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IDENTIFYING ENVIRONMENTAL FACTORS INFLUENCING GOLDEN EAGLE PRESENCE AND REPRODUCTIVE SUCCESS

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By

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Identifying Environmental Factors Influencing Golden Eagle Presence and Reproductive Success

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Declining populations of plant and animal species is a major concern threatening global biodiversity. If we want to conserve threatened species, we must understand the requirements of the species. Recent data suggests Golden Eagle populations in the Western United States are declining. Future threats from expanded energy development, habitat loss and climate change are also a concern. Apparent declines and perceived threats have caused management agencies to classify the Golden Eagle as a species of concern requiring the creation of conservation plans. Yet, an effective conservation plan is dependent on information that is currently lacking. To address this lack of available information, I studied a population of breeding Golden Eagles in south-central Montana which has increased in the last 50 years. I was interested in determining which factors were responsible for the increase in the population and changes in measures of breeding performance. I used information from the current phase to identify which environmental factors are important for the eagles now and assessed whether the identified factors were responsible for the documented changes since the 1960's. I found that Golden Eagles in the current phase were selecting areas for nesting territories based on prey habitat and terrain ruggedness. Within their territories, Golden Eagles selected areas conducive to uplift dependent on proximity to prey habitat, on a western aspect and closer to their nest. My results related to measures of breeding performance were unclear. I found prey habitat was likely not limiting the probability of territories being occupied between phases but instead, anthropogenic disturbance was likely limiting the historic population. My results suggest management plans should focus current protection on areas with prey habitat in close proximity to topography eagles can use to exploit uplift. To better understand the current population trends, I suggest expanding monitoring efforts to areas without a large degree of habitat loss in the last 50 years and to unprotected areas. Golden Eagle populations in these locations may be more indicative of the current status of the population range-wide.

INTRODUCTION

The human population in the United States increased markedly in the past 200 years. Our requirements for food, housing, and transportation all result in habitat loss and degradation that negatively impacts our wildlife populations. For example, in the United States alone over 1.3 million square kilometers of native grasslands have been lost in the past 150 years. When habitats are lost, they are often replaced with urban development, energy infrastructure, or agriculture all to the detriment of native plant and animal species. One such imperiled species is the Golden Eagle (*Aquila chyrsaetos*).

Some intensively monitored populations of Golden Eagles in the western United States have been declining in the last 20 years. In addition, concern over future threats from habitat loss and degradation especially due to continued energy development has caused an increase in concern for Golden Eagle populations in the western United States. Federal and state agencies throughout the region have identified the Golden Eagle as a species worthy of conservation concern and attempts are underway to develop effective management guidelines. Yet, there is little information on population trends outside of a few areas in the region and there is little information on habitat requirements and spatial use by Golden Eagles on the landscape. Understanding the basic requirements of Golden Eagles is essential to the development of any effective conservation plan, and accurately estimating the current status of the population will make measuring the success of conservation actions possible.

I had the opportunity to revisit a historically monitored breeding population of Golden Eagles in south-central Montana with access to historic data on individual territories dating back to 1962. In the first year of the current phase, 2010, I predicted the breeding population would be lower currently than it was in the 1960's due to trends in other parts of the region. To my surprise, the population increased substantially from 33 known breeding territories to 45 known nesting territories. Capitalizing on the unique opportunity to explore the causes of an increasing breeding population, the goals of my project were to: 1) continue adding information to a unique legacy dataset on breeding Golden Eagles in Montana, 2) assess the current status of the Golden Eagle population compared to that in the 1960's, 3) assess environmental factors that influence presence of Golden Eagles on the landscape and within nesting territories, and 4) test which environmental factors are responsible for documented shifts in distribution and productivity. My primary objective was to provide information on habitat requirements and environmental factors responsible for shifts in distribution and productivity to conservation practitioners. If we want to maintain Golden Eagle populations, we must know how they use the landscape and what they need in order to survive. When we have this knowledge, we can then effectively create management guidelines that ensure adequate protection of the species.

My thesis is split between two chapters. Both are in manuscript form and should be read as independent papers. In the first chapter, I assessed which environmental factors influence breeding Golden Eagle presence on the landscape and which factors eagles are choosing within their territories in the current phase only (2010-2013). I also tested the influence of environmental factors on measures of breeding performance. For my second chapter, I used my results from the first chapter to explore whether factors that explain presence and breeding performance in the current phase were responsible for changes in the breeding population since the 1960's. My goal was to provide basic information on the requirements of Golden Eagles and identify factors that influence abundance and reproductive performance to enhance our knowledge of the species and to help guide the creation of management guidelines.

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CHAPTER 1:

FACTORS INFLUENCING PRESENCE AND REPRODUCTIVE SUCCESS OF BREEDING GOLDEN EAGLES

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Abstract

If we want to conserve threatened species, we must learn how they use the landscape and which resources are important for their continued existence. Evidence suggests that Golden Eagle populations in the western United States are declining and an increase in future threats is a concern. Yet we know little on the requirements of Golden Eagles, which hinders the creation of an effective management strategy. I took a multiscaled approach to identify factors influencing the presence of Golden Eagles on the landscape as well as how they use the landscape within their territories. In addition, I tested environmental factors that influenced the probability of nest initiation and nest survival to understand environmental influences on Golden Eagle distribution and breeding success. I found that Golden Eagle territory selection was positively related to percent intermixed shrub and grassland and terrain ruggedness. At the within-territory scale, Golden Eagle selection was best explained by an interaction between ruggedness and proximity to prey habitat, aspect and distance to nest. No environmental variables that I measured could explain nest initiation and results related to nest survival were unclear. My results suggest that to protect and maintain populations of breeding Golden Eagles in the western United States, focus must be placed on maintaining adequate prey habitat in areas with topography conducive to generating uplift that eagles need to effectively capture prey.

Key Words: Golden Eagle, *Aquila chyrsaetos*, resource selection, breeding, Montana

Introduction

Animals choose habitat within a heterogeneous landscape that provides adequate resources and conditions for survival and reproduction (Hall et al. 1997). Preference is predicted by the disproportionate use of habitat in relation to its availability (Johnson 1980) and may be adaptive resulting in fitness benefits to the individuals (Martin 1998). Because of the potential for fitness benefits, conservation practitioners often use information on habitat selection to guide management actions (Manly et al. 2002).

In the past 20 years, studies have indicated that populations of Golden Eagles (*Aquila chyrsaetos*) in the western United States are declining (Kochert and Steenhof 2002, Hoffman and Smith 2003, Good et al. 2007). Recent data suggests the regional population has been stable in the last 50 years, (Millsap et al. 2013), yet most intensive monitoring has shown declines in occupancy rates or measures of breeding performance (Kochert and Steenhof 2002, McIntyre and Schmidt 2012) which complicates the interpretation of the current population status. Nonetheless, state and federal agencies have classified Golden Eagles as a species of conservation concern (United States Fish and Wildlife Service 2008, Montana Natural Heritage Program 2011) due to the documented declines and predicted increase in future threats from energy development (Hunt 2002, Smallwood and Thelander 2007), climate change (McIntyre et al. 2006, Whitfield et al. 2007) and shifts in land use (Kochert and Steenhof 2002, Watson 2010). This increase in attention has exposed the fact there is an insufficiency in knowledge of the basic habitat requirements of Golden Eagles.

Published work on Golden Eagle habitat selection in North America has been based on locations from either direct observations or from VHF animal tracking technology with few relocation points (Marzluff et al. 1997). Limited sampling locations in addition to significant error associated with VHF tracking data (Craighead et al. 1973, Rouys et al. 2001) complicates steps in defining resources selected by individuals. Habitat use also has been described in the United States for far northern breeding Golden Eagles in Alaska (McIntyre et al. 2006). These two efforts have resulted in broad descriptions of habitat characteristics in two distinctly different areas. However, both studies lack detailed, multiscale analyses assessing environmental factors influencing habitat selection by breeding Golden Eagles. Our ability to apply current habitat selection studies are, therefore, limiting in aiding conservation efforts.

If we want to construct an effective conservation strategy, an often overlooked yet extremely important aspect is identifying habitat influences on breeding success. Some Golden Eagle territories are consistently more productive than others (Reynolds 1969, Steenhof et al. 1997, McIntyre 2002). Differences in habitat quality may play an important role in regulating occupancy and productivity of Golden Eagles among territories (Ferrer and Donazar 1996). Therefore, understanding factors that determine both habitat selection and breeding success need to be considered to increase knowledge of Golden Eagle resource requirements and predict the degree of future impacts to Golden Eagle habitat.

Based on the need for information related to breeding Golden Eagle habitat requirements and factors influencing success, I asked two questions: 1) which environmental factors help predict the presence of breeding Golden Eagles and 2) which environmental factors influence Golden Eagle breeding success? The study area where I conducted the work has experienced an increase in Golden Eagles during the last 50 years (R. Crandall unpubl. data). This increase in the population contrasts with current Golden Eagle population trends making this study area an excellent location to examine Golden Eagle related questions. In addition, the current breeding density of Golden Eagles is among the highest reported in the region which further makes this study area worthy of testing predictions related to resource selection and environmental factors that influence breeding success. A high density of Golden Eagles may result in pairs occupying territories of differing qualities which may provide more informative results.

I took a multiscale approach to answering the first question testing environmental factors that may influence presence of breeding Golden Eagles in a resource selection function (RSF) framework at both the territory and within territory level. Habitat selection is considered hierarchical in that different factors influence selection at different spatial scales (Johnson 1980, Lloyd et al. 2005). A multiscale approach allowed for a broader understanding of the resources required by Golden Eagles at these different spatial scales which is needed for a comprehensive understanding of Golden Eagle distribution. Based on the work of Marzluff et al. (1997) and McIntyre et al. (2006), I predicted that Golden Eagle selection would best be explained by the presence of available prey habitat. I also allowed for alternative explanations including the avoidance of anthropogenic disturbances described by Martin et al. (2009) and Watson (2010) and interactions between prey habitat availability and anthropogenic disturbances. For my second question, I also predicted that prey habitat would be the main influence describing the probability of nest initiation and nest survival. I also allowed for alternative explanations including anthropogenic disturbance and biologically significant factors I predicted may influence these measures of breeding performance. My goal was to provide a comprehensive assessment of which factors best predict presence of breeding Golden Eagles and which factors most likely predict measures of reproductive success.

STUDY AREA

I conducted my work in a 2,700 km^2 study area near Livingston, Montana (ca. 45^o 40’ N, 110^{o}34’ W, Figure 1). Elevation in the study area ranges from 1225 to 2600 m. The topography is varied consisting of areas with steep, mountainous terrain to gently rolling hills on the valley floor. Land cover is equally varied ranging from sub-alpine forests in the higher elevations to cottonwood (*Populus* spp.) dominated riparian areas and intermixed sagebrush-steppe and grassland in the lower elevations. Cattle ranching is the primary land use in and around active eagle territories. Land ownership within the study area is a mosaic of private, state, and federal land with most nests located on private land.

Most Golden Eagle research has been focused on public land due to difficulties associated with working on private land. This public land bias has created a large gap in fully assessing the current status of the regional Golden Eagle population. Moreover, resource availability and quality on private land is influenced differently by different grazing regimes, increased human habitation, development and other miscellaneous factors. Ignoring private land in conservation projects has been acknowledged (*see* Bean and Wilcove 1997, Norton 2000) but the problem remains due to the continual lack of effort focusing on private land.

METHODS

Terminology. I used the terminology of Steenhof and Newton (2007) to describe parameters associated with breeding Golden Eagles with the exception of nest initiation where I used the McIntyre and Schmidt (2012) definition (Table 1). Other raptors such as bald eagles (*Haliaeetus leucocephalus*) have been known to appear to be incubating when in reality they are not (Fraser et al. 1983). The frequency of "fake incubation" occurring in Golden Eagles is unknown. Therefore, the terms nest initiation and nest survival should be interpreted as apparent nest initiation and apparent nest survival.

Field Methods. I used data from previous studies (McGahan 1966, 1968, Reynolds 1969, D. Craighead unpubl. data) in addition to talking with knowledgeable local landowners and agency biologists to locate nesting territories beginning in the early spring of 2010. I also searched for new nesting territories by scanning large areas with no known nest sites for the presence of adult Golden Eagles from strategic vantage points using spotting scopes (20-60 x 80) and binoculars

(10 x 42) and located nesting territories opportunistically while traveling throughout the study area. When an adult eagle was located, I waited for evidence of occupancy by a breeding pair. Once a nesting territory was considered occupied, I determined status as either non-nesting or nesting. A pair was classified as nesting only when one of the pair was seen in an incubation posture on a nest. Nesting territories were considered non-nesting when both adults of the pair were seen perched or soaring for greater than 1 continuous hour during the incubation period which often required multiple visits. On average, Golden Eagles leave their nest exposed for far less than one hour per day (Collopy 1984) so one hour was an appropriate time period to determine whether nest initiation had occurred. If the adults were not seen in the early incubation period, the territories were visited again later to confirm whether late nest initiation occurred. Early failures are very difficult to detect in Golden Eagles and therefore may have been categorized as occupied, non-nesting. To minimize misclassifying nesting status, I began nest checks and searching within the first week of the earliest dates of incubation onset and made repeated visits to nesting territories when necessary. The vast majority of nest searching was ground-based surveys (4-wheel drive truck or on foot). I also used fixed-wing aircraft surveys when I believed nest initiation occurred but I was unable to gain access to a property. All fixed-winged aircraft surveys were targeted searches for specific nests and not broad searches for unknown nests.

In the years following the initial discovery of a nesting territory, I recorded some that were not occupied meaning no territorial adults were present. This is a common occurrence with raptors and Golden Eagles specifically (McGahan 1968, Steenhof et al. 1997, McIntyre and Adams 1999). Unoccupied nesting territories were determined from multiple visits (≥ 3) to a nesting territory spanning at least 2 hours per visit where no Golden Eagles exhibiting territorial behavior were seen.

Nesting territories where nest initiation was confirmed or where the status was undetermined were revisited during the nestling period to determine nest survival and productivity rates. Productivity was estimated as the total number of fledged young per successful nest. Nest failures were determined by the lack of live nestlings present in or around the nest.

To assess questions of resource selection, I also trapped and put tracking devices on adult, breeding eagles on the study area. Trapping occurred from early February to late March of 2011-2013. Only known nesting territories with breeding Golden Eagles were targeted for capture. I used road-killed ungulate carcasses for bait which were placed in the territory, typically within 0.5 km of a known nest site, before dawn. I used a net launcher (Trapping Innovation, L.L.C., Kelly, WY) to shoot a 6.1 m x 6.1 m (20ft. x 20ft.) net over the carcass when one or both of the target pair were feeding. Traps were fired using a remote control from afar to minimize the potential for disturbing target adults. Once an adult was captured, I attached a 30-g or 45-g GPS/Argos PTT transmitter (Microwave Telemetry, Columbia, MD). Captured eagles ranged from 3700 to 6100 grams. Therefore, the transmitters were always well under the recommended 3% maximum weight of adults (Gustafson et al. 1997). The transmitters collected 1 point every hour for 15 hours per day for the duration of the breeding season. All trapping and handling of Golden Eagles was approved and certified by University of Montana Institutional Animal Care and Use Committee (AUP #009-12EGDBS-020812).

Territory Selection. I investigated factors influencing selection by breeding Golden Eagles using a resource selection function (RSF) framework (Manly et al. 2002) at multiple spatial scales in order to identify which factors were important at each scale to create a broad understanding of Golden Eagle distribution. I followed Johnson's (1980) definitions of scale targeting the second and third order, which are defined respectively as the home range of an individual and the usage made of various habitat components within the home range. I was first interested in determining which environmental factors influenced the presence of Golden Eagles on the landscape, or what Johnson (1980) defined as the second order.

Within this second order, I further subdivided the projected territory into the core area and the nesting territory as a whole. I defined these two different levels using the tracking information collected from breeding adults. I used relocation data from 10 breeding males and 2 breeding females, and used relocation points only from the nesting period. I defined nesting period as March 15 through July 15 of 2011-2013. In cases where nest failure occurred, the end date for that individual was the date of nest failure determined through tracking data or in the field. Relocation points from GPS transmitters were inspected visually and using internal diagnostics from the tag to ensure any outliers (i.e. inaccurate relocation points) were removed prior to the analysis.

I estimated Minimum Convex Polygons (MCP) using the locations from the tracked individuals to represent two different scales of the nesting territory. I used the 50% MCP's to estimate the size of the core area and the 95% MCP's to estimate the size of nesting territories as a whole. I considered the area represented by the 95% MCP a better estimate of the nesting territory instead of the 100% MCP due to a few large movements made by the adults towards the end of nesting season which would have misleadingly increased the estimate of the territory. I used MCPs instead of another home-range estimator because we were simply using the area estimates provided by the MCP to define the core area and nesting territory. The final product, estimated territories around territory centers or nest sites, is more similar to a MCP than a home range estimate produced by a Kernel Density Estimator for example. All home-range estimates were done using package adehabitatHR in program R (Version 2.15.3, R Core Development Team 2013). I rounded the core area to 1000 m radius surrounding nest sites and the nesting territory estimate to a 2500 m radius based on the estimates from the MCP's.

I projected circles with these radii around used nest sites or nesting territory centers to represent the two spatial scales of each territory. If only one nest was used during the 2010-2013 nesting seasons, this nest was considered the territory center. If different nests were used within a single nesting territory (n=7), I estimated territory centers following the method of McGrady et al. (2002) and McCleod et al. (2002). This is a rather straightforward method in which the geographic center of all used nest locations is estimated and considered territory center. I only projected core area radii around nest sites since a 1000 m radius around the geographic center may not have captured the actual center of use in the territory. In the case of multiple used nest sites, I only extracted covariates from the radii around the nest that was used most frequently to avoid pseudoreplication. I could have done a repeated measures analysis where I used territory as the repeated measure and included covariates from core area estimates from each year, but I wanted to keep the analysis equal for both scales. Also, I may not have had adequate variance for a repeated measure analysis so I determined using only one nest site was the best method to assess selection at the core area scale. The 2500 m radii were projected around the estimated territory centers and always included both nest sites and likely areas of use by birds. All territory projections were done using Geospatial Modelling Environment (GME, Beyer 2012). In cases where radii overlapped between centers of adjacent territories, I bisected the distance between the two nests and considered that the common boundary between the two nesting territories.

This method is similar to that described by McGrady et al. (2002) for delineating Golden Eagle territories that overlap spatially and is justified because Golden Eagles are highly territorial and allow minimal intrusion by other adult Golden Eagles during the breeding season (Watson 2010).

To assess environmental influences on nesting territory selection, I also projected random points within the study area boundaries to represent unused, potential nesting territory centers. Random points were projected in suitable nesting habitat that was not used for nesting by Golden Eagles during the course of my study. I limited randomly projected, unused territory centers to suitable nesting habitat to ensure the area could potentially be used by nesting Golden Eagles. To estimate suitable nesting habitat, I used a 30-m resolution land cover layer (Montana Spatial Analysis Lab 2012) in ArcGIS 10.0 (ESRI Inc., Redlands, CA, USA) and extracted only the land cover types used by Golden Eagles for nesting. Prior to the creation of the layer representing suitable habitat for a nest, I collapsed the land cover types to increase accuracy of the remote sensing data and create more biologically meaningful categories from 77 to 13 land cover types. For potential nesting habitat, I extracted only the land cover types used by eagles in the study area which were coniferous forest, riparian, and cliff and rock. All used nests were within the newly projected layer. Once the potential nesting habitat layer was created, I projected an equal number of random locations as there were used territories with a minimum distance apart equal to the minimum nearest neighbor distance of documented nests on my study area to account for territoriality of the species (Sergio et al. 2006). For both scales, I projected a set of random points within the available nesting habitat layer. I excluded the radius for each given scale around the used nest site for projection of the random points to better assess difference between used sites and random sites. If radii surrounding random sites overlapped, I bisected the distance between territory centers and created a common boundary so territories representing random sites did not overlap just like used nesting territories.

Once all radii were finalized, I extracted covariate information for all estimated territories using a moving window approach (Aldridge et al. 2012). The covariates that I included tested the predictions that I outlined in the introduction and also represented alternative predictions that may explain Golden Eagle territory selection. I used measures of primary prey habitat which I predicted to be the primary factor influencing selection by breeding Golden Eagles. In Montana, McGahan (1966, 1968) and Reynolds (1969) found that eagles' diet consisted primarily of white-tailed jackrabbit (*Lepus townsendii*), desert cottontail (*Sylvilagus audubonii*), mountain cottontail (*Sylvilagus nuttallii*) and Richardson's ground squirrel (*Urocitellus richardsonii*). These species primarily live in open areas consisting of mixed sagebrush and grassland (Yeaton 1972, Hansen and Gold 1977, Johnson and Hansen 1979, Rogowitz 1992, Knick and Dyer 1997) which I included as a covariate (Table 2). As part of the habitat-based prediction, I also included mean terrain ruggedness which has been shown to positively influence presence of breeding Golden Eagles in other studies (McCleod et al. 2002, Sergio et al. 2006, Taipia et al. 2007). Terrain ruggedness was estimated using a 10 m resolution digital elevation model (DEM) layer and I calculated the ruggedness index using the raster package in program R (Version 2.15.3, R Core Development Team 2013). The terrain ruggedness index assigns values to cells in a raster based on difference in elevation between neighboring cells (Riley et al. 1999). Flat areas on the landscape would be assigned a value close to 0 while areas with large difference in elevation between adjoining cells the DEM would be assigned a large value. A primary alternative prediction that I tested was that Golden Eagles resource selection is negatively associated with the presence of anthropogenic disturbance on the landscape which I accounted for with multiple covariates (Table 2). All land cover covariates that I used were taken from the land cover layer with the collapsed habitat types.

Once covariate values were obtained, I used Spearman's correlation coefficients to check for collinearity among covariates with $|r| = 0.60$ as the acceptable threshold. In cases where collinearity occurred, I kept the variable that was more relevant based on the ecology of the Golden Eagle. I then created a candidate model set for both scales *a-priori*, with each model representing the predictions I outlined above related to Golden Eagle territory selection. I used logistic regression to assess the probability of use based on covariates of interest (Manly et al. 2002). I used Akaike Information Criteria adjusted for small sample size (ΔAIC_c) for model selection and considered all models ≤ 2 ΔAIC_c of the top model as competitive (Burnham and Anderson 2002). For all analyses, I also included a null model to compare the ability of my chosen covariates to explain each response variable that I was interested in more than random chance.

To compare which scale was better at predicting the probability of use by breeding Golden Eagles, I used the area under the receiver operator characteristics (ROC) curve, or AUC. The AUC values provided a comparison of the performance and predictive ability of each top model (Hosmer and Lemeshow 2000). I defined the scale with the higher AUC value as the top scale at predicting nest site selection and used the top model associated with that scale for inference (Squires et al. 2008).

Within-Territory Resource Selection. I was also interested in determining which factors were important at the within-territory scale, or third order of habitat selection (Johnson 1980). I used locations from the same 10 breeding males and 2 breeding females to assess resource selection at this scale. I grouped males and females together since the sample size was relatively small. I used the 95% MCP's that I created to estimate territory sizes for the second order habitat selection portion and used these as boundaries with which to project random locations that represented unused, available locations. I used the 95% MCP versus the 100% MCP due to some large movement made by the males towards the end of the nestling season. The difference between the 95% MCP's and the 100% MCP's was large and 100% MCP's often greatly overlapped other, known Golden Eagle breeding territories due to a small number of movements which occurred toward the end of the nestling season. Within each 95% MCP for all 12 Golden Eagles, I projected 1500 random points to represent available, unused locations. The mean number of locations for all birds per breeding season was 1265 locations (SD = 465).

I used covariates that I predicted would have greatest influence on use by Golden Eagles. These included landscape covariates related to prey habitat, human disturbance, and I also included aspect, terrain ruggedness, and distance to nest (Table 2). I used distance to land cover type of interest instead of the land cover type directly associated with the location, which differs from most other resource selection studies. I determined that using distance was more appropriate since Golden Eagles often soar or perch while hunting, and their hunting grounds are often not directly under the individual. I used distance to nest to account for the breeding eagles' continual return to their nest site (Rosenberg and McKelvey 1999, Irwin et al. 2007).

Once I had all covariate information extracted, I again built models that represented predictions related to third-order resource selection by breeding Golden Eagles. I used logistic regression with a random effect of individual to account for unbalanced number of locations for each individual tracked (Gillies et al. 2006). All covariates were checked for collinearity prior to being entered in the modeling process. All covariates were also scaled prior to running the models to aid in model convergence. I used AIC for model selection and considered all models within 2 ΔAIC units of the top model as competitive. I used *k*-fold cross validation with 5 folds to assess model performance of the top model (Boyce et al. 2002). I used Spearman-rank correlation to test the area adjusted frequency of the predicted RSF scores to the RSF score category to assess the predictive ability of the best model (Boyce et al. 2002).

Factors Influencing Nest Initiation and Nest Survival. I also examined which environmental factors influence probability of nest initiation and nest survival of Golden Eagles breeding on my study area. I used all active territories within the study area and separated them out into 1) occupied, non-nesting, 2) occupied, unsuccessful and 3) occupied, successful for each year the nesting territory was monitored. I completed two separate analyses testing factors that influenced probability of nest initiation and then another which tested factors that influenced nest survival. In most studies of breeding Golden Eagles, researchers have noted high variation in occupancy rates. In the 4 nesting seasons that I monitored this breeding population, I only documented 4 unoccupied territories. Because the number of unoccupied territories was small, I did not include factors influencing occupancy in my analysis.

I used the 2500 m buffer around territory centers to extract covariate information to assess factors influencing nest initiation and nest survival. Although I allowed for the possibility of the core area (50% MCP) to better explain territory selection, I assumed that the factors that influence probability of nest initiation and nest survival would be better represented by an area larger than simply the core area. Therefore, I did not entertain a smaller area for covariate extraction for this portion.

Using all the territories as described above, I initially considered covariates which included climatic factors, habitat characteristics and biologically relevant factors all of which may influence breeding success. Nest initiation and productivity rates were nearly identical during each of the 2010-2013 nesting seasons. Therefore, covariates such as weather had limited explanatory power. So, I reduced my chosen variables to 11 nesting territory specific covariates related to prey habitat and anthropogenic disturbance (Table 2). I also used NND to test nesting territory quality. Golden Eagles that use smaller nesting territories are thought to have higher quality nesting territories since they are able to gather the required resources in a smaller area (Collopy and Edwards 1989, Watson 2010). I used NND as a measure of territory size assuming the closer the neighboring territory, the smaller the used territory which was supported by visual observation of my location data. I predicted a positive relationship between NND and the probability of nest initiation or nest survival.

My final models included one model set with response variables of nest initiation with 0 representing no nest initiation and 1 representing apparent initiation. The other model set included a binary response variable representing nest survival where 0 represented nesting failure and 1 represented presence of at least one young at minimum acceptable age for assessing success. Explanatory variables were the covariates that I described above. Covariates that entered the final model sets varied based on collinearity. I used logistic regression with repeated measures in a maximum likelihood framework. I used territory as the repeated measure to account for differences within and among nesting territories. All covariates were scaled prior to running the models to aid in convergence. I used AIC*c* for model selection and considered any model within 2 ΔAIC*c* units from the top as competitive (Burnham and Anderson 2002).

RESULTS

I located 45 Golden Eagle nesting territories within my study area. All were used at least once with most used at least 3 of the 4 nesting seasons. In the 45 territories, I documented 52 used nests with a total of 7 breeding pairs using multiple nest sites. I documented 115 nest initiations from the 2010 through 2013 nesting seasons. Average number of nests per year for all nests in the study area was 28.8 (SD = 1.3). Of the 115 nesting attempts, 74 were successful with an average of 64.3% (SD = 4.4%) successful per year. The average number of young produced per year was 22.8 (SD = 2.4). Productivity per occupied territory was 0.59 (SD = 0.08) young, productivity per nest initiated was 0.79 (SD = 0.08) young and productivity per successful nest was 1.24 (SD = 0.12) young. Of the 52 total nests, 24 were located on trees (46.2%) and 28 were located on cliffs (53.8%). Of the 24 tree nests, 18 were in Douglas firs (75.0%) and 6 were in cottonwoods (25.0%).

Territory Selection. The top models describing the probability of a territory being used by Golden Eagles in my study area at both the entire territory level (2500 m) and the core area (1000 m), included the percent of territory comprised of prey habitat and at the 1000 m scale, an additive effect of terrain ruggedness (Table 3). At the 2500 m scale, there were two other models with 2 AIC*c* units of the best model but each included only one additional parameter so I did not consider those models as competitive (Arnold 2010). The top scale at predicting nesting territory selection was the 1000 m, or core area surrounding a used nest site. The AUC value for the 1000 m level was 0.86 compared to 0.66 at the 2500 m scale. Using the top model from the 1000 m scale, my results suggest Golden Eagles were selecting areas for their nesting territories with intermixed shrub and grassland ($\beta = 7.17$, 95% CI = 4.20 – 10.14) and areas with higher terrain ruggedness ($\beta = 0.41$, 95% CI = 0.10 – 0.72).

Within-Territory Resource Selection. I used 15,182 locations from 12 individuals to assess within-territory resource selection by Golden Eagles during the breeding season. The top model in my model set included an interaction between terrain ruggedness and distance to prey habitat and additive effects of aspect and distance to nest (Table 4). This model was the only competitive model and held 100 % of the model weight and was separated by 83.2 AIC units from the second best model. The interaction term between ruggedness and distance to prey habitat was significant (Table 5) suggesting selection for distance to prey habitat was dependent on terrain ruggedness. Accounting for the interaction, Golden Eagles were selecting locations closer to prey habitat in areas with higher orographic uplift accounted for by terrain ruggedness (Table 5). Golden Eagles were also selecting areas closer to their nests and on western aspects, which is the primary wind direction on the study area (http://www.wrcc.dri.edu/htmlfiles/westwinddir.html). The average Spearman's rho from the *k*-fold cross validation was equal to 0.98 ($p < 0.0001$), indicating the model was effective at predicting selection by Golden Eagles.

Factors Influencing Nest Initiation and Nest Survival. The top model describing probability of nest initiation was the univariate model including percent of territory with 50-100% shrub canopy cover (Table 6). There were two other models within 2 AIC*c* of the best model but neither offered informative parameters (Arnold 2010). The relationship between percent of territory dominated by shrub cover and probability of nest initiation was positive yet the 95% confidence interval overlapped zero therefore I was unable to determine the directionality of this relationship ($\beta = 0.93$, 95% CI = -0.14 – 2.00).

The top model describing the probability of successfully producing young included mean terrain ruggedness and percent of nesting territory comprised of shrub habitat (Table 6). There was one other model within 2 AIC*c* units of the top model but again, this model offered an uninformative parameter so I did not consider it competitive (Arnold 2010). The parameter estimate describing the relationship between mean terrain ruggedness and probability of nest survival was negative ($\beta = -0.66$, 95% CI = -1.29 – -0.18) as well as for percent of territory comprised of shrub habitat although the 95% confidence interval greatly overlapped 0 preventing interpretation of the directionality of the relationship (β = -0.002, 95% CI = -0.392 – -0.388).

DISCUSSION

I found that Golden Eagle habitat selection, both on the second and third order, was best explained by covariates associated with prey habitat and prey acquisition. My results indicated the probability of nest survival was negatively related to terrain ruggedness and that my chosen covariates did a poor job of predicting the probability of Golden Eagles initiating a nest.

Resource Selection. As with many top predators, the presence of Golden Eagles on the landscape was highly correlated with prey habitat. The overwhelming importance of topography, which results in orographic uplift that can be used to aid capturing prey is new, yet follows the hunting style of Golden Eagles. During migration, Golden Eagles almost exclusively use orographic uplift along their route south in the autumn (Bohrer et al. 2012). The use of orographic uplift was explained by the high wing loading of Golden Eagles, which is consistent with a predatory lifestyle but requires stronger updrafts often afforded by orographic uplift (Bohrer et al. 2012). Katzner et al. (2012) noted that Golden Eagles flew at relatively low altitudes over steep slopes and cliffs and local movements, or simply movements not associated with migration, were lower than migratory movements. It could be assumed that breeding Golden Eagle movements are similar to that of local movements made by migrants, meaning they are low and utilize topography which promotes orographic uplift. Therefore, the importance of orographic uplift for breeding birds may be very important and should be included in an assessment of suitable breeding habitat for Golden Eagles.

The human population on my study area has increased by roughly 55% since the 1960’s (Hansen et al. 2002). In addition, nearly all nests on the study area were on private land, which does not have the same protections as National Parks or other conservation areas where most locations where long-term Golden Eagle research has taken place in North America. Thirty years ago managers identified human disturbance as a primary threat to raptor populations (LeFranc and Millsap 1984). Yet, the influence of anthropogenic disturbance on raptor populations has rarely been tested. In fact, Martínez-Abraín et al. (2010) attempted a meta-analysis to quantify effects of recreational activities on breeding parameters for raptors. The only general relationship they found supported was that nests tend to be placed further from roads than would be expected by chance alone. Golden Eagle occupancy was negatively influenced by distance to roads and trails in one of the few tests with this species (Martin et al. 2009). My information from the GPS transmitters allowed for one of the finest-scale and accurate movement based analyses to date for breeding Golden Eagles. Using this fine-scale data, I showed no apparent avoidance of anthropogenic disturbance which may help explain why, despite the increase in human presence, the study area still supports a high number of Golden Eagles. Persecution, primarily through poisoning, is still a major issue for Golden Eagles in Scotland resulting in reduced survival and distribution (Whitfield et al. 2004). Illegal poisoning does occur in the United States, but since Golden Eagles were given protection by the Bald and Golden Eagle Protection Act in 1962, it is likely that poisoning occurs less than it did previously. Direct persecution through activities such as illegal shooting or continuous harassment are likely even less common than poisoning. Therefore, it may be that Golden Eagles in the Western United States are not experiencing a high level of negative interactions with people and are not actively avoiding human presence on the landscape.

Factors Influencing Nest Initiation and Nest Survival. The results from my analysis related to breeding performance showed the probability of nest initiation could not be explained by my covariates and the only significant variable in my top model related to nest survival was terrain ruggedness. The main covariate that I was unable to collect, which would have made this aspect of my analysis more robust was prey abundance. But, prey abundance alone may not explain factors influencing various measures of breeding performance. My results regarding breeding success were similar to McIntyre and Schmidt (2012) who found, despite having annual estimates of prey abundance, that none of their tested covariates were able to predict nest survival. But, they did find that annual prey abundance was able to explain variation in nesting probability. In Idaho, the probability of nest initiation and nest survival for a population of Golden Eagles was influenced by both weather and prey abundance (Steenhof et al. 1997). Sergio et al. (2006) found that percent total grassland in predicted eagle territories was positively related to breeding success. My top model did contain one of my measurements representing prey habitat although it was not a significant predictor describing the probability of nest initiation. While including prey densities would have been desirable, in the absence of prey densities first examining prey habitat was a logical start. In addition, from a management standpoint, understanding the influence of measurable habitat requirements may be easier targets to outline in a management framework since it may be easier to delineate habitat requirements than prey density requirements.

The probability of nest survival was best predicted by terrain ruggedness. Counter to selection, this relationship was negative suggesting the more rugged the area, the lower the probability of nest survival. Ruggedness alone is nearly impossible to interpret as a primary influence on nest survival, especially with a negative influence, which is why I did not include a univariate model of terrain ruggedness. I believe the reason for the importance of ruggedness is due to nesting territories with a high level of relief are located in the more mountainous areas that are typically dominated by conifers. But, the proportion of prey habitat within the territory was not effective at predicting nest survival which would be expected if the more rugged territories had less prey habitat. Therefore, this result is somewhat unclear and likely will require further analysis perhaps after additional data collection.

To effectively create a conservation framework for breeding Golden Eagles in the Western United States, my results suggest protection must focus on maintaining prey habitat. Areas with adequate amounts of prey habitat may also need to have the landscape necessary for Golden Eagles to utilize orographic uplift. Orographic uplift may in fact play a larger role in the presence of Golden Eagles than often considered and may have as large an influence on the presence of eagles to the degree of suitable nesting habitat or even prey availability. Understanding which factors influence nest initiation and nest survival proved more difficult and likely requires more fine-grained information than I had available. Integrating the factors that influence nest survival would increase the effectiveness of any management and continued attempts to identify these factors will be beneficial.

With increased human presence on the landscape and increased resources needed to support a growing human population, the population of plants and animals will continue to be imperiled. Monitoring and conducting research projects on populations of top predators allows conservation practitioners to focus limited resources on species that require stable systems in order to maintain adequate populations. Golden Eagles are top predators and as such, identifying causes of declining population may provide managers with information on larger ecosystem health issues. In western North America, the concern over apparent population declines of Golden Eagles and increased future threats is motivating the conservation community and management agencies to ensure they persist in the region. As we move forward, identifying the status of the population on a broad scale, understanding the factors influencing abundance throughout Western North America and identifying resources needed to maintain and protect the population as a whole will be essential.

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LITERATURE CITED

Aldridge, C.L., D.J. Saher, T.M. Childers, K.E. Stahlnecker, Z.H. Bowen. 2012. Crucial nesting habitat for Gunnison sage-grouse: a spatially explicit hierarchical approach. *Journal of Wildlife Management*, 76: 391-406.

Arnold, T.W. 2010. Uninformative parameters and model selection using Akaike's information criterion. *Journal of Wildlife Management*, 74: 1175-1178.

Bean, M.J., and D.S. Wilcove. 1997. The private-land problem. *Conservation Biology*, 11: 1-2.

Beyer, H.L. 2012. Geospatial Modelling Environment (Version 0.7.1.0). URL: http://www.spatialecology.com/gme.

Bohrer, G., D. Brandes, J. Mandel, K., Bildstein, T. Miller, M. Lanzone, T. Katzner, C. Maisonneuve, and J. Tremblay. 2012. Estimating updraft velocity components over large spatial scales: contrasting migration strategies of Golden Eagles and turkey vultures. *Ecology Letters,* 15: 96-103.

Boyce, M. S., P.R. Vernier, S.E. Nielsen and F.K. Schmiegelow. 2002. Evaluating resource selection functions. *Ecological Modelling*, 157: 281-300.

Burnham, K.P., and D.R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach, 2nd Edn. Springer-Verlag, New York, New York, USA.

Collopy, M. W. 1984. Parental care and feeding ecology of Golden Eagle nestlings. *The Auk*, 101: 753-760.

Collopy, M. W., and T.C. Edwards Jr. 1989. Territory Size, Activity Budget, and Role of Undulating Flight in Nesting Golden Eagles. *Journal of Field Ornithology,* 60: 43-51.

Craighead, J. J., F. C. Craighead, R. L. Ruff, and B. W. O'Gara. 1973. Home ranges and activity patterns of non-migratory elk of the Madison drainage herd as determined by radio-telemetry. *Wildlife Monographs*, 33: 1-50.

Ferrer, M. and J.A. Donazar. 1996. Density-dependent fecundity by habitat heterogeneity in an increasing population of Spanish imperial eagles. *Ecology*, 77:69-74.

Fraser, J. D., L.D. Frenzel, L. D., J.E. Mathisen, F. Martin, and M.E. Shough. 1983. Scheduling bald eagle reproduction surveys. *Wildlife Society Bulletin*, 11: 13-16.

Gillies, C. S., M. Hebblewhite, S.E. Nielsen, M.A. Krawchuk, C.L. Aldridge, J.L. Frair, and C.L. Jerde. 2006. Application of random effects to the study of resource selection by animals. *Journal of Animal Ecology*, 75: 887-898.

Good, R.E., R.M. Nielson, H. Sawyer, and L.L. McDonald. 2007. A population estimate for Golden Eagles in the western United States. *Journal of Wildlife Management*, 71:395-402.

Gustafson, M.E., J. Hildenbrand, and L. Metras. 1997. The North American Bird Banding Manual (Electronic Version). Version 1.0.

Hall, L.S., P.R. Krausman, and M.L. Morrison. 1997. The habitat concept and a plea for standard terminology. *Wildlife Society Bulletin*. 25: 173-182.

Hansen, R.M., and I.K. Gold. 1977. Blacktail prairie dogs, desert cottontails and cattle trophic relations on shortgrass range. *Journal of Range Management*, 30: 210-214.

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

Hoffman, S.W., and J.P. Smith. 2003. Population trends of migratory raptors in western North America, 1977-2001. *Condor*, 105:397-419.

Hosmer, D.W., and S. Lemeshow. 2000. Applied logistic regression. John Wiley and Sons, New York, New York, USA.

Hunt, W.G. 2002. Golden Eagles in a perilous landscape: predicting the effects of mitigation for wind turbine blade-strike mortality. Public Interest Energy Research, California Energy Commission.

Irwin, L.L., L.A. Clark, D.C. Rock, and S.L. Rock. 2007. Modeling foraging habitat of California spotted owls. *Journal of Wildlife Management*, 71: 1183–1191.

Johnson, D.H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology*, 61: 65-71.

Johnson, M.K., and R.M. Hansen. 1979. Foods of cottontails and woodrats in south-central Idaho. *Journal of Mammalogy*, 60: 215-216.

Katzner, T.E., D. Brandes, T. Miller, M. Lanzone, C. Maisonneuve, J.A. Tremblay, R. Mulvihill, and G. T. Merovich Jr. 2012. Topography drives migratory flight of Golden Eagles: implications for on-shore wind energy development. *Journal of Applied Ecology*, 49: 1178-1186.

Knick, S.T. and D.L. Dyer. 1997. Distribution of black-tailed jackrabbit habitat determined by GIS in southwestern Idaho. *Journal of Wildlife Management*, 61:75-85.

Kochert, M.N. and K. Steenhof. 2002. Golden Eagles in the U.S. and Canada: Status, trends, and conservation challenges. *Journal of Raptor Research*, 36:32-40.

LeFranc, M.N., and B.A. Millsap. 1984. A summary of state and federal agency raptor management programs. *Wildlife Society Bulletin*, 12: 274-282.

Lloyd, P., T.E. Martin, R.L. Redmond, U. Langner, and M.M. Hart. 2005. Linking demographic effects of habitat fragmentation across landscapes to continental source-sink dynamics. *Ecological Applications*, 15: 1504-1514.

Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W.P. Erickson. 2002. Resource selection by animals: statistical design and analysis for field studies. Second edition. Kluwer Press, Boston, MA USA.

Martin, J., C.L. McIntyre, J.E. Hines, J.D. Nichols, J.A. Schmutz, and M.C. MacCluskie. 2009. Dynamic multistate site occupancy models to evaluate hypotheses relevant to conservation of Golden Eagles in Denali National Park, Alaska. *Biological Conservation*, 142: 2726-2731.

Martin, T.E. 1998. Are microhabitat preferences of coexisting species under selection and adaptive? *Ecology*, 79: 656-670.

Martínez-Abraín, A., D. Oro, J. Jiménez, G. Stewart, and A. Pullin. 2010. A systematic review of the effects of recreational activities on nesting birds of prey. *Basic and Applied Ecology*, 11: 312-319.

Marzluff, J.M., S.T. Knick, M.S. Vekasy, L.S. Schueck, and T.J. Zarriello. 1997. Spatial use and habitat selection of Golden Eagles in southwestern Idaho. *The Auk*, 114:673-687.

McGahan, J. 1966. Ecology of the Golden Eagle. Thesis, University of Montana, Missoula, USA.

McGahan, J. 1968. Ecology of the Golden Eagle. *The Auk*, 85:1-12.

McGrady, M.J., J.R. Grant, I.P. Bainbridge, and D.R.A. McLeod. 2002. A model of Golden Eagle (*Aquila chrysaetos*) ranging behavior. *Journal of Raptor Research*, 36:62-69.

McIntyre, C.L. 2002. Patterns in nesting area occupancy and reproductive success of Golden Eagles (*Aquila chyrsaetos*) in Denali National Park and Preserve, Alaska, 1988-99. *Journal of Raptor Research*, 36:50-54.

McIntyre, C.L., and L.G. Adams. 1999. Reproductive characteristics of migratory Golden Eagles in Denali National Park, Alaska. *Condor*, 101:115-123.

McIntyre, C.L., M.W. Collopy, J.G. Kidd, A.A. Stickney, and J. Paynter. 2006. Characteristics of the landscape surrounding Golden Eagle nest sites in Denali National Park and Preserve, Alaska. *Journal of Raptor Research*, 40:46-51.

McIntyre, C. L., and J.H. Schmidt. 2012. Ecological and environmental correlates of territory occupancy and breeding performance of migratory Golden Eagles Aquila chrysaetos in interior Alaska. *Ibis*, 154: 124-135.

McLeod, D.R.A., D.P., Whitfield, M.J. McGrady. 2002. Improving prediction of Golden Eagle (*Aquila chrysaetos*) ranging in western Scotland using GIS and terrain modeling. *Journal of Raptor Research*, 36:70-77.

Millsap, B. A., G.S. Zimmerman, J.R. Sauer, R.M. Nielson, M. Otto, E. Bjerre and R. Murphy. 2013. Golden Eagle population trends in the western United States: 1968–2010. *Journal of Wildlife Management*, 77: 1436-1448.

Montana Natural Heritage Program and Montana Fish, Wildlife and Parks. Golden Eagle (*Aquila chrysaetos* <http://FieldGuide.mt.gov/detail_ABNKC22010.aspx> Accessed 13 March 2012.

Norton, D.A. 2000. Conservation biology and private land: shifting focus. *Conservation Biology*, 14: 1221-1223.

Reynolds, H.V. 1969. Population status of the Golden Eagle in south-central Montana. Thesis, University of Montana, Missoula, Montana, USA.

Riley, S. J., S.D. DeGloria, and R. Elliot. 1999. A terrain ruggedness index that quantifies topographic heterogeneity. *Intermountain Journal of Sciences*, 5: 23-27.

Rogowitz, G.L. 1992. Reproduction of white-tailed jackrabbits on semi-arid range. *Journal of Wildlife Management*, 56:676-684.

Rosenberg, D.K. and K.S. McKelvey. 1999. Estimation of habitat selection for central-place foraging animals. *Journal of Wildlife Management*, 63:1028-1038.

Rouys, S., J. Theuerkauf, and M. Krasinska. 2001. Accuracy of radio-tracking to estimate activity and distances walked by European bison in the Bialowizia forest, Poland. *Acta Theriologica*, 46:319–326.

Sergio, F., P. Pedrini, and L. Marchesi. 2006. Adaptive range selection by Golden Eagles in a changing landscape: A multiple modelling approach. *Biological Conservation*, 133: 32-41.

Squires, J. R., N.J. Decesare, J.A. Kolbe, and L.F. Ruggiero. 2008. Hierarchical den selection of Canada lynx in western Montana. *Journal of Wildlife Management*, 72: 1497-1506.

Smallwood, K.S., and C. Thelander. 2008. Bird mortality in the Altamont Pass Wind Resource Area, California. *Journal of Wildlife Management*, 72: 215-223.

Steenhof, K., M.N. Kochert, and T.L. Mcdonald. 1997. Interactive effects of prey and weather on Golden Eagle reproduction. *Journal of Animal Ecology*, 66:350-362.

Steenhof, K. and I. Newton. 2007. Assessing nesting success and productivity. P. 181-192 *In* D.M. Bird and K.L. Bildstein (eds.), Raptor research and management techniques. Hancock House Publishers, Blaine, Washington, USA.

Taipia, L., J. Dominguez, and L. Rodriguez. 2007. Modelling habitat use and distribution of Golden Eagles (*Aquila chrysaetos*) in a low-density area of the Iberian Peninsula. *Biodiversity Conservation*, 16:3559-3574.

Watson, J. 1992. Golden Eagle (*Aquila chrysaetos*) breeding success and afforestation in Argyll. *Bird Study*, 39: 203-206.

Watson, J. 2010. The Golden Eagle. Second edition. Yale University Press, New Haven, Connecticut, USA.

Whitfield, D. P., A.H. Fielding, D.R.A. McLeod and P.F. Haworth. 2004. The effects of persecution on age of breeding and territory occupation in Golden Eagles in Scotland. *Biological Conservation*, 118: 249-259.

Whitfield, D.P., A.H. Fielding, M.J.P. Gregory, A.G. Gordon, D.R.A. McLeod, and P.F. Haworth. 2007. Complex effects of habitat loss on Golden Eagles *Aquila chrysaetos*. *Ibis*, 149: 26-36.

Williams, G. C. 1966. Natural selection, the costs of reproduction, and a refinement of Lack's principle. *American Naturalist*, 100: 687-690.

Yeaton, R.I. 1972. Social behavior and social organization in Richardson’s ground squirrel (*Spermophilus richardsonii*) in Saskatchewan. *Journal of Mammalogy*, 53: 139-147.

Figure 1. Study area with all Golden Eagle nest locations from 2010-2013. Multiple dots in close proximity are indicative of multiple nest sites within one nesting territory.

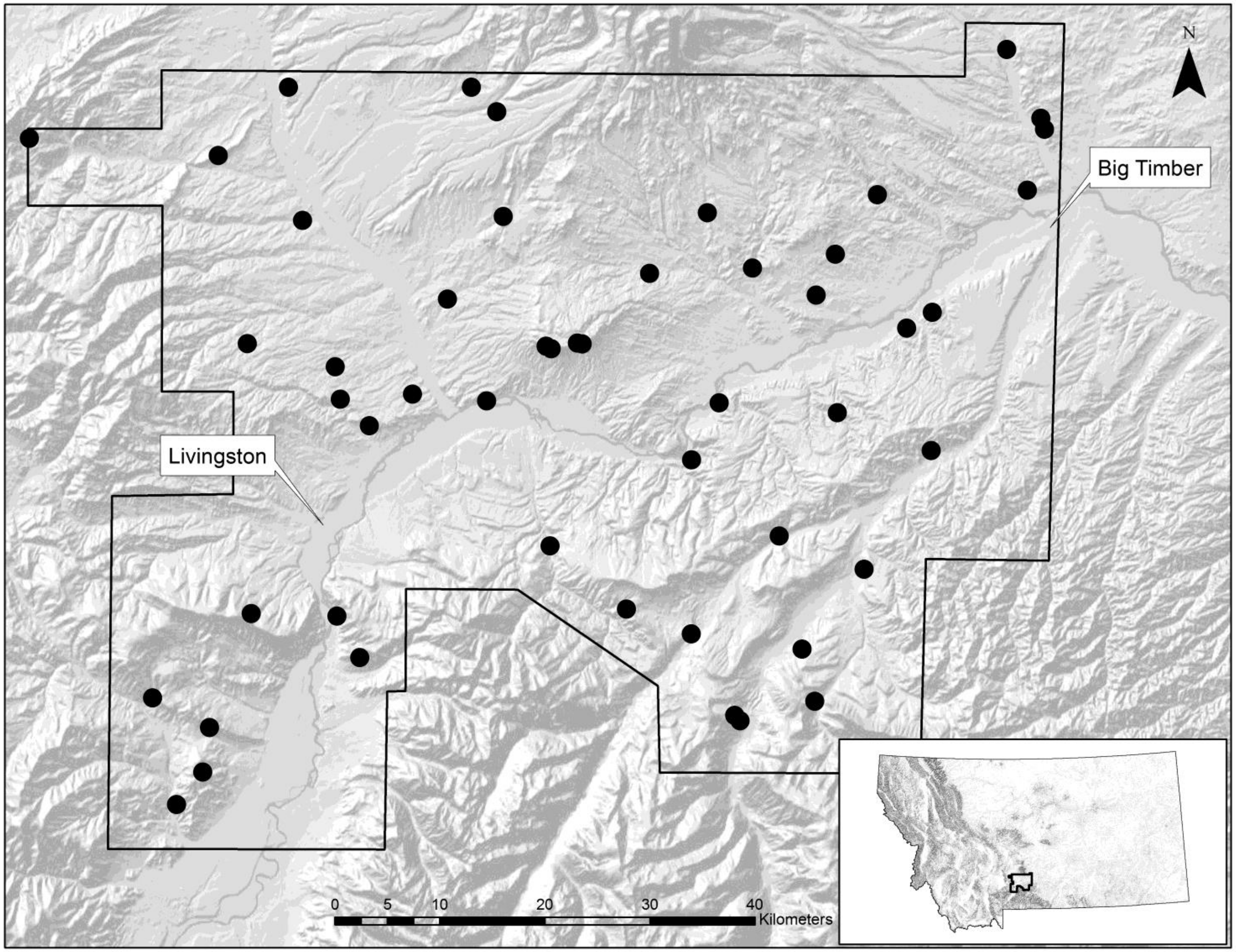

Table 1. Definitions of terms used to describe Golden Eagle breeding parameters. With the exception of nest initiation, all definitions of terms were used following Steenhof and Newton (2007). Nest initiation was used following McIntyre and Schmidt (2012).

Nesting Territory	An area that contains, or has contained, one or more nests and is within the home range of a mated pair known to have bred at least once from 2010-2013
Occupancy	Presence of one or more breeding age Golden Eagles exhibiting territorial behavior such as chasing, undulating flights, or escorting or indivuals showing signs of breeding such as nest building or incubation
Nest Initiation	A pair of breeding age Golden Eagles that appear to lay eggs and incubate
Nest Survival	When a pair successfully raises chicks to the minimum acceptable age for assessing success, which is equal to 8 weeks for Golden Eagles on my study area
Nesting Period	The time from the first egg is laid to when the first chick leaves the nest on its own accord
Nestling Period	The time from the first egg hatches to when at least one chick first leaves the nest on its own accord
Productivity	The total number of young that reach the minimum acceptable age for assessing success

Table 2. All covariates used in the modeling process and the predicted relationship between each covariate and the respective response variable for each analysis. Note that negative relationships for distance covariates represent selection (i.e. probability of use decreases as distance increases) and positive values represent avoidance. The covariate that represented aspect was categorical; western aspect was tested since that is primary wind direction on my study area (http://www.wrcc.dri.edu/htmlfiles/westwinddir.html). The reference category for aspect was north.

Territory Selection	**Description**	**Predicted Relationship**
% Shrub-Grassland	Percent of nesting territory composed of shrub and grassland habitat types	+
TRI	Mean terrain ruggedness index value	+
% Cultivation	Percent of nesting territory in cultivated agriculture	-
% Pasture	Percent of nesting territory in pasture	-
% Developed	Percent of nesting territory developed	-
TRds	Total linear distance of roads in nesting territory	-
Within-Territory RSF		
DSG	Distance to shrub and grassland cover type	-
TRI	Terrain ruggedness index	+
W_ASP	Categorical variable representing western aspect	+
DAg	Distance to agriculture	+
DPast	Distance to pasture	+
DRd	Distance to road	+
DStr	Distance to structure	+
DNest	Distance to nest	-
Nest Initiation and Success		
% Shrub	Percent of nesting territory composed of shrubs	+
% Grassland	Percent of nesting territory composed of grassland	+
TRI	Mean terrain ruggedness index value	+
SC050	Percent of nesting territory with shrub canopy cover from 0-50%	+
SC50100	Percent of nesting territory with shrub canopy cover from 50-100%	+
HC050	Percent of nesting territory with herbaceous canopy cover from 0-50%	+
HC50100	Percent of nesting territory with herbaceous canopy cover from 50-100%	+
TRds	Total linear distance of roads in nesting territory	-
TStr	Total number of structures in nesting territory	-
% Cultivation	Percent of nesting territory in cultivated agriculture	-
% Pasture	Percent of nesting territory in pasture	-
NND	Nearest neighbor distance	-

Table 3. Model selection results from top models describing territory selection by breeding Golden Eagles at the core area and territory sized scale.

1000 m Territory	K	AIC*c*	ΔAIC*c*	Model Likelihood	AIC*c* Weight	Log Likelihood	Cum.Wt
% Shrub-Grassland + TRI	3	87.980	0.000	1.000	0.940	-40.850	0.940
% Shrub-Grassland	2	94.290	6.300	0.040	0.040	-45.070	0.980
% Shrub -Grassland + % Pasture	3	95.890	7.910	0.020	0.020	-44.800	0.990
% Shrub -Grassland + % Developed	4	97.900	9.920	0.010	0.010	-44.700	1.000
Null	1	122.640	34.660	0.000	0.000	-60.300	1.000
2500 m Territory							
% Shrub-Grassland	2	117.500	0.000	1.000	0.450	-56.680	0.450
% Shrub -Grassland + % Pasture	3	119.220	1.720	0.420	0.190	-56.470	0.640
% Shrub-Grassland + TRI	3	119.560	2.060	0.360	0.160	-56.640	0.800
% Shrub-Grassland + % Developed	4	121.020	3.520	0.170	0.080	-56.270	0.880
% Cultivation + % Developed	3	122.530	5.030	0.080	0.040	-58.120	0.910

Table 4. Model selection results showing top models for resource selection function of 3rd order habitat selection by breeding Golden Eagles.

	K	AIC*c*	ΔAIC*c*	Model Likelihood	AIC*c* Weight	Log Likelihood	Cum.Wt
*TRI + DSG + W_ASP + TRI * DSG+ DNest*	7	36009.35	0	1	1	-17997.67	1.00
TRI + DSG + W_ASP+ DNest	6	36092.55	83.20	0.00	0.00	-18040.27	1.00
TRI + DSG + DNest	5	36127.84	118.49	0.00	0.00	-18058.92	1.00
*TRI + W_ASP + TRI * W_ASP + DNest*	6	36210.09	200.74	0.00	0.00	-18099.04	1.00
TRI + W_ASP + DNest	5	36211.83	202.48	0.00	0.00	-18100.92	1.00

Table 5. Coefficient estimates describing probability of use by breeding Golden Eagles for covariates from top model in Table 4.

			95 % CI	
	β	Std. Error	Low	High
TRI	1.12	0.02	1.08	1.16
DSG	-0.20	0.01	-0.22	-0.18
W_ASP	0.19	0.03	0.13	0.25
*TRI * DSG*	-0.12	0.01	-0.14	-0.10
DNest	-0.47	0.02	-0.51	-0.43

Table 6. Model selection results showing top models describing the probability of nest initiation and nest survival for Golden Eagles in south central Montana.

Nest Initiation	K	AIC*c*	ΔAIC*c*	Model Likelihood	AIC*c* Weight	Log Likelihood	Cum.Wt
SC50100	3	177.93	0.00	1.00	0.35	-85.89	0.35
SC50100 + HC050	4	177.98	0.04	0.98	0.34	-84.85	0.69
TRI + SC50100	4	179.85	1.92	0.38	0.13	-85.79	0.82
Null	2	182.03	4.10	0.13	0.04	-88.98	0.87
% Grassland	3	183.58	5.65	0.06	0.02	-88.71	0.89
Nest Success							
TRI +% Shrub	4	152.06	0.00	1.00	0.49	-71.85	0.49
TRI + % Shrub + % Grassland	5	153.95	1.89	0.39	0.19	-71.70	0.68
*TRI + % Shrub + TRI * % Shrub*	5	154.24	2.18	0.34	0.16	-71.85	0.85
% Shrub + % Grassland	4	155.71	3.65	0.16	0.08	-73.68	0.92
Null	2	158.52	6.46	0.04	0.02	-77.21	0.94

CHAPTER 2:

SHIFTS IN DISTRIBUTION OF A BREEDING GOLDEN EAGLE POPULATION EXPLAINED BY LANDSCAPE CHANGE AND ANTHROPOGENIC DISTURBANCE

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ABSTRACT

Increasing human populations and the subsequent impacts to resources required by raptors have caused decreases in some species. The population status of Golden Eagles in the western United States has recently received an increase in attention due to declines in intensively monitored breeding populations and migration counts. Frequently, human-caused disturbance is blamed for this decline although little evidence exists to support this claim due to the lack of time-series data that spans an appropriate time period to make such an assessment. Beginning in 2010, I resurveyed a site with data on breeding Golden Eagle presence and reproductive success dating back to 1962. Since that time, the breeding population has increased roughly 40% providing an anomaly in current Golden Eagle population trends. Although the population has increased, productivity rates have decreased and there are shifts in productivity within territories that were occupied during both phases. I was interested in determining which environmental factors were responsible for the increase in the population and shifts in breeding performance. I found historically unused territories that are currently occupied were likely not limited by prey habitat. Instead, my results suggest anthropogenic disturbance may have been responsible for the lack of breeding Golden Eagles in historically unoccupied territories. The probability of Golden Eagles initiating a nest was negatively related to distance from nest site to road. I found no relationship between any of my tested covariates and the probability of nest survival. My results suggest Golden Eagle populations may have been historically limited by people. As a result, it is possible that Golden Eagle abundance has increased due to declines in persecution in locations where prey habitat has remained relatively stable. To better understand population trends, monitoring should be focused in areas that have not witnessed massive habitat loss or destruction and are outside of protected areas that likely did not have the same level of persecution in the

past. In addition, monitoring efforts should be conducted over an adequate time period to assess population trends. Lastly, I recommend minimizing the probability of direct persecution through continued federal protection, enforcement and education to maintain Golden Eagle populations.

KEY WORDS: Golden Eagle, *Aquila chyrsaetos,* retrospective analysis, breeding habitat, Montana

INTRODUCTION

The presence and reproductive success of raptors is dependent on the availability of prey and nest sites (Hickey 1942, Newton 1979). Increasing human populations can negatively impact the availability and quality of these resources (Sisk et al. 1994, Fahrig 2001) to the detriment of raptor populations (Kochert and Steenhof 2002) and other organisms worldwide (Sala et al. 2000). Factors responsible for declining populations can be assessed by examining which environmental factors are associated with changes in abundance, distribution and productivity of species over time (Martin 1992). Of utmost concern to ecologists and conservation biologists are situations when landscape change negatively impacts species with low or decreasing population sizes (Woodward et al. 2001). A prime example of a species of concern is the Golden Eagle (*Aquila chrysaetos*).

In recent years, Golden Eagle populations in localized areas across Western North America have experienced declines (Leslie 1992, Kochert and Steenhof 2002, Hoffman and Smith 2003, Good et al. 2007). Relative declines of Golden Eagles also have been documented at migration sites (Hoffman and Smith 2003). This differentiation is important because migration sites primarily monitor Golden Eagles that breed in the northern latitudes of Alaska and Canada and overwinter in the Rocky Mountain West (Hoffman and Smith 2003). In contrast, regional breeding populations of Golden Eagles are thought to be non-migratory (Marzluff et al. 1997) and may experience different environmental causes of negative trends. These apparent declines have caused state and federal agencies to designate the Golden Eagle as a species of conservation concern (USFWS 2008, Montana Natural Heritage Program 2011). Yet, the environmental causes of declines are unknown. Current suggestions include habitat loss and degradation (Kochert et al. 1999, Kochert and Steenhof 2002), increased human disturbance (Franson et al. 1995), poisoning (Harmata and Restani 1995, Craig and Craig 1998), electrocution (Harness 1997), changes in grazing regimes (Watson 2010) and impacts from a changing climate (McIntyre et al. 2006, Watson 2010). Yet, little work has been done testing the influence of suggested impacts on Golden Eagle populations. Ultimately, the lack of information on environmental influences on breeding Golden Eagles is hindering the creation of an effective conservation strategy. A critical element needed for empirical assessments is the availability of time series data that spans an appropriate period to make an assessment of potential environmental influences on Golden Eagles.

Beginning in 1962, Jerry McGahan and later Harry Reynolds surveyed an area in south-central Montana for breeding Golden Eagles under the guidance of Dr. John Craighead. They focused on determining population density, productivity rates, prey selection and effects of pesticides on Golden Eagles (McGahan 1968, Reynolds 1969). These data allowed assessments of population change over a half century and provide one of the oldest and most comprehensive baseline datasets on breeding Golden Eagles in the Rocky Mountain West. With access to the legacy dataset, I began monitoring the study site again in 2010 to determine the current status of the population and an interesting trend appeared: nearly all historic territories are currently occupied and the population has increased roughly 40% (Figure 1). In addition, the study area where the original work took place has seen an increase in the human population by at least 55% since the 1960's (Hansen et al. 2002). In light of negative Golden Eagle population trends elsewhere, I had a unique opportunity to examine environmental factors that influence an expanding breeding Golden Eagle population and how landscape change with an increasing human population may affect presence and breeding success of eagles.

I was interested in performing a retrospective analysis using data collected from the 1960's (hereafter referred to as the historic phase) to compare to information collected currently (hereafter referred to as the current phase) on breeding Golden Eagles. Specifically, I was interested in asking which environmental factors influence the observed change in Golden Eagle abundance, distribution and measures of breeding success over time? I separated the analysis into three main sections. First, I attempted to identify factors that influenced the increase in the number of territories. Breeding Golden Eagle populations in Idaho and Scotland were found to be negatively influenced by habitat loss of preferred prey species (Kochert et al. 1999, Marquiss et al. 1985, Watson 1992, Whitfield et al. 2001). Because Golden Eagles negatively react to decreases in prey habitat, I predicted that changes in the amount of prey habitat positively influenced colonization of new territories by Golden Eagles since the historic phase. I allowed for alternate explanations including climate and anthropogenic disturbance as primary factors influencing abundance and distribution.

The second and third sections of my analysis had the goal of identifying factors that influenced changes in the probability of pairs initiating a nest and changes in nest survival. Prey availability and weather can influence the number of Golden Eagle pairs initiating nests and successfully producing young (Steenhof et al. 1997, McIntyre and Schmidt 2012). In the area where I conducted my research, precipitation has decreased and temperatures have warmed in the last 50 years (http://www.ncdc.noaa.gov/). Therefore, I predicted that shifts in the probability of initiating a nest and nest survival were negatively associated with the changes in climate. I also allowed for alternate explanations including changes in the amount of prey habitat and density of breeding pairs. By testing factors influencing both presence and reproductive performance, my goal was determine what has allowed this population to increase while other intensively monitored breeding populations have been decreasing.

STUDY AREA

The location where I conducted my research covers an area approximately 2700 km^2 in size adjacent to the town of Livingston, Montana (ca. 45^o 40’ N, 110^{o}34’ W) on the western edge and Big Timber near the eastern border (Figure 1). Mountains border the study area on three sides with the Crazy Mountains to the north, Absaroka Mountains to the south and Bridger Mountains to the west. All nests were located between 1295 m and 2250 m elevation. Today, the area is dominated by grasslands and sagebrush (*Artemisia spp.*). Forested areas located throughout the study area are composed primarily of Douglas Fir (*Pseudotsuga menziesii*) and Lodgepole Pine (*Pinus contorta*). Riparian areas dominated by Cottonwoods (*Populus spp.*) are also found throughout the lower elevations of the study area. The primary land use now, as in the 1960’s, is ranching (McGahan 1968) with a shift from both cattle and sheep in the 1960’s to primarily cattle currently (http://quickstats.nass.usda.gov/).

METHODS

Terminology. I used terminology to describe activities related to breeding Golden Eagles recommended by Steenhof and Newton (2007) and McIntyre and Schmidt (2012, Table 1). The frequency of “fake incubation” behavior in Golden Eagles is unknown, so the correct interpretation of nest initiations and nesting success should be interpreted as apparent nest initiation and nest survival.

The terminology that I used is the current norm for describing breeding Golden Eagle activity but during the historic phase, the terminology differed. Reynolds (1969) and McGahan (1966,1968) considered a nesting territory occupied only if an eagle pair made an attempt to nest as indicated by direct observation of field sign. Therefore, their definition of occupancy is what I referred to as a nesting territory with a nest initiation. Reynolds (1969) noted specifically in a very low occupancy year that "the low number of nesting pairs observed in 1965 apparently reflects the failure of some adults to nest and not a reduction in numbers of adults on the study area." I expect because apparent occupancy rates were high during the year with the lowest the historic phase definition of occupancy, that overall occupancy using our current definition were likely high during all years of the historic phase. Even so, I was unwilling to assume that all territories monitored each year were occupied therefore I excluded occupancy from my analysis.

Historic Data. Historic data was collected from 1962 to 1968 from McGahan (1966, 1968) and Reynolds (1969). I only used data from 1963-1968 since more effort was put into nest monitoring during those years. During the historic phase, McGahan searched for nests from May through August 1962. Reynolds (1969) used the locations from McGahan (1966) but also searched for new nesting territories by systematically glassing cliffs, buttes, timbered ridges, and ravines from vantage points. At the end of the historic phase, Reynolds was confident that nearly all Golden Eagle nesting territories were discovered on the study area (pers. comm.). I received information on nest locations and breeding performance for each year that a nesting territory was monitored from Reynolds (unpubl. data), both theses, and information from a member of the original field crew (D. Craighead, unpubl. data). From the information that I received, I was able to digitize all historic nest locations in ArcGIS (Esri Inc., Redlands, CA, USA) to aid in spatial analysis and nest searching in the current phase. I was also able to determine nesting status and nest survival for each year a nesting territory was monitored during the historic phase of the study using the available data.

Field Methods – Current Phase. Using the digitized locations of the historic nest locations, I returned to the study area during the early spring of 2010 and focused on checking all historic nesting territories. In addition to checking the historically known territories, I also searched for new nesting territories by glassing potentially suitable nesting habitat similar to Reynolds (1969). I also sought out information on new nesting territories from agency biologists and found a number of new territories based on conversations with local landowners. Once I was at a known nesting territory and saw adults or if I spotted adults while searching for unknown nesting territories, I waited for signs of territorial behavior indicative of breeding adults. When I saw territorial behavior, I considered the nesting territory occupied and attempted to assess whether the pair had initiated a nest. I only determined nest initiation when I saw a bird in incubation posture on a nest. If I saw the pair either soaring or perched for greater than 1 hour, I considered the nesting territory occupied with a non-nesting pair. I chose one hour based on the maximum amount of time Golden Eagles spend away from their nests during the incubation period (Collopy 1984). If I could not easily determine nesting or non-nesting pairs, I repeatedly visited the nesting territory throughout the incubation and nestling period until such a determination could be made. Nearly all nest searching was done either on foot or using 4-wheel drive truck. I also used fixed-wing aircraft when I suspected a nest initiation but could not gain access to the property. All nest searching done via fixed-wing aircraft was targeted and not broad surveys over the entire study area.

I also documented unoccupied territories over the 4 breeding seasons. I determined unoccupied nesting territories by making at least 3 visits that spanned 2 hours or more to previously occupied territories during which time I did not see any adults exhibiting territorial behavior. The number of unoccupied territories during this period was extremely low (n=4) compared to other studies (Kochert and Steenhof 2012, McIntyre and Adams 1999).

When I determined nest initiation, I visited the nesting territory again in the summer to determine nesting survival. I made several visits, when necessary, until I was able to confirm nest survival status. I determined nesting failure by the lack of a live nestling in or around the nest.

Abundance and Distribution. I separated the analysis into the 3 major sections outlined above that examine potential factors influencing 1) abundance and distribution, 2) probability of nest initiation and 3) probability of nest survival. To assess the influence of factors on abundance and distribution, I separated the analysis into a test of climate-related factors on the number of known territories for each year and landscape factors influencing the probability of nesting territory use by breeding eagles. I chose climate variables that represented factors that may influence the prey base through changes in the vegetation. Golden Eagles primarily rely on prey that are associated with open areas; in the Rocky Mountain Region of the Western United States, these prey items include jackrabbits (*Lepus* spp.), cottontail rabbits (*Sylvilagus* spp.), and ground squirrels (*Urocitellus* spp.; McGahan 1966, 1968, Reynolds 1969, Steenhof and Kochert 1988). All of these primary prey species are found in open areas composed of intermixed shrub and grasslands (Yeaton 1972, Hansen and Gold 1977, Johnson and Hansen 1979, Rogowitz 1992, Knick and Dyer 1997). The climate variables that I chose which could influence intermixed shrub and grassland included total precipitation during the breeding season (*BSP*) defined as March 15 to

August 15, previous annual precipitation (*PAP*), snowfall (*TS*), and Palmer Drought Severity Index (*PDSI*). White-tailed jackrabbit (*Lepus townsendii*) reproductive output was negatively influenced by drought-like conditions in Wyoming (Rogowitz 1992). Therefore I predicted breeding season precipitation would be positively associated with abundance and PDSI would be negatively associated with abundance. White-tailed jackrabbits also delayed their first reproductive attempt in years with greater snowfall (Rogowitz 1992) which could result in lower prey availability for Golden Eagles. In addition, Columbian ground squirrels (*Urocitellus columbianus*) significantly delayed emergence from their dens with years of delayed snowmelt (Lane et al. 2012). Ground squirrel emergence is significant because I have found ground squirrel remains in nearly all nests that I have collected prey remains from during the study period (R. Crandall, unpubl. data). In addition, I have seen Golden Eagles frequently hunting near ground squirrel colonies (R. Crandall, unpubl. data). Therefore, I predicted a negative relationship between total snowfall and abundance. Snowfall measurements were from December to April for all years of the study. All weather data was taken from the Livingston, MT airport weather station (http://www.ncdc.noaa.gov/) which is located in the center of the study area.

In addition to climate related covariates, I included site specific habitat covariates to test whether probability of a nesting territory being used was influenced by habitat. In a separate analysis of only the data from the current phase, I found that prey habitat (i.e. intermixed shrub and grassland) was the top predictor of use at the nesting territory and within-nesting territory levels (Chapter 1). To account for the changes in intermixed shrub and grassland, I used aerial photographs from 1965 (USDA Farm Service Agency, Salt Lake City, UT, USA) to manually digitize this habitat type in all known nesting territories. Before digitizing habitat types, I first georeferenced all aerial photos in ArcGIS 10.0 (Esri Inc., Redlands, CA, USA). I then projected all documented nest sites from both phases on the historic photographs. To delineate nesting territories, I followed the methods of McGrady et al. (2002), which involved defining the nesting territory center and then projecting a nesting territory around the identified center with a radius of ½ the average nearest neighbor distance (NND). In nesting territories with a single nest site, I used the nest site as nesting territory center. For nesting territories with multiple nest sites, I estimated the geographic center of all nests and defined that as territory center (McCleod et al. 2002, McGrady et al. 2002). I used ½ the average NND adjusted for each phase to project nesting territories around each nesting territory center. When projected nesting territories overlapped, I bisected the overlap and created a new boundary so the nesting territories did not overlap (McGrady et al. 2002). This is a standard approach because Golden Eagles are highly territorial and only allow slight overlap by other breeding-age eagles. Once I had all nesting territories projected for each phase, I extracted the covariate values. Within all projected territories from the historic phase, I used the manually digitized shrub and grassland layer.

To delineate shrub and grassland habitat types in the current phase, I used a 30-m resolution land cover layer (Montana Spatial Analysis Lab 2012). I collapsed 77 total land cover types into 13 primary land cover types including intermixed shrub and grassland. I then projected all documented nesting territories onto the current land cover data and extracted the percent of each nesting territory comprised of the shrub and grassland cover type (*SG*).

In addition to habitat types, I also tested whether human disturbance may affect occupation. Human disturbance can negatively influence occupancy rates of Golden Eagles (Martin et al. 2009). Other raptors are sensitive to human disturbance as well (Steidl and Anthony 2000, Holmes et al. 1993). Chronic disturbance could even cause Golden Eagles to abandon a nesting territory (Watson 2010). I accounted for human disturbance with two, site-specific covariates, including distance from nest sites to roads (*DRds*) and total linear distance of roads (*TRds*) within nesting territories. Historic roads were manually digitized using the georeferenced aerial photos and only primary roads were included. Primary roads included all roads with the exception of two-tracks. I excluded two-track roads since they are found in high numbers throughout the study area, are travelled infrequently and as such have a lower probability for introducing anthropogenic disturbance. For the current phase, I used a Montana Department of Transportation layer downloaded from the Montana GIS Portal (http://gisportal.msl.mt.gov/geoportal). The layer was updated in 2010 and was comprised of "any and all roads open to public travel" making it directly comparable to the digitized layer that I used for the historic phase.

For all analyses, I used a binary variable to represent each phase. The *Phase* variable was included in all models and I considered the phase only model as the null since my questions all involved a difference between the two phases. Adding *Phase* to all models was a straightforward way for me to test the importance of each phase and the relationship of each phase on my response variables.

I used generalized linear models (GLM) with a Poisson error distribution to test the influence of climate on the number of known territories. I used logistic regression to compare the probability that a territory was being used during each phase for each nesting territory. I originally attempted to use repeated measures logistic regression to test the ability of my chosen covariates to explain the probability of a nesting territory being occupied in each phase but I did not have enough repeated observations to estimate variance. Therefore, I did not use repeated measures for this analysis. I used an information-theoretic approach where I built models *a-*

priori that each represented a prediction to explain the documented changes in abundance and the probability of nesting territory use (Burnham and Anderson 2002). Before model building, I tested all covariates for collinearity using Spearman's correlation coefficients with $|r| > 0.6$ as the threshold for determining collinear covariates. When collinearity occurred, I kept the covariate that was more relevant to Golden Eagle ecology and management. I tested the influence of climate on abundance based on 4 models that included a phase-only model to test whether any of the climate covariates better explained the change in abundance better than phase alone. To test the probability of nesting territory use, I created a model set with my 3 explanatory variables which consisted of 4 total models also including the null. I used Akaike Information Criteria (AIC) adjusted for small sample sizes (AIC*c*) for model selection and considered all models within 2 ΔAIC*c* units of the top model as competitive (Burnham and Anderson 2002).

Factors Influencing Nest Initiation and Nest Survival. I explored the influence of 7 explanatory variables that included influence of weather and prey habitat on the probability of Golden Eagles initiating a nest. I chose weather variables that have been shown to influence nest initiation specifically. My list of climate covariates included pairs of days of precipitation in the early incubation period (*CDPI*), heating degree days (*HDD*), and total snowfall (*TS*) during the early breeding season. Early incubation period was defined as March 1 to April 1 and I defined early breeding season as February 15 to April 15. Pairs of days of continuous precipitation during the early incubation period may influence the decision by the pair to nest based on the difficulty to effectively capture prey (McIntyre and Schmidt 2012). I predicted a negative relationship between continuous days of precipitation and probability of initiating a nest. Heating degree days are a measure of winter severity and are calculated by determining the average temperature for any given day and adding the day's high and low temperature and dividing that value by 2. If the number is above 65, there are no heating degree days that day. If the number is less than 65, it is subtracted from 65 to find the number of heating degree days (www.erh.noaa.gov/cle/climate/info/degreedays.html). The percentage of Golden Eagle pairs initiating nests can be negatively influenced by the number of heating degree days during the early nesting season (Steenhof et al. 1997). I predicted a similar relationship between heating degree days and nest initiations in the breeding population that I monitored. Total snowfall from December to April was the last climate related covariate that I used and I predicted a negative relationship between total snowfall and probability of nest initiation due to difficulty associated with capturing prey and potential negative impacts to prey base.

To explain differences in the probability of nest survival, I tested the number of continuous days above 32^{o} C (*CDA32*) which can negatively influence Golden Eagle nesting success in Idaho (Steenhof et al. 1997). I also used a measure of pairs of continuous days of precipitation during the nestling phase (*CDPN)* which was defined as May 15 to August 15. I also tested the influence of previous annual precipitation and PDSI to explain differences in nest survival predicting similar relationships to abundance.

I also tested landscape factors that may influence the probability of nest initiation and nest survival including percent of each nesting territory with intermixed shrub and grassland and distance from nest sites to roads. Based on the results of previous work showing the importance of prey habitat to presence of Golden Eagles (Chapter 1), I predicted a positive relationship between both measures of breeding performance and percent of nesting territory in shrub and grassland. I predicted a positive relationship between distance from nest to road and a negative relationship between total linear distance of roads and both measures of breeding performance due to the influence of anthropogenic disturbance.

I used repeated measures logistic regression to test the influence of my covariates on probability of binary response variables for nest initiation and nest survival. I used repeated measures using nesting territory in each phase as the repeated measure to account for differences within and among territories. I built 2 model sets each comprised of 12 models *a-prioi* to represent my predictions for factors influencing nest initiation and nest survival and used ΔAIC*c* for model selection. I used the top model for each analysis for inference. I used R (Version 3.0.1, R Core Development Team 2013) for all statistical analyses.

RESULTS

The most notable differences between the historic and current phase included the increase of approximately 40% in the number of known territories since the historic phase while the proportion of nests initiated between phases was relatively constant and the number of young produced per year decreased (Table 2).

Abundance and Distribution. The top model describing the abundance of Golden Eagles on the study area included only the covariate *Phase* indicating difference among time periods (Table 3). The other competitive model in the model set included an additive effect of total snowfall in addition to *Phase* (Table 3) but since it only included the addition of one covariate and was within 2 ΔAIC*c* units of the top model, I did not consider it competitive (Arnold 2010). Therefore, results suggest my chosen climate covariates had little influence on the change in abundance of this eagle population. Considering the *Phase* only model, the beta estimate describing the relationship between *Phase* and abundance was equal to 0.43 (95% CI = 0.22 – 0.65) which suggests significantly more known territories in the current phase.

The top model describing the probability of territory occupation included covariates representing prey habitat, total linear distance of roads within nesting territories and phase. This was the only competitive model in the model set (Table 4). Nesting territory occupation was negatively related to percent of territory in shrub and grassland cover type (β = -1.13, 95% C.I. = -1.99- -0.27). Golden Eagle territory occupation between phases was also negatively associated with linear distance of roads (β = -0.91, 95% C.I. = -1.57- -0.25). Lastly, the current phase had more occupied territories than the historic phase (β = 2.64, 95% C.I. = 1.21- 4.08).

Nest Initiation and Nest Survival. The top model describing the probability of initiating a nest included distance from nest to road and phase (Table 5). The second best model only included the addition of proportion of territory comprised of prey habitat but it was within 2 AIC*c* units of the top model so I did not consider this model competitive (Arnold 2010). There was another competitive model that included total snowfall during the early breeding season (Table 5). The best model was approximately 2.4 times more likely than the total snowfall model but I considered both competitive. After looking at the parameter estimates for distance from nest sites to roads, phase and total snowfall, only distance from nest site to road was able to predict the probability of nest initiation and the relationship was negative (β = -0.38, 95% C.I. = -0.73 – -0.04). The top model describing the probability of successfully producing young included precipitation and phase. But, 7 other models were also competitive therefore there was a high level of model uncertainty (Table 6).

DISCUSSION

I was most interested in assessing whether changes in prey habitat, which was the primary factor influencing presence of Golden Eagles on the landscape (Chapter 1), was the primary factor explaining the increase in number of Golden Eagle territories. Yet, I found a negative relationship between the probability of nesting territory occupation and percent shrub and grassland which suggests the non-occupied territories in the 1960's had adequate prey habitat but were unoccupied. I believe it is possible, based on these results, that human disturbance may have played a larger role in the absence of eagles in the historically unoccupied territories.

Range wide, Golden Eagles have been and continually are impacted by direct persecution (Reynolds 1969, Whitfield et al. 2004, Whitfield et al. 2006, Watson 2010). In the United States direct persecution has likely decreased since the 1960's. In part, the decline in persecution is a result of federal protection but also a change in ranching activity and perhaps a social shift. In 1962, the Bald Eagle Protection Act of 1940 was amended to include Golden Eagles and was cleverly renamed the Bald and Golden Eagle Protection Act. In both Park and Sweet Grass Counties, MT in the 1960's, there were many more sheep grazing then there are currently (http://www.nass.usda.gov). Golden Eagles will, in certain circumstances, feed upon sheep (Reynolds 1969, Olendorf 1976, O'Gara 1978, Watson 2010). Despite protection under the Bald and Golden Eagle Protection Act, the controversy surrounding Golden Eagle predation on domestic sheep resulted in sheepmen continually attempting to limit Golden Eagle populations around lambing pastures by either destroying nests, shooting or poisoning (Olendorf 1976). During my many visits to landowners in the last few years, a common remark I have heard is the number of Golden Eagles present during calving. Nearly all ranchers that I have talked with attribute the presence of Golden Eagles during that time to cattle afterbirth which the eagles feed upon. Lambing operations likely also saw influxes of Golden Eagles in the 1960's but for different feeding opportunities which increased the conflict between ranchers and Golden Eagles. As a result, it is possible that adult Golden Eagles were harassed or had their nests destroyed in higher number than they are now. It could be argued this idea is somewhat supported by results from my previous work showing that Golden Eagles do not appear to actively avoid humans currently (Chapter 1). I found that Golden Eagles show no active avoidance of human presence both at territory and within-territory level. If continued harassment was still an issue, I would expect to have found evidence of avoidance but there was no model support for such relationships.

The relationship between distance from nest sites to roads and probability of nest initiation further suggests human influences may affect Golden Eagles although the relationship was opposite what I predicted. Whether the apparent selection for distance to road and probability of nest initiation is indicative of a benefit derived from nesting closer to roads is unclear. I do not have any explanations for what sort of benefit may exist beyond road kill. While purely speculative, I doubt road kill would be a significant enough source of food to increase the probability of nest initiation. In locations with less overall human presence, distance from nest site to human disturbances has negatively impacted occupancy of Golden Eagles (Martin et al. 2009) which lead to my prediction. It may be that in areas with less overall human disturbance, Golden Eagles are just more wary and the possibility for negative impacts by humans is greater. In addition, the historic territories that were occupied may have experienced less negative interactions with people, perhaps as a result of landowner attitude or lack of sheep, which allowed an occupied territory to be present resulting in nest initiation attempts. The nests in the current phase may have little negative impacts regardless which may be influencing my results. The combination of little human disturbance in historically occupied territories and little disturbance to current nests may explain why the phase variable had not explanatory power in the model. The different results pertaining to presence of territories and breeding success is a great example of the importance of not only assessing factors influencing presence but also breeding success. My results here suggest humans may have played a role in keeping the historic population lower than the current phase but humans may not be negatively influencing the probability of nest initiation. The documented difference may provide insight into the increase in the population density yet a relatively stable nest initiation rate.

None of my chosen covariates had explanatory power describing the probability of nest survival. Often, Golden Eagle breeding success is best explained by prey densities (Steenhof and Kochert 1997, Watson 2010, McIntyre and Schmidt 2012). I did not have historic information on prey densities and I was unable to gather prey densities for the current phase. My analysis would have benefitted from having these data but in my case it was not possible. Considering the probability of nest initiation was most influenced by distance to road which is a stable factor, unlike prey availability, my results may suggest nest survival is influenced more by events such as prey cycles. Prey abundance, in addition to weather, has been shown to influence nest survival of Golden Eagles in Idaho (Steenhof and Kochert 1997) and may have better explained the probability of nest survival in this breeding population as well.

Between the historic phase and the current phase, the population has expanded and appears to have stabilized at the current number of territories that I monitor yearly. Based on what I have documented, I predict the population may be at or near equilibrium since I have traveled the area extensively to document nesting territories and I believe there are few nesting territories that have yet been discovered. The low number of known nesting territories in 2010 was likely not a result not of the colonization of new territories from 2011-2013 but instead a result of a lack of resources to search the area as in-depth as the following years. Since Golden Eagles are highly territorial, lower probability of nest initiation with increased density is reasonable and has been observed for a breeding Golden Eagle population in Italy (Fasce et al. 2011). Density dependent effects on reproduction have been documented in other raptor species as well (Bretagnolle et al. 2008). Unfortunately, I did not have enough data to test the influence of density since I had to remove the first years of each phase, the year with lowest densities as a result of search effort, which limited the amount of data to a point that I was unwilling to include density in my analysis. Without more years of data in the current phase, it may prove difficult to assess the influence of density since I had to omit one entire year of data to test the influence of density. Nevertheless, the population may be showing signs of density dependence (i.e. higher density with lower annual productivity rates) which I hope to test after additional years of data collection.

Long-term data on breeding parameters of wildlife populations are rare. When access to such data exists, it allows a thorough examination of factors influencing population growth rates as well as factors influencing the breeding success of the population. For Golden Eagles on my study area, access to the long-term dataset allowed me to assess factors that have influenced a documented increase in the local breeding population. Since it is widely thought breeding populations in the western United States are declining, there are applied implications to my results. For instance, in areas that have remained relatively stable over the past 50 years, we may find increases in the number of breeding eagles. Golden Eagles must have access to prey. In areas with massive habitat destruction, we would expect populations to decrease. Yet, there may be many areas that have remained relatively intact and have experienced increasing populations. We should focus efforts on these areas to estimate breeding densities and demographic rates to better understand the status of the Golden Eagle in the western United States. Another applied implication is integrating the influence of density to management goals. If the goals of management actions were based on reproductive performance, it would be important to know the population was near equilibrium and may be influenced by density more than available prey habitat. If we want to conserve this species into the future, we must take into account complex interactions to create effective management guidelines.

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LITERATURE CITED

Arnold, T.W. 2010. Uninformative parameters and model selection using Akaike's information criterion. *Journal of Wildlife Management*, *74*: 1175-1178.

Bretagnolle, V., F. Mougeot, and J.C. Thibault. 2008. Density dependence in a recovering osprey population: demographic and behavioural processes. *Journal of Animal Ecology*. 77: 998–1007.

Burnham, K.P., and D.R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach, 2nd Edn. Springer-Verlag, New York, New York, USA.

Collopy, M. W. 1984. Parental care and feeding ecology of Golden Eagle nestlings. *The Auk*, 101: 753-760.

Craig, E.H. and T.H. Craig. 1998. Lead and mercury levels in golden and bald eagles and annual movements of Golden Eagles wintering in east central Idaho 1990-1997. UDDI Bureau of Land Management, Idaho State Office, Boise, ID USA.

Fahrig L. 2001. How much habitat is enough? *Biological Conservation*, 100:65-74.

Fasce, P., L. Fasce, A.Villers, F. Bergese, and V.Bretagnolle. 2011. Long-term breeding demography and density dependence in an increasing population of Golden Eagles *Aquila chrysaetos*. *Ibis*, 153: 581–591.

Franson, J.C., L. Sileo, and N.J. Thomas. 1995. Causes of eagle deaths. Page 68 in E.T. LaRoc, G.S. Ferris, C.E. Puckett, P.D. Doran, and M.J. Mac [Eds.]. Our living resources. USDI, Natl. Biol. Serv., Washington D.C., USA.

Fraser, J. D., L.D. Frenzel, L. D., J.E. Mathisen, F. Martin, and M.E. Shough. *1983*. Scheduling bald eagle reproduction surveys. *Wildlife Society Bulletin*, 11: 13-16.

Good, R.E., R.M. Nielson, H. Sawyer, and L.L. McDonald. 2007. A population estimate for Golden Eagles in the western United States. *Journal of Wildlife Management*, 71:395-402.

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

Hansen, R.M., and I.K. Gold. 1977. Blacktail prairie dogs, desert cottontails and cattle trophic relations on shortgrass range. *Journal of Range Management*, 30: 210-214.

Harmata, A.R. and M. Restani. 1995. Environmental contaminants and cholinesterase in blood of vernal migrant Bald and Golden Eagles in Montana. *Intermountain Journal of Science* 1: 1-15.

Harness, R.E. 1997. Raptor electrocutions caused by rural electric distribution power lines. M.S. thesis, Colorado State Univ., Fort Collins, CO USA.

Hickey, J.J. 1942. Eastern population of the Duck Hawk. *The Auk*, 59: 176-204.

Hoffman, S.W., and J.P. Smith. 2003. Population trends of migratory raptors in western North America, 1977-2001. *Condor*, 105:397-419.

Holmes, T. L., R.L. Knight, L. Stegall, and G.R. Craig. 1993. Responses of wintering grassland raptors to human disturbance. *Wildlife Society Bulletin*, 21: 461-468.

Johnson, M.K., and R.M. Hansen. 1979. Foods of cottontails and woodrats in south-central Idaho. *Journal of Mammalogy*, 60: 215-216

Knick, S.T. and D.L. Dyer. 1997. Distribution of black-tailed jackrabbit habitat determined by GIS in southwestern Idaho. *Journal of Wildlife Management*, 61:75-85.

Kochert, M.N. and K. Steenhof. 2002. Golden Eagles in the U.S. and Canada: Status, trends, and conservation challenges. *Journal of Raptor Research*, 36:32-40.

Kochert, M.N., and K. Steenhof. 2012. Frequency of nest use by Golden Eagles in Southwestern Idaho. *Journal of Raptor Research*, 46: 239-247.

Kochert, M.N., K. Steenhof, L.B. Carpenter, and J.M. Marzluff. 1999. Effects of fire on Golden Eagle territory occupancy and reproductive success. *Journal of Wildlife Management*, 63:773-780.

Lane, J. E., L.E. Kruuk, A. Charmantier, J.O. Murie, and F.S. Dobson. 2012. Delayed phenology and reduced fitness associated with climate change in a wild hibernator. *Nature*. 489: 554-557.

Leslie, D.G. 1992. Population status, habitat and nest-site characteristics of a raptor community in eastern Colorado. M.S. thesis, Colorado State Univ., Fort Collins, CO, USA.

Marquiss, M., D.A. Ratcliff, and R. Roxburgh. 1985. The numbers, breeding success and diet of Golden Eagles in southern Scotland in relation to changes in land use. *Biological Conservation*, 33: 1-17.

Martin, J., C.L. McIntyre, J.E. Hines, J.D. Nichols, J.A. Schmutz, and M.C. MacCluskie. 2009. Dynamic multistate site occupancy models to evaluate hypotheses relevant to conservation of Golden Eagles in Denali National Park, Alaska. *Biological Conservation*, 142: 2726-2731.

Martin, T. E. 1992. Breeding productivity considerations: What are the appropriate habitat features for management? Pages 455-473 in J. M. Hagan and D. W. Johnston, eds. Ecology and Conservation of Neotropical Migrants, Smithsonian Institution Press.

Marzluff, J.M., S.T. Knick, M.S. Vekasy, L.S. Schueck, and T.J. Zarriello. 1997. Spatial use and habitat selection of Golden Eagles in southwestern Idaho. *The Auk*, 114:673-687.

McGahan, J. 1966. Ecology of the Golden Eagle. Thesis, University of Montana, Missoula, USA.

McGahan, J. 1968. Ecology of the Golden Eagle. *The Auk*, 85:1-12.

McGrady, M.J., J.R. Grant, I.P. Bainbridge, and D.R.A. McLeod. 2002. A model of Golden Eagle (*Aquila chrysaetos*) ranging behavior. *Journal of Raptor Research*, 36:62-69.

McIntyre, C. L., and J.H. Schmidt. 2012. Ecological and environmental correlates of territory occupancy and breeding performance of migratory Golden Eagles *Aquila chrysaetos* in interior Alaska. *Ibis*, 154: 124-135.

McIntyre, C.L., and L.G. Adams. 1999. Reproductive characteristics of migratory Golden Eagles in Denali National Park, Alaska. *Condor*, 101:115-123.

McIntyre, C.L., M.W. Collopy, J.G. Kidd, A.A. Stickney, and J. Paynter. 2006. Characteristics of the landscape surrounding Golden Eagle nest sites in Denali National Park and Preserve, Alaska. *Journal of Raptor Research*, 40:46-51.

McLeod, D.R.A., D.P., Whitfield, M.J. McGrady. 2002. Improving prediction of Golden Eagle (*Aquila chrysaetos*) ranging in western Scotland using GIS and terrain modeling. *Journal of Raptor Research*, 36:70-77.

Montana Natural Heritage Program and Montana Fish, Wildlife and Parks. Golden Eagle (*Aquila chrysaetos* <http://FieldGuide.mt.gov/detail_ABNKC22010.aspx> Accessed 13 March 2012.

Newton, I. 1979. Population ecology of raptors. T. and A.D. Poyser, London, United Kingdom.

O'Gara, B.W. 1978. Sheep depredation by Golden Eagles in Montana. Proceedings of the 8th Vertebrate Pest Conference.

Olendorf, R. 1976. The Food Habits of North American Golden Eagles. *American Midland Naturalist*, 95: 231–236

Reynolds, H.V. 1969. Population status of the Golden Eagle in south-central Montana. Thesis, University of Montana, Missoula, Montana, USA.

Rogowitz, G.L. 1992. Reproduction of white-tailed jackrabbits on semi-arid range. *Journal of Wildlife Management*, 56:676-684.

Sala, O.E., F.S. Chapin III, J.J. Amesto, E. Berlow, J. Bloomfield, R. Dirzo, E. Huber-Sanwald, L.F. Huenneke, R.B. Jackson, A. Kinzig, R. Leeman, D.M. Lodge, H.A. Mooney, Martin Oesterheld, N.L. Poff, M.T. Sykes, B.H. Walker, M. Walker, and D.H. Wall. 2010. Global biodiversity scenarios for the year 2100. *Science*, 287: 1770-1774.

Sisk, T. D., A. E. Launer, K. R. Switky, and P. R. Ehrlich. 1994. Identifying extinction threats. *Bioscience*, 44:592–604.

Steenhof, K. 1987. Assessing raptor reproductive success and productivity, p. 157-170. *In* B. A. Giron Pendleton, B.A. Millsap, K.W. Cline, and D.M. Bird (eds.), Raptor management techniques manual. Scientific and Tech. Series No. 10, Natl. Wildl. Fed. Washington, DC, USA.

Steenhof, K. and M.N. Kochert. 1988. Dietary responses of three raptor species to changing prey densities in a natural environment. *Journal of Animal Ecology*, 57:37-48.

Steenhof, K., and I. Newton. 2007. Assessing nesting success and productivity. P. 181-192 *In* D.M. Bird and K.L. Bildstein (eds.), Raptor research and management techniques. Hancock House Publishers, Blaine, Washington, USA

Steenhof, K., M.N. Kochert, and T.L. Mcdonald. 1997. Interactive effects of prey and weather on Golden Eagle reproduction. *Journal of Animal Ecology*, 66:350-362.

Steidl, R.J., and R.G. Anthony. 2000. Experimental effects of human activity on breeding bald eagles. *Ecological Applications*, 10: 258-268.

United States Fish and Wildlife Service (USFWS). 2008. Birds of conservation concern. Arlington, VA. <http://www.fws.gov/migratorybirds/NewReportsPublications/SpecialTopics/BCC2008/BBC2008.pdf> Accessed 12 March 2012.

Watson, J. 2010. The Golden Eagle. Second edition. Yale University Press, New Haven, Connecticut, USA.

Whitfield, D.P., D.R.A. McLeod, A.H. Fielding, R.A. Broad, R.J. Evans, and P.F. Haworth. 2001. The effects of forestry on Golden Eagles on the island of Mull, western Scotland. *Journal of Applied Ecology*, 38: 1208-1220.

Whitfield, D.P., A.H. Fielding, D.R.A. McLeod, and P.F. Haworth. 2004. Modelling the effects of persecution on the population dynamics of Golden Eagles in Scotland. *Biological Conservation*, 119:319-333.

Whitfield, D. P., A.H. Fielding, D.R. McLeod, P.F. Haworth, and J. Watson. 2006. A conservation framework for the Golden Eagle in Scotland: refining condition targets and assessment of constraint influences. *Biological conservation*, 130: 465-480.

Woodward, A.J., S.D. Fuhlendorf, D.M. Leslie Jr., and J. Shackford. 2001. Influence of landscape composition and change on lesser prairie-chicken (*Tympanuchus pallidicinctus*) Populations. *American Midland Naturalist*, 145: 264-274.

Yeaton, R.I. 1972. Social behavior and social organization in Richardson's ground squirrel (*Spermophilus richardsonii*) in Saskatchewan. *Journal of Mammalogy*, 53: 139-147

Figure 1. Study area with nest locations from the historic and current phase.

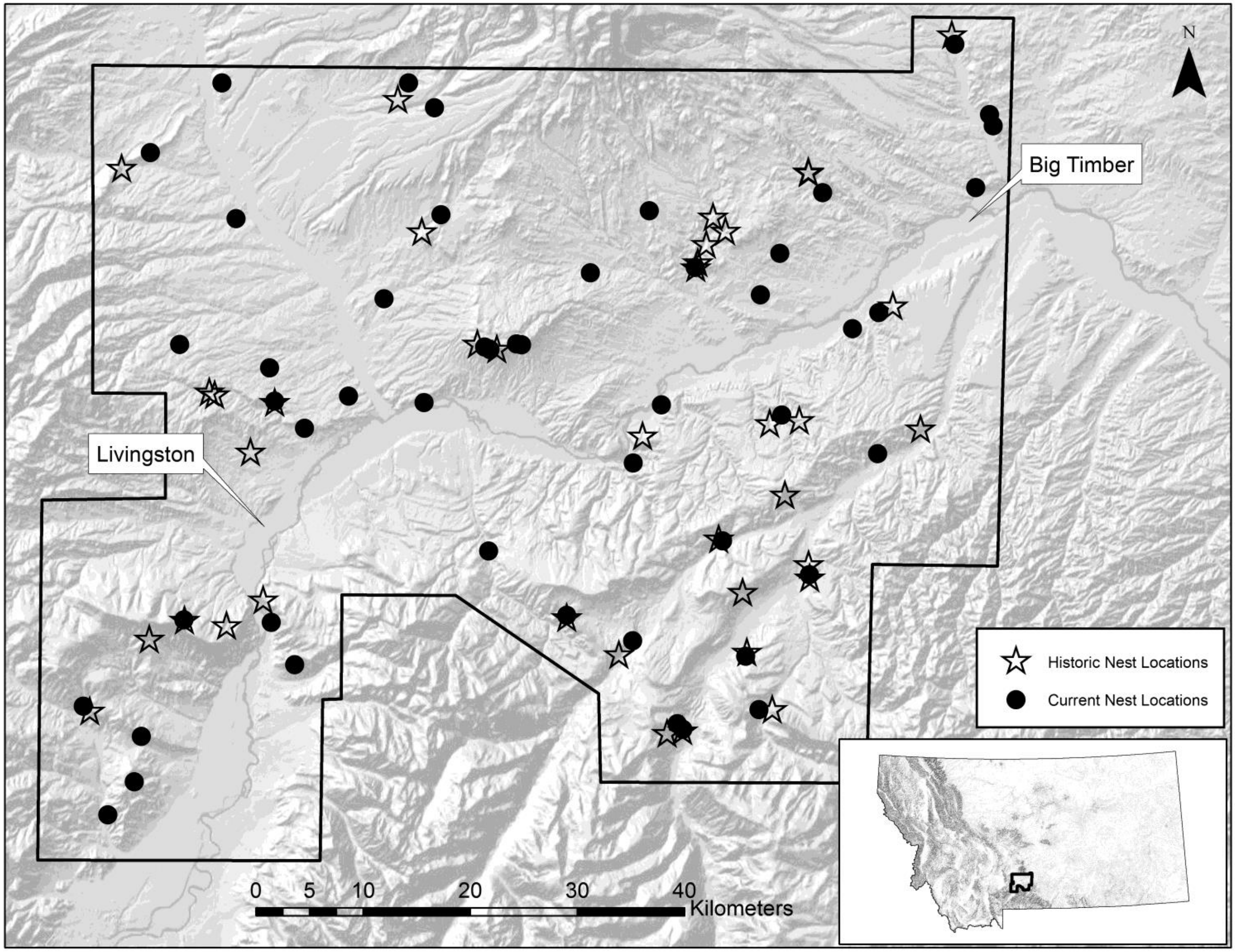

Table 1. Definition of terms used to describe breeding parameters for Golden Eagles.

Nesting Territory	An area that contains, or has contained, one or more nests and is within the home range of a mated pair known to have bred at least once from 2010-2013
Occupancy	Presence of one or more breeding age Golden Eagles exhibiting territorial behavior such as chasing, undulating flights, or escorting or indivuals showing signs of breeding such as nest building or incubation
Nest Initiation	A pair of breeding age Golden Eagles that appear to lay eggs and incubate
Nest Survival	When a pair successfully raises chicks to the minimum acceptable age for assessing success, which is equal to 8 weeks for Golden Eagles on my study area
Nesting Period	The time from the first egg is laid to when the first chick leaves the nest on its own accord
Nestling Period	The time from the first egg hatches to when at least one chick first leaves the nest on its own accord
Productivity	The total number of young that reach the minimum acceptable age for assessing success

Table 2. Summary of nesting and breeding data collected for both phases. Numbers in parentheses are standard deviations. Two nests were not included in the current phase due to access issues.

Year	# Territories Monitored	# Territories Occupied	# Nests Initiated	Total # Successful Nests	Total # Young Produced	# Young per Territory Monitored	# Young per Initiated Nest	# Young per Successful Nest	Proportion of Successful Nests for All Territories Monitored	Proportion of Successful Nests for All Occupied Territories	Proportion of Successful Nests for All Initiated Nests
1963	20	20	13	11	19	1.06	1.46	1.73	0.61	0.58	0.85
1964	22	22	19	18	23	1.05	1.21	1.28	0.82	0.82	0.95
1965	25	24	12	9	13	0.52	1.08	1.44	0.36	0.38	0.75
1966	26	26	17	13	18	0.72	1.06	1.38	0.52	0.52	0.76
1967	31	31	20	13	19	0.68	0.95	1.46	0.46	0.46	0.65
1968	31	27	20	11	19	0.61	0.95	1.73	0.35	0.41	0.55
Summary	25.8 (4.5)	25.0 (3.9)	16.8 (3.5)	12.5 (3.1)	18.5 (3.2)	0.77 (0.23)	1.12 (0.19)	1.50 (0.19)	0.52 (0.18)	0.53 (0.16)	0.75 (0.14)
2010	31	31	30	20	21	0.68	0.70	1.05	0.65	0.65	0.67
2011	42	42	29	18	23	0.55	0.79	1.28	0.43	0.43	0.62
2012	43	41	27	16	21	0.49	0.78	1.31	0.37	0.39	0.59
2013	43	41	29	20	26	0.60	0.90	1.30	0.47	0.49	0.69
Summary	39.8 (5.8)	38.8 (5.2)	28.8 (1.3)	18.5 (1.9)	22.8 (2.4)	0.58 (0.08)	0.79 (0.08)	1.24 (0.12)	0.48 (0.12)	0.49 (0.11)	0.64 (0.05)

Table 3. Top models describing changes in abundance of a breeding Golden Eagle population due to climate related factors. *PAP* is previous annual precipitation, *TAP* is total annual precipitation and *TS* is total snowfall from December to April.

	K	AICc	ΔAICc	Model Likelihood	AICc Weight	Log Likelihood	Cum.Wt
Phase	2	65.00	0.00	1.00	0.60	-29.64	0.60
TS + Phase	3	65.88	0.88	0.64	0.39	-27.94	0.99
PAP +Phase	3	69.05	4.05	0.07	0.99	-29.53	1.00
PAP + TAP + Phase	4	74.17	9.17	0.01	1.00	-29.08	1.00

Table 4. Top models describing probability of nesting territory occupation by Golden Eagles in south central Montana. *SG* is the percent of the nesting territories in the shrub and grassland habitat type. *TRds* is the total linear distance of roads in each nesting territory.

	K	AICc	ΔAICc	Model Likelihood	AICc Weight	Log Likelihood	Cum.Wt
SG + TRds + Phase	4	92.75	0.00	1.00	0.92	-42.19	0.92
SG + Phase	3	99.08	6.33	0.04	0.04	-46.43	0.96
TRds + Phase	3	99.95	7.20	0.03	0.03	-46.86	0.98
Phase	2	100.53	7.78	0.02	0.02	-48.21	1.00

Table 5. Top models describing factors influencing nest initiations by breeding Golden Eagles in south central Montana. *HDD* is heating degree days in early breeding season, *TS* is total snowfall during early breeding season, and *CDPI* is continuous days of precipitation in early incubation period. *DRds* is distance from nests to nearest road and *SG* is the percent of each territory composed of shrub and grassland habitat type. Early incubation period was defined as February 15-March 15 and early breeding season was defined as March 1 to April 1.

	K	AIC*c*	ΔAIC*c*	Model Likelihood	AIC*c* Weight	Log Likelihood	Cum.Wt
DRds + Phase	4	335.69	0.00	1.00	0.31	-163.77	0.31
DRds + SG + Phase	5	336.92	1.22	0.54	0.17	-163.35	0.47
TS + Phase	4	337.55	1.85	0.40	0.12	-164.70	0.59
Phase	3	338.10	2.40	0.30	0.09	-166.01	0.68
*CDPI + TS + CDPI * PI + Phase*	6	338.15	2.46	0.29	0.09	-162.93	0.77
*DRds + SG + DRds * SG + Phase*	6	338.64	2.95	0.23	0.07	-163.17	0.84
CDPI + HDD + Phase	6	339.08	3.39	0.18	0.06	-163.39	0.90
*HDD + TS + HDD * TS + Phase*	6	340.14	4.45	0.11	0.03	-163.92	0.93
SG + Phase	4	340.15	4.46	0.11	0.03	-166.01	0.96
*SG + HDD + SG * HDD + Phase*	6	341.67	5.97	0.05	0.02	-164.68	0.98

Table 6. Top models describing factors influencing nest survival by breeding Golden Eagles in south central Montana. C*DA32* is equal to the continuous number of days above 32°C and *CDPN* is equal to the pairs of consecutive days of precipitation during the nestling phase. The nestling phase was defined as May 15 to August 15. *DRds* is the distance from the nest site to the nearest road and *SG* is the percent of the territory composed of the shrub and grassland habitat type.

	K	AIC*c*	ΔAIC*c*	Model Likelihood	AIC*c* Weight	Log Likelihood	Cum.Wt
CDPN + Phase	4	261.69	0.00	1.00	0.21	-126.75	0.21
Phase	3	261.81	0.12	0.94	0.20	-127.85	0.41
*SG + CDPN + SG * CDPN + Phase*	6	262.38	0.70	0.71	0.15	-124.99	0.56
SG + Phase	4	263.35	1.66	0.44	0.09	-127.58	0.65
DRds + Phase	4	263.37	1.68	0.43	0.09	-127.59	0.74
CDA32 + CDPN + Phase	5	263.58	1.89	0.39	0.08	-126.64	0.82
CDA32 + Phase	4	263.67	1.98	0.37	0.08	-127.74	0.90
DRds + SG + Phase	5	264.15	2.47	0.29	0.06	-126.93	0.96
*DRds + SG + DRds * SG + Phase*	6	266.20	4.51	0.10	0.02	-126.89	0.98
*SG + CDA32 + SG * CDA32 + Phase*	6	266.43	4.75	0.09	0.02	-127.01	1.00