RSF x Slope + Road View + Distance To Road x Road View	Summer	Day	16494.96	0
2	Distance To Road + Slope + Aspect + Habitat Type + Elk RSF + Road View + Distance To Road x Road View			16511.96	16.99

3	Distance To Road + Slope + Aspect + Habitat Type + Elk RSF + Elk RSF x Slope + Road View + Distance To Road x Road View			16513.85	18.89
1	Distance To Road + Slope + Aspect + Habitat Type + Elk RSF + Road View + Distance To Road x Road View	Summer	Crepuscular	3875.35	0
2	Distance To Road + Slope + Aspect + Habitat Type + Elk RSF + Elk RSF x Slope + Road View + Distance To Road x Road View			3876.81	1.46
3	Distance To Road + Slope + Aspect + Habitat Type + Road View + Distance To Road x Road View			3876.99	1.64
1	Distance To Road + Slope + Aspect + Habitat Type + Elk RSF + Elk RSF x Habitat Type + Road View + Distance To Road x Road View	Summer	Night	21211.62	0
2	Distance To Road + Slope + Aspect + Habitat Type + Elk RSF + Elk RSF x Slope + Road View + Distance To Road x Road View			21217.85	6.23
3	Distance To Road + Slope + Aspect + Habitat Type + Elk RSF + Road View + Distance To Road x Road View			21219.22	7.6
1	Distance To Road + Slope + Aspect + Elk RSF + Road View + Distance To Road x Road View	Fall	Day	1034.65	0
2	Distance To Road + Slope + Aspect + Habitat Type + Elk RSF + Road View + Distance To Road x Road View			1038.09	3.44
3	Distance To Road + Slope + Aspect + Habitat Type + Elk RSF + Elk RSF x Slope + Road View + Distance To Road x Road View			1040.07	5.42
1	Distance To Road + Slope + Aspect + Habitat Type + Elk RSF + Road View + Distance To Road x Road View	Fall	Crepuscular	1054.18	0
2	Distance To Road + Slope + Aspect + Habitat Type + Elk RSF + Elk RSF x Slope + Road View + Distance To Road x Road View			1056.18	2
3	Distance To Road + Slope + Aspect + Habitat Type + Road View + Distance To Road x Road View			1057.93	3.75
1	Distance To Road + Slope + Aspect + Habitat Type + Elk RSF + Elk RSF x Slope + Road View + Distance To Road x Road View	Fall	Night	2283.92	0
2	Distance To Road + Slope + Aspect + Elk RSF + Road View + Distance To Road x Road View			2284.65	0.73

3	Distance To Road + Slope + Aspect + Habitat Type + Elk RSF + Road View + Distance To Road x Road View	2285.46	1.54

Figure 3.1. Study area map in the Greater Yellowstone Ecosystem. The red polygon outlines the 5,853km^2 where we calculated SSFs for wolves and elk. The shaded area delineates the boundaries of Yellowstone National Park. Parallel line shapes show where the entire road system was cut into smaller sections and circle shapes on the roadway show the placement of automatic traffic counters. Data from automatic traffic counter in August 2015 were used to generate estimates of Average Daily traffic (ADT) for each road segment. Inset bar graphs show ADT estimates averaged over all years of the study where shaded bars represent different months within the 3 seasons used in this study: white bars for spring (May), black bars for summer (June-September), and gray bars for fall (October). All bar graph y-axes are scaled from zero to 8000 vehicles per day. See Results section for exact dates included in each season.

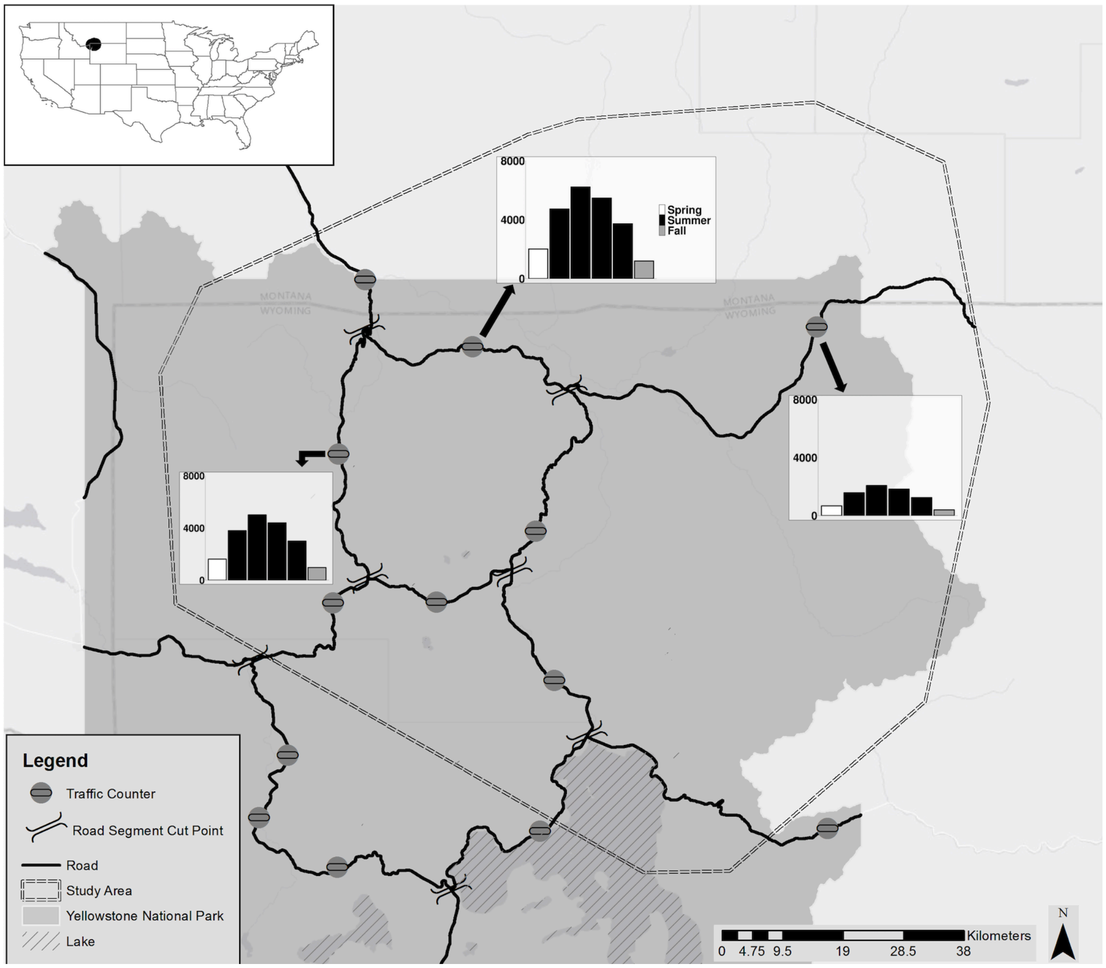


Figure 3.2. Plot showing relative odds of selection based on the wolf's distance to road and the road view value. Panels represent different seasons: Spring (A), Summer (B), and Fall (C). Orange lines represent day, green represent crepuscular, and purple represent night hours. Solid lines represent the odds of selection given Road View is low (habitat is closed), the dashed lines represent selection when Road View is high (habitat is open). Selection for lower x-axis values (smaller distances to road) indicates selection for areas closer to the road. It is important to note that y-axes value ranges differ between seasonal plots.

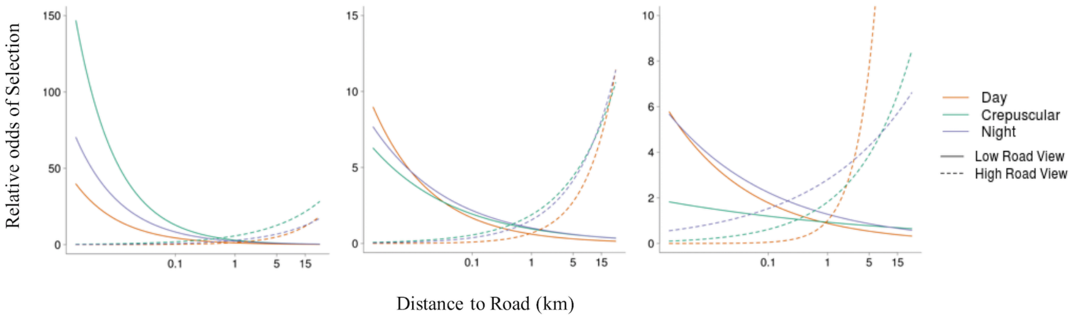
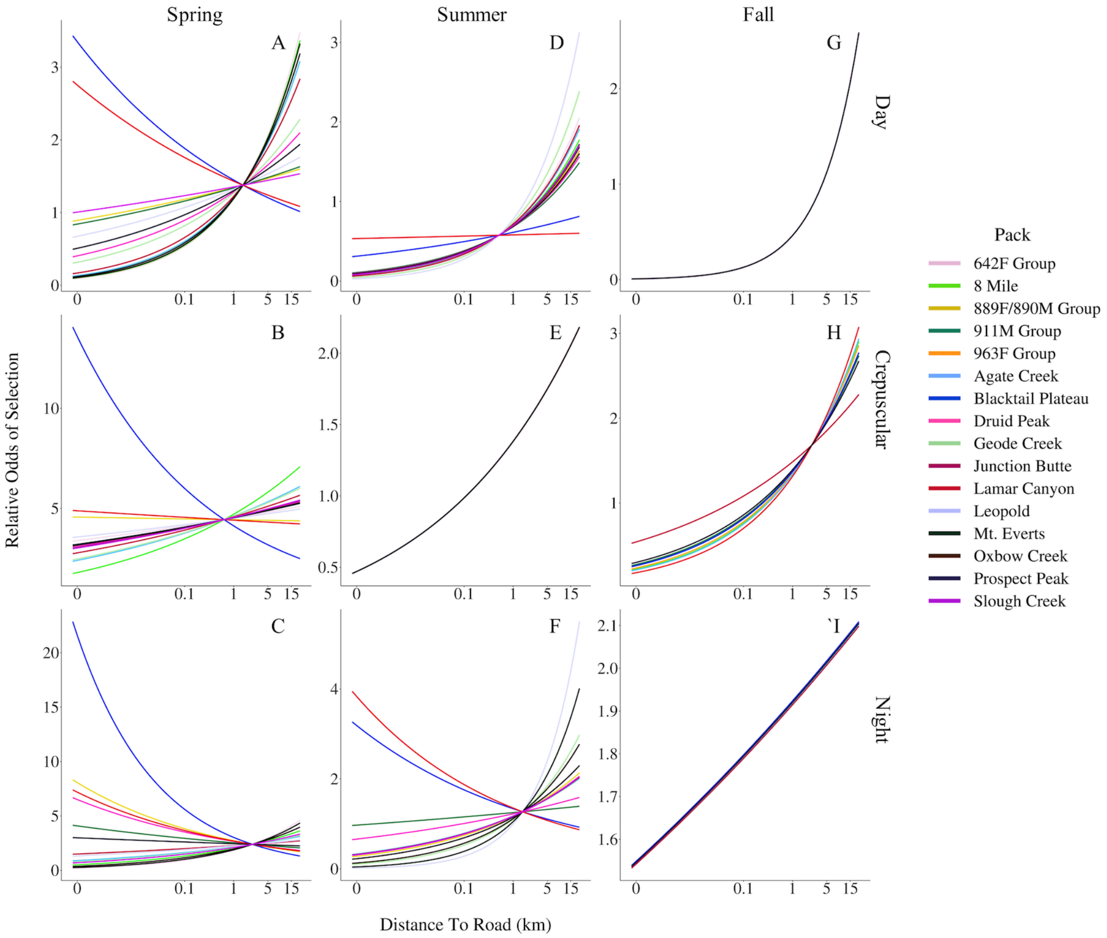


Figure 3.3. Results from MCLR modelling with random intercepts and slopes for each pack's distance to road relationship. Panels represent different seasonal and diel period combinations. Seasons are aligned in columns: spring selection in panels A-C, summer in panels D-F, and fall in panels G-I. Diel periods are separated by rows: day panels in A, D, and G; crepuscular in B, E, and H; and night in panels C, F, and I.



Chapter 3 Supplementary Information

Table S3.1. GPS collared gray wolves from 2001-2017 used to calculate resource selection functions. Yearling age class refers to animals aged 1-2 years, adults are aged >2 years. Social status refers to breeders and leaders of their respective social group (Alpha), breeders that lack the leadership role (Beta), or those that are not breeders or leaders (Subordinate). Years represented refers to the years in which GPS locations were used for each individual. Pack refers to the pack affiliation for that individual during the year of data collection. Individuals may have joined a new pack and have multiple entries in the table.

The table provides the fate of each individual with the year of their death, if appropriate.

Wolf ID	Sex	Age Class	Social Class	Years Represented	Pack	# of 6-Hour GPS Locations	Fate
222M	Male	Yearling	Subordinate	2001	Druid Peak	84	Unknown Fate
220F	Female	Yearling	Subordinate	2001	Leopold	328	Interspecific (2003)
376F	Female	Yearling	Subordinate	2004	Druid Peak	89	Dispersed -> Unknown Fate
392M	Male	Adult	Subordinate	2004	Geode Creek	317	Unknown Fate
470F	Female	Yearling	Subordinate	2005	Leopold	254	Malnutrition (2011)
527F	Female	Adult	Beta	2006	Slough Creek	72	Harvest (2009)
525F	Female	Adult	Subordinate	2006, 2007	Agate Creek	994	Intraspecific (2011)
593F	Female	Yearling	Subordinate	2007	Leopold	266	Unknown Fate
624F	Female	Yearling	Subordinate	2008	Leopold	365	Unknown Fate
625F	Female	Yearling	Subordinate	2008	Leopold	337	Dispersed -> Control Action (2009)
626F	Female	Yearling	Subordinate	2008	Oxbow Creek	366	Natural Unknown (2008)
627M	Male	Adult	Alpha	2008	Oxbow Creek	361	Unknown Fate
692F	Female	Adult	Subordinate	2009	Blacktail Plateau	366	Dispersed -> Poached (2011)
693F	Female	Adult	Alpha	2009	Blacktail Plateau	348	Unknown (2013)
684M	Male	Unknown	Subordinate	2009	Everts	380	Unknown Cause of Death (2014)
685M	Male	Adult	Subordinate	2009	Everts	386	Unknown Cause of Death(2012)
642F	Female	Adult	Subordinate	2010	Blacktail Plateau	375	Harvest (2011)
752F	Female	Yearling	Subordinate	2010	Blacktail Plateau	382	Dispersed -> Harvest (2012)
752F	Female	Adult	Subordinate	2011	642F Group	540	Dispersed -> Harvest (2012)
775M	Male	Yearling	Subordinate	2011	Agate Creek	332	Intraspecific (2011)
777M	Male	Adult	Subordinate	2011, 2012	Blacktail Plateau	491	Dispersed -> Intraspecific (2012)
829F	Female	Adult	Subordinate	2012	Blacktail Plateau	691	Harvest (2012)
777M	Male	Adult	Subordinate	2012	Junction Butte	249	Intraspecific (2012)
832F	Female	Adult	Alpha	2012	Lamar Canyon	661	Harvest (2012)
SW763M	Male	Adult	Subordinate	2013	8 Mile	700	Dispersed
889F	Female	Adult	Alpha	2013	889F/890M Group	454	Dispersed -> Harvest (2014)
890M	Male	Adult	Alpha	2013	889F/890M Group	475	Alive
890M	Male	Adult	Subordinate/Alpha*	2013, 2014	Junction Butte	397	Alive
911M	Male	Adult	Alpha	2014	911M Group	663	Intraspecific (2016)
SW763M	Male	Adult	Alpha	2014	Prospect Peak	700	Alive
907F	Female	Yearling	Subordinate	2014, 2015	Junction Butte	1008	Alive
911M	Male	Adult	Subordinate	2014, 2015	Junction Butte	766	Intraspefic (2016)
968F	Female	Yearling	Subordinate	2015	Junction Butte	439	Harvest (2015)
964M	Male	Yearling	Subordinate	2015	Prospect Peak	711	Alive
910M	Male	Adult	Subordinate	2015, 2016	8 Mile	467	Alive
1005F	Female	Yearling	Subordinate	2016	8 Mile	687	Alive
994M	Male	Yearling	Subordinate	2016	Junction Butte	638	Alive
993M	Male	Adult	Alpha	2016	Lamar Canyon	227	Interspecific (2016)
996M	Male	Yearling	Subordinate	2016	Prospect Peak	705	Alive
962M	Male	Adult	Subordinate	2017	8 Mile	676	Alive
963F	Female	Adult	Subordinate	2017	8 Mile	131	Dispersed
963F	Female	Adult	Alpha	2017	963F Group	82	Alive
1047M	Male	Adult	Subordinate	2017	Junction Butte	715	Alive

*890M changed social status in 2014 and took over the Alpha position.

Table S3.2. MCLR model list displaying covariate combinations used for wolf SSF. All models including term (1 + Distance To Road | Pack) to estimate random intercepts and slopes for each wolf pack’s selection for distance to road.

Model	**Covariates**
MCLR1	Distance To Road + Slope + Aspect + Habitat Type + Elk SSF + (1+ Distance To Road | Pack)
MCLR2	Distance To Road + Slope + Habitat Type + Elk SSF + (1+ Distance To Road | Pack)
MCLR3	Distance To Road + Aspect + Habitat Type + Elk SSF + (1+ Distance To Road | Pack)
MCLR4	Distance To Road + Slope + Habitat Type + Elk SSF + Distance To Water
MCLR5	Distance To Road + Slope + Aspect + Habitat Type + Elk SSF + Distance To Water + (1+ Distance To Road | Pack)
MCLR6	Distance To Road + Slope + Aspect + Habitat Type + Elk SSF + Distance To Road X ADT + (1+ Distance To Road | Pack)
MCLR7	Distance To Road + Slope + Aspect + Habitat Type + Elk SSF + Distance To Road X ADT + Elk SSF X Slope + (1+ Distance To Road | Pack)
MCLR8	Distance To Road + Slope + Aspect + Habitat Type + Elk SSF + Distance To Road X ADT + Elk SSF X Habitat Type + (1+ Distance To Road | Pack)
MCLR9	Distance To Road + Slope + Aspect + Habitat Type + Elk SSF + Road View + Distance To Road X Road View + (1+ Distance To Road | Pack)
MCLR10	Distance To Road + Slope + Aspect + Habitat Type + Elk SSF + Road View + Distance To Road X ADT + (1+ Distance To Road | Pack)
MCLR11	Distance To Road + Slope + Aspect + Habitat Type + Road View + Distance To Road X Road View + (1+ Distance To Road | Pack)
MCLR12	Distance To Road + Slope + Aspect + Road View + Distance To Road X Road View + (1+ Distance To Road | Pack)
MCLR13	Distance To Road + Habitat Type + Elk SSF + Road View + Distance To Road X Road View + (1+ Distance To Road | Pack)
MCLR14	Distance To Road + Slope + Aspect + Elk SSF + Road View + Distance To Road X Road View + (1+ Distance To Road | Pack)
MCLR15	Distance To Road + Slope + Aspect + Habitat Type + Elk SSF + Elk SSF X Habitat Type + Road View + Distance To Road X Road View + (1+ Distance To Road | Pack)
MCLR16	Distance To Road + Slope + Aspect + Habitat Type + Elk SSF + Elk SSF X Slope + Road View + Distance To Road X Road View + (1+ Distance To Road | Pack)
MCLR17	Distance To Road + Slope + Aspect + Habitat Type + Elk SSF + Elk SSF X Habitat Type + (1+ Distance To Road | Pack)

MCLR18	Distance To Road + Slope + Aspect + Habitat Type + Elk SSF + Elk SSF X Distance To Road + (1+ Distance To Road | Pack)
MCLR19	Distance To Road + Slope + Aspect + Habitat Type + Elk SSF + Elk SSF X Slope + (1+ Distance To Road | Pack)

Table S3.3. Spring model selection table. Top AIC models are bolded and outlined.

	Spring Day n = 1643		**Spring Crepuscular** n = 297		**Spring Night** n = 2005	
Model	AIC	ΔAIC	AIC	ΔAIC	AIC	ΔAIC
MCLR1	5129.97	215.09	944.03	32.86	6227.53	210.59
MCLR2	5133.89	219.01	943.70	32.53	6236.90	219.95
MCLR3	5185.39	270.51	956.81	45.64	6281.62	264.68
MCLR4	5133.76	218.89	941.26	30.09	6233.14	216.19
MCLR5	5129.89	215.02	941.57	30.40	6223.90	206.95
MCLR6	5131.47	216.59	945.90	34.73	6229.04	212.10
MCLR7	5112.74	197.86	944.39	33.22	6215.36	198.42
MCLR8	5134.40	219.52	949.35	38.18	6184.71	167.77
MCLR9	4936.40	21.52	913.07	1.90	6059.84	42.89
MCLR10	5079.73	164.85	932.07	20.90	6186.02	169.08
MCLR11	4936.59	21.72	**911.17**	**0.00**	6072.34	55.39
MCLR12	5014.23	99.35	912.53	1.35	6123.10	106.15
MCLR13	4997.09	82.21	926.67	15.50	6127.53	110.58
MCLR14	5014.63	99.75	913.97	2.80	6115.18	98.23
MCLR15	4931.63	16.75	917.54	6.37	**6016.95**	**0.00**
MCLR16	**4914.88**	**0.00**	911.95	0.78	6040.36	23.41
MCLR17	5132.89	218.01	947.49	36.32	6183.13	166.19
MCLR18	5131.95	217.07	943.09	31.92	6159.65	142.70
MCLR19	5111.16	196.28	942.49	31.32	6213.99	197.04

Table S3.4. Summer model selection table. Top AIC models are bolded and outlined.

	Summer Day		**Summer Crepuscular**		**Summer Night**	
	n = 5571		n = 1326		n = 7300	
Model	AIC	ΔAIC	AIC	ΔAIC	AIC	ΔAIC
MCLR1	17051.67	556.70	3957.08	81.73	21711.13	499.51
MCLR2	17069.52	574.56	3958.35	83.00	21733.13	521.51
MCLR3	17642.64	1147.68	4154.08	278.73	22701.91	1490.28
MCLR4	17071.26	576.30	3946.92	71.57	21730.65	519.03
MCLR5	17053.46	558.49	3945.22	69.87	21708.72	497.10
MCLR6	17048.03	553.06	3958.85	83.50	21711.47	499.85
MCLR7	17049.12	554.16	3960.58	85.23	21712.91	501.29
MCLR8	17002.11	507.15	3960.81	85.46	21696.89	485.27
MCLR9	16511.96	16.99	**3875.35**	**0.00**	21219.22	7.60
MCLR10	16843.24	348.27	3911.21	35.86	21476.57	264.95
MCLR11	16577.67	82.70	3876.99	1.64	21239.09	27.46
MCLR12	16727.18	232.22	3895.52	20.17	21363.83	152.21
MCLR13	17048.95	553.98	4058.41	183.06	22214.79	1003.17
MCLR14	16645.94	150.97	3893.19	17.84	21345.79	134.16
MCLR15	**16494.96**	**0.00**	3879.48	4.13	**21211.62**	**0.00**
MCLR16	16513.85	18.89	3876.81	1.46	21217.85	6.23
MCLR17	17005.11	510.15	3959.04	83.69	21696.56	484.93
MCLR18	17009.50	514.54	3958.92	83.57	21686.43	474.81
MCLR19	17052.71	557.75	3958.81	83.46	21712.55	500.93

Table S3.5. Fall MCLR model selection table using AIC. Top models are bolded and outlined.

	Fall Day n = 364		**Fall Crepuscular** n = 372		**Fall Night** n = 793	
Model	AIC	ΔAIC	AIC	ΔAIC	AIC	ΔAIC
MCLR1	1071.24	36.60	1064.20	10.01	2314.45	30.53
MCLR2	1076.19	41.54	1059.21	5.03	2313.17	29.25
MCLR3	1155.67	121.02	1144.57	90.38	2390.01	106.09
MCLR4	1077.95	43.30	1060.94	6.75	2312.61	28.69
MCLR5	1072.69	38.05	1065.95	11.77	2313.88	29.96
MCLR6	1073.01	38.37	1065.67	11.48	2314.23	30.31
MCLR7	1075.01	40.37	1067.66	13.48	2310.17	26.25
MCLR8	1079.06	44.41	1072.84	18.65	2317.66	33.74
MCLR9	1038.09	3.44	**1054.18**	**0.00**	2285.46	1.54
MCLR10	1057.50	22.85	1059.04	4.86	2293.36	9.44
MCLR11	1051.57	16.92	1057.93	3.75	2292.40	8.48
MCLR12	1048.30	13.66	1076.31	22.12	2304.69	20.77
MCLR13	1111.84	77.19	1125.07	70.88	2363.60	79.68
MCLR14	**1034.65**	**0.00**	1077.12	22.94	2284.65	0.73
MCLR15	1046.34	11.70	1061.93	7.74	2289.40	5.48
MCLR16	1040.07	5.42	1056.18	2.00	**2283.92**	**0.00**
MCLR17	1077.26	42.61	1071.37	17.19	2317.83	33.91
MCLR18	1055.34	20.69	1066.20	12.01	2315.66	31.74
MCLR19	1073.24	38.59	1066.20	12.01	2310.49	26.57

Table S3.6. Covariate Parameter estimates for top Spring MCLR wolf SSF models or averaged estimates among models within Δ4 AIC of top model.

Spring Day

Covariate	Coefficient	SE	Lower 95% CI	Upper 95% CI
Aspect_N	-0.1799	0.0857	-0.3513	-0.0085
Aspect_S	0.1513	0.0944	-0.0374	0.3401
Aspect_W	-0.0393	0.0896	-0.2185	0.1399
Slope	-0.2033	0.0403	-0.2838	-0.1228
Burned Forest	0.2778	0.3363	-0.3948	0.9504
Unburned Forest	1.0224	0.3061	0.4103	1.6345
Grassland	-0.2180	0.3250	-0.8680	0.4320
Other Habitat	0.5798	0.3552	-0.1305	1.2901
Shrubland	0.4305	0.3060	-0.1815	1.0426
Elk SSF	0.0222	0.0410	-0.0598	0.1043
Elk SSF X Slope	0.1713	0.0356	0.1001	0.2425
Log Distance To Road	0.1294	0.0808	-0.0323	0.2911
Log Distance To Road X Road View	0.4602	0.0407	0.3788	0.5416
View To Road	0.5077	0.0505	0.4068	0.6087

Spring Crepuscular

Covariate	Coefficient	SE	Lower 95% CI	Upper 95% CI
Aspect_N	-0.3601	0.2042	-0.7602	0.0401
Aspect_S	0.0899	0.2206	-0.3424	0.5222
Aspect_W	0.0869	0.1995	-0.3041	0.4778
Slope	-0.3513	0.0927	-0.5330	-0.1696
Burned Forest	1.7527	0.9044	-0.0198	3.5252
Unburned Forest	1.8546	0.8582	0.1725	3.5366
Grassland	1.2312	0.8690	-0.4721	2.9345
Other Habitat	0.7433	1.0004	-1.2174	2.7040
Shrubland	1.4997	0.8516	-0.1693	3.1688
Elk SSF	-0.0744	0.1211	-0.3117	0.1629
Elk SSF X Slope	0.1612	0.0912	-0.0175	0.3399
Log Distance To Road	-0.0518	0.1142	-0.2756	0.1721
Log Distance To Road X Road View	0.3807	0.0912	0.2020	0.5594
View To Road	0.5663	0.1224	0.3263	0.8063

Spring Night

Covariate	Coefficient	SE	Lower 95% CI	Upper 95% CI
Aspect_N	-0.1255	0.0784	-0.2823	0.0313
Aspect_S	0.2310	0.0833	0.0645	0.3976
Aspect_W	-0.0202	0.0810	-0.1821	0.1417
Slope	-0.2566	0.0351	-0.3268	-0.1865
Burned Forest	0.9417	0.3893	0.1631	1.7202
Unburned Forest	1.4149	0.3708	0.6732	2.1565
Grassland	0.4252	0.4028	-0.3804	1.2309
Other Habitat	0.8569	0.6351	-0.4134	2.1271
Shrubland	1.0563	0.3735	0.3093	1.8033
Elk SSF	1.0706	0.8082	-0.5458	2.6870
Elk SSF X Burned Forest	-1.4637	0.8277	-3.1192	0.1917
Elk SSF X Grassland	-0.8858	0.8240	-2.5337	0.7622
Elk SSF X Other Habitat	-0.9619	0.9463	-2.8545	0.9308
Elk SSF X Shrubland	-1.1768	0.8096	-2.7960	0.4423
Elk SSF X Unburned Forest	-0.4331	0.8116	-2.0563	1.1901
Log Distance To Road	0.0106	0.0766	-0.1426	0.1638
Log Distance To Road X Road View	0.3756	0.0351	0.3053	0.4458
View To Road	0.4350	0.0460	0.3430	0.5271

Table S3.7. Covariate Parameter estimates for top Summer MCLR wolf SSF models or averaged estimates among models within Δ4 AIC of top model.

Summer Day

Covariate	Coefficient	SE	Lower 95% CI	Upper 95% CI
Aspect_N	0.0328	0.0456	-0.0584	0.1240
Aspect_S	0.0504	0.0507	-0.0509	0.1517
Aspect_W	-0.1338	0.0486	-0.2310	-0.0367
Slope	-0.4795	0.0215	-0.5224	-0.4366
Burned Forest	-0.1470	1.5675	-3.2820	2.9879
Unburned Forest	0.0965	1.5662	-3.0359	3.2290
Grassland	-0.5381	1.5691	-3.6763	2.6001
Other Habitat	0.0746	1.5680	-3.0615	3.2106
Shrubland	-0.2269	1.5664	-3.3596	2.9058
Elk SSF	-0.1079	0.8678	-1.8435	1.6278
Elk SSF X Burned Forest	-0.2290	0.8702	-1.9694	1.5114
Elk SSF X Grassland	0.1031	0.8699	-1.6367	1.8428
Elk SSF X Other Habitat	0.2966	0.8742	-1.4518	2.0449
Elk SSF X Shrubland	-0.0217	0.8673	-1.7562	1.7129
Elk SSF X Unburned Forest	-0.1494	0.8680	-1.8853	1.5865
Log Distance To Road	0.3105	0.0527	0.2051	0.4160
Log Distance To Road X Road View	0.4011	0.0236	0.3540	0.4482
View To Road	0.4236	0.0271	0.3694	0.4778

Summer Crepuscular

Covariate	Coefficient	SE	Lower 95% CI	Upper 95% CI
Aspect_N	0.1432	0.0973	-0.0474	0.3338
Aspect_S	0.2834	0.0976	0.0920	0.4748
Aspect_W	0.2112	0.0968	0.0214	0.4010
Slope	-0.5683	0.0445	-0.6555	-0.4811
Burned Forest	-0.1597	0.3747	-0.8941	0.5746
Unburned Forest	0.0922	0.3460	-0.5859	0.7703
Grassland	0.1086	0.3576	-0.5923	0.8095
Other Habitat	0.4434	0.3731	-0.2879	1.1746
Shrubland	0.4780	0.3408	-0.1899	1.1460
Elk SSF	-0.0453	0.0485	-0.1404	0.0498

Elk SSF X Slope	0.0300	0.0411	-0.0505	0.1106
Log Distance To Road	0.1705	0.0558	0.0611	0.2799
Log Distance To Road X Road View	0.2578	0.0438	0.1720	0.3436
View To Road	0.4519	0.0585	0.3372	0.5666

Summer Night

Covariate	Coefficient	SE	Lower 95% CI	Upper 95% CI
Aspect_N	-0.0349	0.0415	-0.1180	0.0482
Aspect_S	0.1940	0.0431	0.1078	0.2801
Aspect_W	-0.0198	0.0424	-0.1046	0.0650
Slope	-0.6002	0.0210	-0.6422	-0.5582
Burned Forest	0.0517	0.2230	-0.3942	0.4977
Unburned Forest	0.6128	0.2172	0.1783	1.0472
Grassland	-0.0847	0.2203	-0.5253	0.3559
Other Habitat	0.6433	0.2386	0.1662	1.1204
Shrubland	0.5191	0.2134	0.0922	0.9460
Elk SSF	-0.2208	0.2311	-0.6829	0.2414
Elk SSF X Burned Forest	0.2069	0.2509	-0.2949	0.7087
Elk SSF X Grassland	-0.0129	0.2492	-0.5112	0.4855
Elk SSF X Other Habitat	0.2253	0.2544	-0.2834	0.7341
Elk SSF X Shrubland	0.1261	0.2314	-0.3367	0.5888
Elk SSF X Unburned Forest	0.3555	0.2365	-0.1175	0.8286
Log Distance To Road	0.2114	0.0661	0.0792	0.3437
Log Distance To Road X Road View	0.2903	0.0186	0.2531	0.3275
View To Road	0.4070	0.0240	0.3591	0.4549

Table S3.8. Covariate Parameter estimates for top Fall MCLR wolf SSF models or averaged estimates among models within Δ4 AIC of top model.

Fall Day

Covariate	Coefficient	SE	Lower 95% CI	Upper 95% CI
Aspect_N	0.3416	0.1769	-0.0052	0.6883
Aspect_S	-0.2809	0.2035	-0.6798	0.1180
Aspect_W	-0.1200	0.1957	-0.5036	0.2637
Slope	-0.6730	0.0852	-0.8400	-0.5060
Burned Forest	-0.8656	0.6673	-2.1735	0.4424
Unburned Forest	-0.4803	0.6166	-1.6888	0.7283
Grassland	-0.9996	0.6429	-2.2597	0.2605
Other Habitat	-1.2773	0.7506	-2.7485	0.1939
Shrubland	-0.6812	0.6025	-1.8621	0.4997
Elk SSF	-0.4519	0.1229	-0.6928	-0.2110
Log Distance To Road	0.5544	0.1336	0.2925	0.8162
Log Distance To Road X Road View	0.4986	0.1162	0.2709	0.7262
View To Road	0.5348	0.1174	0.3047	0.7650

Fall Crepuscular

Covariate	Coefficient	SE	Lower 95% CI	Upper 95% CI
Aspect_N	0.0688	0.1792	-0.2825	0.4201
Aspect_S	0.1183	0.1961	-0.2660	0.5026
Aspect_W	-0.0538	0.1992	-0.4442	0.3366
Slope	-0.7482	0.0964	-0.9372	-0.5593
Burned Forest	-0.3295	0.7286	-1.7575	1.0986
Unburned Forest	-0.5871	0.6483	-1.8578	0.6835
Grassland	0.5454	0.6377	-0.7045	1.7952
Other Habitat	-0.0975	0.7960	-1.6577	1.4627
Shrubland	0.6760	0.6345	-0.5675	1.9196
Elk SSF	-0.1893	0.0909	-0.3675	-0.0110
Elk SSF X Slope	0.0106	0.0809	-0.1479	0.1691
Log Distance To Road	0.2018	0.1147	-0.0231	0.4267
Log Distance To Road X Road View	0.1846	0.0793	0.0292	0.3400
View To Road	0.3829	0.1159	0.1556	0.6101

Fall Night

Covariate	Coefficient	SE	Lower 95% CI	Upper 95% CI
Aspect_N	0.1160	0.1220	-0.1231	0.3550
Aspect_S	-0.0923	0.1380	-0.3628	0.1781
Aspect_W	-0.1146	0.1336	-0.3765	0.1472
Slope	-0.5941	0.0842	-0.7590	-0.4291
Burned Forest	0.2856	0.5103	-0.7146	1.2858
Unburned Forest	0.4963	0.4840	-0.4523	1.4450
Grassland	0.5727	0.4851	-0.3781	1.5234
Other Habitat	0.3858	0.5293	-0.6516	1.4232
Shrubland	0.7827	0.4732	-0.1448	1.7101
Elk SSF	0.1623	0.1088	-0.0509	0.3755
Elk SSF X Slope	-0.1028	0.0544	-0.2095	0.0038
Log Distance To Road	0.0239	0.0652	-0.1039	0.1518
Log Distance To Road X Road View	0.1672	0.0535	0.0623	0.2720
View To Road	0.4062	0.0776	0.2542	0.5583

Summary

The main results in the research article cover SSF outcomes pertaining only to human activity; however, several other interesting habitat use patterns emerged from MCLR models. The results below summarize some of the significant habitat selection estimates for several landscape attributes.

Wolves demonstrated seasonal- and diel-specific selection for different habitat types with a pattern of selecting for unburned forests during the day when limiting sun exposure for thermoregulation is most important (Appendix A Table S6-S8). For example, on spring days, wolves were 2.11 (95% CI: 1.64, 2.71) times more likely to use unburned forests instead of burned forests. This pattern remained during spring crepuscular hours; however, wolves shifted from unburned forests and were 1.47

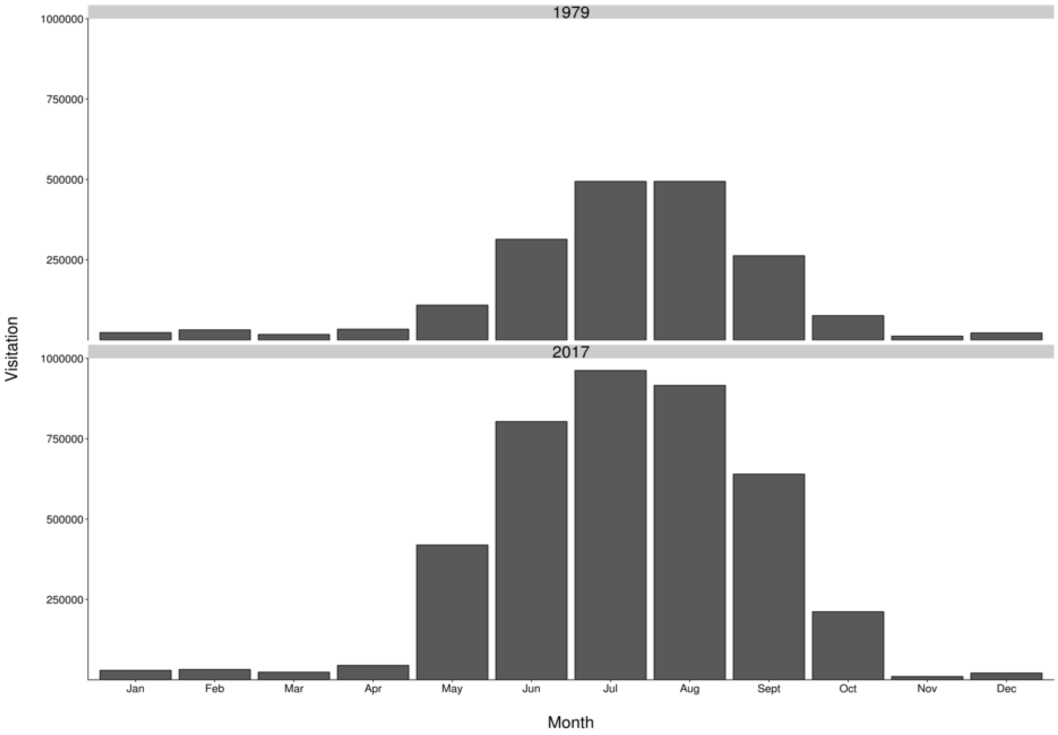
(95% CI: 1.24, 1.75) and 3.54 (95% CI: 2.41, 5.19) times more likely to use shrubland during summer and fall crepuscular hours, respectively. Night habitat type selection varied across all seasons with wolves favoring unburned forest, the other category, or shrubland during spring, summer, and fall, respectively (Appendix A Table S6-S8).

Wolves selected for flatter terrain with lower degree slopes in all seasons and diel periods, which coincides with areas where roads are more likely to occur (Appendix A Table S6-S8). In addition, wolves were 1.39 (95% CI: 1.19, 1.63) more likely to use south rather than north facing aspects on spring days (Appendix A Table S6-S8). During fall days selection shifted and wolves were 1.86 (95% CI: 1.32, 2.64) more likely to use north instead of south aspects.

In addition, wolves displayed varying selection for elk SSF values between the seasons and diel periods (Appendix A Figure S2). Using results from fitted elk SSFs, we designated elk SSF values to each pixel in the study area. We tallied predicted SSF values into 10 equal sized bins (Appendix C). Therefore, each wolf used and available location was assigned a value from 1 to 10 in accordance with its spatial and temporal alignment with the elk SSF. Across all seasons, wolves selected areas with lower SSF values during the day and crepuscular hours. For example, wolves were 2.20 (95% CI: 0.67, 3.72) and 1.39 (95% CI: 0.03, 2.75) more likely to select a patch ranked with a value of 2 instead of a patch with a value of 7 during fall day and crepuscular hours, respectively. This relationship was similar during the night in summer, but night hours during spring and fall departed from this trend.

Wolves were 6.45 (95% CI: 0.00, 22.22) and 1.35 (95% CI: 0.00, 2.78) times more likely to use a patch with a value of 7 instead of a patch with a value of 2 during night hours in spring and fall, respectively. Nonetheless, all 95% CI odds ratio (OR) calculations between unfavorable and favorable elk SSF values (i.e., values of 1-5 vs. 6-10) included OR ≤ 1 ≤ OR indicating there may be no difference in the odds of selection (Hosmer et al. 2013).

Figure S3.1. Yellowstone National Park monthly visitation from 1979 and 2017 (National Park Service 2018). Total visitation in 1979 was 1,892,908 and increased about 120% to 4,116,524 in 2017. In 2017, average monthly visitation from November-April was approximately 4% (27,102/month) of that recorded during May-October (658,985/month).



Elk Step Selection Function Estimation

To account for wolf foraging behavior when selecting habitat resources, we built an elk population SSF under an optimal foraging theoretical framework. We applied the same methodology to generate available locations as we did for wolf GPS locations (Forester et al. 2009, Thurfjell et al. 2014). We also divided the data into nine temporal subsets. The higher order division separated the data into 3 seasons: Spring, Summer, and Fall. The cut points for these seasons were identified by closely inspecting each individual elk's yearly movement to identify the day(s) of the year they migrated to and from their respective summer ranges. We then averaged these elk migration dates to identify the mean ordinal date that elk shifted to and from their summer ranges to subset the data into three seasons: Spring, Summer, and Fall. Spring migration began on May 24 (±13 days). The summer season started on May 31 (±19 days) and ended on October 4 (±45 days). The fall season began on October 13 (±18 days) and extended through the end of our study period, November 1. Time spent migrating to and from Summer ranges was not included in elk SSF models. To ensure all wolf GPS points were included in only one seasonal dataset, we took the midpoint between the end of the previous season and start of the next season. Therefore, the spring season was identified as May 1 to May 27, summer as May 28 to October 6, and fall as October 7 to November 1.

Animal movement and, therefore, habitat selection can vary over the course of the diel period in response to predator movement or thermoregulation needs (Kohl et al. 2018). As such, we divided each season into three diel activity subsets: Day, Night, and Crepuscular. Diel activity periods were delineated spatially and temporally. Crepuscular times included the period buffered by 1 hour before and after sunrise or sunset. We expected wolf selection for higher elk SSF values to be stronger during crepuscular periods since wolves hunt more during those hours (Kohl et al. 2018).

We evaluated the effect of spatial and temporal variables on elk resource selection following similar methods described for wolves, using conditional logistic regression models via the *clogit* call in the *survival* package (Therneau 2015), and fitting generalized estimating equations (GEEs) to account for autocorrelation. Prior to fitting models, we standardized all continuous covariates (elevation, slope, distance to water, openness, and NDVI) to mean = 0 and standard deviation = 1 (Schielzeth 2010).

We fit models using single covariates and biologically relevant combinations resulting in 14 different models in each of the 9 distinct temporal subsets. We performed model selection using QIC and validated top models with 5-fold cross validation as described above (Pan 2001, Boyce et al. 2002). We averaged parameter estimates for models ≤Δ4 QIC.

Figure S3.2 Beta Parameter plot for elk SSF GEEs.

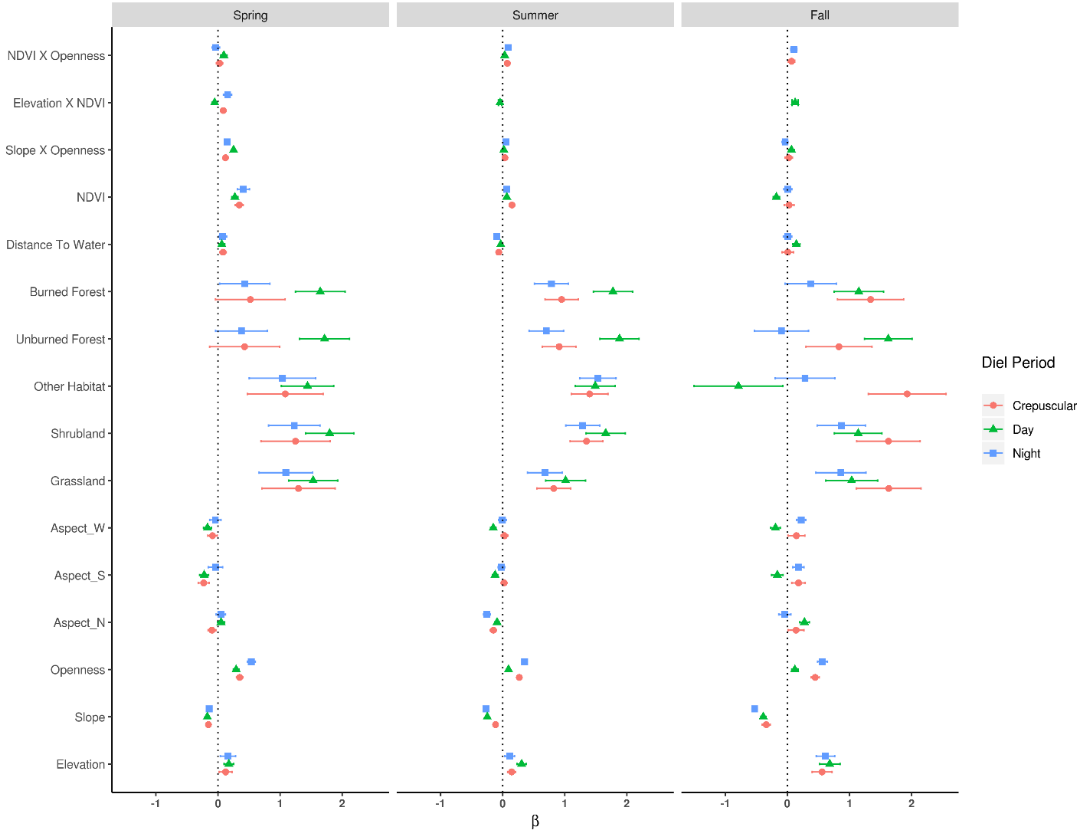


Table S3.9. GEE model list and covariate combinations used for Elk SSFs. GEE models included cluster identification unique to individuals, following methods outlined by Prima et al. (2017).

Model	Covariates
Mod1	Elevation + Slope + Aspect
Mod2	Elevation + Slope + Aspect + Openness
Mod3	Elevation + Slope + Aspect + Openness + Distance To Water
Mod4	Elevation + Slope + Aspect + Openness + NDVI
Mod5	Elevation + Slope + Aspect + Openness + Distance To Water + NDVI
Mod6	Elevation + Slope + Aspect + Openness + NDVI + Habitat Type
Mod7	Elevation + Slope + Aspect + Openness + NDVI + Openness X Slope + Elevation X NDVI
Mod8	Elevation + Slope + Aspect + Openness + NDVI + Habitat Type + Openness X Slope
Mod9	Elevation + Slope + Aspect + Openness + Distance To Water + NDVI + Openness X Slope
Mod10	Elevation + Slope + Aspect + Openness + Habitat Type
Mod11	NDVI + Habitat Type
Mod12	Slope + Openness + NDVI + Habitat Type
Mod13	Elevation + Slope + Aspect + Openness + Distance To Water + NDVI + Habitat Type
Mod14	Elevation + Slope + Aspect + Openness + Distance To Water + NDVI + Habitat Type + NDVI X Openness

Table S3.10. Spring model selection table using QIC. Top models are bolded and outlined.

	Spring Day n = 4974			**Spring Crepuscular** n = 2761			**Spring Night** n = 2014		
Model	QIC	ΔQIC	$\bar{r}_s$	QIC	ΔQIC	$\bar{r}_s$	QIC	ΔQIC	$\bar{r}_s$
Mod1	15923.66	277.45		8821.62	282.25		6438.60	276.58	
Mod2	15850.02	203.81		8699.99	160.61		6279.56	117.54	
Mod3	15849.09	202.88		8699.03	159.65		6279.00	116.98	
Mod4	15798.08	151.87		8670.19	130.82		6259.61	97.60	
Mod5	15797.31	151.10		8670.02	130.64		6259.33	97.32	
Mod6	15748.31	102.10		8550.97	11.60		6174.18	12.17	
Mod7	15649.02	2.81		**8539.38**	**0.00**	**0.66**	**6162.02**	**0.00**	**0.77**
Mod8	**15646.21**	**0.00**	**0.59**	8541.75	2.37		6165.67	3.66	
Mod9	15648.87	2.66		8540.01	0.64		6164.77	2.75	
Mod10	15791.99	145.78		8576.27	36.90		6191.27	29.25	
Mod11	15886.39	240.18		8614.32	74.95		6248.79	86.77	
Mod12	15767.96	121.75		8553.27	13.89		6167.42	5.40	
Mod13	15747.91	101.70		8550.66	11.28		6174.29	12.28	
Mod14	15743.40	97.19		8551.66	12.28		6175.63	13.61	

Table S3.11. Summer model selection table using QIC. Top models are bolded and outlined.

	Summer Day n = 13725			**Summer Crepuscular** n = 6703			**Summer Night** n = 6483		
Model	QIC	ΔQIC	$\bar{r}_s$	QIC	ΔQIC	$\bar{r}_s$	QIC	ΔQIC	$\bar{r}_s$
Mod1	43714.16	358.80		21404.56	393.72		20488.35	580.51	
Mod2	43720.44	365.07		21231.14	220.31		20202.01	294.18	
Mod3	43722.10	366.74		21230.82	219.99		20196.12	288.28	
Mod4	43708.52	353.16		21200.75	189.92		20198.07	290.24	
Mod5	43709.71	354.35		21199.35	188.52		20191.29	283.45	
Mod6	43355.76	0.40		21019.81	8.98		19921.80	13.96	
Mod7	43357.16	1.79		21017.71	6.88		19919.77	11.93	
Mod8	43364.16	8.80		21011.52	0.69		19908.68	0.85	
Mod9	43359.36	3.99		21018.89	8.06		19916.57	8.73	
Mod10	43358.20	2.83		21040.56	29.73		19922.55	14.71	
Mod11	43730.76	375.39		21177.98	167.15		20264.73	356.89	
Mod12	43423.89	68.52		21035.92	25.09		19951.97	44.13	
Mod13	43356.31	0.95		21017.99	7.16		19917.24	9.40	
Mod14	**43355.36**	**0.00**	**0.70**	**21010.83**	**0.00**	**0.76**	**19907.84**	**0.00**	**0.77**

Table S3.12. Fall model selection table using QIC. Top models are bolded and outlined.

	Fall Day n = 2330			**Fall Crepuscular** n = 1124			**Fall Night** n = 2626		
Model	QIC	ΔQIC	$\bar{r}_s$	QIC	ΔQIC	$\bar{r}_s$	QIC	ΔQIC	$\bar{r}_s$
Mod1	7304.78	68.21		3527.18	103.14		8052.84	288.38	
Mod2	7305.97	69.40		3452.02	27.98		7844.04	79.58	
Mod3	7303.11	66.54		3453.86	29.82		7846.10	81.64	
Mod4	7297.06	60.49		3454.09	30.05		7846.58	82.13	
Mod5	7293.24	56.66		3455.88	31.84		7848.62	84.16	
Mod6	7242.63	6.06		3425.95	1.92		7766.79	2.34	
Mod7	**7236.57**	**0.00**	**0.88**	3429.32	5.29		7769.20	4.74	
Mod8	7244.12	7.55		3428.01	3.97		7764.99	0.54	
Mod9	7238.65	2.08		3429.57	5.53		7769.88	5.42	
Mod10	7252.23	15.65		**3424.04**	**0.00**	**0.83**	**7764.46**	**0.00**	**0.94**
Mod11	7431.29	194.71		3510.19	86.15		8153.89	389.43	
Mod12	7308.00	71.42		3435.17	11.14		7811.71	47.26	
Mod13	7239.18	2.60		3427.62	3.58		7768.77	4.32	
Mod14	7241.24	4.67		3427.71	3.67		7765.60	1.14	

Elk SSF Predictive Surfaces

In order to make a predictive elk SSF geospatial layer for each temporal subset, model parameter estimates were averaged for all models within 4 QIC of the top-ranking model and incorporated into the exponential model (equation 1) defined by Manly et al. (2007).

$$w(i) = \exp\,(\beta_1 x_1 + \ldots\ \beta_n x_n)$$

eqn. 1

where the relative probability of selection, *w*, for habitat patch, i, is determined by the exponentiation of parameter estimates from averaged SSF's within 4 QIC of the top model, β, multiplied by covariates, *x*. We assigned raster layers for each covariate. Each pixel, i, within the study area was assigned an attribute value from each covariate raster and these values were used as the x values in equation 1. Following Boyce et al. (2002), we divided these values into 10 bins so that each bin included the same number of pixels within the study area.

Figure S3.3. Spring day elk resource selection predictive surface.

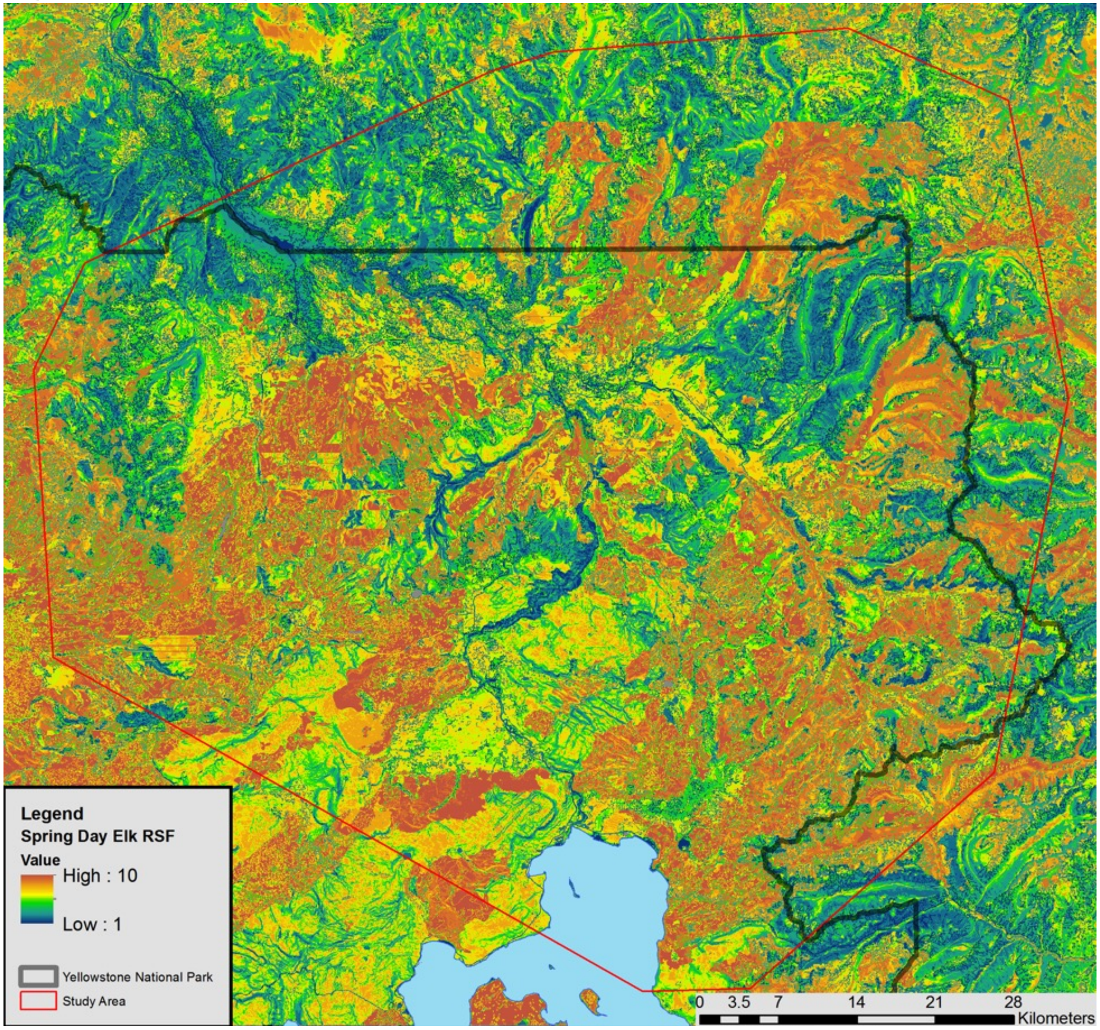


Figure S3.4. Spring crepuscular elk resource selection predictive surface.

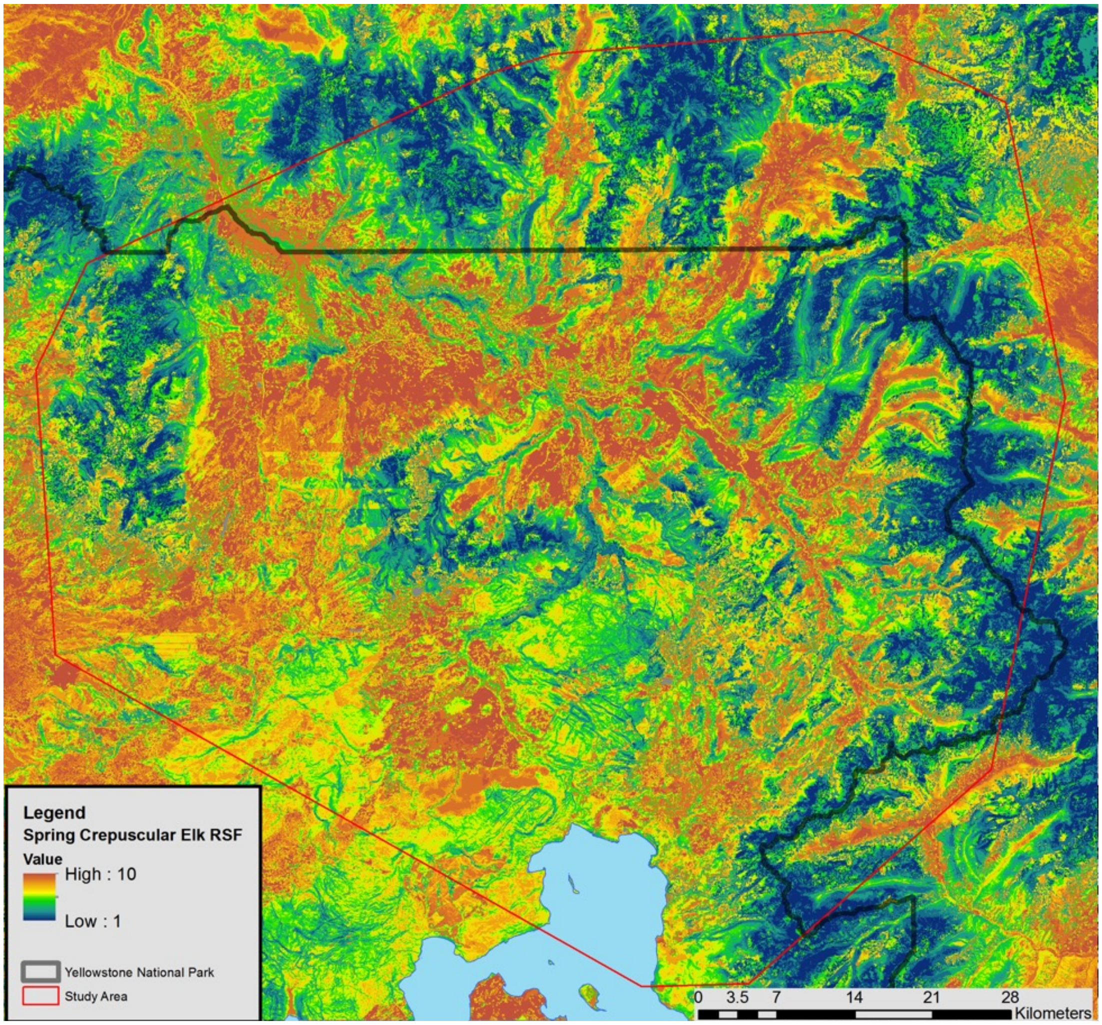


Figure S3.5. Spring night elk resource selection predictive surface.

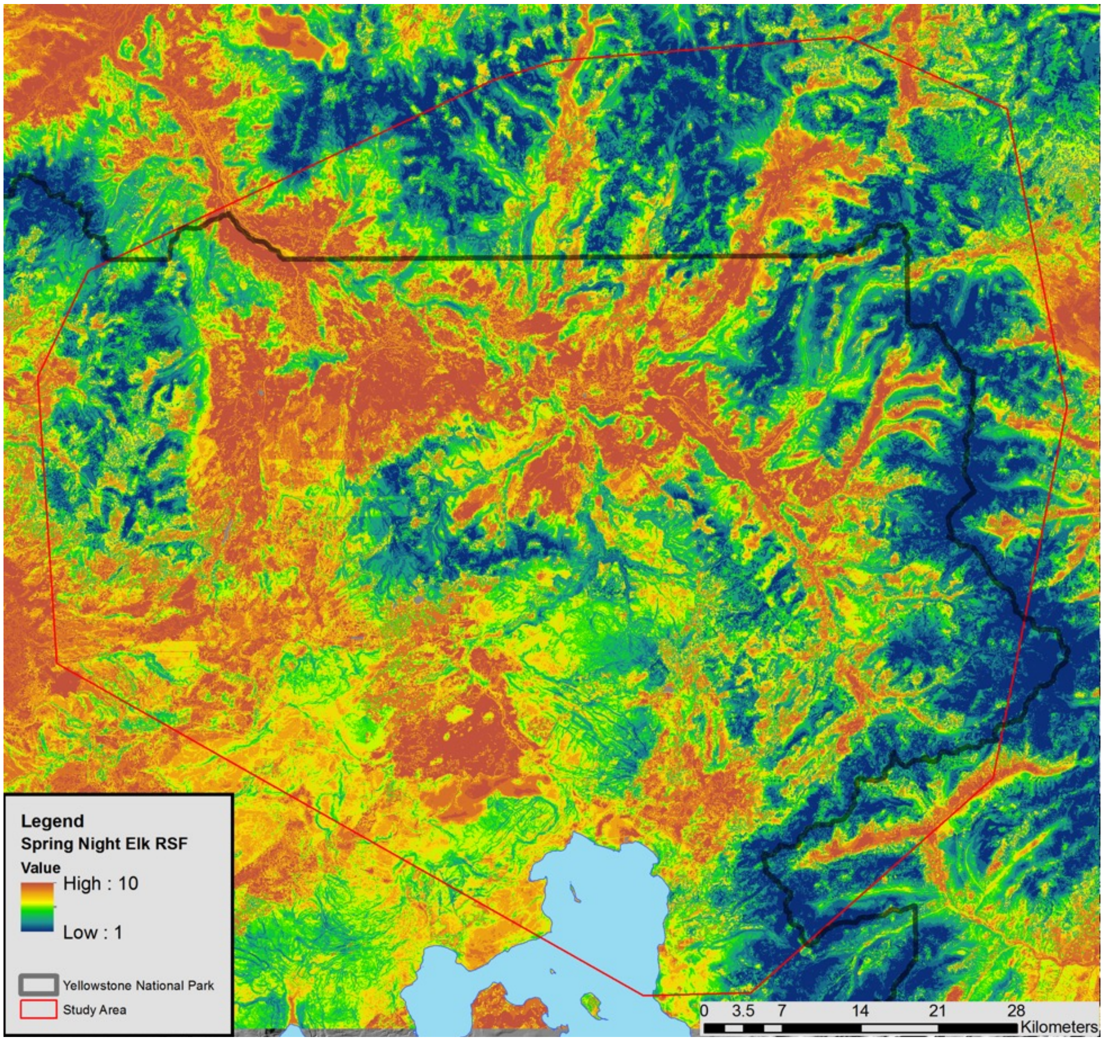


Figure S3.6. Summer day elk resource selection predictive surface.

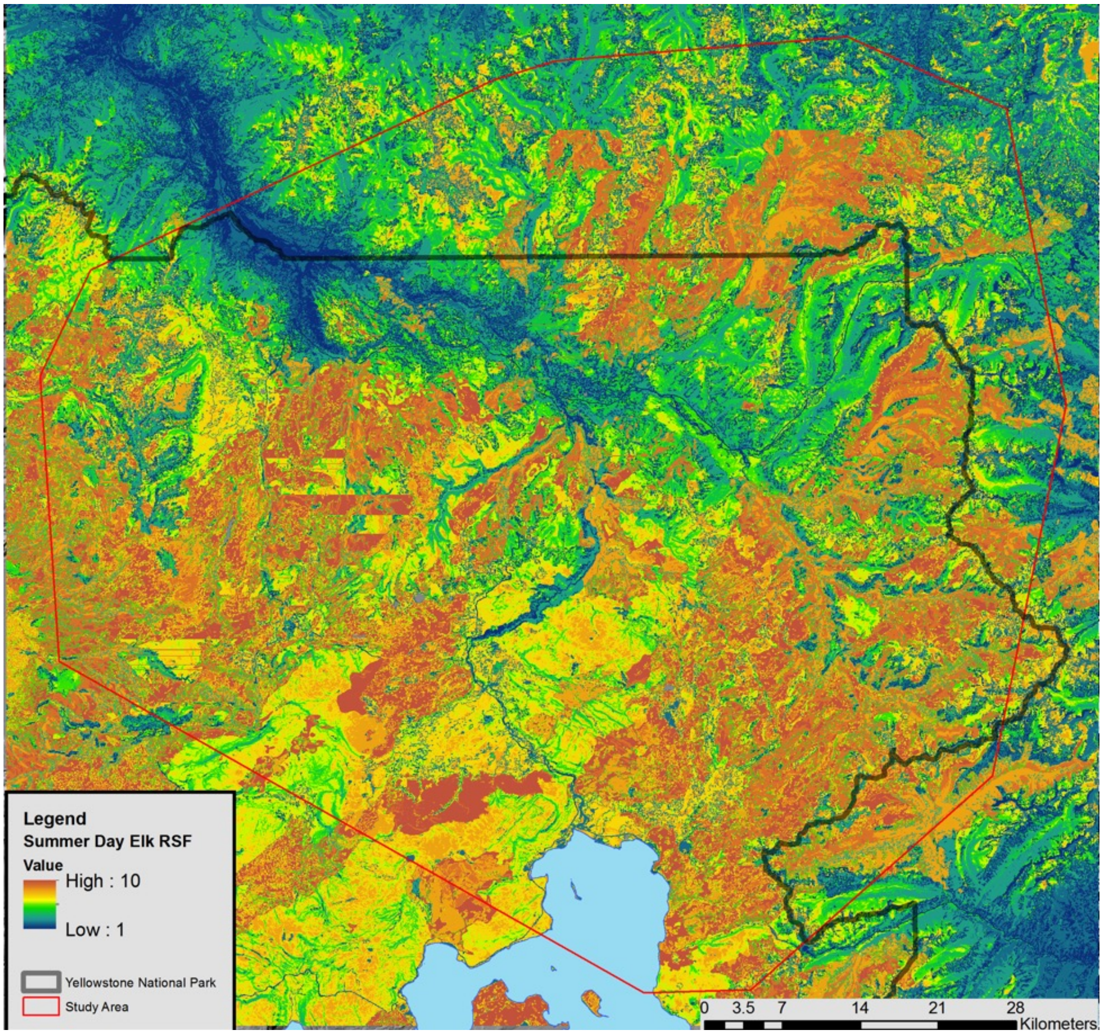


Figure S3.7. Summer crepuscular elk resource selection predictive surface.

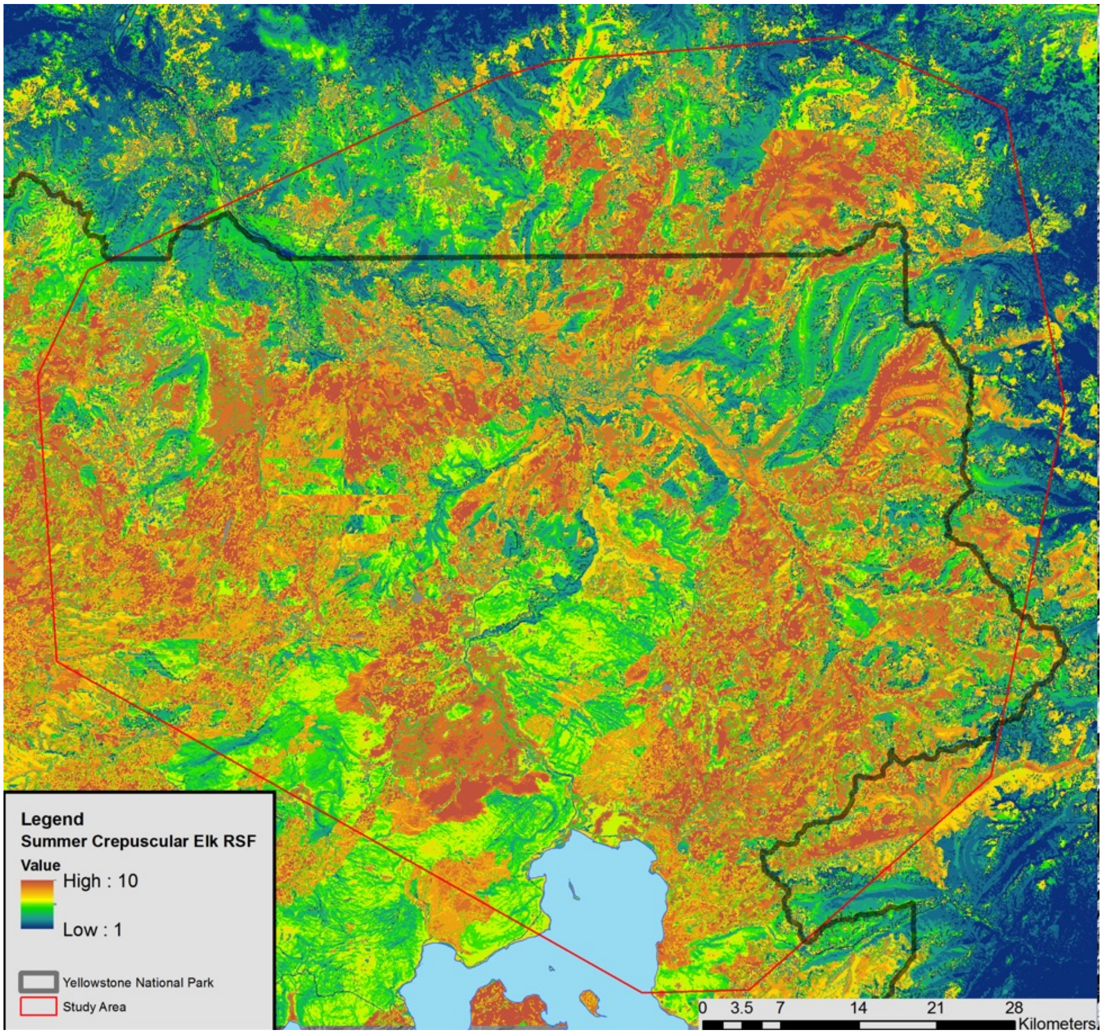


Figure S3.8. Summer night elk resource selection predictive surface.

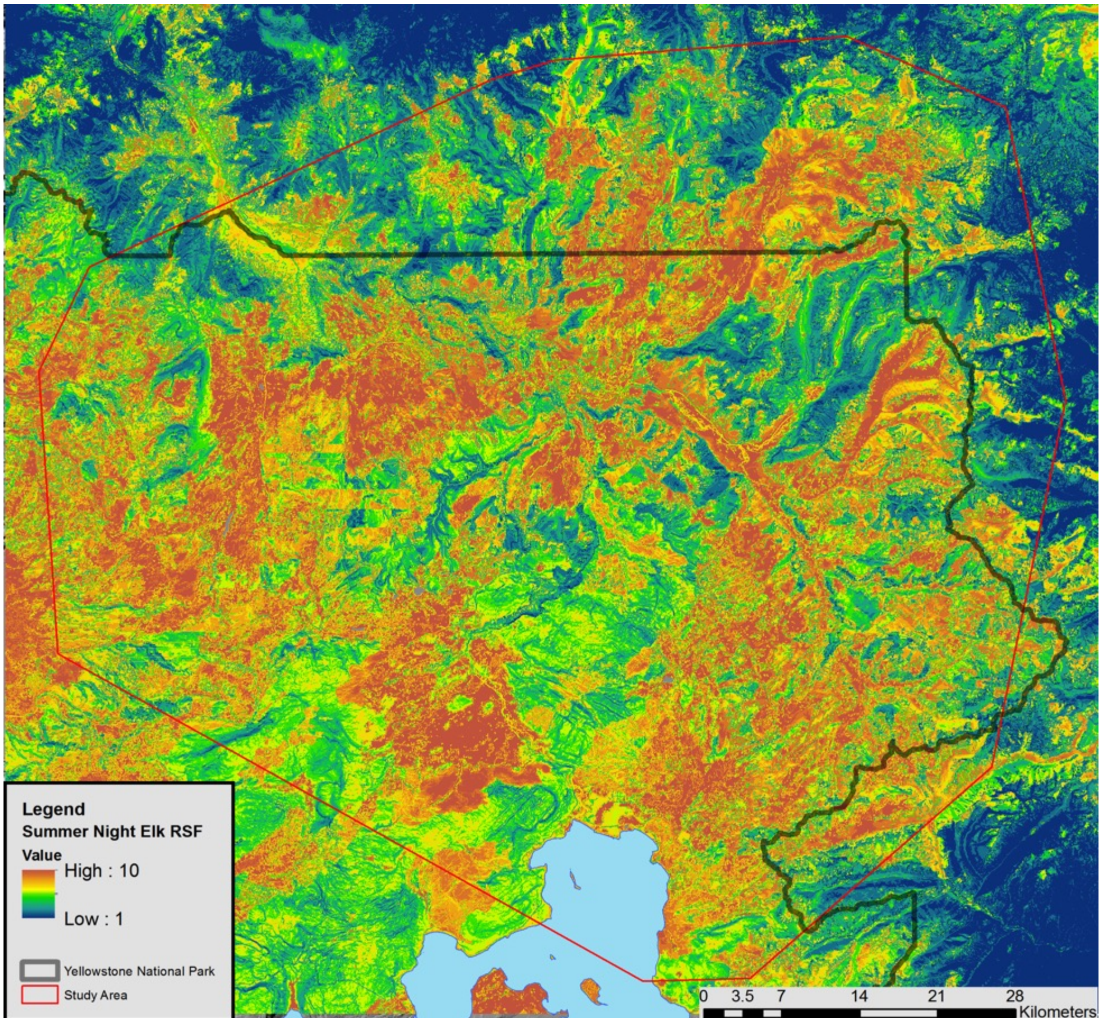


Figure S3.9. Fall day elk resource selection predictive surface.

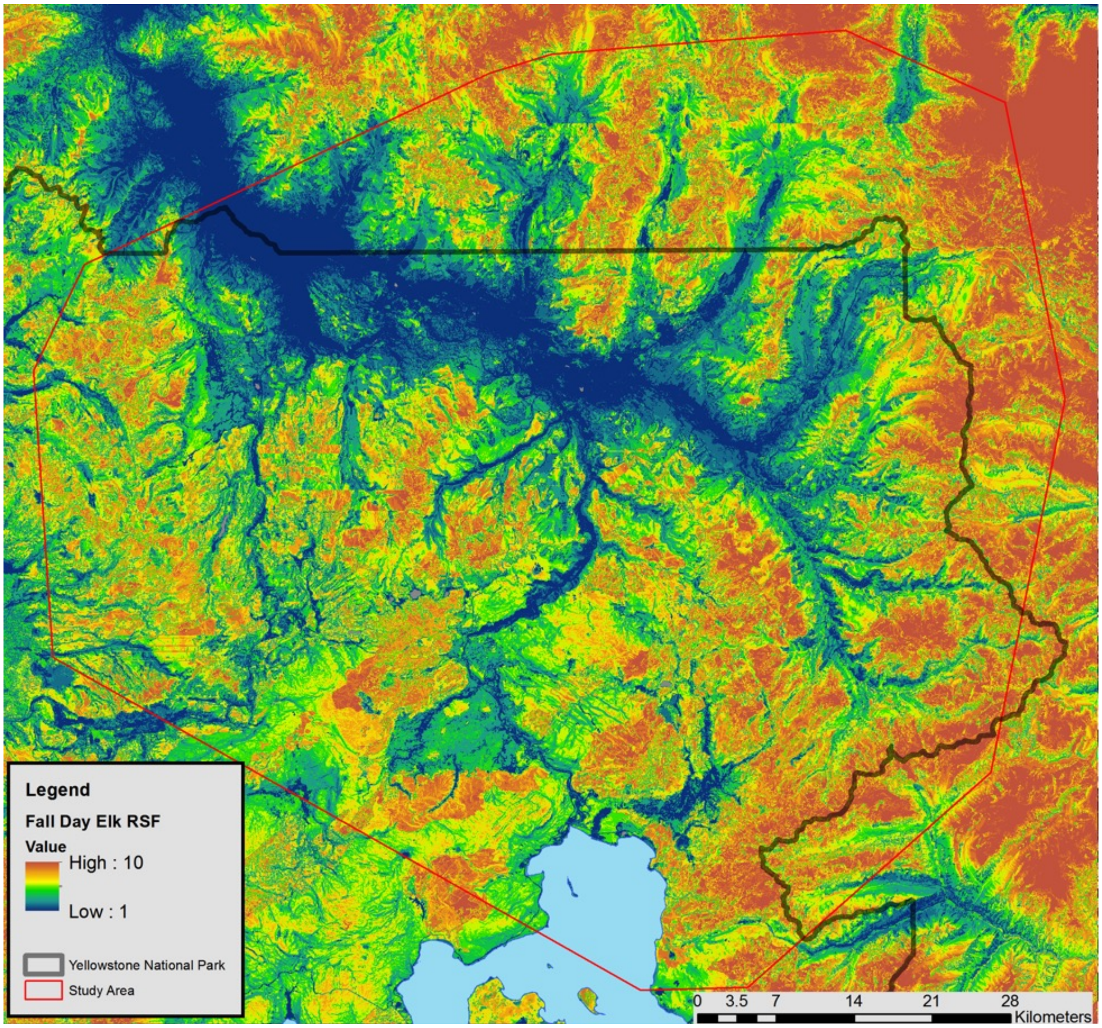


Figure S3.10. Fall crepuscular elk resource selection predictive surface.

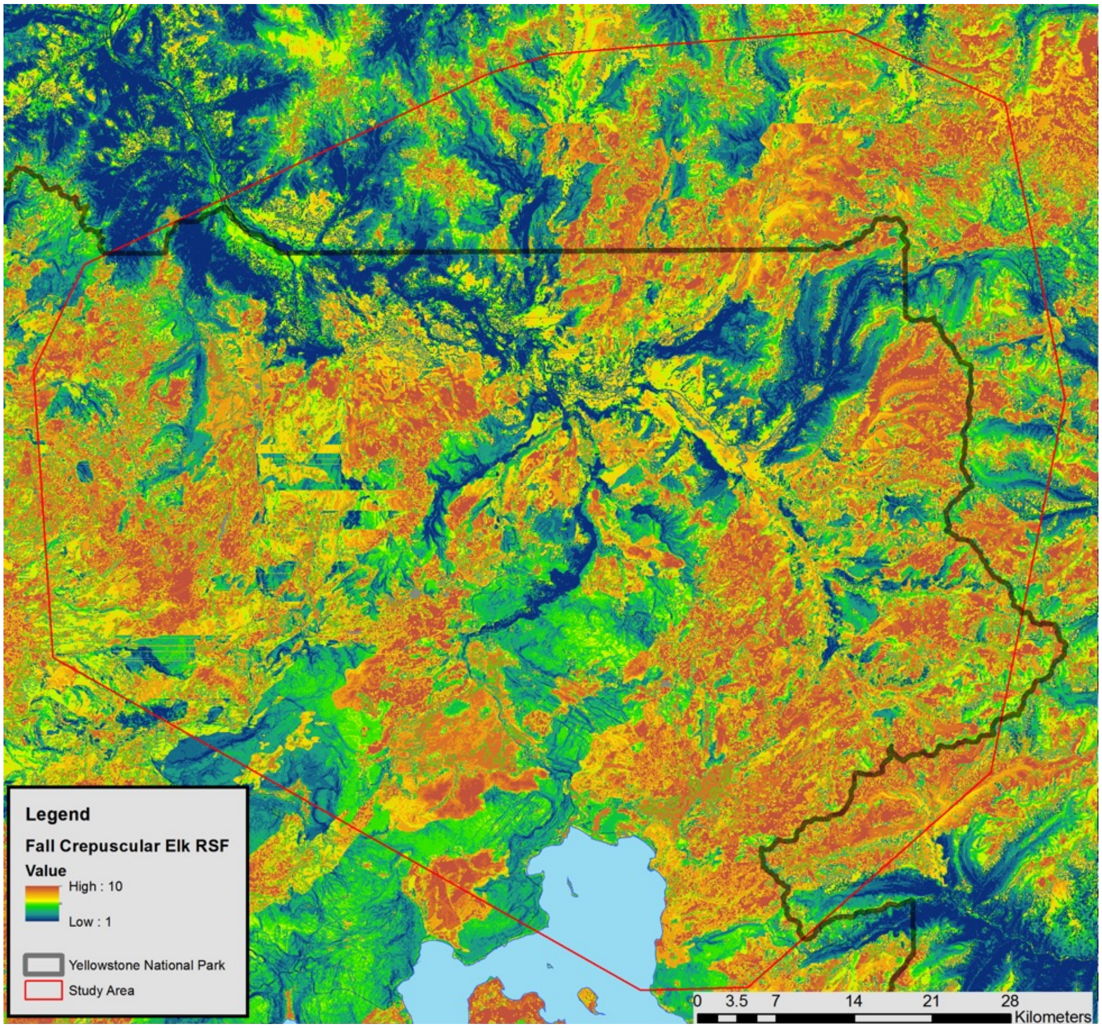
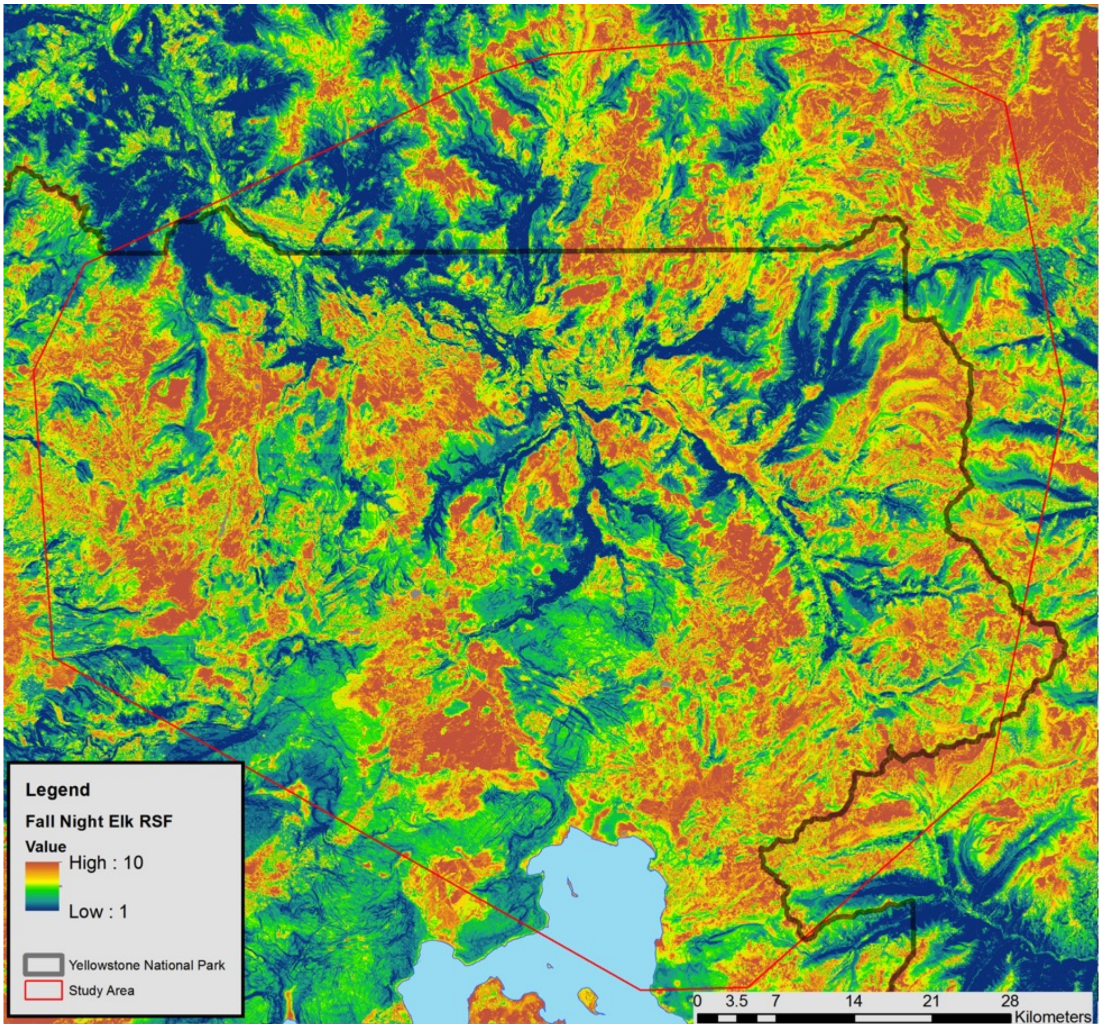


Figure S3.11. Fall night elk resource selection predictive surface.



CHAPTER 4

Linking energetic costs to hunting behavior, life history, and sociality in large carnivores

Abstract

Large carnivore physiology and morphology has led to evolutionary distinct patterns in hunting and social behavior. As a result, predation by sympatric large predators in Yellowstone National Park (YNP) display differences in prey composition, acquisition rates, and energetic efficiency. Moreover, these two large carnivores display differing hunting modalities, where wolves are characteristic group coursing predators while solitary cougars use ambush predation techniques. We deployed tri-axial accelerometer GPS collars on cougars (*Puma concolor*) and wolves (*Canis lupus*) to simultaneously identify and quantify fine-scale behavior allocation, prey composition, prey acquisition rate, and energy expenditure. Elk (*Cervus canadensis*) was the most prominent prey in each predators' diets, but cougars selected for smaller age and sex classes than wolves. Using tri-axial accelerometers we quantified overall dynamic body acceleration (ODBA) and split each individual carnivore's time into 3 behavior phases associated with predation (foraging, killing, and handling) and tested the influence of individual, spatial, and prey characteristics to the time allocated to each activity. Overall, cougars spent more time handling carcasses and less time foraging (54% ± 12% of total time; $n = 184$ vs. 46% ± 12% of total time; $n = 160$) than wolves (33% ± 14% of total time; $n = 133$ vs. 66% ± 14% of total time; $n = 127$).

Further, there was a positive relationship between prey mass and time required to both hunt and kill prey. Given the strong linear relationship between ODBA and volume of oxygen consumed (VO_2), previous studies were able to calibrate and calculate energy expenditure with cougars in a laboratory setting. Using information from 149 field-confirmed kills, we found that cougars expended more energy to successfully kill larger prey. For cougars, we compared daily and seasonal energy expenditure with consumption rates (edible biomass available per individual) in order to better understand the relationship between reproductive status and caloric demands for female cougars. Solitary female cougars expended the most kilojoules per day (30,237 ± 10,079 kj/day) but were able to offset this by consuming more prey which led to energetic consumption excesses of 57,419 ± 31,327 kj/day of . In contrast, female cougars with young of any age expended less energy (20,406 ± 1,747 kj/day), but due to increases in group size and the energy required to care for young, consumed less prey biomass and had lower overall excess calories consumed per day (+3,460 ± 12,090), with some animals experiencing negative energy deficits. Converting energetic currency back to biomass suggests that some individuals were killing an excess equivalent of 11 adult female mule deer or 3 adult female elk per season. This surplus energy consumption is most likely explained by high rates of kleptoparatism by dominant scavengers like grizzly bears (*Ursus arctos*), black bears (*U. americanus*), and wolves. Our analyses demonstrate that the combination of predation (e.g. GPS collars) and ecophysiological (e.g. tri-axial accelerometers) methods can reveal metabolic drivers in predator-prey dynamics and the costs of life-history traits like reproduction.

Introduction

Physiological performance guides evolutionary processes and species' behavioral patterns (Krebs and Davies 1981). Further, energy exchange through ecosystems not only shapes the trophic web, but also impacts the individual survival and reproductive success of ecosystem participants (Lotka 1922, Withers et al. 2016). Predator hunting behavior, which incurs significant movement related energetic costs (Garland 1983, Halsey et al. 2015), involves managing opportunities to maximize energetic gains while minimizing losses (Williams et al. 2014). As a result, animals employ different hunting and social strategies to boost energetic efficiency (Wilson et al. 2012, Amélineau et al. 2014). The comparison of cougars (*Puma concolor*) and wolves (*Canis lupus*) – large carnivores that are sympatric in some systems and rely on the same primary prey – provides an opportunity to compare predator hunting behavior, prey selection, and energetic efficiency (Metz et al. 2012, Ruth et al. 2019).

Perhaps the most striking differences between these two apex predators that potentially influences energetics are their respective hunting behaviors (partially driven by morphology) and social structures (MacNulty et al. In press, Ruth et al. 2019). With respect to hunting, cougars are ambush predators that use rough terrain and vegetative cover to stalk their for prey, then use retractile claws, supinating muscular forelimbs, and canines to grab and kill prey (Murphy and Ruth 2010). In contrast, wolves are coursing predators that typically hunt in groups, chase down prey over long distances, and use only their canines and incisors to grab, subdue, and kill (MacNulty et al. 2007, MacNulty et al. 2009). Each of these hunting methods with their corresponding morphological and social characteristics impart constraints and advantages which presumably have consequences on energetic gains and losses.

With regard to social structure, cougars are predominantly solitary while wolves are cooperative breeders that live in kin-structured groups (Mech and Boitani 2003, Ruth et al. 2019). There are tradeoffs between solitary versus group living. Benefits to being social include sharing prey acquisition costs (Carbone et al. 1999, Metz et al. 2011, Hubel et al. 2016b), defense against inter- or intra-specific competitors (Vucetich et al. 2004, Cassidy et al. 2015), and rearing offspring (Clutton-Brock et al. 1999, Sparkman et al. 2011, Stahler et al. 2013). Nonetheless, there are disadvantages to social living. While more capable hunters may yield higher success or larger prey (Mech and Boitani 2003), the division of food resources amongst the group allocates less food per individual (Thurber and Peterson 1993, Metz et al. 2011). Wolves can benefit from splitting up and hunting in smaller groups or alone, creating feeding opportunities across the landscape where other pack members can obtain biomass without expending energy associated with hunting and killing prey (Mech 1966, Metz et al. 2011, Hubel et al. 2016b).

These divergent social strategies go beyond the hunting phase and lead to differences in prey handling behavior. Interference competition occurs when members of one species limits the access to a common resource for another species, usually through aggressive behavior (Levin 2009). For example, cougars are subordinate predators (Elbroch and Kusler 2018) and lose control of carcasses to sympatric predators like grizzly bears (*Ursus arctos*), black bears (*Ursus* *americanus*), and wolves (Murphy et al. 1998, Ruth et al. 2010, Elbroch et al. 2015). In response, cougars cache carcasses and use latrine and bed locations away from the kill site to reduce detection probability from scavengers (Beier et al. 1995, Murphy and Ruth 2010). Wolves are also vulnerable to kleptoparasitism by many scavenger species (Wilmers et al. 2003), but their group size enables wolves to mitigate biomass loss through more rapid consumption of their kills before they are detected by large scavengers (MacNulty et al. 2001, Ballard et al. 2003, Smith et al. 2003, Wilmers et al. 2003). When aggressive interactions occur between wolves and grizzly bears at carcasses, bears are dominant and regularly limit wolves' access to the food resource (MacNulty et al. 2001, Tallian et al. 2017).

Understanding differences in how sociality and hunting modality influence diet, behavior, and energy expenditure could shed light on predation patterns. Predation studies often focus on quantifying diet composition and kill rates (kills/predator/time), using global positioning system (GPS) collars (Anderson and Lindzey 2003, Knopff et al. 2009, Ruth et al. 2010, Metz et al. 2012). Prey composition varies based on community composition and season (Metz et al. 2012), but average prey size scales positively with predator mass (Carbone et al. 1999). Cougars and wolves are similarly sized, with cougars being slightly bigger (Gittleman 1985). In YNP, they select similar prey species, and respond to seasonal changes in prey availability by selecting for more abundant or vulnerable sex and age classes (Metz et al. 2012, Wilmers et al. 2020); however, these changes have consequences for individual energetics, as well as prey population vital rates (Vucetich et al. 2011, Ruth et al. 2019). While kill rates are one component of estimating impacts of predation on prey populations, consumption rates (edible biomass/predator/time) may be more informative to understanding a predator's survival and reproductive success (Miller et al. 2013). Ultimately, consumption rates provide an estimate of total biomass consumed by the predator allowing for comparison to total energy expenditures (Miller et al. 2014).

Until recently, quantification of mammalian energetics have been coarse calculations measured over weeks with doubly labelled water (Halsey 2011) or derived using information on basal metabolic rate and observed prey acquisition rates (Ackerman et al. 1986, Elbroch et al. 2014, Ruth et al. 2019). Recent technological advances have coupled GPS collars with tri-axial accelerometers which have the ability to record movement signatures of free ranging animals to remotely identify behaviors and quantify energetic expenditure (Watanabe et al. 2005, Wilson et al. 2006, Williams et al. 2014, Wang et al. 2015). An animal's energetic requirements can be summarized by an animal's body mass and morphology, diet and digestion, thermoregulatory conditions, growth, reproductive state, and environment (McNab 2009, Tomlinson et al. 2014, Halsey 2016, Withers et al. 2016). Further, movement-based accelerometry can be used to estimate field metabolic rate (FMR), allowing for comparison of the energetic costs of essential behaviors like raising young and foraging for food (Wilmers et al. 2017). In practice, these studies use accelerometer signatures to calculate an animal's overall dynamic body acceleration (ODBA) which has significant linear relationships with oxygen consumption from laboratory trials with captive animals (Halsey et al. 2009, 2011, Qasem et al. 2012). Energetics can be derived by correlating smoothed ODBA over a 2-second running mean to laboratory-obtained oxygen consumption rates to estimate energetic expenditures of free-ranging animals (Wilson et al. 2006, Shepard et al. 2008, Halsey et al. 2009, Williams et al. 2014, Wilmers et al. 2017).

Accelerometry-informed behavior identification and energetics has been used in a variety of studies on both terrestrial and marine species. Most of these studies have relied on a combination of high-frequency accelerometers (8-64 Hz) and frequent GPS fix rates (1-15 minutes) to infer behavior of wild animals (Halsey et al. 2011, Williams et al. 2014, Wang et al. 2015, Wilmers et al. 2017). However, frequent GPS fix rates significantly reduce battery life on GPS collars, requiring either repeated collaring attempts over short time periods or remotely dropping collars. Capture and handling of wild animals carries inherent risk, for both biologists and the animals, elevated research costs, and ethical questions from some that prefer noninvasive methods (Darimont et al. 2008). In addition, many pressing conservation questions (e.g. habitat use, predation patterns) can be answered with extended GPS fix rates and require monitoring that extends over longer time periods to assess the impact of environmental change.

In this paper, we first aim to evaluate and compare prey composition between cougars and wolves using GPS cluster methods. Second, we simultaneously identify, quantify, and compare fine-scale behavior allocation for a solitary, ambush hunter (cougar) versus a coursing, group hunter (wolf) using tri- axial accelerometer GPS collars. Finally, since previous studies have calibrated and correlated ODBA to caloric expenditures for cougars (Williams et al. 2014, Wang et al. 2017), we estimated energetic expenditures across seasonal and life history stages in cougars and related patterns to observed prey consumption rates obtained from GPS cluster methods. We predict that hunting style and sociality imparts behavior allocation differences between cougars and wolves leading wolves to spend more time foraging. But, we expect prey characteristics (e.g species and mass) and spatial characteristics (e.g. terrain and vegetative openness) to influence cougar and wolf behavior at kill sites. Given the different hunting styles these predators utilize, we expect wolf killing surges to be preceded by accelerometer running signatures (e.g. indicating chase behavior), whereas cougar accelerometer signatures should display low-frequency movements indicating cryptic stalking behavior (Williams et al. 2014). Further, we expect cougar energetics to be largely driven by the season (e.g. cost travel through snow) and the female cougar's reproductive status (e.g. cost of providing for young).

Methods

Study Area

Yellowstone's Northern Range (NR) is a 1,531 km^2 area situated on both sides of the northern boundary of YNP and is prime wintering habitat for ungulates. On the NR, vegetation consists of grasslands interspersed with patches of douglas fir (*Pseudotsuga menziessi*), lodgepole pine (*Pinus contorta*) and juniper (*Juniperus occidentalis*). Moreover, topography varies with rugged, mountainous areas adjacent to rolling plateaus ranging from 1,500-2,200m in elevation. Eight different ungulates inhabit the NR: elk (*Cervus canadensis*), bison (*Bison bison*), mule deer (*Odocoileus hemionus*), white-tailed deer (*Odocoileus virgianus*), moose(*Alces alces*), pronghorn antelope (*Antilocarpa americana*), bighorn sheep (*Ovis canadensis*), and introduced mountain goats (*Oreamnos americanus*; Lemke 2004).

Carnivore Collar Data and Monitoring

We used GPS location and tri-axial accelerometer data from cougars and wolves collared from 2015-2017. Cougars were captured using snow-tracking and trained hounds during winter following protocols approved by the NPS Institutional Animal Care and Use Committee (IACUC; Permit: IMR_YELL_Stahler_Cougars_2015). Cougars (3 adult females, 1 subadult male) were fitted with Vectronic-Aerospace (Berlin, Germany) Vertex Plus Iridium or GPS Plus downloadable satellite communication collars, programmed to take GPS fixes at 30-min, 1-hour, or 3-hour intervals depending on season. Wolves (1 adult female, 2 adult male, and 1 subadult male) were captured during Yellowstone National Park's annual wolf capture operations using helicopter darting techniques following protocols approved by IACUC (Permit: IMR_YELL_Smith_wolves_2012). Wolf Vertex Plus Iridium GPS collars were programmed to gather location data at 30-min, 1-hour, and 6-hour intervals depending on season. Both cougar and wolf collars included tri-axial accelerometers set to 16Hz.

Yellowstone Wolf Project (YWP) personnel conducted fixed-wing aerial surveys throughout the year to collect information on wolf pack demography, behavior, and predation (Smith et al. In press). This ongoing research provided information on wolf pack sizes and composition. Cougar reproductive status (e.g. solitary and maternal female with young kittens, kittens, or yearlings) was determined through remote camera surveys and direct observations to monitor kitten survival.

GPS cluster predation analysis and prey composition

Cougar and wolf predation patterns were similarly evaluated using established GPS cluster methodologies (Knopff et al. 2009, Metz et al. 2012). Possible predation events for both carnivores were identified and searched during 3 separate seasons: late winter (March), summer (May-July), and early winter (mid-November to mid-December). These three seasonal study periods were chosen to capture seasonal variation in prey vulnerability associated with both the decline in prey health over the winter and neonate availability in summer (Metz et al. 2012). For wolves, winter GPS clusters were classified as ≥ 2 one-hour GPS fixes within 100m of its nearest neighbor. Summer predation clusters were identified as ≥ 2 thirty-minute GPS fixes within 100m of its nearest neighbor. The smaller GPS fix rate used in summer facilitated detection of seasonal smaller prey items, such as neonate ungulates. Cougar predation events were identified during the same seasons outlined for wolf predation but following cluster identification protocols outlined by Knopff et al. (2009). For all seasons, we identified cougar clusters as ≥ 2 three-hour locations within 6 days and 200m of its nearest neighbor. This larger GPS fix interval has been previously demonstrated to be sufficient for identifying cougar predation events and finding prey remains given cougar's handling time (Knopff et al. 2009).

All possible cougar and wolf predation event sites were investigated on foot with a 5-14 day lag after the animal left the area in order to minimize disruption to feeding patterns and field personnel safety during seasons when grizzly bears were still active. When prey remains were located, they were identified to species, age (using tooth eruption or cementum annuli), and sex when possible. We estimated seasonal and pooled diet composition for cougars and wolves. In addition, field personnel examined kill sites for natural sign (e.g. visual observation, tracks, scats, and inverted hide) of scavengers, and attempted to estimate when and if the carcass was usurped by dominant scavengers.

Behavior Phase Identification and ODBA calculation

We used tri-axial accelerometers to continuously measure movement at a rate of 16x/second on the 3 major axes of the body (x: transverse sway, y: anterior-posterior surge, z: dorsal-ventral heave) for wolves and cougars. We used these data to classify focal behaviors into 3 phases: foraging for prey, killing prey, and handling prey (Williams et al. 2014). We used GPS clusters and known kill locations from cluster searches to help narrow search windows to identify these behaviors. With the search window narrowed, we created time series plots of raw accelerometer data from all 3 axes to visualize behaviors (e.g. resting, walking, running, killing, and feeding; Figure 4.1; Wang et al. 2015). In addition, we used known kill locations correlated with GPS clusters to identify the surge in accelerometer measurements associated with killing prey. The behaviors immediately following this surge were assigned as the prey handling period, or when feeding behavior had begun. We then calculated the duration of time between when handling started and the animal left the carcass area (e.g. moved >400m away, the distance cougars can bed away from a kill; Beier et al. 1995). We used this distance criteria for wolves for consistency. Next, we classified the behaviors occurring after the first minute displaying travel behavior (e.g. walking or running) away from the kill site as the start of foraging for the next kill. Times when animals left the carcass to set up latrine or bed sites were included in handling time, as these behaviors are often lost in GPS data and are essential to calculating overall energetic costs, and these behaviors are not associated with foraging for the next kill.

We summarized ODBA values into 1-minute intervals from tri-axial accelerometer measurements into the three focal behavior phases. We calculated ODBA following previously established methods (Shepard et al. 2008, Qasem et al. 2012). After splitting the data into 1-minute intervals, we linked ODBA data with our focal behavior phase identification and spatially to kills identified through GPS cluster searches. We compared ODBA calculations for behaviors within species. In addition, we calculated the duration (hours) for each behavior to compare behavior budgets within and across species.

Linear Regression Analysis

We used linear regression to test the effects of prey species characteristics, spatial covariates, and predator movement patterns as explanatory variables for the duration and magnitude of species-and behavior-specific ODBA from verified kill locations. Prior to analysis, we split the total dataset by behavior phase (e.g. kill, handling, and forage) and predator species (e.g. cougar and wolf) and ran linear regression models separately.

Following Williams et al. (2014) we expected prey size (weight in kg) and ODBA prior to the kill surge to be influential covariates determining kill surge ODBA. To estimate prey size, we used season-specific growth curves developed for our study area to approximate live weight (Murphy 1998, Metz et al. 2011), based on the age and sex of prey determined at kill site visits. We calculated ODBA for the 5 minutes preceding the kill surge to understand how activity prior to killing influenced the magnitude of ODBA values during the kill surge. We included prey species, age, and sex; as well as habitat openness and topographic roughness index (TRI). We extracted kill site spatial characteristics from raster data with a 30m resolution.

We included reproductive status of each study individual and the number of individuals in their respective cougar group or wolf pack. Cougar reproductive status was classified as groups that included young kittens or pups (< 6 months of age), young of year (6 months-1 year), yearlings (1-2 years old), or adults (> 2 years old). Each reproductive group experiences significantly different energetic responsibilities associated with raising, defending, and provisioning young (Ruth et al. 2019). Wolf packs usually include multiple generations, thereby including individuals from multiple reproductive statuses. Therefore, we characterized a wolf pack as having pups < 6 months old or by the age class that comprises the highest proportion in the pack (e.g. yearling or adult animals).

We estimated edible biomass available at each kill, by first calculating live weights as described above, and assuming 68% of large prey (>40kg) carcasses (Wilmers et al. 2003) and 79% of small prey (<40kg) carcasses were available and edible (Miller et al. 2013). Kleptoparasitism was incorporated as a categorical variable for small and large scavenger species detected at kill sites. We characterized red fox and coyote as small scavengers and grizzly bear, black bear, wolf, and cougar as large scavengers. While avian scavengers can remove significant biomass (Wilmers et al. 2003), their offtake was not included in this analyses. We used kill sites without scavenger sign as the reference category, In addition, we included vegetative openness and TRI associated with the kill site.

To test for differences of mean time spent performing each behavior, we ran unpaired t-test's with predator species as a grouping variable and analysis of variance (ANOVA) to estimate the significance of reproductive status and season as grouping variables. We used AIC model selection to identify the best fit model within each group and provide parameter estimates using model averaged coefficients for all models within Δ4 AIC of the top model.

Cougar energetics

We estimated seasonal energy expenditure for cougars using calculated ODBA values and methods outlined in Williams et al. (2014). First, we converted ODBA to VO_2 using:

$$VO_2 = 3.52 + 58.42(ODBA) \tag{2}$$

where VO_2 is measured in mL $O_2 \cdot kg^{-1} \cdot min^{-1}$. This was translated to energetic units using a conversion of 20.1 J/ml O_2.

$$\text{Energetic Cost}_{Cougar} = \frac{VO_2 \times cougar\ mass \times 20.1}{1000}. \tag{3}$$

While we initially hoped to correlate ODBA to caloric expenditures for both species, we lacked calibrated and correlated observations from captive wolves to infer expenditures in wild animals (See Williams et al. 2014, Wang et al. 2015 for more information on accepted calibration methods). Thus, estimates of behavior-specific energy expenditures were only calculated for cougars.

Body size scales positively with metabolic requirements (Tomlinson et al. 2014, Halsey 2016, Withers et al. 2016), so we attempted to separate individual consumption rates for collared individuals within family groups. Using previously derived edible biomass from prey carcasses, we calculated prey consumption rates for individuals by first estimating the number, age, and sex of all cougars within a family group. We assigned a weight to each individual within the cougar family groups using average values from previous literature (Logan and Sweanor 2001). We then divided the maternal female's mass at the time of capture by the combined family group weight to calculate the proportion of total weight the maternal female represented compared to the cumulative weight of all individuals in the family group. To assign individual consumption weight (kg prey biomass/cougar) we multiplied this proportion of the family group weight by the total edible weight obtained from each carcass. Consumption rates were estimated by dividing this consumption weight obtained by the collared individual by the number of days monitored during that season to give consumption rate in kg/cougar/day.

Our model used the wet meat energy value from white-tailed deer (*Odocoileus virginianus*), 7,908 kilojoules/kg, to represent the per kilogram energy content of meat from any species (Davison et al. 1978). We multiplied this value by the edible weight of carcasses detected from GPS clusters. The final product gave the total kilojoules (kj) consumed through ingesting prey biomass for the entire season. Comparing this value to the total kilojoules expended over the same time period allowed us to directly quantify if individuals are meeting field metabolic requirements.

Results

Prey Composition

We hiked 4,577 km to search 724 (94.76%) cougar GPS clusters, detecting prey remains at 188 cluster sites (Table S4.1). This analysis required that kills were made in succession in order to continuously monitor behavior and energetic expenditures. Thus, we did not use 22 kills that were not consecutively foraged and handled, leaving 149 prey carcasses for analysis. Using kill site information from field visits and accelerometer signatures, 149 of these were determined to be killed by GPS collared cougars but we detected instances of other cougars scavenging these carcasses. In addition, we hiked 1,700 km to search 485 (84.94%) wolf GPS clusters and detected prey remains at 80 cluster sites, 55 of which were killed by the tri-axial accelerometer collared wolf in the pack. At 25 carcasses, feeding behavior commenced without a characteristic surge preceding, indicating the animal likely scavenged.

Prey composition differed by predator species and season. Both species' diets were predominately elk, the most abundant prey species in the study area. Cougar diet was composed of elk (52.35%) followed by mule deer (*Odocoileus hemionus*; 34.23%), yellow-bellied marmot (*Marmota flaviventris*; 6.04%), pronghorn (*Antilocapra americanus*; 3.73%), red fox (*Vulpes vulpes*; 2.01%), coyote (*Canis latrans*; 0.67%), and unknown species (0.67%; Table S4.2). Wolf diet was more diverse, mainly comprised of elk (63.75%), followed by bison (16.25%), mule deer (12.50%), pronghorn (2.50%), bighorn sheep (2.50%), moose (1.25%), and badger (*Taxidea taxus*; 1.25%; Table S4.2). Cougar seasonal diet changed slightly with greater diversity in summer, but elk and mule deer composed the vast majority of their diet in all seasons (Figure S4.1). Similarly, wolves displayed the most diverse diet during the summer season with elk and bison representing the majority (Figure S4.1); however, we abstained from calculating significance of seasonal prey composition changes due to small sample size (see Ruth et al. 2019 and Metz et al. 2012 for more on this topic).

Behavior Phase Identification and ODBA Calculations

Across all seasons, the average weight of wolf-killed prey was 157.15 ± 133.70 (6.3 -720.6) kg and cougar-killed prey 71.96 ± 70.91 (2.94 - 310.19) kg, a significant difference of 85.19 kg ($t(66.37) = -4.48$, $p < 0.001$). The top model describing 1-min ODBA during the kill surges is best described by the weight of prey killed and the average ODBA of the 5-minutes immediately preceding the kill surge ($R^2 = 0.23$; Table 4.1). Cougar ODBA increased as prey size increased (β: 0.12 ± 0.02, 95%CI: 0.07,0.17; Figure 4.2a). In addition, if cougars displayed more movement prior to the kill surge, the average ODBA during the kill surge increased (β: 0.11 ± 0.03; Figure 4.2b). Mean ODBA during cougar kill surges decreased in areas of higher TRI (β: -0.004 ± 0.02, 95%CI: -0.05, 0.04) and increased in areas with more vegetative openness (β: 0.03 ± 0.03, 95%CI: -0.02, 0.08; Table S4.4). Wolves displayed similar patterns with top models including prey weight, average ODBA prior to the kill surge, TRI, and openness ($R^2 = 0.14$-0.16; Table 4.2). Kill surge ODBA increased with prey weight (β: 0.07 ± 0.07, 95%CI: -0.05, 0.20; Figure 4.2a) and with higher ODBA prior to the kill (β: 0.22 ± 0.07, 95%CI: 0.08, 0.35; Figure 4.2b). In addition, wolf kill surge ODBA displayed negative relationships with TRI (β: -0.09 ± 0.07, 95%CI: -0.23, 0.04) and openness (β: -0.003 ± 0.07, 95%CI: -0.13, 0.13; Table S4.4). Kill durations varied with surges lasting 1.52 ± 1.25 minutes (0.02 ± 0.01% of total time) for cougars and 3.56 ± 3.35 minutes (0.09 ± 0.06% of total time) for wolves.

Even though prey carcasses were larger for wolves, cougars across all reproductive statuses spent more time handling their prey carcasses, averaging 49.62 hours (52% ± 12% of total time; $n = 184$) compared to 13.88 hours (33% ± 14% of total time; $n = 133$) for wolves ($t(217.26) = 9.45$, $p < 0.0001$). For handling adult elk carcasses only, cougars across all reproductive statuses spent on average 96.95 ± 80.63 hours compared to wolves averaging 20.69 ± 15.22 hours.

To better understand factors influencing prey handling behavior, we fit two groups of linear regression models with handling time as the response for one set of models and total ODBA as the response for the second set of models. The top cougar models explaining handling time selected by AIC included carcass edible weight, scavengers detected, reproductive status, TRI, and vegetative openness (R^2 = 0.31-0.32; Table S4.8). Handling time increased with increasing weight of prey carcasses (β: 20.78 ± 3.48, 95%CI: 13.95, 27.61) and with increased TRI (β: 5.06 ± 3.03, 95%CI: -0.89, 11.01). Compared to solitary cougars, maternal females displayed decreased handling time. Females with yearlings handled carcasses the fastest (β: -28.22 ± 7.01, 95%CI: -41.95, -14.49; Table S4.10). Both small and large scavengers increased handling time for cougars, but 95% CI substantially overlapped zero (Table S4.10). The top models for wolf handling time included carcass edible biomass, scavengers detected, reproductive status, number of individuals in the pack, TRI and openness (R^2 = 0.24-0.32; Table S4.9). Wolf handling time increased with prey carcass edible biomass (β: 7.27 ± 1.75, 95%CI: 3.84, 10.70) and for packs that were comprised of mostly adult wolves (β: 7.92 ± 6.25, 95%CI: -4.33, 20.18). Packs with pups < 60 months of age spent less time handling kills (β: -3.28 ± 5.26, 95%CI: -13.58, 7.02). As TRI increased for carcass sites, wolves handled kills faster (β: -2.09

± 1.58, 95%CI: -5.20, 1.01). Wolf handling decreased minimally has vegetation openness increased (β: -1.51± 1.53, 95%CI: -4.50, 1.49; Table S4.10).

Wolves and cougars display different behaviors while handling carcasses. For example, cougars keep cryptic kill sites by caching carcasses and sometimes bedding long distances away (Ruth et al. 2010). On the other hand, wolves tend to stay closer to kill sites during the handling phase by setting up bed sites within the carcass area and do not set up latrine sites. Nonetheless, wolves may leave kill areas often to return to the denning location during pup rearing season. We tested the influence of the same predictors used in the handling time regression models above to see if they influenced total ODBA observed while handling carcasses. Given the strong linear relationship between ODBA and energy expenditure, it can be assumed that factors leading to increased ODBA would also contribute to increased energetic expenditure (Williams et al. 2014). The top cougar models (R^2 = 0.31-0.32; Table S4.5) displayed increased ODBA as carcass biomass increased (β: 148.92 ± 58.14, 95%CI:34.97-262.87; Table S4.7). In addition, ODBA had positive relationships with TRI (β: 56.07 ± 35.97, 95%CI: -14.42, 126.56) and both small (β: 176.56 ± 90.90, 95%CI: -1.61, 354.73) and large scavengers (β: 73.46 ± 109.16, 95%CI: -140.49, 287.41). Female cougars with yearlings exhibited the least ODBA (β: -425.95 ± 82.40, 95%CI: -587.46, -264.44), followed by young kittens < 6 months of age (β: -316.61 ± 149.71, 95%CI: -610.03,-23.18) and kittens aged 6 months to 1 year (β: -241.09 ± 122.78, 95%CI: -481.74, -0.45). The top wolf models (R^2 = 0.25-0.27,; Table S4.6) showed increased ODBA as carcass weight increased (β: 437.47 ± 87.50, 95%CI: 265.98, 608.97). In addition, ODBA decreased with the presence of smaller scavengers (β: -196.84 ± 155.42, 95%CI: -501.46, 107.78) and increased with larger scavengers (β: 151.39 ± 192.36, 95%CI: -225.63, 528.42). ODBA displayed a negative relationship with TRI (β: -90.99 ± 68.77, 95%CI: -225.78, 43.80) and a positive relationship with vegetative openness (β: 7.20 ± 72.85, 95%CI: -135.59, 149.99). Wolves increased ODBA as wolf pack size increased (β: 11.49 ± 24.85, 95%CI: -37.21, 60.19; Table S4.7)

Across all seasons, cougars averaged 52.95 ± 46.74 hours (46% ± 12% of total time; *n* = 160) foraging for kills while wolves averaged significantly different at 34.41 ± 35.50 hours (66% ± 14% of total time; *n* = 127) foraging (*t*(203.94) = 3.37, p = 0.0009). Cougars displayed little seasonal variation in foraging time (*F*(2,146) = 0.071, p = 0.931). Wolves spent less time foraging during late winter (25.82 ± 25.64 hours) compared to summer (38.78 ± 40.13 hours) and early winter (61.38 ± 44.45 hours; *F*(2,78) = 2.94, p = 0.059). Wolves were more likely to feed on a carcass across several feeding periods compared to cougars. Wolves averaged 1.58 ± 1.42 temporally separated handling events per carcass compared to cougars averaging 1.11 ± 0.37 handling events per carcass (*t*(89) = -3.02, p = 0.003). Since monitoring days were different among individuals, we calculated the proportion of time spent in each behavior phase over the course of the season to allow direct comparison of behavior time budgets (Figure 4.3).

We identified instances of possible kleptoparasitism by other mammalian meat eaters during cluster site surveys. Across all seasons, 17.85 ± 18.98% of cougar carcasses were visited by large scavengers (grizzly bear, black bear, wolf, or other cougar) and 37.04 ± 26.58% of carcasses were visited by smaller scavengers (coyote or red fox). We documented large scavengers (grizzly bears, black bears, or other wolves) at 14.51 ± 8.98% of wolf carcass sites and smaller mammalian scavengers at 60.07 ± 47.02% of wolf carcass sites.

Cougar consumption rate and energetics

Cougar prey consumption rates displayed individual variation, but also across seasons, and reproductive statuses (Table S4.11). We did not include the sole subadult male cougar in this section of the analysis since much of his consumption was highly correlated to his maternal female who is already represented and subadult physiology and behavior can be drastically different from calibrated measurements on adults (Withers et al. 2016). Individual prey consumption rates ranged from 1.54 to 20.35 kg/day with an average of 7.38 ± 5.19 kg/day. Seasonal differences were not significant ($F(2,15) = 0.30$, p = 0.744), with early winter averaging 7.12 ± kg/day, late winter averaging 6.89 ± 6.05 kg/day, and summer averaging 8.88 ± kg/day. Reproductive status significantly influenced consumption rate ($F(3,14) = 3.64$, p = 0.04). Solitary females displayed the highest consumption rates 11.18 ± 4.17 kg/day, followed by females with young kittens (<6 months old; 7.68 ± NA), females with yearlings (3.10 ± 1.66 kg/day), and females with kittens (6 months – 1 year old; 3.52 ± 1.69 kg/day; Table 4.3).

We estimated seasonal and daily energetic expenditure (DEE) for cougars using tri-axial accelerometers. Across all seasons cougar DEE averaged 25,780 ± 9,884 kj/day. There was minimal variation across seasons (*F*(2,657) = 0.63, p = 0.535), and cougars expended the highest average DEE during early winter (27,237 ± 9,396). Cougars averaged 24,273 ± 7,115 kj/day in late winter and 26,802 ± 9,496 kj/day in summer. Similar to consumption rates, cougars displayed more variation in DEE across reproductive statuses (*F*(3,656) = 65.19, p < 0.0001), where solitary females expended the most average DEE (30,237 ± 10,079 kj/day). Females with young kittens displayed the lowest DEE (17,749 kj/day), followed by females with kittens (20,653 ± 1,449 kj/day) and females with yearlings (21,170 ± 1,076 kj/day; Figure 4.4).

Using consumption rates and seasonal and DEE estimates allowed us to calculate behavior-specific expenditures and energetic surpluses or deficits for cougars. Cougars averaged 78 ± 94 kj per kill surge. Mirroring our results showing the impact of prey size on ODBA, cougars expended more energy to kill large prey (prey >40kg; 110 ± 121 kj) than small prey (Prey <40kg; 49 ± 41 kj). Cougars expended an average of 45,329 ± 23228 kj per foraging bout (e.g. inter-kill interval) and 43,656 ± 21,365 kj during the handling period of each carcass. Season influenced whether the energetic deficit was positive or negative (*F*(2,15) = 1.65, p = 0.224). On average, cougars were reaching their daily field metabolic needs through predation in all seasons with the highest positive energetic surplus in summer (34,766 ± 27,503 kj/day) compared to early winter (22,717 ± 40,618 kj/day) and late winter (33,462 ± 44,404 kj/day). In addition, these energetic deficits varied across reproductive statuses (*F*(3,14) = 1.49, p = 0.26). Solitary females, maternal females with yearlings and maternal females with kittens had a surplus of 57,419 ± 31,327 kj/day, 3,137 ± 12,403 kj/day, and 5,956 ± 14,247 kj/day, respectively. Females with young kittens suffered the largest average deficit at 5,560 kj/day (Figure S4.4).

Discussion

Evolutionary differences in morphology between sympatric cougars and wolves, which has led to divergent hunting modalities and social organizations potentially influencing energetic efficiencies (Ruth et al. 2019). Our results from GPS cluster searches demonstrated how these differences lead to contrasting prey compositions where wolves tend to utilize larger prey demographic classes and species (Table S4.3, Figure S4.2-S4.3; Ruth et al. 2010, 2019, Metz et al. 2011, 2012). Second, our results confirm that tri-axial accelerometer signatures can be used to identify and compare characteristic predatory behavior phases which allowed us to uncover variables that influence activity patterns associated with calculated ODBA and duration of time spent in each behavior phase. Finally, we extended cougar ODBA calculations to energy expenditure, demonstrating the energetic costs of successful reproduction and kleptoparasitism by large scavenges like grizzly bears, black bears, gray wolves, and other cougars.

Behavior Phase Identification and ODBA Calculations

Tri-axial accelerometer signatures have been used to remotely identify killing behaviors of wild felid species (Williams et al. 2014, Wang et al. 2015, Wilmers et al. 2017) and included in predictive GPS cluster models to identify predation events (Blecha and Alldredge 2015, Ebinger et al. 2016, Mahoney and Young 2017). While we were unable to remotely classify all behavioral aspects involved in a hunt (MacNulty et al. 2007), this study represents the first to remotely uncover killing behavior of wild gray wolves through identification of killing surges from tri-axial accelerometer signatures. Moreover, we were able to reveal kills for both wolves and cougars that were undiscovered by field personnel, which could be used to improve future kill rate estimates (Blecha and Alldredge 2015). Further, we were able to identify an instance where a yearling male (M201) and his maternal female (F202; both equipped with tri-axial accelerometers) cooperatively killed an elk calf in late winter, further evidence displaying opportunity teaching in a young carnivore (Elbroch and Quigley 2013).

The results of linear regression models estimating the influence of various predictors on the amplitude of ODBA during kill surges showed that ODBA increased as the prey size increased (Williams et al. 2014; Figure 4.2). Previous research has shown that greater cryptic behavior prior to kills led to less energy expenditure required to successfully kill prey for cougars (Williams et al. 2014), but we hypothesized that wolves would not display the same relationship given their hunting style often include extended pursuits prior to a killing surge (Kunkel et al. 2007, MacNulty et al. 2007, Ruth et al. 2019). The average time kill surges lasted was longer for wolves (3.56 vs. 1.52 minutes) compared to cougars, demonstrating how these killing styles are expressed through the accelerometers). The modelling demonstrated that kill surge ODBA increased if wolves exhibited more activity (e.g. ODBA) prior to the surge. For wolf killing behavior, this may point to the complexities of disentangling killing behavior when only one individual is monitored by an accelerometer collar in the wolf pack. Wolves exhibit complicated, collaborative hunting where individuals of different age and sex groups often carry out predictable roles during hunts (MacNulty et al. 2009). Most of the kills identified in this study were carried out by larger adult males whom are less likely to be involved in the chasing and selecting of the individual prior to the attacking of prey (MacNulty et al. 2009). Thus, the low frequency ODBA measurements prior to kill surges could suggest that the animal was shadowing animals directly involved in the chase of prey and assisted with the final blow to the prey. In addition, small prey packages (e.g. calf and fawn ungulates) may not require as much pursuit by wolves before making the killing surge.

Our data revealed that wolves spend 20% more time foraging on average than cougars (Figure 4.3). This discrepancy is explained by cougars spending more time handling (20% more than wolves) carcasses compared to wolves, well-documented behavioral differences between these two carnivores (Ruth et al. 2019). Nonetheless, we assigned behavior without direct observation, inevitably combining a suite of complex cougar and wolf behaviors into the “foraging” and “handling” behavior categories. It is well documented that wolves spend considerable time and can travel great distances maintaining territory boundaries through scent-marking and active defense (Mech and Boitani 2003, Cassidy et al. 2015). Moreover, wolves display highly adaptive social intelligence that allows them to problem solve and respond to changes in their physical (e.g. interactions with terrain features and anthropogenic development; (Whittington et al. 2005, Anton et al. in press) and social environments (e.g. interactions between hostile adversarial wolf packs or competitors, annual influx of new littermates, or rivals for opportunities to mate; Packard 2003, 2012). Similarly, cougars can exhibit complex behaviors in response to their physical environment (Wang et al. 2017) and intra- and inter-specific competitors (Logan and Sweanor 2010, Ruth and Murphy 2010). While considered an exclusively solitary species, cougars display tradeoff decisions pertaining to social interactions that may impact behavior and energetic patterns (Elbroch et al. 2017). Moreover, these differing foraging allocation patterns likely contribute to nonequivalent responses in prey movement patterns (Kohl et al. 2019).

Linear regression models showed handling times for both predators were primarily determined by the edible biomass available for each carcass (Table S4.8-S4.10). Moreover, TRI had opposing impacts on cougars and wolves. In areas of high TRI (e.g steep, often rocky terrain), cougar handling time increased. These areas are often sought out by cougars, presumed to impede successful fleeing by prey, facilitate concealment of carcasses from competitors and provide cougars superior escape terrain if their carcass happens to be detected by bears or wolves (Hopcraft et al. 2005, Ruth and Murphy 2010, Ruth et al. 2019). In contrast, wolf handling time decreased in areas of high TRI. Since these areas are more difficult to travel through, wolves could be hindered if encounters with competitors occurred. In general, these trends validate habitat use differences between the two species and reflect the affinity cougars possess for rugged areas while wolves are more likely to select open areas with lower degree slopes (Knopff et al. 2014, Kohl et al. 2018, Ruth et al. 2019).

Both predators fed on carcasses for shorter periods of time when members of the group were young and with smaller sized prey carcasses (Table S4.10). For wolves, this was partly due to the shared responsibility of raising young, which led to frequent trips back to the denning area to feed and care for pups (Packard 2003). Wolf ODBA at kill sites was primarily determined by the size of the prey carcass. Even once carnivores, have successfully killed prey, they must exert significant effort to rip through hide, tear meat away, and chew on bones (Peterson and Ciucci 2003, Ruth et al. 2019), which would explain greater collar movement while feeding. ODBA increased with pack size, demonstrating intra-pack competition for the shared resource that pushes wolves to feed quickly on carcasses before their pack mates (Peterson and Ciucci 2003). For cougars, the shortest handling times were recorded for females with yearlings, likely the result of the carcass being shared between larger yearling young that require more sustenance than their younger counterparts (Ruth et al. 2019). Moreover, models determining ODBA calculations during the handling period indicated that prey size and an interaction term between small scavengers and prey size were significant predictors (Table S4.7). While larger prey requires more movement-based feeding, the presence of small scavengers may require cougars to periodically defend the carcass and chase off coyotes and red foxes away from the carcass area.

Normally, kills have strong localizing effects for large carnivores (Murphy and Ruth 2010), but we see less of an effect on wolves as we saw in cougars. The 1-minute behavior phase identification we performed showed that wolves would frequently revisit older kills and scavenged carcasses as they foraged for new kills or moved to and from denning areas. This strategy allowed them to consume prey biomass from previous kills or found carcasses foraging, extending consumption times in order to sustain higher foraging costs. In contrast, cougars rarely revisited kill sites. Instead, they opted to increase initial handling time and fully consume kills before beginning foraging for their next prey kill.

Cougar Energetics and Consumption Rate

Field metabolic rate calculations can be applied to population study to better understand landscape, seasonal, or individual differences in vulnerability to change (Halsey 2011, Halsey et al. 2011). Thus, a critical aspect of predation studies is to measure the degree to which an individual is able to meet their metabolic needs. Cougar energetic expenditure patterns were strongly tied to a female's reproductive status (Figure 4). Female cougars give birth to 1-4 kittens, which remain dependent for 12-24 months as they approach similar mass as the maternal female (Logan and

Sweanor 2001, 2010). During this time of dependence, maternal females are responsible for providing sustenance, leading to increased foraging and energetic costs. Maternal females with young less than 1 year old kept smaller home ranges, localizing more to a core area to minimize movement costs, leading to less overall DEE (Beier et al. 1995, Logan and Sweanor 2001, Ruth et al. 2019). These smaller home ranges enable them to travel shorter distances over shorter amounts of time, leading to less overall ODBA, and therefore energy expenditure, per kill. The availability and ease of catching small prey (e.g. neonate elk and mule deer, and yellow-bellied marmots) is likely extremely important for lactating females as they undergo an energetically expensive period and is further evidence for the peak in births occurring during this period (Ruth et al. 2019). In contrast, solitary female cougars expended considerably more energy (Figure 4.4). This seemed to be partially explained by higher prey acquisition and consumption rates, which required more activity to forage and subdue prey (Table 4.3); however, ODBA-informed energy expenditure is movement based and speaks to not only solitary females holding larger home ranges (Logan and Sweanor 2001, Ruth et al. 2019), but also to their drive to find mates and successfully reproduce (Ruth et al. 2019). Cougars are poly-estrus and are capable of entering estrus immediately after their young perish or disperse (Seidensticker et al. 1973, Logan and Sweanor 2010). Female cougars can spend considerable time travelling to find mates and then long time periods with a male to ensure successful copulation (Seidensticker et al. 1973, Logan and Sweanor 2010). Given cougars often exist at low-densities, solitary female cougars likely expend significant energy traveling the landscape in search of and spending time with mates (Ruth et al. 2019).

Further, after converting prey biomass consumption from kg/day to daily energy consumption (DEC; kj/day), maternal females displayed modest energy returns and often displayed negative energy deficits, especially when assuming the additional cost of lactation for females with young kittens, which was not directly quantified (Figure S4.4). Females with yearlings expended similar energy through lower overall activity, but shared each carcass with relatively large young, leading to less overall consumption. Even though we found that solitary females expended the most DEE, they offset this by consuming more prey biomass (Table S4.11) and consistently displayed positive energy gains, consuming more energy than they expended (Figure S4.4). Our estimates of average cougar FMR are higher than previously published values based on expected caloric expenditures from kill rates and allometric scaling (Ackerman et al. 1986 [12,600-23,100 kj/day], Laundré 2005 [10,164-11,363 kj/day], Ruth et al. 2019 [12,446-18,520]). Additionally, this would explain why kill rate estimates derived from projected FMR, using those methods, have been previously biased low as well (Laundré 2005, Knopff et al. 2010).

Nonetheless, we attempted to estimate total biomass consumed, but it is likely an overestimate since we did not account for instances where cougars abandoned carcasses due to kleptoparasitism (Wilmers et al. 2003, Ruth et al. 2010, Elbroch et al. 2014). Large scavenger sign, such as grizzly bear, black bear, or wolf activity, occurred at 17.85 ± 18.98% percent of cougar kills. Since cougars are subordinate to bears and wolves at carcass sites, they likely lost feeding opportunities (Murphy et al. 1998, Ruth and Murphy 2010, Elbroch and Kusler 2018, Ruth et al. 2019), but this can be difficult to determine during kill site surveys (Ruth et al. 2010, Elbroch et al. 2014). Previous studies have attempted to account for carcasses lost to large scavengers by comparing handling times by cougars at carcass sites with and without scavengers detected (Murphy et al. 1998, Ruth et al. 2010, Elbroch et al. 2014). However, our data showed no difference in handling time (and in some cases longer handling times) at carcasses where large scavenger sign was detected, possibly implying cougars remained near carcasses after being displaced to obtain any remaining food after the dominant scavenger had left (Figure 4.5a; Tallian et al. 2017, Ruth et al. 2019). In some cases, the cost of hunting for a new kill outweighs the risk of attempting to obtain food from the existing carcass (Wilmers et al. 2003). Nonetheless, we found cougars with higher proportions of scavenger sign detected at carcasses, dealt with losing food resources by killing additional prey (Ruth et al. 2019). If they had been able to consume every carcass, they captured, this would have been well above their energetic requirements, evidence that suggests there was likely significant biomass lost to kleptoparasitism (Figure 4.5b). After converting the extra projected kilojoules consumed to kg of biomass, this amounted to some cougars possibly killing up to 11 extra adult mule deer does or 3 adult elk cows in a season (Table 4.3). In turn, these cougars incurred significantly greater energetic foraging costs and killing risks over time (Gorman et al. 1998, Ruth et al. 2019), especially if multiple larger prey species (e.g. adult elk) were killed in this time period (Figure

4.6). This interference competition not only directly impacts individual cougars who lose opportunities to feed, but also may indirectly impact prey abundance as predation can be a driver of prey populations (Vucetich et al. 2011, Krofel et al. 2012, Elbroch et al. 2015, Tallian et al. 2017). Annually, wolf and cougar predation distributes hundreds of carcasses on the Yellowstone landscape for a large suite of scavengers (Ruth et al. 2019). This represents a substantial impact throughout the food web, improving ecosystem function and complexity (Stahler et al. In press).

Our results provide new information on the costs and benefits of differing hunting modalities and sociality in large carnivores that help explain time and activity allocation and the resultant energetic expenditures. Many estimates of large-carnivore energetics are underestimated and cannot be directly linked to specific behaviors; however, instantaneous rates of energy expenditure from tri-axial accelerometers can help disentangle the cumulative effects of interspecific competition among large carnivores and the life history traits that drive population dynamics.

Table 4.1. AIC model selection from linear regression models determining the influence of covariates on the ODBA displayed during the killing surge by cougars.

Model	K	logLik	AIC	ΔAIC	R^2
Prey Size + ODBA(5-min prior)	4	-20.83	49.95	0	0.23
Prey Size + ODBA(5-min prior) + Openness	5	-19.85	50.16	0.205	0.23
Prey Size + ODBA(5-min prior) + Openness + TRI	6	-19.84	52.32	2.365	0.23
Prey Size + ODBA(5-min prior) + Openness + TRI + Openness x TRI	7	-19.44	53.73	3.777	0.23
Prey Size + ODBA(5-min prior) + Openness + Prey Species	10	-16.27	54.26	4.304	0.24
Prey Size + ODBA(5-min prior) + Openness + Prey Species + Prey Size x Prey Species	12	-15.54	57.56	7.611	0.24
Prey Size + Openness	4	-28.25	64.81	14.856	0.14
Prey Size + Openness + TRI	5	-28.25	66.96	17.008	0.14
Prey Size	3	-30.8	67.79	17.835	0.12
Prey Size + TRI	4	-30.77	69.84	19.891	0.11
ODBA(5-min prior) + Openness + Prey Species + Prey Age + Prey Age x Prey Species	21	-10.83	70.88	20.933	0.23
Prey Species + Prey Size	8	-27.38	71.87	21.92	0.13
ODBA(5-min prior) + Openness + Prey Species + Prey Age + Openness x Prey Species	19	-14.3	72.45	22.501	0.21
ODBA(5-min prior) + Openness + TRI + Prey Species + Prey Age + Prey Sex + TRI x ODBA(5-min prior)	18	-15.65	72.53	22.577	0.20
ODBA(5-min prior) + Openness + TRI + Prey Species + Prey Age + Prey Sex + Openness x TRI	18	-15.74	72.71	22.753	0.20
ODBA(5-min prior) + Openness + TRI + Prey Species + Prey Age + Prey Sex + Openness x ODBA(5-min prior)	18	-15.89	73	23.048	0.20
Prey Species + Prey Size + Prey Species x Prey Size	10	-26.44	74.6	24.652	0.12
ODBA(5-min prior) + Openness + Prey Species + Prey Age + Prey Sex + Prey Age x Prey Species	23	-10.58	75.91	25.962	0.22
ODBA(5-min prior) + Openness + TRI + Prey Species + Prey Age + Prey Sex + Prey Age x Prey Species	24	-10.49	78.59	28.636	0.22
Prey Species	8	-34.85	86.72	36.764	0.04
Prey Sex	4	-39.97	88.22	38.268	0.00
Prey Species + Prey Sex + Prey Age + Openness	15	-27.62	88.82	38.871	0.08
Prey Species + Prey Sex	10	-34.26	90.11	40.157	0.03
Prey Species + Prey Sex + Prey Age + Openness + TRI	16	-27.61	91.31	41.357	0.08
Prey Species + Prey Sex + Prey Age + Openness + TRI + Openness x TRI	17	-27.61	93.85	43.9	0.07
Prey Species + Prey Sex + Prey Age + TRI	15	-30.31	94.19	44.242	0.05
Prey Species + Prey Sex + Prey Species x Prey Sex	13	-33.71	96.09	46.136	0.02
Prey Species + Prey Sex + Prey Age + Prey Species x Prey Sex	17	-29.54	97.72	47.77	0.05
Prey Species + Prey Sex + Prey Age + Prey Sex x Prey Age	18	-28.78	98.79	48.833	0.05
Prey Species + Prey Sex + Prey Age + Prey Species x Prey Age	21	-25.8	100.82	50.864	0.06

Table 4.2. AIC model selection from linear regression models determining the influence of covariates on the ODBA displayed during the killing surge by wolves.

Model	K	logLik	AIC	ΔAIC	R^2
Prey Size + ODBA(5-min prior)	4	-33.48	75.76	0	0.16
Prey Size + ODBA(5-min prior) + Openness	5	-33.48	78.18	2.42	0.14
Prey Size + ODBA(5-min prior) + Openness + TRI	6	-32.45	78.65	2.888	0.16
Prey Size + ODBA(5-min prior) + Openness + TRI + Openness x TRI	7	-32.43	81.24	5.477	0.14
Prey Size + TRI	4	-36.94	82.68	6.919	0.05
Prey Size	3	-39.03	84.54	8.781	-0.01
Prey Size + Openness + TRI	5	-36.9	85.02	9.26	0.03
Prey Size + Openness	4	-38.79	86.38	10.623	-0.02
Prey Sex	4	-41.83	92.43	16.674	-0.04
Prey Size + ODBA(5-min prior) + Openness + Prey Species	11	-32.31	92.76	16.999	0.07
Prey Species + Prey Size	9	-36.87	95.74	19.984	-0.05
Prey Species	9	-38.82	99.48	23.722	-0.03
Prey Size + ODBA(5-min prior) + Openness + Prey Species + Prey Size x Prey Species	14	-31.56	101.61	25.852	0.03
Prey Species + Prey Size + Prey Species x Prey Size	12	-35.52	102.48	26.717	-0.07
Prey Species + Prey Sex	11	-38.81	105.49	29.729	-0.07
Prey Species + Prey Sex + Prey Species x Prey Sex	12	-38.44	107.97	32.216	-0.08
Prey Species + Prey Sex + Prey Age + Prey Species x Prey Sex	16	-34.55	114.7	38.943	-0.03
Prey Species + Prey Sex + Prey Age + TRI	16	-34.71	115.02	39.26	-0.04
ODBA(5-min prior) + Openness + TRI + Prey Species + Prey Age + Prey Sex + Openness x ODBA(5-min prior)	19	-28.27	115.08	39.319	0.11
Prey Species + Prey Sex + Prey Age + Openness	16	-35.42	116.44	40.684	-0.06
Prey Species + Prey Sex + Prey Age + Prey Sex x Prey Age	17	-33.88	117.46	41.701	-0.03
ODBA(5-min prior) + Openness + Prey Species + Prey Age + Openness x Prey Species	19	-29.72	117.97	42.213	0.06
ODBA(5-min prior) + Openness + TRI + Prey Species + Prey Age + Prey Sex + Openness x TRI	19	-30.08	118.7	42.944	0.05
ODBA(5-min prior) + Openness + TRI + Prey Species + Prey Age + Prey Sex + TRI x ODBA(5-min prior)	19	-30.13	118.79	43.034	0.05
Prey Species + Prey Sex + Prey Age + Openness + TRI	17	-34.7	119.1	43.342	-0.06
ODBA(5-min prior) + Openness + Prey Species + Prey Age + Prey Age x Prey Species	20	-29.53	122.39	46.632	0.04
Prey Species + Prey Sex + Prey Age + Openness + TRI + Openness x TRI	18	-34.6	123.21	47.451	-0.08
ODBA(5-min prior) + Openness + Prey Species + Prey Age + Prey Sex + Prey Age x Prey Species	22	-27.56	128.87	53.117	0.06
Prey Species + Prey Sex + Prey Age + Prey Species x Prey Age	20	-33.53	130.4	54.645	-0.10
ODBA(5-min prior) + Openness + TRI + Prey Species + Prey Age + Prey Sex + Prey Age x Prey Species	23	-26.91	133.27	57.515	0.05

Table 4.3. Estimates of female cougar consumption rates for different seasons and reproductive status phases. Consumption rates (kg/day) were estimated as proportional to the mass of the collared female compared to the total mass of all cougars in the family group. We used measurements and scaling equations to obtain mass-specific daily energetic expenditure (DEE;kj/day) and compared this to daily energetic consumption (DEC; kj/day) using prey biomass consumption rates to obtain an energetic deficit value (kj/day). In addition, we estimated the biomass deficit (kg/day) and multiplied this by average seasonal weights of adult female mule deer and adult female elk to calculate the number of animals a cougar is kill in excess or would need to kill to meet their energetic demands.

Cougar	Season	Year	Reproductive Status	Number of Individuals	Days Monitored	Kills Detected	Carcasses Scavenged	Group Consumption Rate	Individual Consumption Rate	DEE (kj/day)	DEC (kj/day)	Deficit (kj/Day)	Deficit (kg/Day)	± Deer/Season	± Elk/Season
F202	Early Winter	2016	Kittens	5	33	10	0	15.53	3.11	22364 ± 5558	24,011	970	0.12	0.1	0.0
F202	Late Winter	2016	Yearlings	4	36	5	2	8.1	2.17	21788 ± 6132	16,859	-5,534	-0.70	-0.6	-0.2
F202	Summer	2016	Young Kittens	5	42	11	0	7.68	1.54	17128 ± 4246	11,975	-5,561	-0.70	-0.7	-0.2
F202	Late Winter	2017	Kittens	5	17	5	0	19.76	5.98	19397 ± 5684	47,275	26,737	3.38	1.5	0.4
F202	Early Winter	2018	Solitary	1	25	3	4	-	13.97	37114 ± 10422	108,178	69,580	8.80	4.6	1.3
F202	Late Winter	2018	Solitary	1	48	5	2	-	6.1	36332 ± 9486	47,941	11,608	1.47	1.8	0.5
F202	Summer	2018	Solitary	1	63	17	0	-	12.29	34731 ± 6468	95,646	60,915	7.70	11.1	3.0
F202	Late Winter	2019	Solitary	1	23	7	1	-	20.35	35091 ± 5467	156,780	121,689	15.39	8.8	2.3
F202	Summer	2019	Solitary	1	55	10	0	-	7.71	37826 ± 9004	60,962	22,448	2.84	3.6	1.0
F207	Late Winter	2017	Solitary	1	20	3	0	-	9.18	20616 ± 4554	69,588	48,972	6.19	3.1	0.8
F207	Summer	2017	Solitary	1	71	15	1	-	9.37	22145 ± 4920	74,066	51,608	6.53	10.6	2.9
F207	Late Winter	2018	Kittens	3	14	2	1	4.82	2.88	19507 ± 3744	21,276	1,768	0.22	0.1	0.0
F209	Early Winter	2017	Yearlings	3	34	5	1	6.33	2.11	19928 ± 5871	16,358	-2,397	-0.30	-0.2	-0.1
F209	Late Winter	2017	Kittens	4	29	5	0	8.43	2.11	21343 ± 5280	16,429	-5,650	-0.71	-0.5	-0.1
F209	Summer	2017	Yearlings	3	66	27	1	15.06	5.02	21796 ± 5276	39,139	17,344	2.19	3.3	0.9
F209	Late Winter	2018	Solitary	1	45	10	0	-	11.28	20113 ± 3418	88,215	68,103	8.61	9.6	2.5
F209	Summer	2018	Solitary	1	33	8	0	-	10.37	19516 ± 4120	81,953	61,846	7.82	5.9	1.6

Figure 4.1. Example tri-axial accelerometer readings for a cougar (panel A) and a solitary wolf (panel B). The left most plot for each panel displays the killing surge for both animals, followed by feeding behavior that would take place during the handling phase. The right most plot shows traveling behavior that would be used to signify the start of foraging behavior. Each behavior plot displays 5-minutes of accelerometer data.

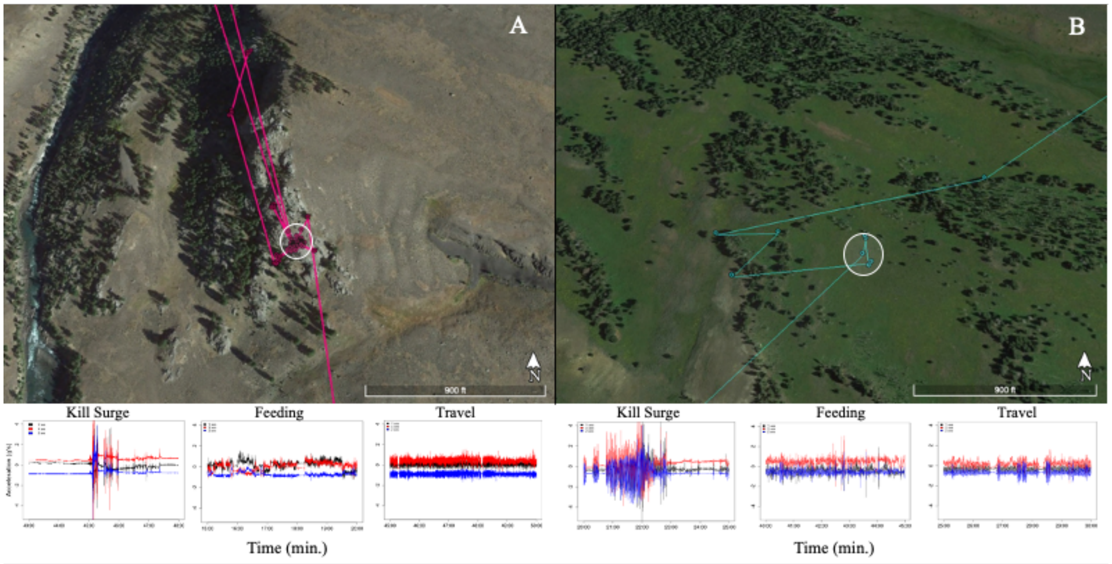


Figure 4.2. Predicted relationships between prey weight (kg) and the overall dynamic body acceleration (ODBA) displayed during a kill surge (Panel A) for cougars (black lines) and wolves (gray lines). Panel B displays the predicted influence of ODBA measurements for the 5-min prior to a kill surge on the amplitude of ODBA measurements during kill surges. Shaded gray areas denote the 95% confidence intervals.

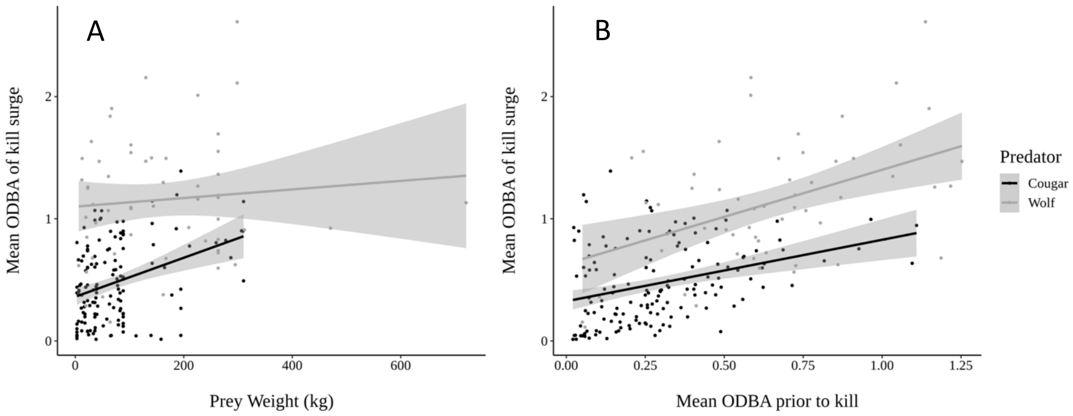


Figure 4.3. Using tri-axial accelerometer measurements we identified three behavior phases associated with predator hunting patterns. Using known kills from GPS cluster searches, we delineated seasonal cougar and wolf movements into these behaviors at 1-min intervals. The plot below shows the proportion of time spent in each behavior phase during a season. Cougar are shown in black and wolves are in gray.

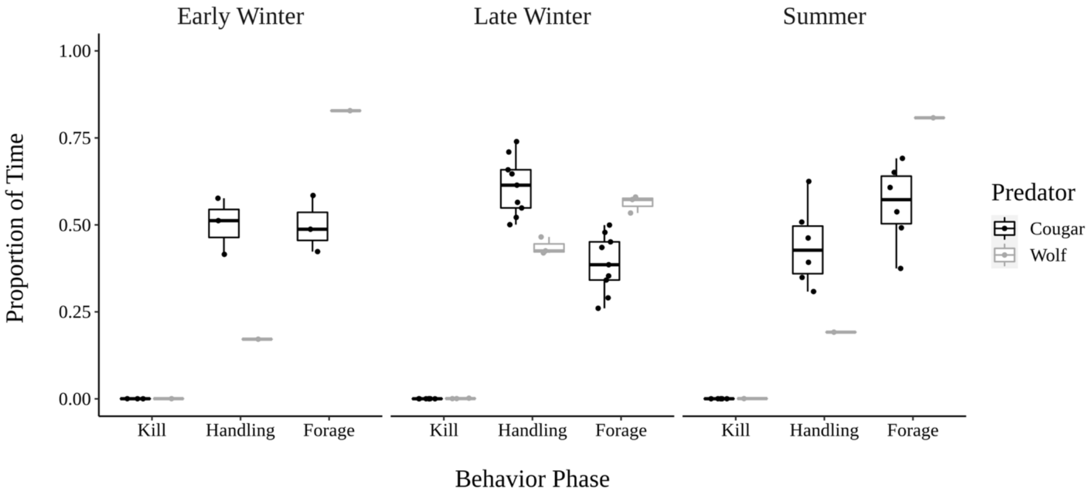


Figure 4.4. We calculated daily energetic expenditure (DEE; kj/day) for maternal and solitary females at different stages of reproductive status. Solitary females travelled mostly alone and did not take care of any young, maternal females with yearlings cared for dependent young > 1 year old, maternal females with kittens cared for young between 6 months and 1 year old, and maternal females with young kittens cared for dependent offspring < 6 months old.

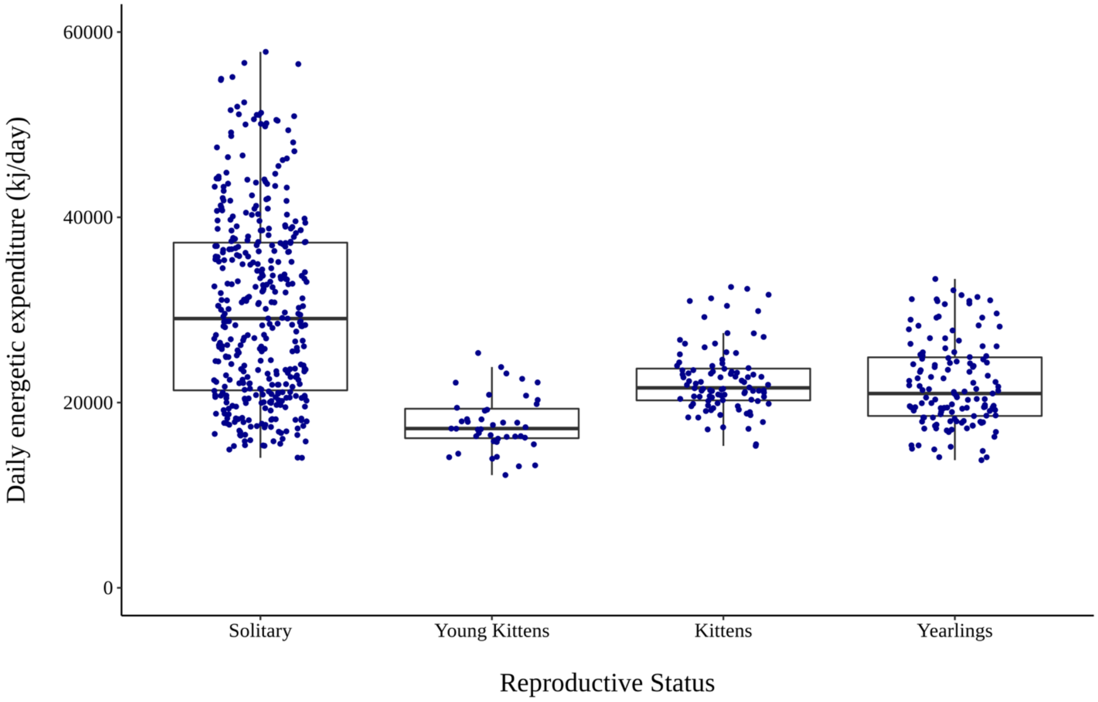


Figure 4.5. During GPS cluster searches, we noted natural sign left from large scavengers like grizzly bear, black bear, wolf and other cougars. We estimated the time spent handling from behavior phase identification and found that animals were spending more time on carcasses where large scavenger sign was detected (Panel A). Using seasonal consumption rates and proportion of carcasses with large scavenger sign showed that animals experiencing higher amounts of kleptoparasitism may be killing an excess amount prey to make up for biomass lost (Panel B).

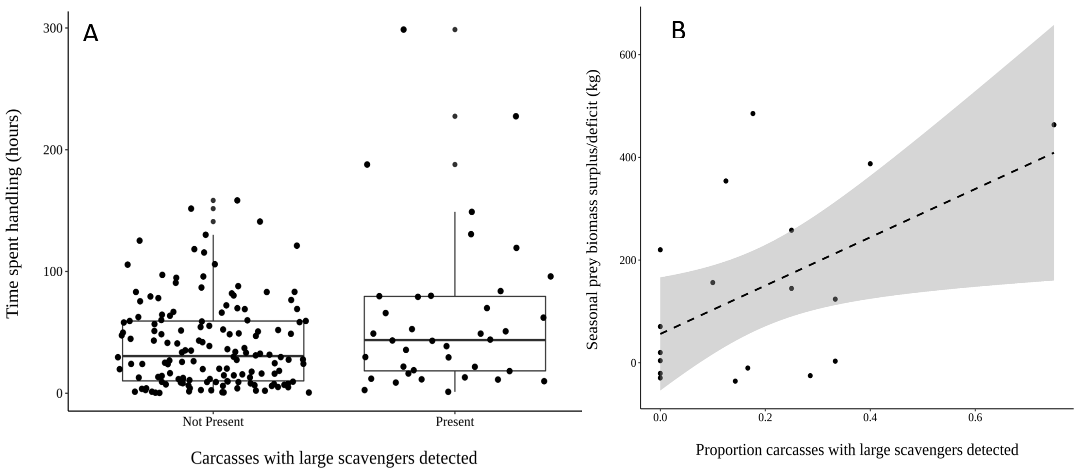
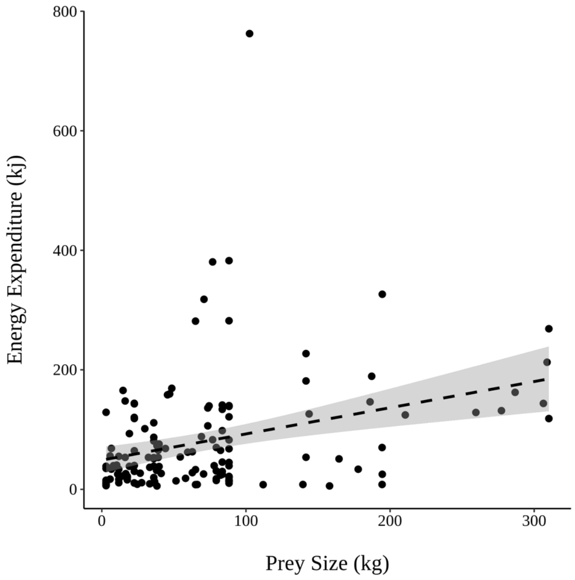


Figure 4.6. Cougar kills were identified using 1-minute behavior phase identification from animals fitted with tri-axial accelerometers. Prey killed were assigned weights given season- and species- specific growth information. Energy expenditure during kill surges was calculated and related to the prey size.



CHAPTER 4 Supplementary Information

Table S4.1. Cougar GPS cluster search results including carcasses detected per individual by each season.

Animal ID	Season	Year	Age	Sex	Clusters Searched	Clusters Not Searched	Clusters Total	Days Monitored	Carcasses
F202	Early Winter	2016	Adult	Female	20	9	29	32	9
F202	Later Winter	2016	Adult	Female	34	1	35	37	9
F202	Summer	2016	Adult	Female	33	0	33	61	12
F202	Later Winter	2017	Adult	Female	14	0	14	19	5
F202	Early Winter	2018	Adult	Female	24	0	24	30	6
F202	Later Winter	2018	Adult	Female	37	0	37	48	9
F202	Summer	2018	Adult	Female	60	0	60	62	18
F202	Later Winter	2019	Adult	Female	26	0	26	45	9
F202	Summer	2019	Adult	Female	66	1	67	74	13
F207	Later Winter	2017	Adult	Female	28	15	43	31	3
F207	Summer	2017	Adult	Female	40	4	44	62	18
F207	Later Winter	2018	Adult	Female	29	4	33	57	5
F209	Early Winter	2017	Adult	Female	27	0	27	33	6
F209	Later Winter	2017	Adult	Female	29	0	29	31	5
F209	Summer	2017	Adult	Female	96	1	97	70	31
F209	Later Winter	2018	Adult	Female	40	0	40	56	9
F209	Summer	2018	Adult	Female	79	1	80	72	13
M201	Later Winter	2016	Yearling	Male	42	4	46	59	8
Total					724	40	764	879	188

Table S4.2. Wolf GPS cluster search results.

Animal ID	Season	Year	Age	Sex	Pack	Clusters Searched	Clusters Not Searched	Clusters Total	Days Monitored	Carcasses	Confirmed Kills
993M	Late Winter	2016	Adult	Male	Lamar Canyon	82	3	85	29	13	8
1012M	Late Winter	2016	Subadult	Male	Prospect Peak	41	0	41	12	7	4
821F	Late Winter	2016	Adult	Female	Prospect Peak	75	7	82	29	16	13
994M	Summer	2016	Adult	Male	Junction Butte	236	33	269	81	38	26
994M	Early Winter	2016	Adult	Male	Loner	51	43	94	15	6	4
Total						485	86	571	166	80	55

Table S4.3. Prey Composition for cougars and wolves calculated from GPS cluster searches in Yellowstone National Park.

		Cougar		Wolf	
Prey Species	Sex-Age Clas	total	%	Total	%
Elk	Calves	55			
	Cows	13		10	
	Bulls	4		21	
	Unknown	6		20	
	Total	78	52.35%	51	63.75%
Mule deer	Fawns	30		3	
	Does	10			
	Bucks	1		1	
	Unknown	10		6	
	Total	51	34.23%	10	12.50%
Bison	Calves			5	
	Cows			2	
	Bulls			4	
	Unknown			1	
	Total	0	0.00%	13	16.25%
Pronghorn	Fawns	5		1	
	Does	1			
	Bucks				
	Unknown			1	
	Total	6	4.03%	2	2.50%
Bighorn Sheep	Fawns			1	
	Ewe				
	Rams				
	Unknown			1	
	Total	0	0.00%	2	2.50%
Moose	Calves			1	
	Cows				
	Bulls				
	Unknown				
	Total	0	0.00%	1	1.25%
Yellow-Bellied Ma	Adult	5			
	Unknown	4			
	Total	9	6.04%	0	0.00%
Red Fox	Adult	2			
	Unknown	1			
	Total	3	2.01%	0	0.00%
Coyote	Adult	1			
	Unknown				
	Total	1	0.67%	0	0.00%
Badger	Unkown			1	
	Total			1	1.25%
Unknown	Total	1	0.67%	0	0.00%
Total all prey		149		80	

Figure S4.1. Seasonal diet composition for wolves and cougars in Yellowstone National Park.

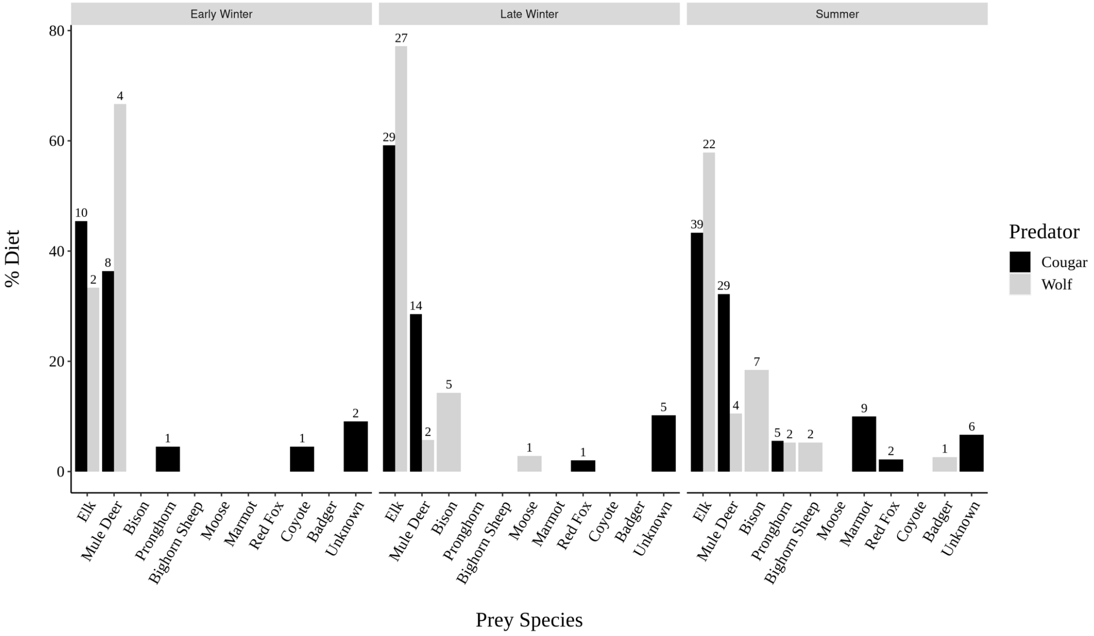


Figure S4.2. Cougar prey composition was primarily elk and mule deer. This figure displays age and sex-specific composition for cougar-killed elk and mule deer.

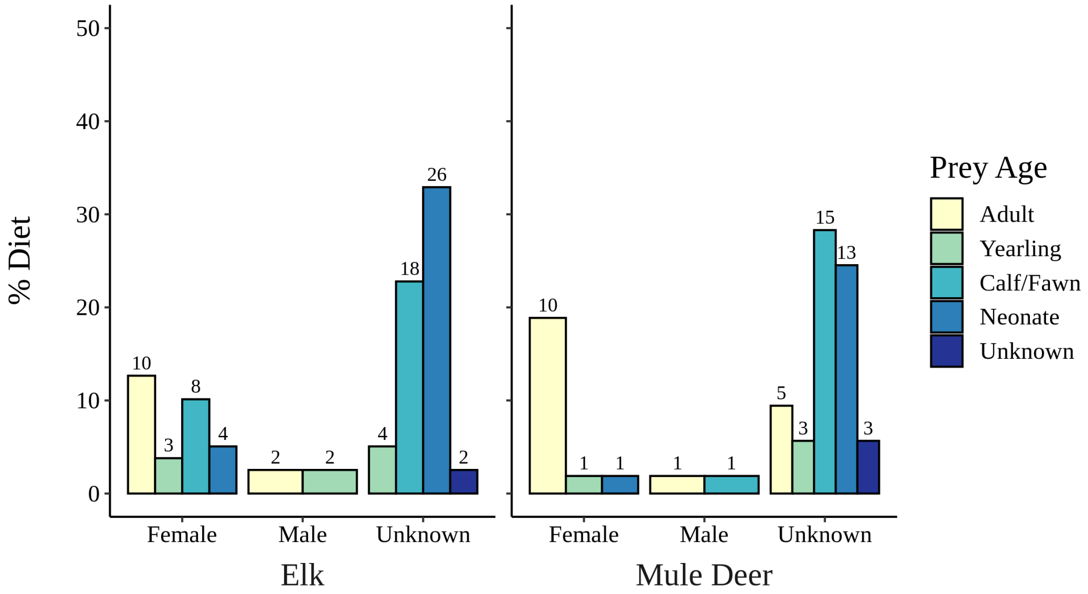


Figure S4.3. Wolf prey composition was primarily elk and bison, but for comparative purposes with Figure S2 we display age and sex-specific composition for wolf-killed elk and mule deer.

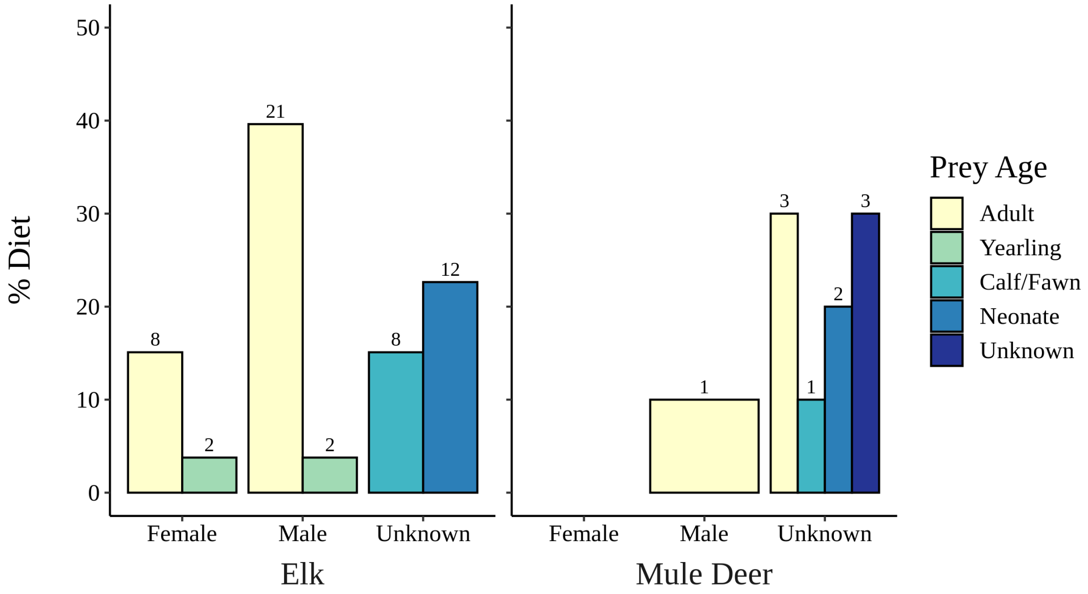
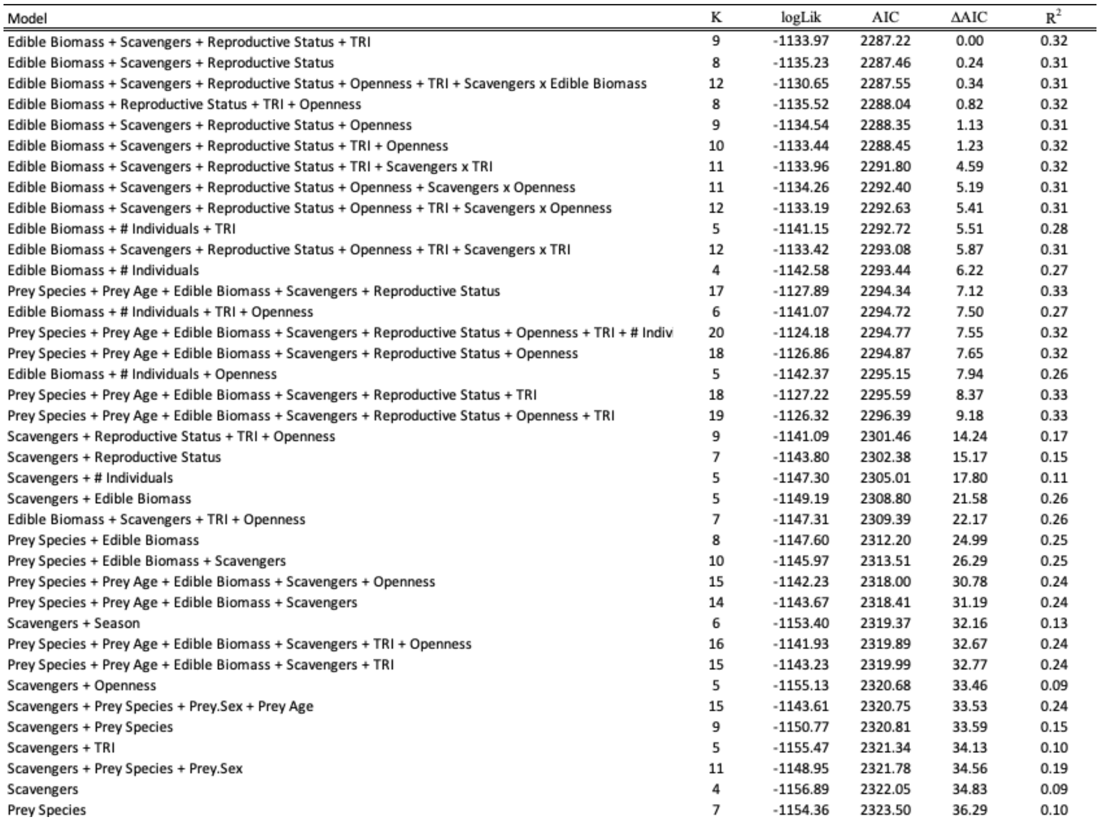


Table S4.4. Averaged coefficients from models within 4ΔAIC based on all models within of the top model testing for influence on kill surge ODBA.

	Cougar				Wolf			
Covariate	Coefficient	SE	Lower 95% CI	Higher 95% CI	Coefficient	SE	Lower 95% CI	Higher 95% CI
(Intercept)	0.48	0.02	0.43	0.53	1.14	0.06	1.02	1.27
Prey Size	0.12	0.02	0.07	0.17	0.07	0.07	-0.05	0.20
ODBA(5-min prior)	0.11	0.03	0.06	0.16	0.22	0.07	0.08	0.35
Openness	0.03	0.03	-0.02	0.08	-0.003	0.07	-0.13	0.13
TRI	-0.004	0.02	-0.05	0.04	-0.09	0.07	-0.23	0.04
Openness x TRI	-0.02	0.03	-0.07	0.03	-	-	-	-

Table S4.5. AIC model selection table for models determining influence of variables on cougar ODBA displayed during prey handling period.



Model	K	logLik	AIC	ΔAIC	R^2
Edible Biomass + Scavengers + Reproductive Status + TRI	9	-1133.97	2287.22	0.00	0.32
Edible Biomass + Scavengers + Reproductive Status	8	-1135.23	2287.46	0.24	0.31
Edible Biomass + Scavengers + Reproductive Status + Openness + TRI + Scavengers x Edible Biomass	12	-1130.65	2287.55	0.34	0.31
Edible Biomass + Reproductive Status + TRI + Openness	8	-1135.52	2288.04	0.82	0.32
Edible Biomass + Scavengers + Reproductive Status + Openness	9	-1134.54	2288.35	1.13	0.31
Edible Biomass + Scavengers + Reproductive Status + TRI + Openness	10	-1133.44	2288.45	1.23	0.32
Edible Biomass + Scavengers + Reproductive Status + TRI + Scavengers x TRI	11	-1133.96	2291.80	4.59	0.32
Edible Biomass + Scavengers + Reproductive Status + Openness + Scavengers x Openness	11	-1134.26	2292.40	5.19	0.31
Edible Biomass + Scavengers + Reproductive Status + Openness + TRI + Scavengers x Openness	12	-1133.19	2292.63	5.41	0.31
Edible Biomass + # Individuals + TRI	5	-1141.15	2292.72	5.51	0.28
Edible Biomass + Scavengers + Reproductive Status + Openness + TRI + Scavengers x TRI	12	-1133.42	2293.08	5.87	0.31
Edible Biomass + # Individuals	4	-1142.58	2293.44	6.22	0.27
Prey Species + Prey Age + Edible Biomass + Scavengers + Reproductive Status	17	-1127.89	2294.34	7.12	0.33
Edible Biomass + # Individuals + TRI + Openness	6	-1141.07	2294.72	7.50	0.27
Prey Species + Prey Age + Edible Biomass + Scavengers + Reproductive Status + Openness + TRI + # Indiv	20	-1124.18	2294.77	7.55	0.32
Prey Species + Prey Age + Edible Biomass + Scavengers + Reproductive Status + Openness	18	-1126.86	2294.87	7.65	0.32
Edible Biomass + # Individuals + Openness	5	-1142.37	2295.15	7.94	0.26
Prey Species + Prey Age + Edible Biomass + Scavengers + Reproductive Status + TRI	18	-1127.22	2295.59	8.37	0.33
Prey Species + Prey Age + Edible Biomass + Scavengers + Reproductive Status + Openness + TRI	19	-1126.32	2296.39	9.18	0.33
Scavengers + Reproductive Status + TRI + Openness	9	-1141.09	2301.46	14.24	0.17
Scavengers + Reproductive Status	7	-1143.80	2302.38	15.17	0.15
Scavengers + # Individuals	5	-1147.30	2305.01	17.80	0.11
Scavengers + Edible Biomass	5	-1149.19	2308.80	21.58	0.26
Edible Biomass + Scavengers + TRI + Openness	7	-1147.31	2309.39	22.17	0.26
Prey Species + Edible Biomass	8	-1147.60	2312.20	24.99	0.25
Prey Species + Edible Biomass + Scavengers	10	-1145.97	2313.51	26.29	0.25
Prey Species + Prey Age + Edible Biomass + Scavengers + Openness	15	-1142.23	2318.00	30.78	0.24
Prey Species + Prey Age + Edible Biomass + Scavengers	14	-1143.67	2318.41	31.19	0.24
Scavengers + Season	6	-1153.40	2319.37	32.16	0.13
Prey Species + Prey Age + Edible Biomass + Scavengers + TRI + Openness	16	-1141.93	2319.89	32.67	0.24
Prey Species + Prey Age + Edible Biomass + Scavengers + TRI	15	-1143.23	2319.99	32.77	0.24
Scavengers + Openness	5	-1155.13	2320.68	33.46	0.09
Scavengers + Prey Species + Prey.Sex + Prey Age	15	-1143.61	2320.75	33.53	0.24
Scavengers + Prey Species	9	-1150.77	2320.81	33.59	0.15
Scavengers + TRI	5	-1155.47	2321.34	34.13	0.10
Scavengers + Prey Species + Prey.Sex	11	-1148.95	2321.78	34.56	0.19
Scavengers	4	-1156.89	2322.05	34.83	0.09
Prey Species	7	-1154.36	2323.50	36.29	0.10

Table S4.6. AIC model selection table for models determining influence of variables on wolf ODBA displayed during prey handling period.

Model	K	logLik	AIC	ΔAIC	R^2
Scavengers + Edible Biomass	5	-623.29	1257.39	0.00	0.27
Edible Biomass + # of Individuals	4	-624.85	1258.24	0.85	0.25
Edible Biomass + # of Individuals + TRI	5	-623.97	1258.74	1.35	0.26
Edible Biomass + Scavengers + TRI + Openness	7	-622.11	1259.78	2.39	0.27
Edible Biomass + # of Individuals + Openness	5	-624.83	1260.46	3.07	0.24
Edible Biomass + # of Individuals + TRI + Openness	6	-623.96	1261.08	3.69	0.25
Edible Biomass + Scavengers + Reproductive Status + TRI	8	-621.97	1261.96	4.57	0.26
Edible Biomass + Scavengers + Reproductive Status	7	-623.26	1262.07	4.68	0.25
Edible Biomass + Reproductive Status + TRI + Openness	7	-624.02	1263.60	6.20	0.23
Edible Biomass + Scavengers + Reproductive Status + TRI + Scavengers x TRI	10	-620.40	1263.98	6.59	0.27
Edible Biomass + Scavengers + Reproductive Status + Openness	8	-623.17	1264.38	6.98	0.24
Edible Biomass + Scavengers + Reproductive Status + TRI + Openness	9	-621.94	1264.45	7.05	0.25
Edible Biomass + Scavengers + Reproductive Status + Openness + TRI + Scavengers x TRI	11	-620.04	1265.96	8.57	0.27
Edible Biomass + Scavengers + Reproductive Status + Openness + TRI + Scavengers x Openness	11	-621.06	1268.00	10.61	0.25
Prey Species + Edible Biomass	9	-624.00	1268.58	11.18	0.21
Edible Biomass + Scavengers + Reproductive Status + Openness + Scavengers * Openness	10	-622.76	1268.72	11.33	0.23
Prey Species + Edible Biomass + Scavengers	11	-622.61	1271.09	13.70	0.22
Prey Species + Prey Age + Edible Biomass + Scavengers	15	-621.91	1281.32	23.93	0.19
Prey Species + Prey Age + Edible Biomass + Scavengers + TRI	16	-620.44	1281.51	24.12	0.20
Prey Species + Prey Age + Edible Biomass + Scavengers + Openness	16	-621.82	1284.28	26.89	0.18
Prey Species + Prey Age + Edible Biomass + Scavengers + TRI + Openness	17	-620.43	1284.73	27.34	0.19
Prey Species + Prey Age + Edible Biomass + Scavengers + Reproductive Status + TRI	18	-620.17	1287.55	30.16	0.18
Prey Species + Prey Age + Edible Biomass + Scavengers + Reproductive Status	17	-621.89	1287.66	30.27	0.16
Prey Species + Prey Age + Edible Biomass + Scavengers + Reproductive Status + Openness	18	-621.78	1290.77	33.37	0.15
Prey Species + Prey Age + Edible Biomass + Scavengers + Reproductive Status + Openness + TRI	19	-620.11	1290.88	33.49	0.17
Prey Species + Prey Age + Edible Biomass + Scavengers + Reproductive Status + Openness + TRI + # of Individuals	20	-619.92	1294.08	36.69	0.16
Scavengers + Prey Species + Prey Sex	13	-654.75	1340.70	83.31	0.16
Scavengers + TRI	6	-664.37	1341.83	84.44	0.04
Prey Species	9	-660.86	1342.15	84.76	0.08
Scavengers	5	-667.69	1346.15	88.75	-0.02
Scavengers + Prey Species	11	-660.34	1346.35	88.96	0.07
Scavengers + Openness	6	-667.20	1347.48	90.09	-0.02
Scavengers + # of Individuals	6	-667.58	1348.24	90.85	-0.03
Scavengers + Reproductive Status + TRI + Openness	9	-664.02	1348.46	91.07	0.01
Scavengers + Season	7	-667.23	1349.94	92.55	-0.04
Scavengers + Prey Species + Prey Sex + Prey Age	17	-653.34	1349.96	92.56	0.14
Scavengers + Reproductive Status	7	-667.33	1350.13	92.73	-0.04

Table S4.7. Averaged coefficients from models within 4ΔAIC of top models for covariates influencing cougar and wolf ODBA while handling prey carcasses.

	Cougar				Wolf			
Covariate	Coefficient	SE	Lower 95% CI	Higher 95% CI	Coefficient	SE	Lower 95% CI	Higher 95% CI
(Intercept)	647.52	65.70	518.76	776.28	484.18	186.12	119.40	848.96
Edible Biomass	148.92	58.14	34.97	262.87	437.47	87.50	265.98	608.97
Small Scavengers	176.56	90.90	-1.61	354.73	-196.84	155.42	-501.46	107.78
Large Scavengers	73.46	109.16	-140.49	287.41	151.39	192.36	-225.63	528.42
Reproductive Status: Young Kittens	-316.61	149.71	-610.03	-23.18	-	-	-	-
Reproductive Status: Kittens	-241.09	122.78	-481.74	-0.45	-	-	-	-
Reproductive Status: Yearlings	-425.95	82.40	-587.46	-264.44	-	-	-	-
TRI	56.07	35.97	-14.42	126.56	-90.99	68.77	-225.78	43.80
Openness	39.41	39.17	-37.36	116.19	7.20	72.85	-135.59	149.99
Edible Biomass x Small Scavengers	294.78	130.01	39.97	549.59	-	-	-	-
Edible Biomass x Large Scavengers	68.84	90.24	-108.04	245.72	-	-	-	-
# of Individuals	-	-	-	-	11.49	24.85	-37.21	60.19

Table S4.8. Model selection table using AIC for models testing the influence of individual, group, prey, and spatial characteristics on cougar handling time.

Model	K	logLik	AIC	ΔAIC	R^2
Edible Biomass + Scavengers + Reproductive Status + TRI	9	-759.16	1537.59	0.00	0.32
Edible Biomass + Reproductive Status + TRI + Openness	8	-760.55	1538.11	0.52	0.32
Edible Biomass + Scavengers + Reproductive Status	8	-760.74	1538.49	0.90	0.31
Edible Biomass + Scavengers + Reproductive Status + TRI + Openness	10	-759.03	1539.62	2.03	0.32
Edible Biomass + Scavengers + Reproductive Status + Openness	9	-760.51	1540.29	2.70	0.31
Edible Biomass + Scavengers + Reproductive Status + TRI + Scavengers x TRI	11	-759.01	1541.91	4.32	0.32
Edible Biomass + Scavengers + Reproductive Status + Openness + TRI + Scavengers x Openness	12	-758.62	1543.49	5.91	0.31
Edible Biomass + # Individuals + TRI	5	-766.59	1543.58	6.00	0.28
Edible Biomass + # Individuals	4	-767.7	1543.67	6.08	0.27
Edible Biomass + Scavengers + Reproductive Status + Openness + TRI + Scavengers x TRI	12	-758.85	1543.95	6.36	0.31
Edible Biomass + Scavengers + Reproductive Status + Openness + TRI + Scavengers * Edible Biomass	12	-758.85	1543.95	6.37	0.31
Edible Biomass + Scavengers + Reproductive Status + Openness + Scavengers * Openness	11	-760.24	1544.36	6.78	0.31
Edible Biomass + # Individuals + TRI + Openness	6	-766.58	1545.74	8.15	0.27
Edible Biomass + # Individuals + Openness	5	-767.69	1545.8	8.21	0.26
Scavengers + Edible Biomass	5	-768.61	1547.64	10.05	0.26
Prey Species + Prey Age + Edible Biomass + Scavengers + Reproductive Status	17	-754.69	1547.95	10.36	0.33
Prey Species + Prey Age + Edible Biomass + Scavengers + Reproductive Status + TRI	18	-753.67	1548.49	10.90	0.33
Edible Biomass + Scavengers + TRI + Openness	7	-767.37	1549.51	11.93	0.26
Prey Species + Prey Age + Edible Biomass + Scavengers + Reproductive Status + Openness	18	-754.43	1550	12.42	0.32
Prey Species + Prey Age + Edible Biomass + Scavengers + Reproductive Status + Openness + TRI	19	-753.49	1550.73	13.15	0.33
Prey Species + Prey Age + Edible Biomass + Scavengers + Reproductive Status + Openness + TRI + # Individuals	20	-753.21	1552.84	15.25	0.32
Prey Species + Edible Biomass	8	-768	1553.02	15.43	0.25
Prey Species + Edible Biomass + Scavengers	10	-766.64	1554.84	17.25	0.25
Prey Species + Prey Age + Edible Biomass + Scavengers	14	-765.2	1561.46	23.87	0.24
Prey Species + Prey Age + Edible Biomass + Scavengers + TRI	15	-764.56	1562.65	25.06	0.24
Prey Species + Prey Age + Edible Biomass + Scavengers + Openness	15	-764.91	1563.36	25.77	0.24
Scavengers + Prey Species + Prey.Sex + Prey Age	15	-765.11	1563.74	26.16	0.24
Prey Species + Prey Age + Edible Biomass + Scavengers + TRI + Openness	16	-764.35	1564.74	27.15	0.24
Scavengers + Prey Species + Prey.Sex	11	-771.77	1567.43	29.85	0.19
Scavengers + Reproductive Status + TRI + Openness	9	-775.08	1569.42	31.83	0.17
Scavengers + Reproductive Status	7	-777.93	1570.64	33.06	0.15
Scavengers + Season	6	-779.82	1572.21	34.63	0.13
Scavengers + Prey Species	9	-776.52	1572.31	34.73	0.15
Scavengers + # Individuals	5	-782.38	1575.18	37.59	0.11
Scavengers + TRI	5	-782.78	1575.97	38.38	0.10
Scavengers	4	-784.63	1577.52	39.94	0.09
Scavengers + Openness	5	-783.82	1578.05	40.46	0.09
Prey Species	7	-782.32	1579.43	41.84	0.10

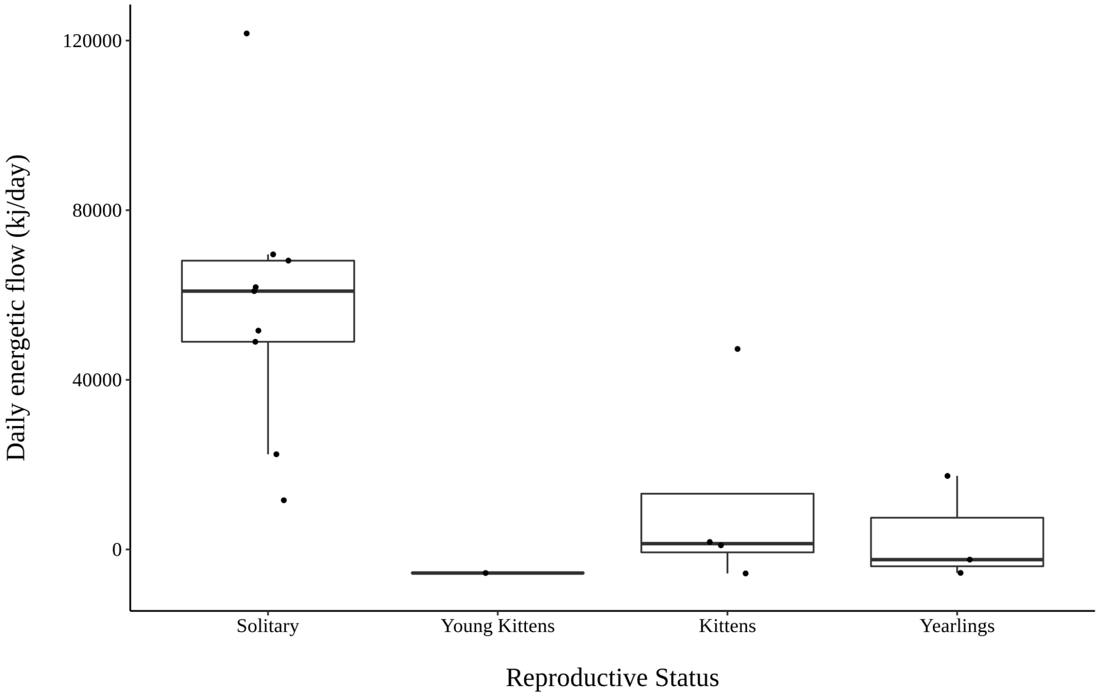
Table S4.9. Model selection table using AIC for models testing the influence of individual, group, prey, and spatial characteristics on wolf handling time.

Model	K	logLik	AIC	ΔAIC	R^2
Edible Biomass + Reproductive Status + TRI + Openness	7	-307.12	629.8	0.00	0.30
Edible Biomass + Scavengers + Reproductive Status + TRI	8	-306.61	631.25	1.45	0.30
Edible Biomass + Scavengers + Reproductive Status + TRI + Scavengers x TRI	10	-304.12	631.43	1.63	0.32
Edible Biomass + Scavengers + Reproductive Status	7	-308.34	632.24	2.43	0.28
Edible Biomass + # of Individuals + TRI + Openness	6	-309.59	632.33	2.53	0.26
Edible Biomass + # of Individuals + TRI	5	-310.99	632.79	2.99	0.25
Edible Biomass + # of Individuals	4	-312.23	632.98	3.18	0.24
Edible Biomass + # of Individuals + Openness	5	-311.23	633.27	3.47	0.24
Edible Biomass + Scavengers + Reproductive Status + TRI + Openness	9	-306.36	633.3	3.50	0.29
Scavengers + Edible Biomass	5	-311.31	633.44	3.64	0.24
Edible Biomass + Scavengers + Reproductive Status + Openness + TRI + Scavengers x TRI	11	-304.12	634.12	4.31	0.31
Edible Biomass + Scavengers + TRI + Openness	7	-309.33	634.21	4.41	0.26
Edible Biomass + Scavengers + Reproductive Status + Openness	8	-308.22	634.48	4.68	0.27
Edible Biomass + Scavengers + Reproductive Status + Openness + TRI + Scavengers x Openness	11	-305.67	637.22	7.42	0.29
Edible Biomass + Scavengers + Reproductive Status + Openness + Scavengers x Openness	10	-307.95	639.08	9.28	0.25
Prey Species + Edible Biomass	9	-311.42	643.41	13.61	0.20
Prey Species + Edible Biomass + Scavengers	11	-308.88	643.63	13.83	0.23
Prey Species + Prey Age + Edible Biomass + Scavengers	15	-307.42	652.33	22.53	0.21
Prey Species + Prey Age + Edible Biomass + Scavengers + Reproductive Status + TRI	18	-302.7	652.61	22.81	0.26
Prey Species + Prey Age + Edible Biomass + Scavengers + Reproductive Status	17	-304.91	653.7	23.90	0.23
Prey Species + Prey Age + Edible Biomass + Scavengers + TRI	16	-306.63	653.89	24.09	0.21
Prey Species + Prey Age + Edible Biomass + Scavengers + Openness	16	-306.88	654.4	24.60	0.21
Prey Species + Prey Age + Edible Biomass + Scavengers + TRI + Openness	17	-305.81	655.5	25.70	0.22
Prey Species + Prey Age + Edible Biomass + Scavengers + Reproductive Status + Openness + TRI	19	-302.55	655.76	25.96	0.25
Prey Species + Prey Age + Edible Biomass + Scavengers + Reproductive Status + Openness	18	-304.85	656.91	27.11	0.22
Prey Species + Prey Age + Edible Biomass + Scavengers + Reproductive Status + Openness + TRI + # of Individuals	20	-302.5	659.24	29.44	0.24
Scavengers + Prey Species + Prey Sex	13	-322.26	675.72	45.91	0.22
Scavengers + TRI	6	-331.94	676.97	47.16	0.11
Scavengers + Season	7	-331.13	677.73	47.93	0.11
Scavengers + Reproductive Status + TRI + Openness	9	-328.68	677.8	48.00	0.14
Scavengers	5	-334.28	679.34	49.54	0.07
Scavengers + # of Individuals	6	-333.32	679.73	49.93	0.08
Scavengers + Reproductive Status	7	-332.21	679.88	50.08	0.09
Scavengers + Openness	6	-334.14	681.38	51.58	0.06
Scavengers + Prey Species	11	-328.12	681.9	52.10	0.13
Scavengers + Prey Species + Prey Sex + Prey Age	17	-320.37	684.02	54.22	0.21
Prey Species	9	-332.27	684.96	55.16	0.07

Table S4.10. Averaged coefficients from models within 4ΔAIC of top models for covariates influencing cougar and wolf handling time for prey carcasses.

	Cougar				Wolf			
	Coefficient	SE	Lower 95% CI	Higher 95% CI	Coefficient	SE	Lower 95% CI	Higher 95% CI
(Intercept)	55.43	5.44	44.77	66.09	18.61	5.93	6.99	30.22
Edible Biomass	20.78	3.48	13.95	27.61	7.27	1.75	3.84	10.70
Small Scavengers	10.41	7.69	-4.66	25.47	4.01	3.45	-2.75	10.78
Large Scavengers	10.68	8.89	-6.74	28.11	4.47	3.93	-3.22	12.17
Reproductive Status: Young Kittens	-8.56	12.41	-32.89	15.77	-	-	-	-
Reproductive Status: Kittens	-7.66	10.41	-28.06	12.74	-	-	-	-
Reproductive Status: Yearlings	-28.22	7.01	-41.95	-14.49	-	-	-	-
TRI	5.06	3.03	-0.89	11.01	-2.09	1.58	-5.20	1.01
Openness	1.01	3.32	-5.50	7.52	-1.51	1.53	-4.50	1.49
Small Scavengers x TRI	-	-	-	-	-4.86	3.41	-11.54	1.82
Large Scavengers x TRI	-	-	-	-	-6.53	3.49	-13.37	0.31
# of Individuals	-	-	-	-	-0.91	0.51	-1.91	0.08
Reproductive Status: Adults	-	-	-	-	7.92	6.25	-4.33	20.18
Reproductive Status: Young Kittens	-	-	-	-	-3.28	5.26	-13.58	7.02

Figure S4.4. Calculated daily energy deficits (kj/day) using daily energetic expenditure (DEE; kj/day) and and daily energetic consumption (DEC; kj/day) from consumption rates gained from GPS cluster searches for cougars in Yellowstone National Park.



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