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GOLDEN EAGLE RESOURCE SELECTION AND ENVIRONMENTAL DRIVERS OF REPRODUCTION IN THE NORTHERN RANGE OF YELLOWSTONE NATIONAL PARK

By

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Golden Eagle Resource Selection and Environmental Drivers of Reproduction in the Northern Range of Yellowstone National Park

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ABSTRACT

In the United States (US), National Parks are considered the "crown jewels" of protected lands. However, the importance of National Parks to wildlife populations and the species that inhabit them is not often quantified, thus, requiring a better understanding of National Parks as a conservation tool. Golden eagles (*Aquila chrysaetos*) are a North American species of conservation concern and territories in the northern range of Yellowstone National Park (YNP) are relatively dense. However, average reproductive rates over the past ten years (2011-2020) have been low (productivity = 0.34, nest success = 28%). The contrast of high density and low reproduction has stimulated questions regarding what environmental factors limit reproductive success. The overall objective of this study is to identify spatial and temporal components of golden eagle habitat that explain reproductive demographics in YNP's northern range. To accomplish, I first examined resource selection at multiple spatial scales during two seasonal periods influential to reproduction. I found that golden eagles select home ranges in areas with low forest cover and in close proximity to open water. Within the home range I found that golden eagles select for increasingly rugged topography and upper slopes increasing to ridgelines. Additionally, I found weak evidence that eagles are selecting prey habitat based on season. I then used the resource selection analysis findings coupled with yearly weather variation to examine their effects on nest initiation/egg-laying and successfully fledging nestlings. Results indicate that increasing occasions of prolonged precipitation and severe weather negatively influence both nest initiation and success. I found weak evidence that home ranges with more rugged terrain and territories in closer proximity to neighboring territories positively influence nest success. The resource selection analysis reaffirms the importance of increased openness and topography near prey habitat on eagle presence and daily needs. Overall, my study advances our understanding of the drivers of low reproductive rates of golden eagles in the northern range of YNP. Harsh weather negatively influences nest initiation and success with weak evidence of a positive effect for spatially distributed resources. Given the potential consequences of low reproductive success in YNP, research will need to address other life-history stages to better understand population status.

Table of Contents

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List of Tables

(2011-2019). *Note:* π represents the probability that a nonbreeder (A) is correctly identified as a nonbreeder (pA). Posterior means, standard deviations (SD), 95% credible intervals (CRI), and Rhat.

Table 2.5 Period specific summaries (mean and standard deviation [SD]) for covariates included in models for apparent nest initiation and nest success. TMAX (maximum temperature °C), SWE (snow water equivalence kg/m^2), PRCP2 (# of occasions with precipitation on two or more consecutive days), PRCP3 (# of occasions with precipitation on three or more consecutive days), Severe (Relative to period, # of days with precipitation ≥ 1 SD above mean and max temperature ≤ 1 SD below the mean), TRI (terrain ruggedness index), TPI (topographical position index), Cougar (probability of successful cougar kill), Biomass (edible biomass (kg), acquired per wolf per day), NND (distance (m) between nearest neighboring eagle territory centers).

Table 2.6 Winter period variable (centered and scaled) coefficient estimates on the probability of apparent nest initiation are reported as log odds. Posterior means, standard deviations (SD), 95% credible intervals (CRI), posterior f value (f), and Rhat. *Note*: f is the probability that the true sign of the effect is equal to the sign of the mean effect. TMAX (winter period mean maximum temperature °C), SWE (winter period mean snow water equivalence kg/m^2), PRCP2 (# of occasions with precipitation on two or more consecutive days during winter period), PRCP3 (# of occasions with precipitation on three or more consecutive days during winter period), Severe (# of days with winter period precipitation ≥ 6.5mm and max temperature ≤ 1 -6.4 °C), TRI (terrain ruggedness index), TPI (topographical position index), Cougar (probability of successful cougar kill), Biomass (edible biomass (kg), acquired per wolf per day), NND (distance (m) between nearest neighboring eagle territory centers).

Table 2.7 Nest initiation period variable (centered and scaled) coefficient estimates on the probability of nest success are reported as log odds. Posterior means, standard deviations (SD), 95% credible intervals (CRI), posterior f value (f), and Rhat. *Note*: f is the probability that the true sign of the effect is equal to the sign of the mean effect. TMAX (nest initiation period mean maximum temperature °C), SWE (nest initiation period mean snow water equivalence kg/m^2), PRCP2 (# of occasions with precipitation on two or more consecutive days during nest initiation period), PRCP3 (# of occasions with precipitation on three or more consecutive days during nest initiation period), Severe (# of days with nest initiation period precipitation ≥ 6.5mm and max temperature ≤ -0.5 °C), TRI (terrain ruggedness index), TPI (topographical position index), Cougar (probability of successful cougar kill), Biomass (edible biomass (kg), acquired per wolf per day), NND (distance (m) between nearest neighboring eagle territory centers).

Table 2.8 Incubation period variable (centered and scaled) coefficient estimates on the probability of nest success are reported as log odds. Posterior means, standard deviations (SD), 95% credible intervals (CRI), posterior f value (f), and Rhat. *Note*: f is the probability that the true sign of the effect is equal to the sign of the mean effect. SWE (incubation period mean snow water equivalence kg/m^2), PRCP2 (# of occasions with precipitation on two or more consecutive days during incubation period), PRCP3 (# of occasions with precipitation on three or more consecutive days during incubation period), TRI (terrain ruggedness index), TPI (topographical position index), Cougar (probability of successful cougar kill), Biomass (edible biomass (kg), acquired per wolf per day), NND (distance (m) between nearest neighboring eagle territory centers).

List of Figures

consecutive days during incubation period), PRCP3 (# of occasions with precipitation on three or more consecutive days during incubation period). (A & B) TRI (terrain ruggedness index), TPI (topographical position index), Cougar (probability of successful cougar kill), Biomass (edible biomass (kg), acquired per wolf per day), NND (distance (m) between nearest neighboring eagle territory centers).

Introduction

Biodiversity is decreasing across the globe (Sala et al. 2000, Munns 2006). One strategy employed to curtail diminishing biodiversity has been the designation of areas for conservation. Over 200,000 protected areas worldwide conserve approximately 15% of the earth's terrestrial surface, constituting significant resource allocations (Chape et al. 2005, UNEP-WCMC and IUCN 2016). The protected areas buffer portions of the world's natural environments from a growing list of anthropogenic threats. Examples include the proliferation of environmental contaminants, fragmentation of landscapes, and introduction of highly competitive exotic species (Sala et al. 2000, Munns 2006). Designating areas for conservation is a successful large scale conservation strategy when areas are systematically and strategically located (Zuidema et al. 1996, Knight and Cowling 2007). However, history has biased the world's network of conservation areas toward infertile and rugged landscapes since factors driving selection and implementation are typically not biological or predictable, rather economical, social, and political (Knight and Cowling 2007).

The highest tier of protection outlined by the International Union for Conservation of Nature is the designation of strict nature reserves and wilderness areas (Dudley 2008). In the United States (US), National Parks are the "crown jewels" of protected lands and, in many cases, have designated wilderness within their boundaries, significantly limiting direct human impact to these environments. Yellowstone National Park (YNP), established in 1872, set forth this model for landscape preservation that has been adopted by countries throughout the world. National Parks inspire people to appreciate the intrinsic value of natural environments and the diversity of species they support. However, their importance to wildlife populations and the species that inhabit them is not often quantified. Further, knowledge of how wildlife within National Park boundaries contributes to broader populations is frequently lacking.

Biodiversity in National Parks is vulnerable, regardless of the regulations that limit direct human impacts within their boundaries. Development of surrounding areas can potentially isolate portions of the landscape, resulting in population declines associated with the insular effects of land-bridge islands (Diamond 1972, Wilson and Willis 1975, Newmark 1995). Evidence suggests the rates of local extinction for specific mammals in US National Parks exceed the rates of colonization (Newmark 1995), suggesting that there is a need for a better understanding of National Parks as a conservation tool for the diversity of species that inhabit them.

YNP has made significant efforts to conserve and promote wildlife populations. A few of the more notable efforts include: 1) the conservation of the last wild population of plains bison (*Bison bison*) (White et al. 2015), 2) the resurgence of grizzly bear (*Ursus arctos*) populations (van Manen et al. 2017), 3) the restoration of native trout populations (YCR 2011), and 4) the reintroduction of gray wolves (*Canis lupus*). YNP has also monitored a suite of resident and migratory bird species (Baril et al. 2011, Walker et al. 2020). Part of this effort has captured the population resurgence of bald eagles (*Haliaeetus leucocephalus*), osprey (*Pandion haliaetus*), and peregrine falcons (*Falco peregrinus*) from the effects of widespread organochlorine pesticide use (Anderson 1972, Baril et al. 2015). In recent years, YNP has initiated multiple monitoring efforts to address species and communities of conservation concern.

Golden eagles (*Aquila chrysaetos*) are a North American species of conservation concern (USFWS 2008). Population trend estimates in North America are variable, allowing for uncertainty in population trajectory. Some studies suggest population declines (Kochert and Steenhof 2002, Hoffman and Smith 2003, USFWS 2016), while others suggest stable (Millsap et al. 2013, Nielson et al. 2014, USFWS 2016) or increasing populations (Crandall et al. 2015). However, much of this work does not account for reproductive rates or span an appropriate amount of time to identify accurate population trends. Kochert and Steenhof (2002) identified only four long term studies (e.g., > 20 years) of nesting golden eagles in North America. Except for a stable population in Alaska, declines reported in other areas are attributed to the impacts of fire on prey habitat, increased change in land use, and urbanization. Current concerns about the population status of golden eagles across the western US have focused on their interaction with energy development (e.g. wind, gas), human activity (Hunt 2002, Watson 2010, Pagel et al. 2013, Tack and Fedy 2015), and environmental contaminants (e.g. lead, poison for pest control; Bortolotti 1984, Newton 1998, Herring et al. 2017, Katzner et al. 2018). Recent demographic analyses have shown that any additive mortality posed by an increase in anthropogenic threats is likely to trigger population declines or exacerbate any declines that may be ongoing (Tack et al. 2017; Wiens et al. 2017, 2018).

Due to these growing concerns for the population status of golden eagles in North America, YNP initiated a territory survey and reproductive monitoring program in 2011. The ongoing effort has identified a minimum of 28 territories, 20 of which are in the northern range of YNP (Figure 1.1). The resulting density in the northern range (approximately one territory per 50 km^2) is relatively high compared to other North

American populations (one territory per 18.5-252 km^2; Katzner et al. 2020). Likewise, territory occupancy rates have been consistently high (100% occupancy, 2011-2020).

In contrast to territory occupancy rates, productivity, defined as the total number of young fledged per occupied territory, and nest success, defined as the percent of occupied territories that fledge at least one nestling, has been low, with an observed average of 0.34 (SD = 0.24) and 28% (SD = 19%), respectively (Figure 1.2; Walker et al. 2020, Haines unpubl. data). Low productivity results from apparent infrequent nesting attempts and high nest failure rates (Baril et al. 2017). On unprotected private and public lands to the north (Livingston, MT, Crandall et al. 2015) and east (Big Horn Basin, WY, Preston et al. 2017) of YNP, golden eagle densities are similar but have substantially higher productivity. In Livingston, productivity is 0.67 (2010-2016, Crandall et al. 2015), while in the Big Horn Basin, it is 0.81 (2009-2016, Preston et al. 2017). The observed difference in reproduction is likely due to variation of prey and weather across the region, but is confounded with eagle density, which may be expected to vary in response to habitat differences.

Golden eagle reproduction is commonly correlated with prey abundance, often interacting with weather (Bates and Morretti 1994, Steenhof et al. 1997, Watson 2010, McIntyre and Schmidt 2012, Preston et al. 2017, Schmidt et al. 2018, Katzner et al. 2020). Carrion is widely recognized as an important golden eagle food resource during the winter months, including early breeding season. However, the importance of carrion to individual eagle life history traits varies across their range, and is dependent on the abundance of live prey and winter conditions that influence the availability of food resources (Watson 2010, Katzner et al. 2020). In YNP, most prey species identified at nest sites are unavailable prior to egg-laying (Haines unpubl. data), suggesting carrion as an important food source in winter.

Prior to carnivore recovery (e.g. wolf reintroduction, cougar (*Puma concolor*) recolonization, and grizzly bear increase), the northern Yellowstone elk herd numbered at least 19,000 individuals in the mid-1990s (Evans et al. 2006). With no primary predator to exhibit top down population control, the overabundant elk herd commonly experienced considerable die-offs as a result of limited resources in severe winters. The timing of these abundant winter die-offs occurred roughly when golden eagles initiate nesting (late February to early April), presumably, providing a reliable food source for eagles at a much-needed time. Today, the northern elk herd numbers around 6,000 – 8,000 individuals (NYCWWG 2018) and winter elk die-off events are consequently less abundant, leaving large carnivores as the primary contributor of carrion to the landscape. Therefore, the abundance of carnivore contributed carrion may not match historic winter die-offs. It may be that current eagle densities in YNP's northern range are a historical relict reflecting food abundance of the past and the low eagle reproductive rates may be a response to the decrease in carrion availability. There are potential population-level consequences to low productivity of YNP eagles, suggesting a need to understand better local dynamics and ultimately aid in our understanding of demography in YNP and across the region.

The overall objective of this study is to identify spatial and temporal components of golden eagle habitat that influence reproductive demographics in YNP's northern range. I address four specific objectives. First, I estimate golden eagle home-range at multiple spatial and temporal scales from a sample of territorial individuals. Second, given that home range is a decision-making process shaped by natural selection to increase fitness (Powell and Mitchell 2012), I use home-range estimates to analyze the selection of habitat components across multiple spatial and temporal scales. Third, using findings from the first and second objectives, I identify the variability of resources selected by eagles across all territories in the study area. Fourth, I use the findings from the first three objectives, coupled with yearly weather variation, to address their effects on nest initiation/egg-laying and successfully fledged nestlings. The study identifies limitations to golden eagle reproduction by accounting for the effects of weather and variation in resources at the territory, thus contributing to our knowledge of habitat and reproductive demographics.

Chapter 1: Golden Eagle Resource Selection at Multiple Spatial and Temporal Scales in Yellowstone National Park's Northern Range

Introduction

Fundamental to species conservation is understanding how species use their habitat. Habitat is defined here as the species-specific resources and conditions present in an area that drives occupancy, survival, and reproduction (Hall et al. 1997). As such, wildlife management uses current knowledge of how species interact with available resources (Morrison et al. 2012). Habitat quality refers to the ability of the environment to provide conditions appropriate for individual and population persistence (Hall et al. 1997). Natural selection should then favor the ability of individuals to distinguish between high- and low-quality habitat (Clark and Shutler 1999, Johnson 2007). Therefore, identifying resources selected by individuals can provide inference for habitat quality across species populations.

Resource selection is the use of resources relative to their availability (Johnson 1980, Manly et al. 2002) assessed across multiple spatial and temporal scales. Johnson (1980) outlined four hierarchical orders of selection, analogous with spatial scale: species geographical range (first order), selection of home range (second order), selection of habitat components within home range (third order), and selection of specific items within habitat components (fourth order). Temporal scale can include time of day, seasonality, and variation among years. Importantly, these two dimensions of scale are not independent, and what scale we measure the effect of resources on selection is question dependent (Boyce 2006). For example, the northern spotted owl (*Strix occidentalis caurina*), a species synonymous with old-growth forests, shows strong selection for old-growth forests at the first and second order, however, weak to no selection for old-growth at the third. Therefore, an important consideration of spatial scale is resolution or sample-unit size (e.g. how finely a resource unit or covariate is measured), since large resolution can negate habitat heterogeneity (Boyce 2006). Further, examining selection at multiple spatial scales reveals the hierarchical process of selection and helps to identify important resources that may be interpreted differently if only measured at a single scale (e.g. no effect, opposite slopes; Rettie and Messier 2000, Boyce et al. 2003).

Golden eagles (*Aquila chrysaetos*) are widely distributed across the northern hemishphere (Watson 2010), and are typically associated with rugged topography and wide-open landscapes. When available, they exploit medium sized mammals and birds (hares, rabbits, marmots, ground squirrels, grouse, waterfowl), young ungulates, reptiles, and carrion (Watson 2010). In North America, golden eagles are a species of conservation concern (USFWS 2008). Population trend estimates are variable, allowing for uncertainty in population trajectory. Some studies suggest population declines (Kochert and Steenhof 2002, Hoffman and Smith 2003, USFWS 2016), while others suggest stable (Millsap et al. 2013, Nielson et al. 2014, USFWS 2016) or increasing populations (Crandall et al. 2015). Current concerns about the population status of golden eagles across the western US have focused on their interaction with energy development (e.g. wind, gas), human activity (Hunt 2002, Watson 2010, Pagel et al. 2013, Tack and Fedy 2015), and environmental contaminants (e.g. lead, poison for pest control) (Bortolotti 1984, Newton 1998, Herring et al. 2017, Katzner et al. 2018).

The northern range of Yellowstone National Park (YNP) contains a relatively dense local population of territorial golden eagles (YNP Golden Eagle Project [YNPGEP] unpubl. data). Since 2011, 20 territories have been identified within this area of the park (Figure 1.1). Golden eagles in the northern range have experienced low reproductive rates over the last ten breeding seasons. Productivity, defined as the total number of young fledged per occupied territory, and nest success, defined as the percent of occupied territories that fledge at least one nestling, has been low, with an observed average of 0.34 (SD = 0.24) and 28% (SD = 19%), respectively (Figure 1.2; Walker et al. 2020, YNPGEP unpubl. data). The average productivity in YNP is less than half of what has been observed in neighboring areas (Crandall et al. 2015, Preston et al. 2017).

Home range behavior is a presumed decision-making process shaped by natural selection to increase fitness (Powell and Mitchell 2012). The presence of raptors is strongly dependent on the availability of prey and nesting substrate (Newton 1979). For most raptors, home range, defined as an area routinely used by an animal to meet its daily needs (Burt 1943, Fieberg and Börger 2012, Powell and Mitchell 2012), is the restricted area that contains the nest, hunting range, and seasonally defended nesting territory (Watson 2010). The nesting territory is the area that contains, or historically contained, one or more nests within the home range of a mated pair (Steenhof et al. 2017). On average, in YNP and elsewhere, some golden eagle territories are consistently more productive than others (Steenhof et al. 1997, McIntyre 2002), offering support for differences in habitat quality across home ranges. Therefore, identification of the resources golden eagles select may provide insight into what components of golden eagle habitat drive reproduction in YNP.

To aid in understanding golden eagle reproduction in YNP's northern range I empirically identified habitat components selected by eagles during seasonal periods influential to reproduction. Additionally, given the potential variation in habitat quality at the home range, I identified how resources eagles select vary between individual home ranges. As a function of extreme seasonal variation in weather (e.g. winter and summer), resources vary significantly. This variation is predicted to influence the physical condition of female eagles prior to egg-laying (Newton 1979), and thus, the ability to successfully rear and fledge nestlings. Therefore, I hypothesized that the area used by an eagle and the resources selected would vary as a function of the seasonal period, given the disparity of available resources between time of egg-laying (late March to early April), incubation, and the rearing of nestlings (early April to late July). I predicted 1) as a function of season, eagles will select resources associated with prey habitat components, and 2) independent of season, eagles will select topographic features known to promote flight, territory defense, and nesting substrate. The study informs park management of what resources in YNP influence golden eagle presence on the landscape. Further, it identifies resources selected for daily activity and needs across two seasonal periods that influence reproductive success.

Study Area

The study was conducted on the ~1,000 km^2 portion of the northern range within the protected boundaries of YNP (Figure 1.1). Elevation varies from ~1,600 m in valleys and canyons to greater than 3,000 m along mountain ridges and peaks (Despain 1990). Forested areas of the northern range consist of Douglas fir (*Pseudotsuga menziesii*) and lodgepole pine (*Pinus contorta*) at the low elevation with subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*) at high elevation. Non-forested areas are dominated by big sagebrush (*Artemesia tridentata*) and Idaho fescue (*Festuca idahoensis*). Climate is characterized by long, cold winters and short, cool summers with average precipitation of 40-75 cm across the elevational gradient (Despain 1990). Within this area, golden eagles nest primarily on cliffs, and preliminary data from the last nine years suggests that golden eagle diet may be composed primarily of carrion in the non-breeding season (Haines pers. obs.). During the breeding season, prey includes Sciurids (e.g., ground squirrels and marmots), ungulate fawns, grouse, and other bird species (Baril et al. 2017). From the collection of prey remains and motion-triggered cameras at the nest, the specific prey species detected most frequently during the breeding season are yellow-bellied marmot (*Marmota flaviventris*), dusky grouse (*Dendragapus obscurus*), and Uinta ground squirrel (*Urocitellus armatus*; Haines unpubl. data).

Methods

Golden Eagle Capture and Telemetry Deployment

To estimate seasonal home-ranges and evaluate resource selection of golden eagles in YNP, I conducted capture efforts for territorial individuals. Capture occurred during December 2018, and January, February, and December 2019. I used a remote-triggered bow-net (Jackman et al. 1994) and net launcher (Trapping Innovations, L.L.C., Jackson, WY, US) baited with road-killed carrion to lure eagles. The bow-net and net launcher were camouflaged using the surrounding vegetation and snow with carrion secured to capture eagles. Trap sites were located ≤ 3 km from known nest sites to minimize the capture of non-target individuals. Manipulation at the trap site was done during dark hours of morning and night to prevent onlooking eagles from becoming wary. Active trap sites were monitored ≤ 1.5 km away using 10x42 binoculars and 20-60x80 spotting scopes. Once eagles were positioned correctly at the trap site, traps were manually triggered using a remote radio-control.

I outfitted eagles with 70 g solar GPS/Argos PTT transmitters (Microwave Telemetry Inc., Columbia, Maryland, US), applied using a break-away backpack style attachment with non-abrasive Teflon® ribbon. Weights of eagles captured in YNP ranged from 3900 to 5800 g. Thus, the transmitters were < 3% of body weight, which is the standard accepted maximum (Gustafson et al. 1997). The transmitters collect a maximum of one location every hour for 15 hours/day. Captured eagles received a USGS leg band and a unique alphanumeric visual identification leg band.

Seasonal Periods

Given the extreme temporal variation of weather and prey resources throughout the annual cycle in YNP, it is expected that area used by an eagle (Watson et al. 2014) and the resources selected will vary in response. Therefore, before estimating seasonal home range for all individuals, I first identified winter and spring/summer (hereafter, summer) periods. Winter began November 15 and ended March 10. During this time, weather conditions are relatively constant, with low temperatures and precipitation primarily in the form of snow). Additionally, much of the live prey golden eagles consume (e.g. marmots, ground squirrels) is not available in winter. I defined the summer period from March 11 to August 5. Golden eagles in YNP initiate egg-laying near the end of March (YNPGEP unpubl. data) and nesting behavior limits the amount of area used with most eagle activity near the nest site at this time. The end date is based on mean annual fledge dates between middle and late July, with observations as late as early August (YNPGEP unpubl. data).

Censoring Data

Golden eagle foraging activity and defense is diurnal (Katzner et al. 2020). Therefore I was interested in selection during daylight hours. Given the decreased hours of daylight in winter, dark hours can account for many location data points. Additionally, location data from dark hours can bias estimates of selection toward resources close to roost sites. I defined the start and end of daylight hours with the end of sunrise and the start of sunset. I used the R (R Core Team 2019) package *suncalc* (Thieurmel and Elmarhraoui 2019) to censor data to daylight hours. Additionally, I removed inaccurate locations resulting from insufficient GPS fixes by visually inspecting the data over a map of the region.

Home Range Resource Selection

I used the use-available design for estimating selection of home range location (i.e. 2nd order selection) following DeCesare et al. (2012) that compares individual seasonal home ranges (used) to the population seasonal home range (available). Analyses were implemented in program R (R Core Team 2019) using base functions and specific R packages. I first separated location data from tracked individuals into the seasonal periods. Then I estimated home range for all individuals using a kernel density estimator (KDE). KDE estimates > 95% are areas that eagles may have only visited briefly or areas used while moving between specific portions of their home range and overestimate home range area. Therefore, I estimated seasonal home range for each individual (used) using a 95% KDE with the *adehabitatHR* package (Calenge 2006). To identify used resources for each individual home range, I randomly sampled locations equal to the approximate mean number of GPS fixes collected per individual within each 95% KDE. To estimate population home range (available), I pooled locations for all individuals and estimated a 99% KDE for each season. To ensure that individual home range estimates (used) were within the population home range (available), I buffered the 99% KDE by 7000 m. To identify available resources for each individual I randomly sampled locations equal to approximately four times the mean number of GPS fixes collected per individual within the population home range. I then extracted covariate values for all used and available points from a geo-referenced raster stack using the *raster* package (Hijmans 2019).

Within Home Range Resource Selection

To estimate resource selection within the home range (i.e. 3rd order selection) I followed a use-available design that compares GPS locations from tracked individuals (used) to randomly sampled locations within the home range (available; Manly et al. 2002). I first extracted covariate values from the season-specific locations of tracked individuals (used). I then randomly sampled 2,000 points within the 95% KDE seasonal home range estimates for all tracked individuals and extracted covariate values (available). Covariate values for 3rd order selection were from the same raster stack used for 2nd order selection using the *raster* package (Hijmans 2019).

Resource Covariates

Typically, golden eagles are associated with rugged topography, hunting wide open landscapes dominated by short vegetation and restricted tree cover (Watson 2010, Katzner et al. 2020). I included multiple topographic covariates in the RSF model identified previously in studies to promote flight, nesting substrate, and territory defense

(Mcgrady et al. 2002, Watson et al. 2014, Crandall et al. 2015, Duerr et al. 2019). These topographic covariates included a terrain ruggedness index (TRI), topographical position index (TPI) and aspect. TRI provides a measure of topographic heterogeneity by calculating the sum change in elevation from a raster cell of a digital elevation model (DEM) and its eight neighbor raster cells (Riley et al. 1999). Higher values of TRI are equivalent to higher levels of ruggedness. TPI compares the elevation of each raster cell of a DEM to the mean elevation from a neighborhood of cells. Positive TPI values represent locations closer to ridge or ridgetop (e.g. higher values than the mean), and negative values represent locations near valleys or valley bottoms (e.g. values lower than the mean). TRI, TPI, and aspect were calculated from a 30 m resolution DEM (Gesch et al. 2002). Given aspect is a circular measure in degrees or radians, I converted it into Euclidean vectors of eastness (positive values face east, negative values face west) and northness (positive values face north, negative values face south; Roberts 1986, Duerr et al. 2019).

During the winter period of interest (Nov 15-Mar 10), carrion is the dominant nutrition source for eagles (Watson et al. 2019, Haines pers. obs.). The most reliable carrion source through winter likely comes from predation by gray wolf (*Canis lupus*) and cougars (*Puma concolor*) (Wilmers et al. 2003*b*). In a study of female elk response to hunting domains of wolf and cougar in northern YNP, the relative probability of wolf and cougar making a successful kill was modeled as a function of vegetative openness (range 0 [dense forest] – 289 [open grassland], Kohl et al. 2019). Wolves select open areas to hunt while cougars tend to hunt in moderately forested areas (Figure 1.3; Kohl et al. 2019). To model selection for areas where probability of wolf kill is highest, I modeled selection as a function of the raw openness values since probability continues to increase up to the high end of openness. To model selection for areas where probability of cougar kill is highest, I first reclassified the openness raster with the fitted probabilities of cougar kill (range = 0.5% - 8.8%; Kohl et al. 2019). By reclassifying the raster, I account for the non-linear probability of cougar kill and the increasing range of openness values, thus modeling selection for increasing kill probability or moderately forested areas. Therefore, selection along this gradient estimates the relative probability eagles are physically using areas where probability of elk kill is higher, thus increasing the probability of encountering wolf and cougar kills.

Golden eagles in YNP prey upon various mammal and bird species during the summer period (Mar 11-Aug 15); therefore, I included landscape covariates associated with prey habitat. I used a 30 m resolution landcover raster obtained from the National Land Cover Database (NLCD; Homer et al. 2012). Landscape covariates included distance to open water, distance to shrub and grassland, and distance to forest. The presence of water generally increases species diversity, grass and shrub communities support ground squirrels and other small mammals, and forest is important winter habitat for species like dusky grouse (Stauffer and Peterson 1985). I used distance to these landcover types since golden eagle foraging activity is typically characterized by visually inspecting the landscape while soaring or from perched locations. Therefore, it is more appropriate to consider proximity to these resources than the resources measured directly at used locations (Crandall et al. 2015, Domenech et al. 2015). Additionally, interpretation of "distance to" is a proximity measure; negative estimates suggest selection for close proximity to the given covariate (e.g. a negative estimate for distance to forest suggests the relative probability of selection decreases as distance increases from forest).

For animals that occupy discrete home ranges with a tendency to return to some central place, there is an expectation of declining use as distance increases from the central place (Rosenberg and McKelvey 1999). Not accounting for the distance from the central place can result in bias for covariates that are disproportionately available near the central place. Therefore, I included distance from all used and available locations to the nest for the 3rd order analysis. It is appropriate for species that exhibit this behavior to consider this covariate as part of the null model (Rosenberg and McKelvey 1999). I created a distance to nest raster for each individual with nest site data from the YNPGEP (unpubl. data). For tracked individuals with an occupied nest in the given year (a nest that contains eggs, young, or incubating bird; Steenhof et al. 2017), I used the specific nest. For tracked individuals that did not breed, I used the approximate geographic center of all known nests in the territory.

I used pairwise Pearson's correlation coefficient to determine collinearity between covariates prior to RSF analysis. Covariates were considered collinear with a correlation coefficient, $|r|$, > 0.60. All covariates considered had a $|r| < 0.60$, therefore, all were included. All covariates were centered and scaled so that estimates were comparable.

Data Analysis

I used a hierarchical random effects resource selection function (RSF) in a Bayesian framework (Manly et al. 2002, Thomas et al. 2006) to estimate the relative probability of resources selected by eagles at two spatial scales while accounting for seasonal period. I chose this approach to simultaneously provide inferences of resource selection by individuals and the population. The model consists of three parts: a data (likelihood) model, a parameter model, and a hyperparameter model (Thomas et al. 2006). The likelihood for relative probability of selection by individual i at observation j in season s, denoted as $PRES_{i,j,s}$ is modeled as a Bernoulli random variable, $PRES_{i,j,s} \sim Bern(p_{i,j,s})$. I modeled individual relative probabilities of selection for resource covariates listed above using the logit-link function:

$$logit(p) = \beta 0_{ijs} + \beta 1_{ijs} * x1_{js} \ldots + \beta k_{ijs} * xk_{js}$$

Where p is the relative probability of selection, β0 is the intercept term, β1…βk are the coefficients estimated for covariates x1…xk.

This model treats individual-specific parameters (e.g. βx_i) as random effects with their prior distributions informed by the population parameters (hyperparameters) (e.g. $\mu_{\beta x}$) prior distributions (hyperpriors). For example, βx_i is modeled as a normal random variable, $\beta x_i \sim Normal(\mu_{\beta x}, \sigma_x^2)$, with $\mu_{\beta x}$ representing the population mean effect of covariate x on selection and σ_x^2 as the variance of the effect among individuals within the population. Hyperparameters were modeled with uninformed prior distributions for population means (e.g. $\mu_{\beta x} \sim Normal(\mu = 1, \sigma^2 = 1000)$) and variances (e.g. $\sigma_x^2 \sim Gamma(\alpha = 0.1, \beta = 0.1)$). All covariates were evaluated as random effects.

The model was formulated in program R and implemented using the *jagsUI* package (Kellner 2019). I ran three Markov Chain Monte Carlo (MCMC) chains of 6,000 iterations and retained 3000 values per chain after discarding 3000 for burn-in. Model convergence was assessed with the Gelman-Rubin diagnostic ($Rhat$) value (Gelman and Rubin 1992) of less than 1.01. Additionally, convergence was assessed by visual inspection of trace plots (grassy chains) and posterior distributions.

Relevant assumptions of the RSF are 1) the distribution of measured covariates for available resources is constant during the study period, 2) resources available to individuals are correctly identified, 3) animals have free and equal access to all available resources, and 4) the resources sampled are random and independent. These assumptions were generally upheld for this analysis. The most difficult to validate is the correct identification of available resources since the data are based on a 30m resolution landcover raster created outside of this study. With the potential error in the landcover raster and GPS fixes, it may be that some resources are misidentified. Assuming that error is minimal, a large sample size of locations should help reduce the effect of misidentified resources. The assumption of equal access to all available resources is difficult to uphold for most animals. Independent of inter- and intra-specific competition, access is not significantly constrained by landscape features for golden eagles.

Seasonal variation in selection was assessed for each covariate with the population and individual (random effects) posterior distributions 95% credible interval relative to zero. All posterior distributions coefficient estimates are log odds and reported as the mean ($\bar{x}$) and 95% credible interval (CRI). Additionally, I report the probability the true sign of the effect is equal to the sign of the estimated mean effect (f).

Results

Golden Eagle Capture and Home Range Summary

A total of ten golden eagles were captured during trapping efforts, with seven individuals captured during the initial trapping period ending February 2019. Of the seven individuals, one eagle was previously banded outside YNP and did not receive a transmitter. One eagle, outfitted with a transmitter, died of lead poisoning after spending time outside YNP during the autumn hunting season. Too little data from the poisoned eagle was acquired to include in the analysis. Three additional birds outfitted with a transmitter in December 2019 had too little data to date to include in this study. Therefore, data on five eagles (4 females, 1 male) were used to investigate resource selection.

After censoring for daytime hours and season, the mean number of locations used for winter and summer home range estimates and resource selection was 1424.4/bird (SD = 235.3) and 1726.8/bird (SD = 13.6; Table 1.1), respectively. Home range area varied between season and individual with mean winter and summer home range estimates of 220.3 km^2 (SD = 282.1) and 32.1 km^2 (SD = 16.9), respectively (Table 1.1). Mean values and percent cover for topographic variables and landcover type from within respective home range estimates (winter, summer) for covariates included in the final 2nd and 3rd order model are presented in Table 1.2.

Home Range Resource Selection

Resource selection at the 2nd order showed no difference between seasonal periods. Therefore, the final 2nd order model did not account for seasonal variation. The effect of vegetative openness was positive and did not include zero ($\bar{x} = 0.54$, 95% CRI = 0.07, 0.99, f = 0.98) providing strong evidence that eagle home ranges are positively associated with areas of increasing vegetative openness. The effect of distance to open water was negative and weakly included zero ($\bar{x} = -0.90$, 95% CRI = -1.88, 0.09, f = 0.97) providing evidence that eagle home ranges are associated with areas in close proximity to open water. The estimated effect for all other covariates strongly included zero providing no strong evidence that eagles selected for these resources at this scale (Table 1.3). TPI and aspect were not included in the final 2^{nd} order model since there was no evidence for an effect at this scale.

Within Home Range Resource Selection

Resource selection at the 3^{rd} order included a subset of covariates with weak evidence for seasonal variation in their effect. These covariates included distance to nest, distance to grass and shrub, and the probability of cougar kill (Table 1.4). The effect for distance to nest was negative for both winter and summer and did not include zero, but magnitude of the mean effect was non-zero ($\bar{x} =$ -3.13, 95% CRI = -5.70, -0.58, f = 0.99; and $\bar{x} =$ -0.96, 95% CRI = -1.77, -0.14, f = 0.98 respectively). Therefore, eagles selected negatively for areas further from the nest within the home range during both winter and summer. The effect of TRI was positive and did not include zero ($\bar{x} = 1.01$, 95% CRI = 0.71, 1.32, f = 1.00), providing strong evidence eagles selected positively for increasingly rugged areas. The effect of TPI was positive and did not include zero ($\bar{x} = 0.38$, 95% CRI = 0.08, 0.69, f = 0.99), providing strong evidence eagles selected for upper slopes and ridgelines above valley bottoms. The estimated effect of all other covariates included zero providing weak or no evidence that eagles selected for these resources at this scale (Table 1.4). Aspect and distance to open water were not included in the final 3^{rd} order model since there was no evidence of an effect at this scale.

Discussion

I found weak evidence for variation in how eagles are selecting resources associated with prey habitat between seasonal periods. Strong evidence may require more telemetered individuals and years of data, a finer resolution of the resource covariates (Boyce 2006), or the analysis of resource selection at a finer spatial scale (Johnson 1980, Manly et al.

2002). However, the multi-scale approach taken here does illuminate the hierarchical process of resource selection (Rettie and Messier 2000), providing more robust inference for resources across spatial scales. This method identifies resources selected by eagles that would otherwise be overlooked if only measured at a single scale. Clear examples include the effects of vegetative openness and distance to open water selected at the larger spatial scale (2nd order; Table 1.3), where TRI and TPI were selected at the finer spatial scale (3rd order; Table 1.4).

My prediction of seasonal variation in selection for resources associated with prey habitat was weakly supported in this study. A seasonal difference in selection for proximity to grass and shrub communities was detected at the 3rd order, with no effect in winter, but weak evidence of an effect for summer (Figure 1.4), suggesting eagles are using areas associated with prey habitat in summer. I predicted this finding given the phenology of ground squirrels and other small mammals. Alternatively, the importance of forest was likely outweighed as a source of prey by other year-round uses (e.g. perch sites) supported by no variation in the estimated effect.

Selection for proximity to open water, detected at the 2nd order, may be driven by increased prey species diversity, other landscape characteristics close to water, or generally preferred when available. Further, with no effect at the 3rd order, open water is accounted for at the larger spatial scale and plays a more important role in determining the presence of the home range. Therefore, at this coarse scale, it is difficult to associate the importance of this resource to golden eagle daily needs.

Since carrion is expected to be a primary source of food during winter months, testing selection for variables that increase the probability of encounters is appropriate.

My findings identified at the 2nd order, with no variation between seasons, increased vegetative openness (correlated with the probability of wolf kill) is an important characteristic of the landscape influencing home range selection (Figure 1.5). Though evidence of an effect at the finer scale is weak, results indicate a 93% probability eagles are selecting for increasing openness. Given the effect at the larger spatial scale, evidence of an effect at the finer scale emphasizes the importance of low forest cover resources. This definitive characteristic of golden eagle habitat increases the probability of encountering wolf kills during winter months and is consistent with scavenger observations at wolf kills (Wilmers et al. 2003*b*, *a*).

Kohl et al. (2019) estimated that the highest probability of successful cougar kills occur in moderately forested areas and areas of increasing ruggedness. Additionally, a study of scavenger diversity at cougar kills in the Greater Yellowstone Ecosystem detected golden eagles as the third most frequent scavenger (Elbroch et al. 2017). With no effect detected at the 2nd order, results at the 3rd order provide weak evidence eagles are selecting these moderately forested areas. Disentangling any seasonal variation is difficult with such a small sample size, but individual (random) effects suggest there may be some common effect during winter (Figure 1.6). All individuals in winter positively selected for moderately forested areas, though one individuals estimate strongly overlapped zero suggesting no selection. Alternatively, selection in summer appears more random, with two individuals negatively selecting for moderately forested areas. Strong evidence of selection for increasing ruggedness, coupled with the results of selection for moderately forested areas, suggests these eagle habitat components increase the probability of encountering cougar kills in winter.

The solitary nature of cougars and their ability to kill disproportionately larger animals provide, on average, more available biomass to scavenging animals, as opposed to wolves who typically kill in packs and consume more of each kill (Elbroch and Wittmer 2012, Elbroch et al. 2017). Therefore, given these shared habitat characteristics, the abundance of cougars in this system may be particularly important to the provisioning of carrion during winter months. Future work should examine selection for proximity to known cougar and wolf kills from concurrent studies in the northern range of YNP. This data may allow fine-scale inference for the contributions of other apex predators that would otherwise be very difficult or impossible to obtain.

As predicted, there was no seasonal variation detected for the effect of topographic variables included in these models. At the 3rd order, estimates provided strong evidence of an effect for both TRI and TPI with credible intervals not including zero. An important mechanism of flight, particularly for large soaring birds, is supplemental updraft (Duerr et al. 2015), primarily achieved through thermal and orographic properties. Orographic updraft occurs at relatively low altitudes and is driven by the horizontal deflection of winds off features of the landscape (Alerstam and Hedenstrom 1998, Duerr et al. 2015). Increased ruggedness and ridgelines provide appropriate landscape structures to promote orographic updraft. With weak evidence of an effect for increasing TRI at the 2nd order, this characteristic of the landscape may additionally play a role in home range selection. Unlike TRI, TPI had no effect at the 2nd order, suggesting that supplemental updraft generated from increasing TPI and the availability of high vantage perch locations are selected at the finer scale. The effect of increasing TPI on behavioral responses is likely selected to fulfill daily activity. With substantial variation in topography across the species range, eagles will likely select high values of available TRI and TPI relative to the overall landscape. Therefore, other components of the environment are likely more important to home range selection.

The 3rd order selection findings provide strong evidence for an effect of distance to nest with zero not included in the credible intervals for both winter and summer (Figure 1.7). Therefore, not accounting for the importance of this central place could influence the inferences of resources near this central place. The magnitude and variability of the effect vary between seasons, likely due to behavior and home range area. In winter, eagles are not directly using nest sites but are regularly returning to this core area of the home range. With a larger winter home range, the magnitude of the effect will be greater due to increased availability away from this central location (Beyer et al. 2010) and more variable since there is no or very limited use at the nest. The smaller and less variable effect in summer results from a smaller home range and direct use of the nest site.

Modeling resource selection can be used to address multiple ecological questions such as habitat suitability indices, identification of threats, or predicting species distributions (Johnson et al. 2004, Dussault et al. 2006, Miller et al. 2014). My overarching objective linked resources eagles select to biological processes of reproduction in YNP during two seasonal periods critical to reproduction. The variation of resources within home range estimates indicate substantial differences in availability, especially when accounting for home range size. For example, given the proposed importance of grass and shrub communities on the presence of prey, large home range estimates have more area of this resource than the total area of smaller home range estimates. As the basis for conducting this study, this variation is of particular interest to its effects on reproduction. It may be that increased area of selected resources results in higher reproductive rates. However, some evidence indicates that a smaller home range may indicate higher quality (Pfeiffer and Meyburg 2015), suggesting that low prey availability results in larger home ranges and poorer reproductive success.

Capture efforts resulted in a smaller than ideal sample size. Unfortunately, the loss of one individual to lead poisoning and the restriction of adding a transmitter to a previously banded individual further reduced the small sample size. Additionally, failure to pass funding legislation by the federal government, resulting in a government shutdown through January 2019, prevented capture efforts for targeted individuals during this time. Eagles with transmitters currently occur in YNP, and locational information is available, and future studies should provide more statistical power and stronger inference. Random effects models will typically result in high variability of the estimated effects when the sample size is small because of individual variation, as shown in this study. Despite the variability, the advantage of a hierarchical RSF is the simultaneous analysis of individuals within the model. Individual estimates allow further interpretation of results, which is particularly important when sample size is small. For example, how one or more individual(s) may be influencing overall population estimates. Overall, the results from this analysis provide a baseline for habitat selection in YNP and are generally in agreement with predictions, despite the lack of strong evidence for an effect of many covariates tested. My study reaffirms the importance of increased openness and topography near prey habitat on eagle presence and selection (Katzner et al. 2020, Watson 2010)

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Tables and Figures

Table 1.1 Number of GPS locations per eagle used for seasonal home range estimates (kernel density estimate [KDE]) and estimated seasonal home range area (km^2) per eagle. Female (F), Male (M).

		Locations		Home Range km^2	
ID	Sex	Winter	Summer	Winter	Summer
Eagle 1	F	1781	1719	312.50	45.67
Eagle 2	M	1518	1743	14.48	44.40
Eagle 3	F	1333	1738	63.42	43.07
Eagle 4	F	1325	1724	676.58	12.23
Eagle 5	F	1165	1710	34.40	15.12

Table 1.2 Summary of variables within home range estimates per season and eagle. Terrain ruggedness index (TRI), topographical position index (TPI), vegetative openness (Open), and cougar kill probability/moderately forested areas (Cougar) are summarized as the mean and standard deviation (SD). Grass and Shrub, Forest, and Open water are summarized as percent cover.

ID	Season	TRI	TPI	Open	Cougar	% Grass Shrub	% Forest	% Open Water
Eagle 1	Winter	17.71 (12.77)	0.00 (1.86)	185.04 (90.69)	0.04 (0.03)	0.71	0.26	0.01
Eagle 1	Summer	15.06 (11.08)	0.01 (1.71)	171.00 (92.85)	0.04 (0.03)	0.75	0.22	0.00
Eagle 2	Winter	24.62 (11.63)	0.01 (1.97)	177.81 (90.39)	0.04 (0.03)	0.68	0.30	0.01
Eagle 2	Summer	23.36 (12.58)	0.02 (1.86)	149.88 (112.27)	0.03 (0.03)	0.55	0.41	0.01
Eagle 3	Winter	16.43 (11.55)	0.00 (1.91)	212.70 (89.66)	0.03 (0.03)	0.74	0.22	0.01
Eagle 3	Summer	16.97 (11.06)	0.01 (1.96)	198.29 (97.09)	0.03 (0.03)	0.71	0.25	0.01
Eagle 4	Winter	20.65 (13.73)	0.00 (1.99)	116.46 (95.54)	0.04 (0.03)	0.55	0.43	0.00
Eagle 4	Summer	15.92 (9.87)	0.01 (1.61)	219.37 (53.20)	0.04 (0.03)	0.81	0.17	0.01
Eagle 5	Winter	15.79 (14.02)	-0.01 (1.91)	132.30 (94.93)	0.04 (0.03)	0.50	0.42	0.01
Eagle 5	Summer	19.55 (15.98)	0.04 (2.14)	124.86 (97.00)	0.04 (0.02)	0.45	0.44	0.02

Table 1.3 Variable (centered and scaled) coefficient estimates for 2^{nd} order (home range) selection are reported as log odds. Posterior means, standard deviations (SD), 95% credible intervals (CRI), posterior f value (f), and Rhat. *Note*: f is the probability that the true sign of the effect is equal to the sign of the mean effect. Terrain ruggedness index (TRI), distance to forest (Dforest), distance to grass and shrub (Dgrass), vegetative openness (Open). cougar kill probability/moderately forested areas (Cougar), distance to open water (Dwater).

			CRI			
Variable	Mean	SD	2.5%	97.5	f	Rhat
TRI	0.14	0.20	-0.24	0.50	0.83	1.00
Dforest	-0.22	0.28	-0.75	0.33	0.83	1.00
Dgrass	-0.14	0.16	-0.47	0.16	0.85	1.00
Open	0.54	0.25	0.07	0.99	0.98	1.00
Cougar	-0.05	0.17	-0.39	0.27	0.65	1.00
Dwater	-0.90	0.50	-1.88	0.09	0.97	1.00

Table 1.4 Variable (centered and scaled) coefficient estimates for 3rd order (within home range) selection are reported as log odds. Coefficent estimates with seasonal variation are represented by winter (w) and summer (s). Posterior means, standard deviations (SD), 95% credible intervals (CRI), posterior f value (f), and Rhat. *Note*: f is the probability that the true sign of the effect is equal to the sign of the mean effect. Distance to nest (Dnest), Terrain ruggedness index (TRI), topographical position index (TPI), distance to forest (Dforest), distance to grass and shrub (Dgrass), cougar kill probability/moderately forested areas (Cougar), vegetative openness (Open).

			CRI			
Variable	Mean	SD	2.5%	97.5	f	Rhat
Dnest(w)	-3.13	1.31	-5.70	-0.58	0.99	1.00
Dnest(s)	-0.96	0.41	-1.77	-0.14	0.98	1.00
TRI	1.01	0.16	0.71	1.32	1.00	1.00
TPI	0.38	0.16	0.08	0.69	0.99	1.00
Dforest	-0.55	0.39	-1.33	0.25	0.94	1.00
Dgrass(w)	0.02	0.16	-0.31	0.35	0.54	1.00
Dgrass(s)	-0.23	0.22	-0.67	0.20	0.89	1.00
Cougar(w)	0.15	0.15	-0.15	0.46	0.87	1.00
Cougar(s)	0.13	0.22	-0.31	0.57	0.77	1.00
Open	0.44	0.35	-0.24	1.10	0.93	1.00

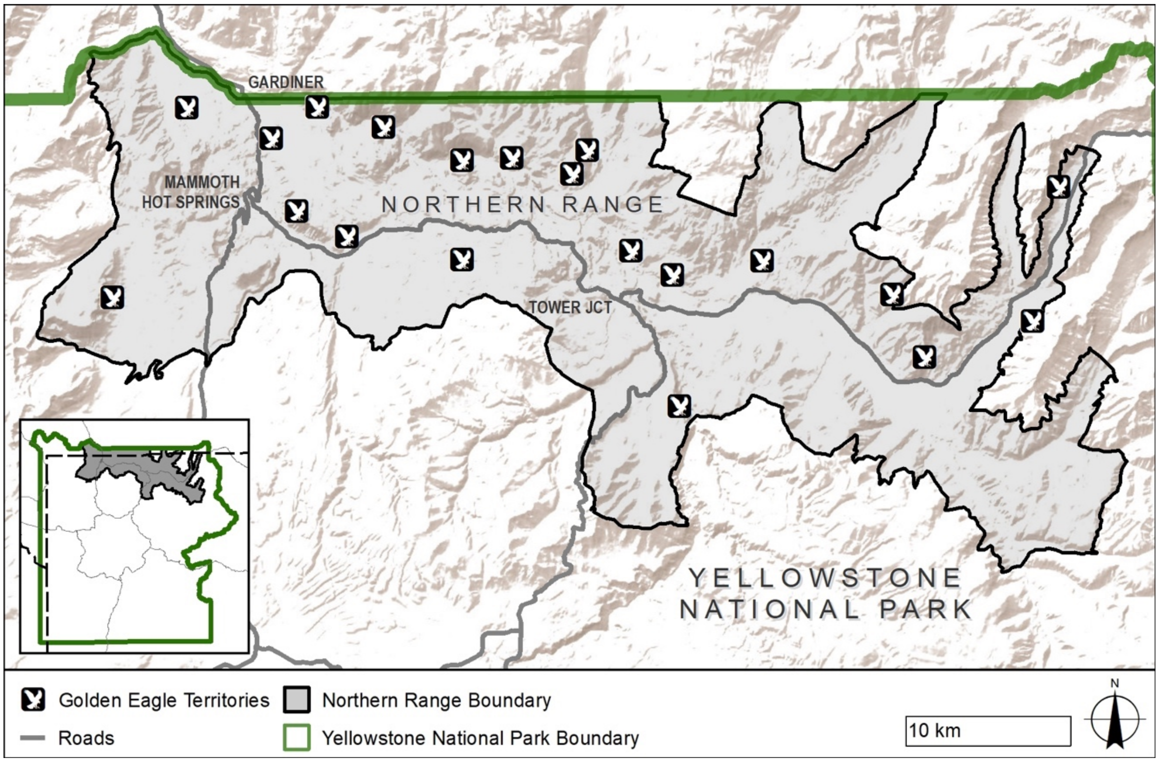

Figure 1.1 Yellowstone National Park northern range study area with golden eagle territories.

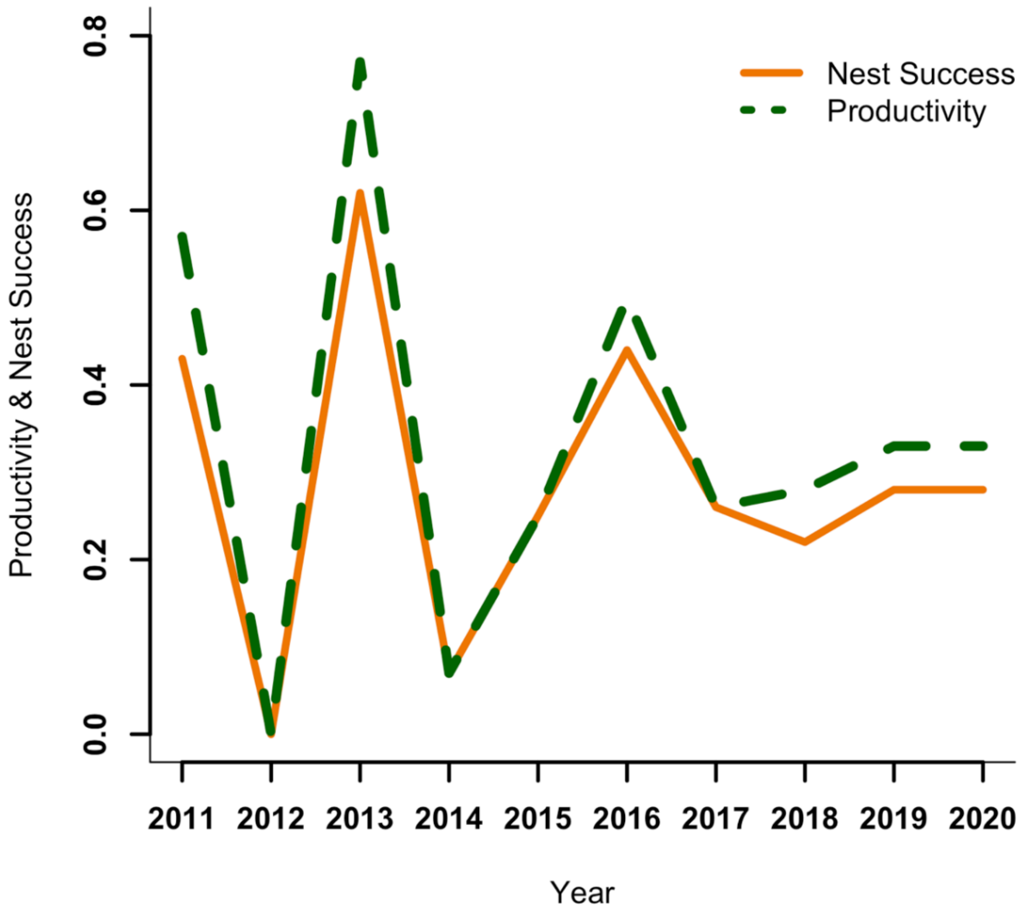

Figure 1.2 Annual estimates of golden eagle productivity and nest success in the northern range of Yellowstone National Park, 2011-2020.

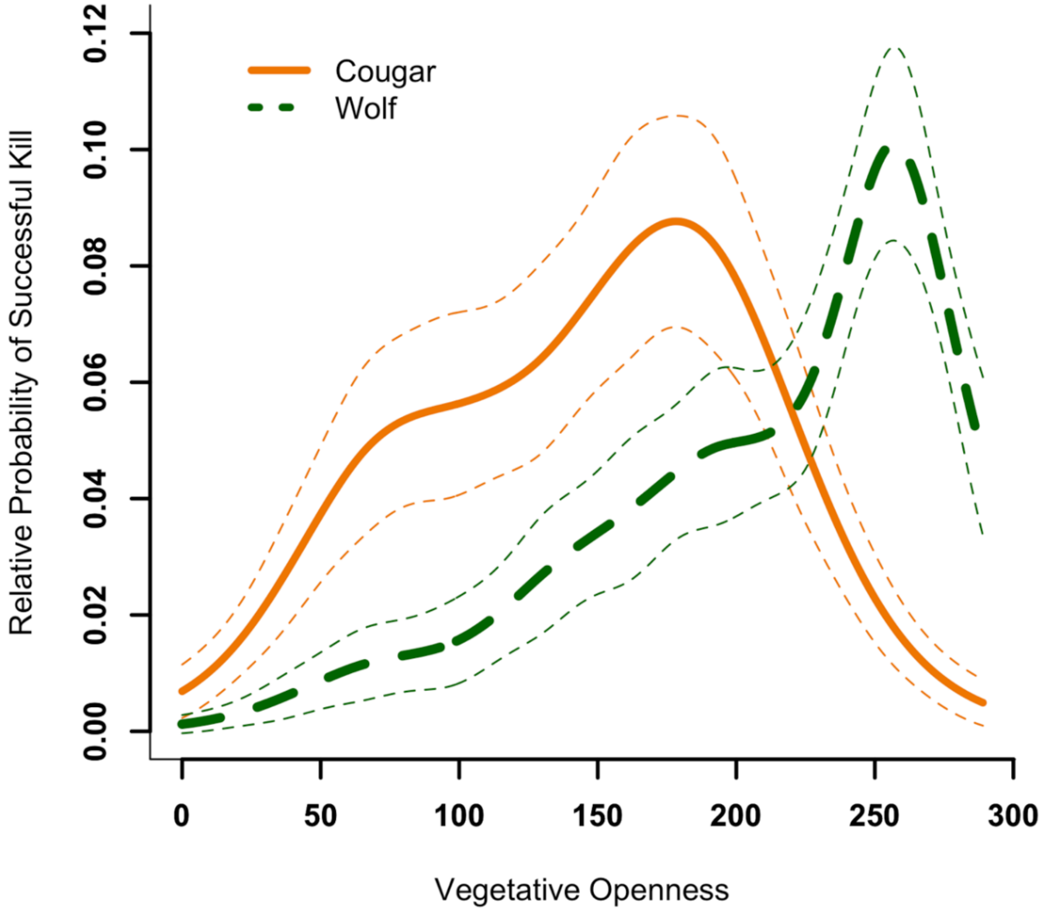

Figure 1.3 Relative probability of successful wolf and cougar kill as a function of vegetative openness (adapted from Kohl et al. 2019). Bold lines are fitted estimates and small dashed lines represent 95% CI.

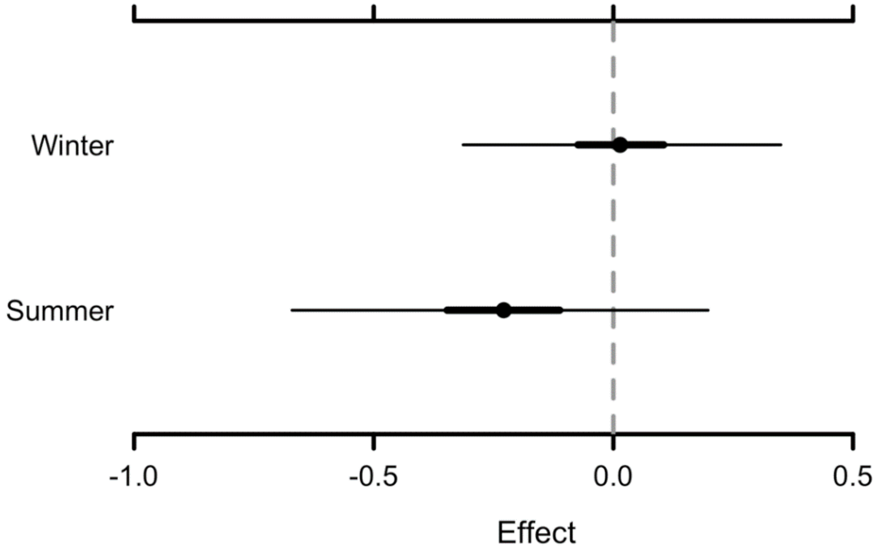

Figure 1.4 Winter and summer effect of distance to grass and shrub. Points represent the mean estimate. Bold and thin lines represent 50% and 95% credible intervals, respectively.

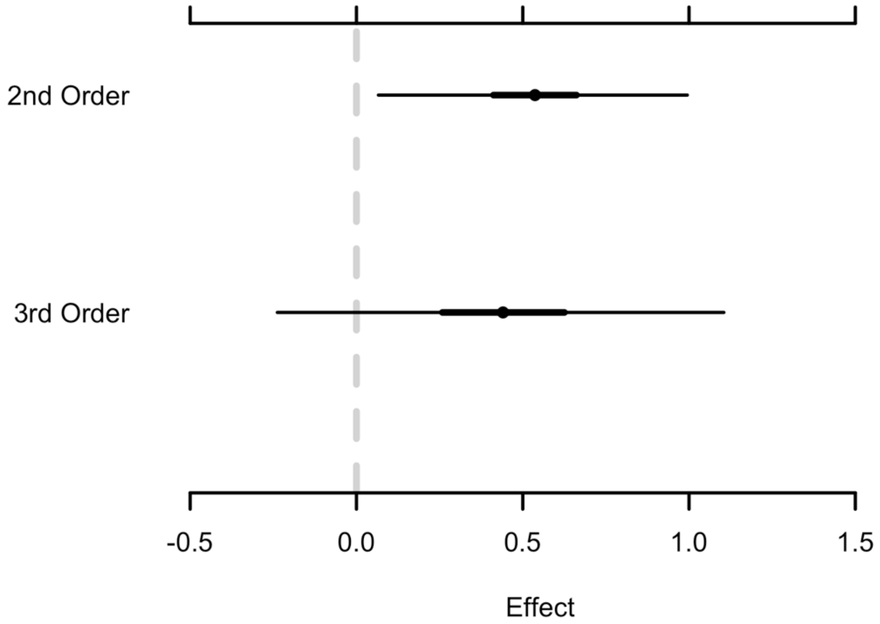

Figure 1.5 2^{nd} order (home range) and 3^{rd} order (within home range) effect of vegetative openness. Points represent the mean estimate. Bold and thin lines represent 50% and 95% credible intervals, respectively.

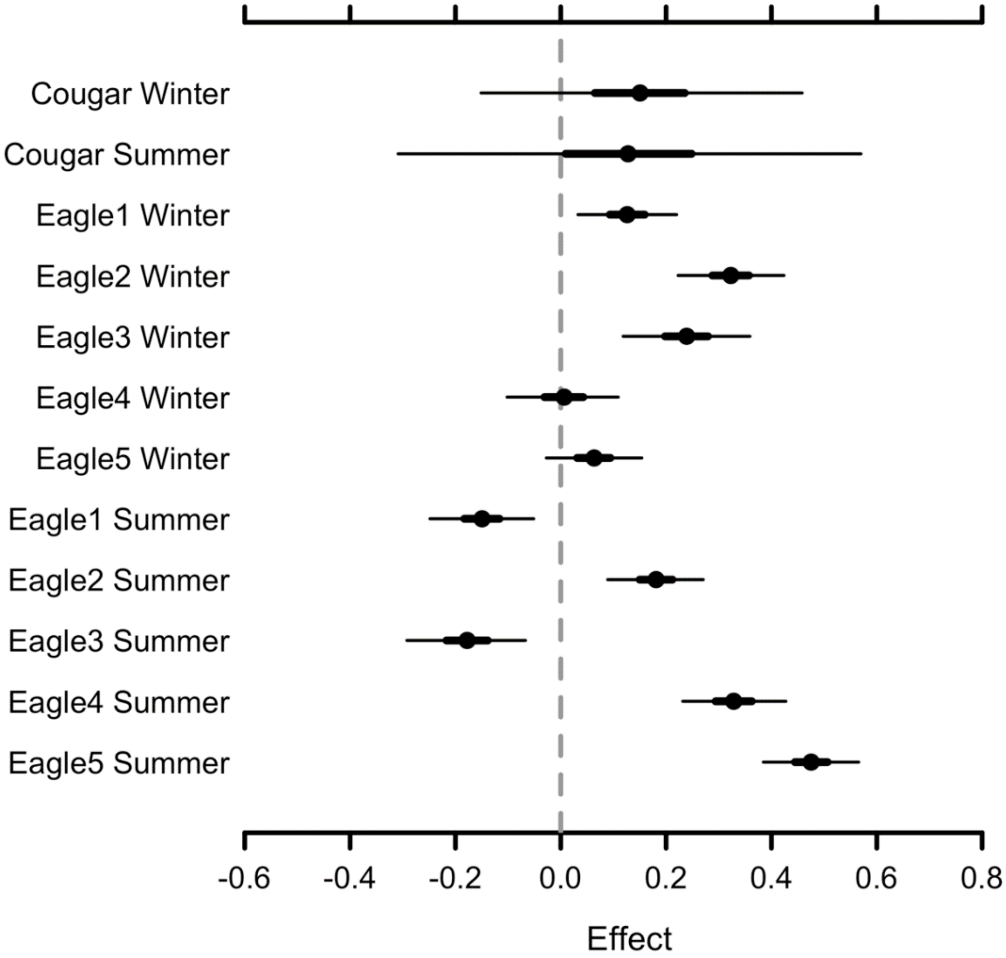

Figure 1.6 Winter and summer effect of probability of successful cougar kill/moderately forested areas for population and individual eagle. Points represent the mean estimate. Bold and thin lines represent 50% and 95% credible intervals, respectively.

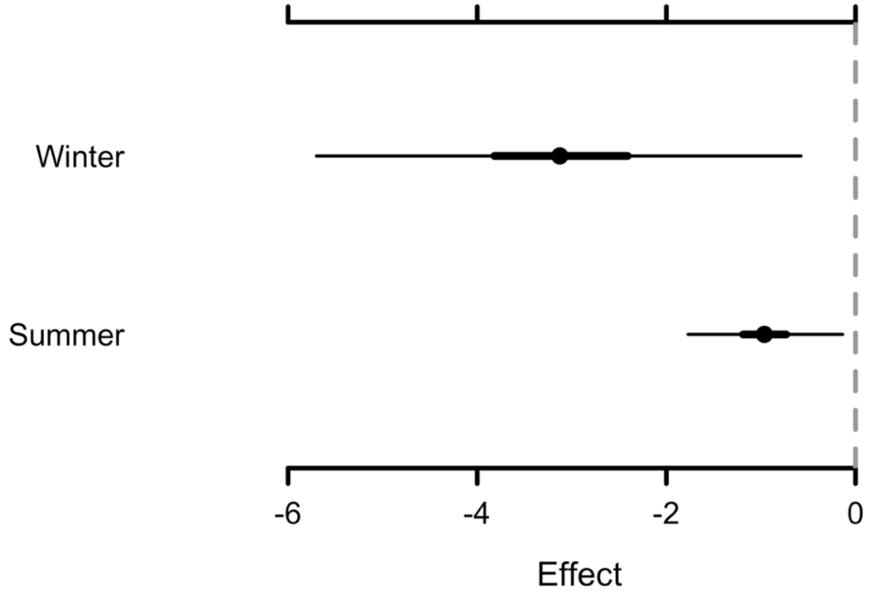

Figure 1.7 Winter and summer effect for distance to nest. Points represent the mean estimate. Bold and thin lines represent 50% and 95% credible intervals, respectively.

Chapter 2: Spatial and Temporal Drivers of Golden Eagle Reproduction in the Northern Range of Yellowstone National Park

Introduction

Life history theory suggests animals balance their investment in provisioning for young against their chances to survive and reproduce in the future (Roff 1993, Erikstad et al. 1998). Broadly defined, individual fitness is a function of survival of both the individual and their offspring, and reproduction, regulated through spatial, temporal, and individual variability (Franklin et al. 2000). Inherently, sources of variation may affect fitness components differently, thus complicating our understanding of population dynamics for a given species. Fretwell and Lucas (1969) introduced the notion that habitat influences fitness, suggesting individuals occupying habitats that maximize their survival and lifetime reproductive success will contribute the most to future generations (Newton 1989, Franklin et al. 2000, Johnson 2007). Habitat is defined here as the species-specific resources and conditions present in an area that drives occupancy, survival, and reproduction (Hall et al. 1997). Often, the habitat occupied by a species spans a gradient from low to high quality (Franklin et al. 2000, Johnson 2007). Therefore, ecological research has sought to measure the effect of species' habitat on the survival and reproduction of individuals across the low to high gradient of habitat quality (Franklin et al. 2000, Johnson 2007).

This study focuses on golden eagle (*Aquila chrysaetos*) habitat in the northern range of Yellowstone National Park (YNP) by examining the correlation between spatial and temporal habitat components and reproductive success. Habitat selection theory suggests that species habitat preferences should be under selection and adaptive, whereby individuals select habitat components that promote fitness advantages (Morris 1989, Martin 1998, Chalfoun and Schmidt 2012, Gibson et al. 2016). Here, I consider the weather and biotic and abiotic resources selected by golden eagles in the northern range of YNP as sources of temporal and spatial variation.

Golden eagles are a North American species of conservation concern (USFWS 2008), and population trend estimates in North America are variable, creating uncertainty in population trajectory. Some studies show declines (Kochert and Steenhof 2002, Hoffman and Smith 2003, USFWS 2016), while others suggest stability (Millsap et al. 2013, Nielson et al. 2014) or even increases (Crandall et al. 2015). Current concerns about the population status of golden eagles across the western US have focused on their interaction with energy development (e.g. wind, gas), human activity (Hunt 2002, Watson 2010, Pagel et al. 2013, Tack and Fedy 2015), and environmental contaminants (e.g. lead and poison for pest control; Bortolotti 1984, Newton 1998, Herring et al. 2017, Katzner et al. 2018).

YNP initiated in 2011 a golden eagle territory survey and reproductive monitoring program. The primary goal was to locate golden eagle territories parkwide and summarize annual reproductive rates. Since 2011, 28 territories have been identified parkwide, 20 of which are in the northern range of YNP (Figure 2.1). Density across the northern range is approximately one territory per 50 km^2, relatively high compared to other North American populations (range = one territory per the range of 18.5-252 km^2; Katzner et al. 2020). Nesting territory occupancy, which is determined by the annual presence of a bonded pair in the territory (Steenhof et al. 2017), has remained 100%. However, productivity (the total number of young fledged per occupied territory) and nest success (the percent of occupied territories that fledge at least one nestling) have been low. The ten-year average for productivity is 0.34 (range = 0-0.80) and 28% (range = 0%-60%) for nest success (Figure 2.2; Walker et al. 2020, YNP Golden Eagle Project [YNPGEP] unpubl. data), a result of infrequent nesting attempts and high nest failure rates.

Prey abundance and weather are primary factors driving raptor reproductive success (e.g. egg-laying, nest success; Newton 1979). It is well established that golden eagles may forgo breeding in a given year, a presumed result of food-stressed females not meeting the conditional requirements for egg-laying (hereafter, nest initiation; Newton 1979, Katzner et al. 2020). Life history theory suggests that long-lived species have a fixed level of investment in young as a means to maximize their survival (Erikstad et al. 1998). Therefore, as a long-lived species, when prey abundance is low or weather conditions poor, eagles commonly choose not to breed (Steenhof et al. 1997, Watson 2010).

Carrion is widely recognized as an important golden eagle food resource during the winter months, including early breeding season (Katzner et al. 2020, Watson 2010). However, the importance of carrion to individual eagle life history traits varies across their range. It is dependent on the abundance of prey species (Bates and Morretti 1994, Steenhof et al. 1997, Kochert et al. 2002, Watson 2010, McIntyre and Schmidt 2012, Preston et al. 2017, Schmidt et al. 2018) and winter conditions that influence the availability of food resources. In YNP, most prey species identified at nest sites are unavailable prior to nest initiation (Haines unpubl. data), suggesting carrion is an important food source in winter.

Nest failure (e.g. failure to hatch eggs, failure to fledge nestlings) is associated with the indirect and direct effects of inclement weather (Newton 1979, 1998, Bradley et al. 1997, Watson 2010, Anctil et al. 2014), often interacting with food availability (Steenhof et al. 1997). Indirectly, weather may impact reproductive success by reducing the availability of prey, either by limiting the activities of prey itself or by limiting the predator's ability to detect or effectively hunt prey (Watson 2010). The direct effects of weather on golden eagle reproductive success are less commonly known but suggested a result of weather extremes. In Montana, Phillips and Beske (1990) reported that 71% of golden eagle nests containing chicks failed shortly after a three-day blizzard in April 1984. By contrast, overheating of nestlings has also been recorded as a cause of nest failure (Beecham and Kochert 1975, Kochert et al. 2019).

Animals select home ranges to increase the contributions of spatially distributed resources that benefit fitness (Powell and Mitchell 2012). For most raptors, home-range, defined as an area routinely used by an animal to meet its daily needs (Burt 1943, Fieberg and Börger 2012, Powell and Mitchell 2012), is the restricted area that contains the nest, hunting range, and seasonally defended nesting territory (Watson 2010). The nesting territory is the area that contains, or historically contained, one or more nests within the home range of a mated pair (Steenhof et al. 2017). On average, some golden eagle territories in YNP are more productive than others, suggesting differences exist in the quality of spatially distributed resources at the home range. Weather, a temporal habitat condition, may be more influential on reproduction where individuals occupy a home range with lower quality resources (Steenhof et al. 1997, Newton 1998).

My objective establishes linkages between temporal and spatial components of golden eagle habitat and the probability of apparent nest initiation and nest success. Specifically, I examined the influence of weather conditions and resources selected by eagles on reproductive data collected over a nine-year period (2011-2019). I developed hypotheses related to weather and selected resources on apparent nest initiation and nest success. *Nest initiation weather hypothesis*: Length and severity of winter weather events prior to the nest initiation period reduces prey availability, thereby indirectly affecting a female eagle's ability to meet conditional requirements for nest initiation. I predicted that increasing occasions of prolonged precipitation and severe weather during winter would reduce the probability of nest initiation. Alternate *nest success weather hypotheses*: 1) Length and severity of weather during the nest initiation period reduces prey availability, affecting adult eagle condition, thereby limiting the ability to maintain appropriate incubation and brooding requirements. I predicted that increasing occasions of prolonged precipitation and severe weather during the nest initiation period would reduce the probability of successfully fledging nestlings. 2) Length and severity of weather during the incubation and brooding period (hereafter, incubation period) will impact incubating adults and young nestlings. predicted that increasing occasions of prolonged precipitation during the incubation period would reduce the probability of successfully fledging nestlings. *Resource selection hypothesis*: The proportion of resources selected by golden eagles within their home range will influence apparent nest initiation and nest success. I predicted a greater proportion of selected resources in the home range would increase the probability of egg laying and successfully fledging nestlings. This study identifies limitations to golden eagle reproduction by accounting for the effects of weather and variation in resources at the home range, thus contributing to our knowledge of habitat and reproductive demographics.

Study Area

The study was conducted on ~1,000 km^2 of the northern range within the protected boundaries of YNP (Figure 2.1). Elevation varies from ~1,600 m in valleys and canyons to greater than 3,000 m along mountain ridges and peaks (Despain 1990). Forested areas of the northern range consist of Douglas fir (*Pseudotsuga menziesii*) and lodgepole pine (*Pinus contorta*) at the lower elevations with subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*) at upper elevations. Non-forested areas are dominated by big sagebrush (*Artemesia tridentata*) and Idaho fescue (*Festuca idahoensis*). Climate is characterized by long, cold winters and short, cool summers with average precipitation of 40-75 cm across the elevational gradient (Despain 1990). Within this area, golden eagles nest primarily on cliffs. Preliminary data suggests that golden eagles' food resources may be limited to carrion in the nonbreeding season (Haines unpubl. data). During the breeding season, golden eagles forage on various live prey such as Sciurids (e.g., ground squirrels and marmots), ungulate fawns, grouse, and other bird species (Baril et al. 2017). From the collection of prey remains and motion-triggered cameras at the nest, the specific prey species detected most frequently are yellow-bellied marmot (*Marmota flaviventris*), dusky grouse (*Dendragapus obscurus*), and Uinta ground squirrel (*Urocitellus armatus*).

Methods

Occupancy and Reproduction

I used a ground-based monitoring approach to collect data on nesting territory occupancy (hereafter, occupancy) and reproductive status. Monitoring efforts were initiated each year near the end of March, when eagles initiate nesting. Monitoring was conducted using 10x42 binoculars and 20-60x60 spotting scopes within eagle nesting territories to observe adult behavior and determine nesting status. Occupancy was determined by 1) the presence of a mated pair of birds, 2) a single bird exhibiting territorial behavior, 3) locating nest structures that contain new material or fresh greenery, or 4) other reproduction-related activities (i.e., adult in incubation posture, observations of young in the nest; Steenhof et al. 2017, Driscoll 2010). At occupied territories, I determined nest initiation by an eagle on the nest in incubation posture. I presumed nests with incubating eagles contained eggs; therefore, I use the term apparent nest initiation (McIntyre and Schmidt 2012, Crandall et al. 2015). To determine the lack of nest initiation, I first checked all known nests within the territory. If no incubating eagle was observed at the known nests, I observed pair behavior to indicate unknown nests. In many instances, determining nest initiation activity required multiple nesting territory visits. For initiated nests, I visited the territory ≥ 2 times to determine if the nest failed or nestlings reached 80% of their fledging age (approximately 56 days old) or older (Steenhof and Newton 2007). From these observations, I calculated annual measures of productivity and nest success.

Weather Covariates

I examined the influence of weather events that may indirectly affect nest initiation and directly or indirectly affect nest success. I calculated weather metrics for the 1) winter period (Jan. 1 – Mar. 15), 2) nest initiation period (Mar. 1 – Apr. 15), and 3) incubation period (Apr. 1 – Jun. 15). The dates for each of the three periods were based on observed egg laying and incubation dates. I predicted that indirect effects would be the result of weather events prior to nest initiation and incubation. In contrast, direct effects would be the result of severe weather events during the incubation period.

I used 1 km^2 gridded weather data to obtain daily weather estimates at the home range (defined below) from the Daymet dataset (Thornton et al. 2017) using the R (R Core Team 2019) package *FedData* (Bocinsky 2019). The weather data included precipitation (PRCP), maximum temperature (TMAX), and snow water equivalent (SWE). I averaged daily estimates for each weather variable for each 1 km^2 grid cells in each home range. I used daily estimates of precipitation and maximum temperature for each period of interest (winter, nest initiation, incubation) to derive weather events (e.g., prolonged periods of rain) that may impact reproduction. For precipitation, I included the number of occasions with precipitation on two or three or more consecutive days (PRCP2, PRCP3; respectively) since duration may have a greater effect than precipitation totals. For winter and nest initiation periods only, I calculated the number of days with a combination of precipitation greater than or equal to one standard deviation (SD) above the mean and maximum temperature less than or equal to one SD below the mean (WIN-SEVERE, NEST-SEVERE). Additionally, I included mean estimates of precipitation, maximum temperature, and snow water equivalent for each of the three periods.

Abiotic and Biotic Resource Covariates

I determined the effect of resources golden eagles select within their home range on apparent nest initiation and success. Resource selection analyses were implemented in program R (R Core Team 2019) using base functions and specific R packages (see chapter 1; Haines unpubl. data). I estimated selection for multiple abiotic and biotic landscape variables associated with flight, nesting substrate, territory defense, and prey habitat at multiple spatial and temporal scales. Here, I consider how resources eagles select vary within the home range during the breeding period, March 11 to August 5. These dates encompass the range of observed nest initiation (March 28 – April 10) and fledge dates (June 24 – August 5) in YNP (YNPGEP, unpubl. data).

Breeding season home range was estimated using 95% kernel density estimator (KDE) from location data collected during the given breeding period. Average home range size was 32.1 km^2 (SD = 16.9). I accounted for variation in resources between home ranges by applying a 30 km^2 circular area around each territory center using the *sampSurf* package (Gove 2020). The territory center was approximately the middle point of all known nest site locations in each territory. All landscape covariates were extracted from each 30 km^2 area using the *raster* package (Hijmans 2019) and summarized as the mean value or percent cover.

An important flight mechanism, particularly for large soaring birds, is supplemental updraft (Duerr et al. 2015) achieved by orographic and thermal properties. Orographic updraft occurs at relatively low altitudes and is driven by the horizontal deflection of winds off features of the landscape (Alerstam and Hedenstrom 1998, Duerr et al. 2015). Topographic variables selected by eagles in YNP included a terrain ruggedness index (TRI) and a topographical position index (TPI) (see Chapter 1; Haines unpubl. data). TRI provides a measure of topographic heterogeneity by calculating the sum change in elevation from a raster cell of a digital elevation model (DEM) and its eight neighbor raster cells (Riley et al. 1999). Higher values of TRI are equivalent to higher levels of ruggedness. TPI compares the elevation of each raster cell of a DEM to the mean elevation from a neighborhood of cells. Positive TPI values represent locations closer to ridge or ridgetop (e.g. higher values than the mean), and negative values represent locations near valleys or valley bottoms (e.g. values lower than the mean). Increased ruggedness and ridgelines provide appropriate landscape structures to promote orographic updraft. I calculated TRI and TPI from a 30 m resolution DEM (Gesch et al. 2002) using the *raster* package (Hijmans 2019) and summarized each as the mean value across the home range for each territory.

Golden eagles forage across several different landcover types to obtain a diverse array of prey items, including mammal and bird species. A primary resource driving reproduction is prey abundance (Newton 1979). However, there are limited data available to estimate abundance of eagle prey in YNP. Therefore, I used landcover covariates to infer prey availability and perch sites that benefit foraging strategies. I used a 30 m resolution landcover raster obtained from the National Land Cover Database (NLCD; Homer et al. 2012). Landscape covariates considered for this analysis included grassland and shrub, and forest. Grass and shrub communities support ground squirrels, among other small mammals, and have a high propensity for generating thermal updraft. Forest support perch sites and are important dusky grouse winter habitat (Stauffer and Peterson 1985). I extracted landcover type for each home range and summarized type as percent cover.

The most reliable source of carrion in winter likely comes from carnivore predation. A study of gray wolf (*Canis lupus*) and cougar (*Puma concolor*) hunting domains in YNP modeled the relative probability of wolf and cougar making a successful elk kill as a function of vegetative openness (range = 0 [dense forest] – 289 [open grassland], Kohl et al. 2019). The highest probability of a successful wolf kill (range = 0.1% - 10.1%) occurs at the high end of vegetative openness (Figure 2.3; Kohl et al. 2019). Therefore, I extracted the raw openness values (OPEN) for each home range and summarized them as the mean value. The highest probability of a successful cougar kill (range = 0.5% - 8.8%, Kohl et al. 2019) occurs in moderately forested areas. To account for the effect of moderately forested areas, I reclassified the openness raster with the fitted probabilities of cougar kill using the *raster* package (Hijmans 2019). I then extracted cougar kill probabilities (COUGAR) for each home range and summarized them as the mean value.

To further address the effect of carrion on nest initiation and success, I considered annual estimates of edible biomass (kg) acquired per wolf per day during late winter/early spring in the northern range of YNP (Yellowstone National Park Wolf Project, unpubl. data). The timing of these estimates align well with the period prior to nest initiation, essentially providing an index of carrion availability from wolves in the study area at a critical time.

Finally, I used nearest neighbor distance (NND) measurements to address resource variation not accounted for by other covariates. A higher density of nesting territories may indicate better habitat quality, thus, requiring a smaller area for resource procurement (Watson 2010, Pfeiffer and Meyburg 2015). I calculated NND as the shortest distance between neighboring territory centers using the *nabor* package (Elseberg et al. 2012).

Testing for Collinearity

After all covariates were extracted for each eagle territory and prior to analysis, I used pairwise Pearson’s correlation coefficient to determine collinearity between covariates. Covariates were considered collinear with a correlation coefficient, |r|, > 0.60. If collinear, I retained the covariates most appropriate for biological explanation and interpretation.

Data Analysis

I used a multievent capture-recapture model in a Bayesian framework (Catlin et al. 2019) to estimate annual transition probabilities (ψ) of nest initiation and nest success and the effect of covariates on these probabilities. The multievent model is a modified multistate model that allows for uncertain state assignment (Pradel 2005, Genovart et al. 2012, Catlin et al. 2019). In this model, an event is the observation of the state of an individual territory. Events are coded in the capture histories (Genovart et al. 2012). In this study, I directly observed an incubating bird, nest success, and failure, but observed birds that were not breeding could be either non-breeders or breeders I failed to detect. Therefore, I included a state uncertainty parameter on the detection of the nonbreeding state.

There were four states in which territories could transition in this model: nonbreeding (A), breeding (B), breeding successful (C), and breeding failed (D) (Table 2.1). I divided the observation process (p) into four categories: nonbreeding detected (pA), breeding detected (pB), breeding successful detected (pC), breeding failed detected (pD). To account for uncertainty in state assignment (π), I modeled the probability that a nonbreeding territory was correctly detected as nonbreeding (Table 2.2).

I modeled the effect for weather and the abiotic and biotic landscape covariates listed above for each territory *i* probability of state transition using the logit-link function:

$$logit(\psi_i) = \beta 0 + \beta 1 * x1_i \ldots + \beta k * xk_i$$

Where ψ is the probability of state transition, β0 is the intercept term, β1…βk are the coefficients estimated for covariates x1…xk.

The model was formulated in program R and implemented using the $jagsUI$ package (Kellner 2019). I ran three Markov Chain Monte Carlo (MCMC) chains of 20,000 iterations and retained 10,000 values per chain after discarding 10,000 for burn-in. To address the effects of weather on nest initiation, I modeled winter period weather. To address the effects of weather on nest success, I modeled both nest initiation and incubation period weather. For each model I included the same set of landscape covariates, BIOMASS, and NND. All covariates were evaluated as fixed effects. Prior to analysis all covariates were centered and scaled. I assessed the effect of each covariate using the posterior distributions 95% credible interval (CRI) relative to zero. Model convergence was assessed with the Gelman-Rubin diagnostic ($Rhat$) value (Gelman and Rubin 1992) of less than 1.01. Additionally, I used visual inspection of trace plots (grassy chains) and posterior distributions to assess model convergence. All posterior coefficient estimates are log odds and reported as the mean ($\bar{x}$) and 95% CRI. Additionally, I report the probability the true sign of the effect is equal to the sign of the estimated mean effect (f).

Results

Occupancy and Reproduction

For this study, I used data from 19 of the 20 known territories in YNP's northern range. Territories were monitored as they were discovered, therefore not all 19 territories were monitored in each year. At the end of the ninth breeding season (2011-2019), occupancy remained 100% across all territories for all years monitored. With a total of 148 territory surveys across all nine monitoring years, I detected 56 nonbreeding events, 68 nest initiation events, 38 nest success events, 30 nest failure events, and 24 unknown breeding status events.

Probability of NonBreeding, Apparent Nest Initiation, Nest Success, and Nest Failure

Transition probability (ψ) estimates from reproductive monitoring data are reported as the mean ($\bar{x}$) and 95% CRI (Table 2.3). The probability that an eagle territory will remain nonbreeding (A→A) was $\bar{x} = 0.68$ (95% CRI = 0.62 – 0.74). The probability that an eagle territory will transition from nonbreeding to breeding (A→B) was $\bar{x} = 0.32$ (95% CRI = 0.26 – 0.38). The probability that a breeding territory will successfully fledge at least one nestling (B→C) was $\bar{x} = 0.59$ (95% CRI = 0.49 – 0.67). Finally, the probability that a breeding territory will fail in fledging at least one nestling (B→D) was $\bar{x} = 0.41$ (95% CRI = 0.32 – 0.51).

Probability of State Observation and State Uncertainty

Generally, except for observing the nonbreeding state (pA), probability of observing all other breeding states was very high. State observation probabilities are reported as the mean ($\bar{x}$) and 95% CRI (Table 2.4). The probability of observing the nonbreeding state (pA) was $\bar{x} = 0.75$ (95% CRI = 0.68 – 0.81). The probability of observing the breeding state (pB) was $\bar{x} = 0.98$ (95% CRI = 0.92 – 1.00). The probability of observing the breeding successful state (pC) was $\bar{x} = 0.98$ (95% CRI = 0.91 – 1.00). The probability of observing the breeding failed state (pD) was $\bar{x} = 0.97$ (95% CRI = 0.89 – 1.00). Finally, given the uncertainty of correctly observing the nonbreeding state, the probability of a nonbreeding territory correctly observed as nonbreeding (π) was $\bar{x} = 0.96$ (95% CRI = 0.86 – 1.00).

Collinearity of Covariates

I assessed collinearity for all covariates respective to the period of interest (winter, nest initiation, incubation). No abiotic or biotic landscape covariates were strongly correlated with weather. However, TRI, OPEN, GRASS_SHRUB, and FOREST relative to each other all have correlation coefficients $|r| > 0.6$. Resource selection analysis provided strong evidence that eagles are selecting for increasing ruggedness within the home range while selection for OPEN, GRASS_SHRUB, and FOREST were weakly supported (see chapter 1; Haines unpubl. data). Therefore, I selected TRI to include each model. Mean precipitation and number of occasions with precipitation on three or more consecutive days (PRCP3) during the winter had a $|r| = 0.7$. Given the assumption that prolonged periods of precipitation have a greater impact on reproduction, I selected PRCP3 to include in the nest initiation model. No weather covariates included in the same nest success models have a $|r| > 0.6$.

Covariates Influencing Apparent Nest Initiation

Covariates included on the probability of apparent nest initiation were mean winter TMAX and SWE, PRCP2, PRCP3, WIN-SEVERE, TRI, TPI, COUGAR, BIOMASS, and NND (Table 2.5). The additive model indicates that only PRCP3 had strong evidence of an effect on apparent nest initiation ($\bar{x} = -0.52$, 95% CRI = -1.00 – -0.05, f = 0.98; Table 2.6). This result suggests that increasing occasions of precipitation (e.g. snow, rain) on three or more consecutive days during the winter period negatively influenced the probability of apparent nest initiation.

Covariates Influencing Nest Success

Two models addressed the effects of weather on the probability nest success. I included the same set of abiotic and biotic landscape covariates (TRI, TPI, COUGAR, BIOMASS, NND; Table 2.5) to each additive model to assess their effect on nest success in relation to weather experienced. I assessed the effects of weather prior to the incubation period on nest success using weather covariates from the nest initiation period (mean TMAX and SWE, PRCP2, PRCP3, and NEST-SEVERE; Table 2.5). To assess the effects of weather during incubation on nest success, I used weather covariates from the incubation period (mean SWE, PRCP2, and PRCP3; Table 2.5).

Weather during nest initiation period best explained nest success. In the nest initiation period model, multiple coefficient estimates did not include zero (Table 2.7, Figure 2.4A). In contrast, all coefficient estimates for weather in the incubation period model included zero (Table 2.8, Figure 2.4B). Here I report the nest initiation period model coefficient estimates for covariates with strong evidence of an effect. TMAX was negative ($\bar{x} =$ -2.06, 95% CRI = -3.81 – -0.49, f = 1.00), suggesting probability of nest success decreased with increasing temperature during nest initiation. SWE was negative ($\bar{x} =$ -1.16, 95% CRI = -2.38 – -0.10, f = 0.99), suggesting probability of nest success decreased with higher amounts of accumulated snow during nest initiation. NEST-SEVERE was negative ($\bar{x} =$ -1.23, 95% CRI = -2.35 – -0.27, f = 1.00), suggesting probability of nest success decreased with increasing days of severe weather. With the 95% CRI including zero, but a 97% probability of a positive effect, there was weak evidence for a positive effect of TRI ($\bar{x} = 0.85$, 95% CRI = -0.04 – 1.82, f = 0.97), suggesting probability of nest success increased with increasing ruggedness at the home range. Finally, with the 95% CRI including zero, but a 93% probability of a negative effect, there was weak evidence for the negative effect of NND ($\bar{x} =$ -0.59, 95% CRI = -1.44 – 0.19, f = 0.93), suggesting that probability of success decreased with increasing distance from neighboring eagle territories.

Discussion

This study indicates that golden eagle reproduction, at least partially, is regulated through temporal effects of weather and habitat resources within the home range. Golden eagles in the northern range of YNP have demonstrated a low probability of apparent nest initiation ($\psi = 0.32$), suggesting that female condition for egg-laying is not regularly met. My findings suggest that the probability of nest initiation is partially explained by increasing occasions of precipitation on three or more consecutive days in winter. The effect of prolonged precipitation supports the prediction that duration will negatively influence nest initiation. Increased occasions of precipitation on three or more consecutive days can limit both prey activity and the species' ability to successfully hunt (Steenhof et al. 1997, Watson 2010). Further, during winter, precipitation is primarily in the form of snow, and carrion is more likely to be covered with increasing duration, thus, limiting detection. I found no strong evidence for other temporal and spatial covariates that explain nest initiation.

The probability of successfully fledging nestlings ($\psi = 0.59$) is partially explained by multiple weather covariates prior to nest initiation (Mar. 1 – Apr. 15). My findings suggest negative effects on successful fledging for increasing mean maximum temperature, mean snow water equivalence, and severity (identified as the number of days with both precipitation ≥ 6.5mm [1 SD ≥ mean] and maximum temperature ≤ -0.5°C

[1 SD ≤ mean]). The negative effect of increasing mean temperatures through March and early April is difficult to discern on its own, particularly in the context of the other weather variables found here. Therefore, further analysis with more years of data may be required in order to make inferences on the negative effect of increasing temperature. The negative effect of snow may generally indicate some lasting effect of severe winters on nest success. However, when snow on the ground persists longer into the breeding season, small mammals gain increased cover from predators (Sonerud 1986, Hansson 1987). Therefore, increased snow cover may limit detection of prey as golden eagles become more reliant on small mammals. I found a reduction in nest success as the occasions of severe weather during the nest initiation period increased. In this study severity incorporates both temperature and precipitation. As mentioned previously, increasing occasions of severe weather may limit prey activity or hunting abilities. Disentangling how low temperatures and high precipitation affect prey and eagle activity requires further research related to both predator and prey movement and energetics. Ultimately, for female eagles who have met egg-laying conditional requirements, results suggest inclement weather during the nest initiation period has a lasting effect on successfully fledging nestlings.

I found weak evidence for a positive effect of increasing ruggedness on nest success. Multiple golden eagle resource selection functions have demonstrated strong selection for increasing ruggedness (Watson et al. 2014, Crandall et al. 2015, LeBeau et al. 2015, Duerr et al. 2019). In turn, this promotes supplemental updraft (Duerr et al. 2015), resulting in increased prey acquisition and territory defense while conserving energy required for flight. I also found weak evidence for a negative effect of nearest neighbor distance. The probability of nest success decreases with increasing distance from neighboring eagle territories. This result suggests a connection between spatially aggregated resources, territory density, and nest success.

In Idaho, Steenhof et al. (1997) found nest initiation was positively related to jackrabbit abundance and inversely related to winter severity. However, they emphasize that during peaks of the jackrabbit cycle, the effects of winter severity could not be detected. The correlation between lagomorph abundance and reproductive success has been detected across many other golden eagle populations (Bates and Morretti 1994, Watson 2010, McIntyre and Schmidt 2012, Preston et al. 2017, Schmidt et al. 2018, Katzner et al. 2020). However, lagomorphs are not abundant in YNP (Gunther et al. 2009, Hodges et al. 2009) and are highly infrequent in prey remains and photographs from motion-triggered cameras at the nest. During winter, the prey identified at nest sites are unavailable or limited, suggesting carrion as a primary food source. Wolf kill biomass, included here, is an estimate of edible biomass (kg) acquired per wolf per day. This estimate does not account for spatial variation of the resource, nor does it account for what is actually available for scavenging animals (wolves may consume most of the kill), potentially limiting its explanatory power. Therefore, it remains unclear if the increased availability of carrion has a positive effect on nest initiation.

Extreme weather, variation in prey availability, and the recovery of large carnivores within YNP (Smith et al. 2003) present a unique system for golden eagles. Prior to carnivore recovery, the northern Yellowstone elk herd numbered at least 19,000 individuals in the mid-1990s (Evans et al. 2006). With no primary predator to exhibit top down population control, the overabundant elk herd commonly experienced considerable die-offs as a result of limited resources in severe winters. The timing of these abundant winter die-offs occurred roughly when golden eagles initiate nesting (late February to early April), presumably, providing a reliable food source for eagles at a much-needed time. Today, the northern elk herd numbers around 6,000 – 8,000 individuals (NYCWWG 2018), and winter elk die-off events are consequently less abundant. Therefore, the abundance of carnivore contributed carrion on the landscape may not match the historic winter die-offs. It may be that current eagle densities in YNP's northern range are a historical relict reflecting food abundance of the past, and low eagle reproductive rates may be a response to the decrease in carrion availability.

In Scotland, golden eagle density was highest in regions where carrion was most abundant (Watson 2010). The study suggests that if carrion densities suddenly decreased, eagle populations would decline since alternative live prey could not support the current populations (Watson 2010). This prediction was supported by a decline in eagle density since the 1960s in the Highland area of Scotland as a result of changes in red deer (*Cervus elaphus*) management, which subsequently reduced carrion density (Watson et al. 1989).

My study advances our understanding of the low reproductive rates of golden eagles in the northern range of YNP. Further, the study informs park management of what spatial and temporal habitat components influence reproductive success. Results from this study suggest harsh weather in YNP negatively influences nest initiation and success. A positive effect for spatially distributed resources selected by eagles on reproduction is only weakly supported. However, average home range was approximated from a small sample of telemetered eagles (see chapter 1; Haines unpubl. data) and represented as a circular area around each territory center. The method provides a coarse representation of actual home range shape and size. Therefore, the variation of spatially distributed resources extracted from the home range is a coarse approximation of actual availability. If home range can be approximated better for each territory, inference for the effect of spatially distributed resources may improve. Alternatively, though nearly impossible to quantify, individual quality could better explain low reproductive rates rather than habitat quality (Zabala and Zuberogoitia 2014). The ecological relationships between habitat and fitness are inherently complex. The fitness components addressed in this study cannot fully assess the advantages of selected resources since habitat can influence multiple life-history stages (e.g. adult survival, juvenile survival; Gibson et al. 2016). Therefore, given the potential consequences of low reproductive success in YNP, research will need to address other life-history stages to better understand population status in the northern range of YNP.

Management Implications

The study highlights the need to understand better how food resources in YNP affect eagle reproduction. This will require more data on prey selection (e.g. nest cameras), the demography of prey species, and carrion. Given low reproductive rates, a study of food supplementation (Ward and Kennedy 1994) may help address if limited prey resources in winter and early spring influence reproductive success. As a long-lived species, adult survival is a primary component of population stability (Tack et al. 2017). Currently, not enough data have been collected to estimate survival of golden eagles in YNP. However, when considering the mean annual survival rates of juvenile ($\bar{x} = 0.70$, CRI = 0.66 – 0.74), sub-adult ($\bar{x} = 0.80$, CRI = 0.77 – 0.83), and adult ($\bar{x} = 0.87$, CRI =

0.84 – 0.89) survival from outside YNP (USFWS 2016) and the mean annual probability estimates of nest initiation ($\bar{x} = 0.32$, CRI = 0.26 – 0.38) and success ($\bar{x} = 0.59$, CRI = 0.49 – 0.68) from this study, lambda (λ) is $\bar{x}$ = 0.98 (CRI = 0.92 – 1.03). Consequently, the estimated λ suggests the local population in YNP has the potential to decline over time, if not mediated by immigration from outside the area. Therefore, continued efforts to outfit eagles with GPS transmitters (e.g. multiple age classes) will provide the appropriate data to estimate survival and identify threats to the population.

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Tables and Figures

Table 2.1 Multievent model state transition matrix (ψ) for nonbreeding (A), breeding (B), breeding success (C), and breeding failed (D) golden eagle territories in Yellowstone National Park (2011-2019).

State	Nonbreeding$_{t+1}$	Breeding$_{t+1}$	Breeding-success$_{t+1}$	Breeding-fail$_{t+1}$
Nonbreeding$_t$	$\psi_{A \to A}$	$\psi_{A \to B}$	0	0
Breeding$_t$	0	0	$\psi_{B \to C}$	$\psi_{B \to D}$
Breeding-success$_t$	0	0	0	0
Breeding-fail$_t$	0	0	0	0

Table 2.2 Multievent observation probabilities (p) for nonbreeder (A), breeder (B), breeder success (C), and breeder fail (D) golden eagles in Yellowstone National Park (2011-2019). *Note:* π represents the probability that a nonbreeder (A) is correctly identified as a nonbreeder (pA).

Observation	Nonbreeder	Breeder	Breeder-success	Breeder-fail
Seen nonbreeding	pA $\times\pi$	pB $\times(1-\pi)$	0	0
Seen breeding	0	pB	0	0
Seen breeding-success	0	0	pC	0
Seen breeding-fail	0	0	0	pD

Table 2.3 Multievent state transition probabilities ψ for nonbreeding (A), breeding (B), breeding success (C), and breeding failed (D) golden eagle territories in Yellowstone National Park (2011-2019). Posterior means, standard deviations (SD), 95% credible intervals (CRI), and Rhat.

		CRI			
Transition	Mean	SD	2.5%	97.5%	Rhat
$\mathrm{A} \rightarrow B$	0.32	0.03	0.26	0.38	1.00
$\mathrm{B} \rightarrow C$	0.59	0.05	0.49	0.68	1.00
$\mathrm{B} \rightarrow D$	0.41	0.05	0.32	0.51	1.00
$\mathrm{A} \rightarrow A$	0.68	0.03	0.62	0.74	1.00

Table 2.4 Multievent observation probabilities (p) for nonbreeder (A), breeder (B), breeder success (C), and breeder fail (D) golden eagles in Yellowstone National Park (2011-2019). *Note:* π represents the probability that a nonbreeder (A) is correctly identified as a nonbreeder (pA). Posterior means, standard deviations (SD), 95% credible intervals (CRI), and Rhat.

			CRI		
Detection	Mean	SD	2.5%	97.5%	Rhat
pA	0.75	0.03	0.68	0.81	1.00
pB	0.98	0.02	0.92	1.00	1.00
pC	0.97	0.02	0.91	1.00	1.00
pD	0.97	0.03	0.89	1.00	1.00
π	0.96	0.04	0.86	1.00	1.00

Table 2.5 Period specific summaries (mean and standard deviation [SD]) for covariates included in models for apparent nest initiation and nest success. TMAX (maximum temperature °C), SWE (snow water equivalence kg/m^2), PRCP2 (# of occasions with precipitation on two or more consecutive days), PRCP3 (# of occasions with precipitation on three or more consecutive days), Severe (Relative to period, # of days with precipitation ≥ 1 SD above mean and max temperature ≤ 1 SD below the mean), TRI (terrain ruggedness index), TPI (topographical position index), Cougar (probability of successful cougar kill), Biomass (edible biomass (kg), acquired per wolf per day), NND (distance (m) between nearest neighboring eagle territory centers).

	Period		
Covariates	Winter	Nest Initiation	Incubation
TMAX	-1.64 (1.64)	3.92 (1.77)	-
SWE	179.69 (49.17)	254.1 (82.99)	232.92 (102.17)
PRCP2	7.38 (2.21)	4.67 (1.7)	6.97 (1.56)
PRCP3	4.59 (1.89)	2.76 (1.36)	4.19 (1.37)
Severe	0.79 (1.16)	0.89 (1.49)	-
TRI	19.13 (4.91)	19.13 (4.91)	19.13 (4.91)
TPI	0 (0.02)	0 (0.02)	0 (0.02)
COUGAR	0.04 (0.01)	0.04 (0.01)	0.04 (0.01)
BIOMASS	6.99 (2.3)	6.99 (2.3)	6.99 (2.3)
NND	4200.91 (1482.99)	4200.91 (1482.99)	4200.91 (1482.99)

Table 2.6 Winter period variable (centered and scaled) coefficient estimates on the probability of apparent nest initiation are reported as log odds. Posterior means, standard deviations (SD), 95% credible intervals (CRI), posterior f value (f), and Rhat. *Note*: f is the probability that the true sign of the effect is equal to the sign of the mean effect. TMAX (winter period mean maximum temperature °C), SWE (winter period mean snow water equivalence kg/m^2), PRCP2 (# of occasions with precipitation on two or more consecutive days during winter period), PRCP3 (# of occasions with precipitation on three or more consecutive days during winter period), Severe (# of days with winter period precipitation ≥ 6.5mm and max temperature ≤ 1 -6.4 °C), TRI (terrain ruggedness index), TPI (topographical position index), Cougar (probability of successful cougar kill), Biomass (edible biomass (kg), acquired per wolf per day), NND (distance (m) between nearest neighboring eagle territory centers).

			CRI			
Variable	Mean	SD	2.5%	97.5%	f	Rhat
TMAX	-0.05	0.29	-0.62	0.52	0.57	1.00
SWE	0.19	0.20	-0.20	0.58	0.83	1.00
PRCP 2	0.21	0.20	-0.18	0.60	0.85	1.00
PRCP 3	-0.52	0.24	-1.00	-0.05	0.98	1.00
Severe	0.04	0.20	-0.36	0.45	0.58	1.00
TRI	-0.24	0.20	-0.64	0.14	0.90	1.00
TPI	0.20	0.17	-0.14	0.54	0.88	1.00
Cougar	-0.31	0.19	-0.69	0.07	0.94	1.00
Biomass	-0.31	0.24	-0.81	0.15	0.90	1.00
NND	-0.13	0.19	-0.52	0.25	0.74	1.00

Table 2.7 Nest initiation period variable (centered and scaled) coefficient estimates on the probability of nest success are reported as log odds. Posterior means, standard deviations (SD), 95% credible intervals (CRI), posterior f value (f), and Rhat. *Note*: f is the probability that the true sign of the effect is equal to the sign of the mean effect. TMAX (nest initiation period mean maximum temperature °C), SWE (nest initiation period mean snow water equivalence kg/m^2), PRCP2 (# of occasions with precipitation on two or more consecutive days during nest initiation period), PRCP3 (# of occasions with precipitation on three or more consecutive days during nest initiation period), Severe (# of days with nest initiation period precipitation ≥ 6.5mm and max temperature ≤ -0.5 °C), TRI (terrain ruggedness index), TPI (topographical position index), Cougar (probability of successful cougar kill), Biomass (edible biomass (kg), acquired per wolf per day), NND (distance (m) between nearest neighboring eagle territory centers).

			CRI			
Variable	Mean	SD	2.5%	97.5%	f	Rhat
TMAX	-2.06	0.85	-3.81	-0.49	1.00	1.00
SWE	-1.16	0.58	-2.38	-0.10	0.99	1.00
PRCP 2	0.37	0.33	-0.26	1.03	0.87	1.00
PRCP 3	0.34	0.40	-0.45	1.15	0.80	1.00
Severe	-1.23	0.53	-2.35	-0.27	1.00	1.00
TRI	0.84	0.47	-0.04	1.81	0.97	1.00
TPI	0.49	0.41	-0.29	1.30	0.89	1.00
Cougar	0.21	0.35	-0.46	0.92	0.73	1.00
Biomass	0.16	0.72	-1.21	1.65	0.58	1.00
NND	-0.59	0.42	-1.44	0.19	0.93	1.00

Table 2.8 Incubation period variable (centered and scaled) coefficient estimates on the probability of nest success are reported as log odds. Posterior means, standard deviations (SD), 95% credible intervals (CRI), posterior f value (f), and Rhat. *Note*: f is the probability that the true sign of the effect is equal to the sign of the mean effect. SWE (incubation period mean snow water equivalence kg/m^2), PRCP2 (# of occasions with precipitation on two or more consecutive days during incubation period), PRCP3 (# of occasions with precipitation on three or more consecutive days during incubation period), TRI (terrain ruggedness index), TPI (topographical position index), Cougar (probability of successful cougar kill), Biomass (edible biomass (kg), acquired per wolf per day), NND (distance (m) between nearest neighboring eagle territory centers).

			CRI			
Variable	Mean	SD	2.5%	97.5%	f	Rhat
SWE	-0.33	0.37	-1.07	0.38	0.82	1.00
PRCP 2	-0.04	0.39	-0.82	0.72	0.54	1.00
PRCP 3	-0.46	0.36	-1.20	0.25	0.90	1.00
TRI	0.61	0.42	-0.18	1.47	0.93	1.00
TPI	-0.08	0.33	-0.71	0.57	0.60	1.00
Cougar	0.19	0.29	-0.36	0.76	0.75	1.00
Biomass	0.72	0.42	-0.04	1.60	0.97	1.00
NND	-0.63	0.37	-1.39	0.07	0.96	1.00

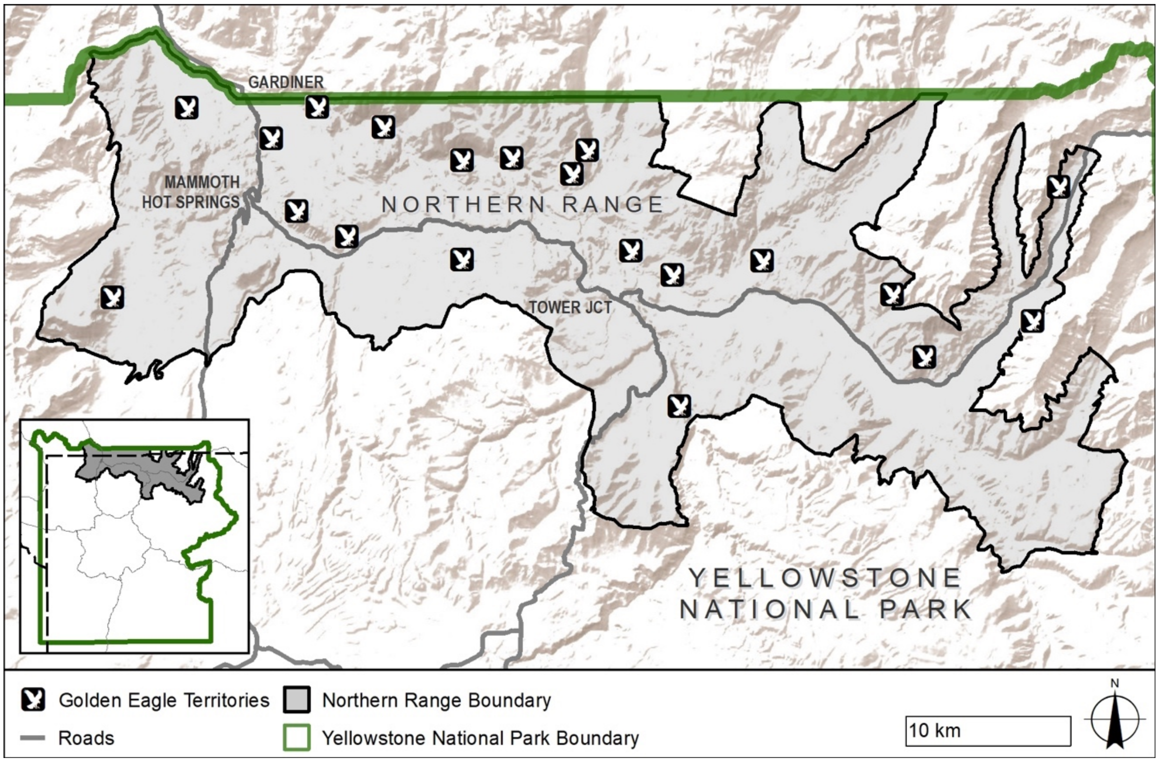

Figure 2.1 Yellowstone National Park northern range study area with golden eagle territories.

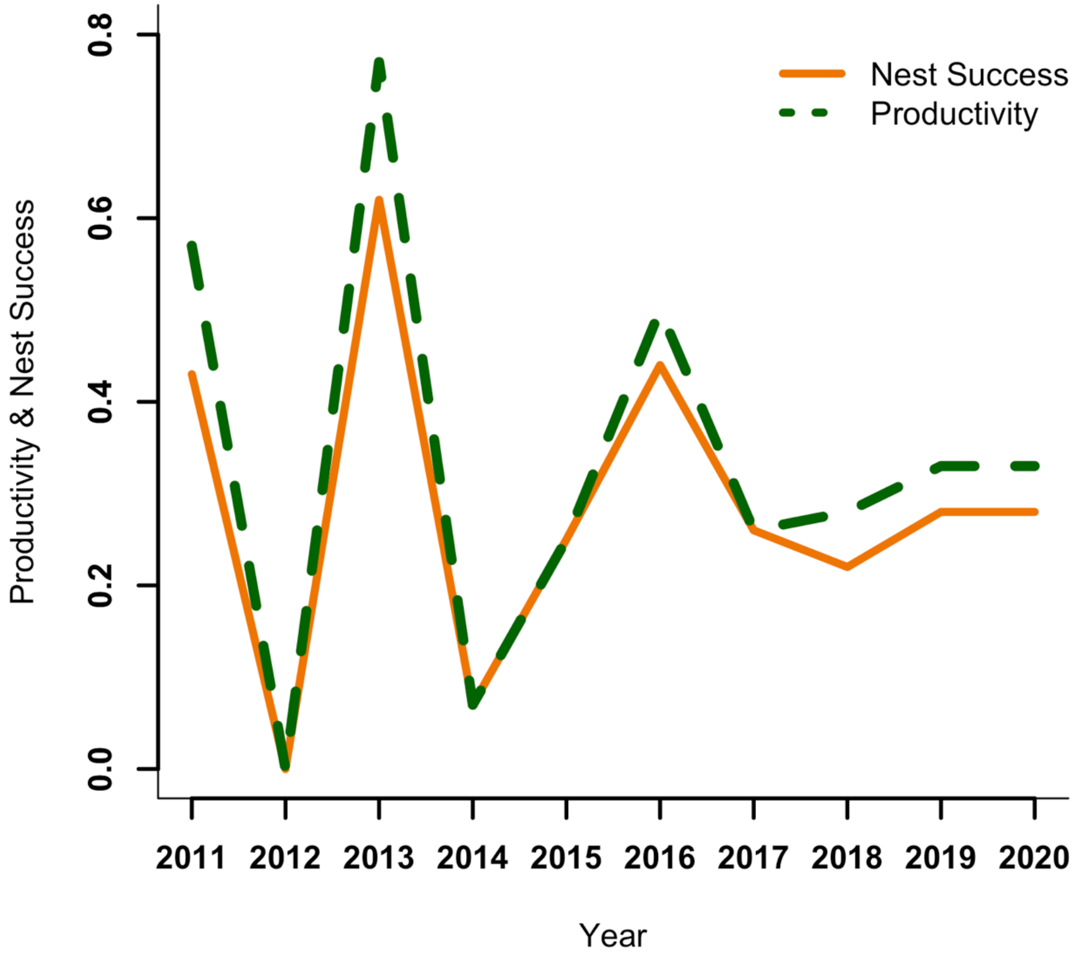

Figure2.2 Annual estimates of golden eagle productivity and nest success in the northern range of Yellowstone National Park, 2011-2020.

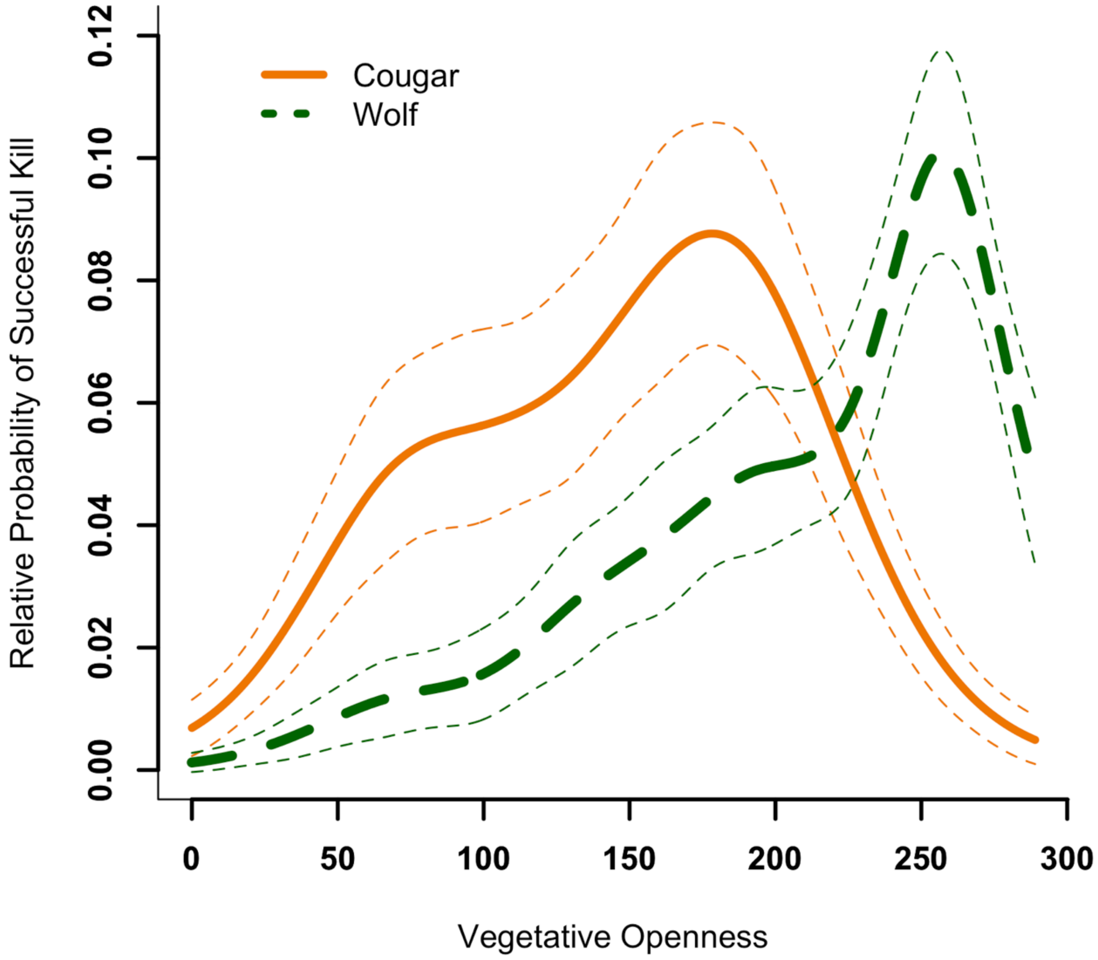

Figure 2.3 Relative probability of successful wolf and cougar kill as a function of vegetative openness (adapted from Kohl et al. 2019). Bold lines are fitted estimates and small dashed lines represent 95% CI.

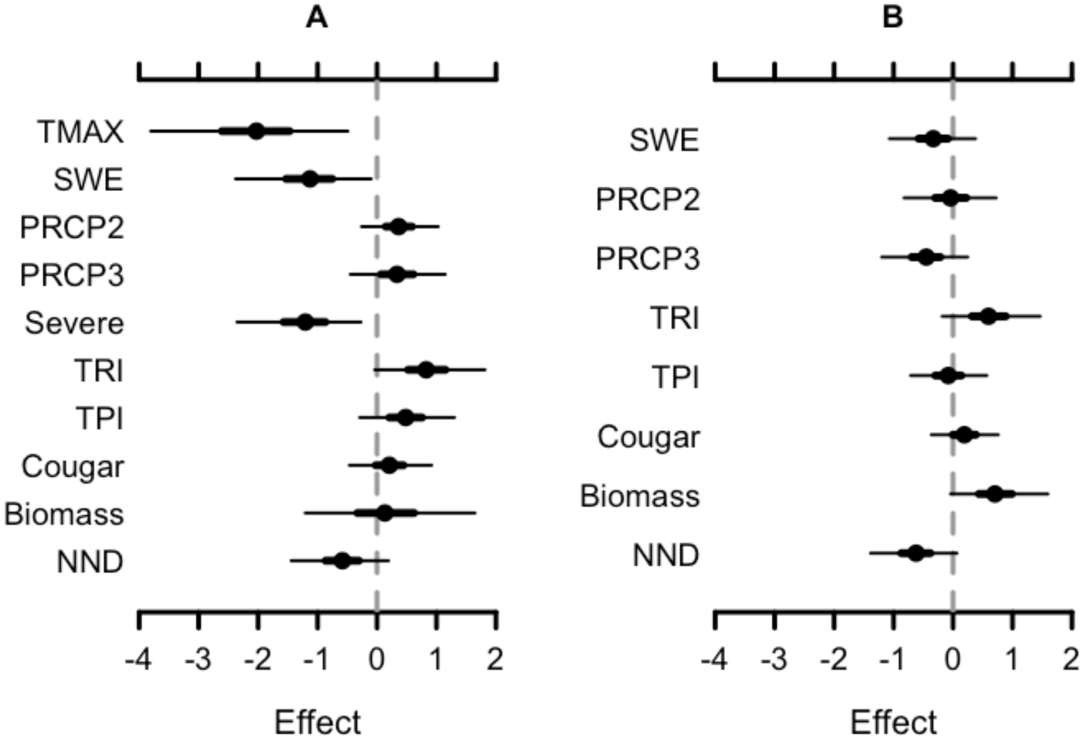

Figure 2.4 (A) Effect of nest initiation period weather and abiotic and biotic resources variables on nest success. TMAX (nest initiation period mean maximum temperature °C), SWE (nest initiation period mean snow water equivalence kg/m^2), PRCP2 (# of occasions with precipitation on two or more consecutive days during nest initiation period), PRCP3 (# of occasions with precipitation on three or more consecutive days during nest initiation period), Severe (# of days with nest initiation period precipitation $\geq$ 6.5mm and max temperature $\leq$ -0.5 °C). (B) Effect of incubation period weather and abiotic and biotic resources variables on nest success. SWE (incubation period mean snow water equivalence kg/m^2), PRCP2 (# of occasions with precipitation on two or more consecutive days during incubation period), PRCP3 (# of occasions with precipitation on three or more consecutive days during incubation period). (A & B) TRI (terrain ruggedness index), TPI (topographical position index), Cougar (probability of successful cougar kill), Biomass (edible biomass (kg), acquired per wolf per day), NND (distance (m) between nearest neighboring eagle territory centers).