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HABITAT SELECTION AND FACTORS INFLUENCING NEST SURVIVAL OF GOLDEN EAGLES IN SOUTH-CENTRAL MONTANA

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ABSTRACT.—Golden Eagle (*Aquila chrysaetos*) population trends in the western United States are unclear, but an increase in future threats is causing concern for the species. Understanding the resource requirements of Golden Eagles will be essential to the creation of an effective management approach. Yet, we currently lack sufficient information on the basic habitat requirements of Golden Eagles, which hinders creation of a successful conservation plan. We took a multiscaled approach to identify factors influencing habitat selection of breeding Golden Eagles in south-central Montana. In addition, we tested environmental factors we predicted would influence daily nest survival rates to understand environmental influences on breeding success. From the 2010–2013 nesting seasons, we located 45 nesting territories and identified 115 apparent nest initiations (defined as nests where eggs have apparently been laid). We collected 15,182 telemetry locations from 12 breeding Golden Eagles. We found that Golden Eagles selected home ranges based on the percent of intermixed shrub and grassland and terrain ruggedness. At the within-home range scale, Golden Eagles selected areas based on aspect, distance to their nest, and an interaction between proximity to prey habitat and terrain ruggedness. Despite Golden Eagle selection of rugged topography, daily nest survival was negatively influenced by topographic ruggedness. Based on our results, we suggest that to maintain breeding pairs of Golden Eagles in areas similar to our study area, management should focus on preserving adequate prey habitat in areas with rugged topography. However, territories with higher ruggedness may not be as productive; therefore, management goals should be clear and environmental factors influencing both habitat selection and reproductive success should be considered when possible.

KEY WORDS: *Golden Eagle*; Aquila chrysaetos; *habitat selection*; *Montana*; *nest survival*; *reproductive rate*; *resource selection*; *telemetry.*

SELECCIÓN DE HÁBITAT Y FACTORES QUE INFLUYEN EN LA SUPERVIVENCIA EN NIDO DE *AQUILA CHRYSAETOS* EN EL CENTRO SUR DE MONTANA

RESUMEN.—Las tendencias poblacionales de *Aquila chrysaetos* en el oeste de los Estados Unidos son inciertas, pero existe un interés de conservación por la especie debido al aumento de las amenazas en el futuro. Entender los requerimientos ecológicos de *A. chrysaetos* es esencial para la creación de una estrategia de gestión efectiva. No obstante, carecemos actualmente de información necesaria sobre los requerimientos básicos de hábitat de *A. chrysaetos*, lo que dificulta la creación de un plan de conservación efectivo. Utilizamos un enfoque de múltiples escalas para identificar los factores que influyen en la selección de hábitat de individuos reproductivos de *A. chrysaetos* en el centro sur de Montana. Además, evaluamos los factores ambientales que predijimos que influirían las tasas diarias de supervivencia en los nidos, para entender la influencia de variables ambientales sobre el éxito reproductivo. En las estaciones reproductoras del periodo 2010–2013, localizamos 45 territorios de cría e identificamos 115 inicios de nidificación aparente (definida ésta como nidos donde aparentemente hubo puesta de huevos). Obtuvimos 15,182 localizaciones mediante telemetría vía satélite de 12 individuos reproductores de *A. chrysaetos*. Encontramos que el águila real seleccionó sus áreas de campeo en base a la combinación de estepa arbustiva y pastizal y la irregularidad del terreno. Dentro del área de campeo, *A. chrysaetos* escogió áreas basadas en la orientación, la distancia al nido y la interacción entre la proximidad al hábitat con presencia de presas y la irregularidad del terreno.

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A pesar de que *A. chrysaetos* seleccionó una topografía irregular, la supervivencia en los nidos estuvo influida negativamente por la irregularidad del terreno. En base a nuestros resultados, sugerimos que para mantener parejas reproductoras de *A. chrysaetos* en zonas similares al área de estudio, la gestión se debería enfocar hacia la preservación de hábitats adecuados para las presas, en áreas con topografía irregular. Sin embargo, los territorios con mayor irregularidad pueden no ser tan productivos; por lo tanto, los objetivos de gestión deben ser claros y debe considerarse, cuando sea posible, los factores ambientales que influyen en la selección de hábitat y el éxito reproductor.

[Traducción del equipo editorial]

Animals choose habitats within a heterogeneous landscape that provide adequate resources and conditions for survival and reproduction (Hall et al. 1997). Preference is measured by the disproportionate use of habitat in relation to its availability (Johnson 1980), and preference 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).

Populations of Golden Eagles (*Aquila chrysaetos*) in the western United States and Alaska have been reported as stable (Millsap et al. 2013), declining (Kochert and Steenhof 2002, Hoffman and Smith 2003, Good et al. 2007), and increasing (Crandall 2013), which complicates our understanding of the current population status. The most intensive monitoring shows declines in occupancy rates or measures of breeding performance (Kochert and Steenhof 2002, McIntyre and Schmidt 2012). Due to the unknown status of the population and perhaps more importantly, a known increase in future threats from factors such as energy development (Hunt 2002, Smallwood and Thelander 2008), climate change (McIntyre et al. 2006, Whitfield et al. 2007) and changes in land use (Kochert and Steenhof 2002, Watson 2010), federal and some state agencies classify Golden Eagles as a species of conservation concern (U.S.F.W.S. 2008, M.N.H.P. and M.F.W.P. 2011). This increase in attention exposes an insufficiency in knowledge of the basic habitat requirements of Golden Eagles, which hinders the creation of an effective conservation strategy.

Published work on Golden Eagle habitat selection in North America has been based on locations collected from either direct observations or VHF tracking, with relatively few data points, except in one very recent example (Watson et al. 2014). Limited sampling locations in addition to significant error associated with VHF tracking data (Craighead et al. 1973, Rouys et al. 2001) complicates the task of understanding habitat selection by individuals. Habitat use has been described for breeding Golden Eagles in Alaska, where eagles use mainly low shrubs at the territory scale (McIntyre et al. 2006). At the within-home-range scale, Golden Eagles in Idaho select landscapes conducive to uplift and black-tailed jackrabbit (*Lepus californicus*) habitat (Marzluff et al. 1997, Watson et al. 2014). These efforts have resulted in broad descriptions of habitat and landscape characteristics in distinctly different areas. All studies lack detailed, multiscaled analyses assessing environmental factors, including topography and structural habitat characteristics, influencing habitat selection by breeding Golden Eagles.

Development of an effective conservation strategy requires identifying the relationship of resource characteristics, both vegetative and topographic, not only to the presence of Golden Eagles, but also to breeding success. Some Golden Eagle territories are consistently more productive than others (Reynolds 1969, Steenhof et al. 1997, McIntyre 2002), suggesting breeding performance may be influenced by differences in habitat quality (Ferrer and Donazar 1996). Because the Golden Eagle is a wide-ranging species, attempts to identify differences in habitat quality that influence breeding success across its range in the western United States are difficult. Integrating investigations of factors influencing breeding success in smaller scale studies can provide much needed information on this important aspect of Golden Eagle ecology.

In this study, we investigated (1) which environmental factors influence resource selection of Golden Eagles breeding in south-central Montana and (2) which environmental factors influence Golden Eagle daily nest survival (DSR) in south-central Montana. We took a multiscaled approach to test environmental and anthropogenic factors that may influence resource selection in breeding Golden Eagles at both the home-range and within-home-range scales in south-central Montana. Habitat selection is considered hierarchical in that different factors influence selection at different spatial scales (Johnson 1980, Lloyd et al. 2005). We predicted that Golden Eagle habitat selection would be

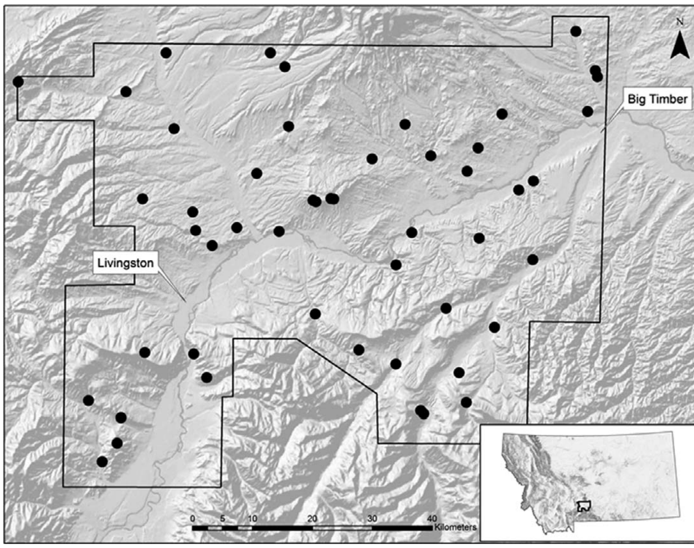

Figure 1. Study area with all Golden Eagle nest locations from 2010–2013. Multiple dots in close proximity are indicative of multiple nest sites within one nesting territory.

influenced by the presence of available prey habitat (Marzluff et al. 1997, McIntyre et al. 2006). We tested for alternative explanations, including avoidance of anthropogenic disturbances and interactions that included prey habitat availability and disturbances (Martin et al. 2009, Watson 2010). We also predicted that prey habitat would be the main influence on DSR. We allowed for alternative explanations including anthropogenic disturbance and tested the importance of year to see whether there were differences in DSR among years. Our goal was to provide a comprehensive assessment of the factors that influence habitat selection and measures of reproductive success for Golden Eagles.

METHODS

Study Area. We conducted our work in a 2700 km^2 study area near Livingston, Montana (ca. 45°40′N, 110°34′W, Fig. 1). Elevation in the study area ranges from 1225 to 2600 masl. 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 subalpine forests in the higher elevations to cottonwood-dominated (*Populus* spp.) riparian areas and intermixed sagebrush-steppe and grassland in the lower elevations. Cattle ranching is the primary land use in and around occupied eagle territories. Land ownership within the study area is a mosaic of private, state, and federal land, with most nests located on private land.

Terminology. We used the terminology of Steenhof and Newton (2007) to describe parameters associated with breeding Golden Eagles with the exception of "nest initiation" for which we used the McIntyre and Schmidt (2012) definition (Table 1). We used the nest initiation definition of McIntyre and Schmidt (2012) because other raptors, such as Bald Eagles (*Haliaeetus leucocephalus*), sometimes appear to be incubating when in reality they are not (Fraser et al. 1983). The frequency of "false 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. We used data from previous studies (McGahan 1966, 1968, Reynolds 1969, D. Craighead unpubl. data) in addition to talking with landowners and agency biologists to locate nesting territories beginning in the early spring of 2010. We also searched for new nesting territories by scanning large areas with no known nest from strategic vantage points using spotting scopes and binoculars and opportunistically while traveling throughout the study area. To minimize misclassifying nesting status, we began nest checks and searching within the first week of the earliest dates of incubation onset and made repeated visits to nesting territories

Table 1. 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).

TERM	DEFINITION
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 individuals showing signs of breeding such as nest building or incubation
Nest initiation	Nest where eggs have apparently been laid
Nest survival	Probability that a nesting attempt survives from the laying of the first egg until one nestling reaches the minimum acceptable age for assessing success, which is equal to 8 wk for Golden Eagles on our study area
Nesting period	Time between the laying of the first egg and the departure from the nest of at least one nestling of its own accord.

when necessary. We conducted nest searches by ground-based surveys (4-wheel drive truck or on foot) and used fixed-wing aircraft surveys to confirm nest initiation when we were unable to gain access to a property. Throughout the 2010–2013 nesting seasons, we surveyed the study area extensively and became very familiar with the area. Based on our familiarity with the study area and the lack of breeding-age birds observed outside of known territories, we were confident that we located nearly all nesting territories within the study area. After we confirmed nest initiation, the nest site was not visited again until later in the nesting season to document nest survival. If we detected young at a nest site, we used a photographic ageing guide to determine the age of the nestlings (Driscoll 2010). Nests with young were visited until young were at or exceeded the minimum acceptable age to fledge, which is 51 d (Brown et al. 2013).

In the years following the initial discovery of a nesting territory, we observed some that were not occupied. This is a common occurrence in raptors and Golden Eagles specifically (McGahan 1968, Steenhof et al. 1997, McIntyre and Adams 1999). Nesting territories were classified as unoccupied after multiple visits (≥3) to a nesting territory spanning at least 2 hr per visit in which no Golden Eagles exhibiting territorial behavior were seen.

We trapped and tagged adult, breeding eagles from known nesting territories within the study area before eagles initiated nesting (early February to late March) from 2011 to 2013. We used road-killed ungulate carcasses for bait and a net launcher (Trapping Innovations, L.L.C., Kelly, Wyoming, U.S.A.) for captures. We attached a 30-g or 45-g GPS/Argos PTT transmitter (Microwave Telemetry, Inc., Columbia, Maryland, U.S.A.) using a cross-chest harness of Teflon ribbon with a breakaway point at the breast patch. The transmitters collected a maximum of one location every hr for 15 hr/d during daytime hours for the duration of the breeding season.

Resource Selection Analyses. We investigated factors influencing selection by breeding Golden Eagles using a resource selection function (RSF) framework (Manly et al. 2002). We 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 of various habitats within the home range. We were first interested in determining which environmental factors influenced the presence of Golden Eagles on the landscape (second order habitat selection; Johnson 1980).

Selection of Home Range. Within the second order, we further subdivided the scale into the core home range (hereafter referred to as the core area) and the home range. We used tracking information collected in our study area from 10 breeding males and two breeding females during the nesting season (March 15 through July 15) to estimate the size of the core area and the home range. We then used those estimates to project core areas and home ranges to all known nesting territories in our study area. The 12 birds that we used to estimate core areas and home ranges were from 10 territories; two individuals were a pair from a single territory and one male died and was replaced with a new male that was also captured and fitted with a transmitter. The remaining tagged eagles were the only individual marked in their respective nesting territory. In cases where nest failure occurred, the end date for the tracked individual was the date of nest failure determined through tracking data or field observations. GPS telemetry locations were inspected visually and internal diagnostics from the tag were used to remove any outliers (i.e., inaccurate locations) prior to estimating core areas and home ranges.

We estimated core areas and home ranges using Minimum Convex Polygons (MCP) from the transmittered individuals. We defined the core area as the 50% MCP and we defined the home-range area as the 95% MCP (Millsap et al. 2015). We used MCPs to estimate the core area and the home-range area rather than a different home-range estimator because our objective for this phase of the analysis was simply to estimate average core areas and home ranges from the tagged birds in our study area and then apply those estimates to all nesting territories, not only nesting territories with satellite-tracked individuals. Minimum convex polygons were estimated using the package adehabitatHR in program R (Version 3.0.1, R Development Core Team 2013).

We projected estimated core areas and home ranges around home-range centers within the study area. If only one nest was used in a nesting territory during the study period, the location of that nest was considered the home-range center. We only projected core areas around home-range centers determined by a used nest site. When there were multiple used nest sites within a nesting territory, we used the location of the most frequently used nest as home-range center for our core-area scale analysis. We projected home ranges around home-range centers defined as the geographic center of all used nest locations within a nesting territory (McGrady et al. 2002, McLeod et al. 2002, McIntyre et al. 2006). We projected core areas around used nest sites, as a core area projected around a home-range center estimated from multiple used nests may not have captured the actual epicenter of use at the core-area scale. Radii representing the home-range scale always included all used nest sites and the likely areas used by birds. In cases where estimated home ranges overlapped, we bisected the distance between the two nests and considered that the common boundary between the two home ranges. This method was described by McGrady et al. (2002) for delineating Golden Eagle nesting territories that overlap spatially. Our tracking data supported minimal overlap between neighboring eagles' home ranges during the nesting season. To maintain consistency, we only used estimated home ranges and core areas for assessing second-order habitat selection, even in nesting territories where we had estimated core areas and home ranges for a transmittered eagle.

To assess environmental influences on second-order habitat selection, we projected random points in nesting habitat within the study area that were not located within the estimated core areas and home ranges to represent available home-range centers. We limited randomly projected available home-range centers to suitable nesting habitat to ensure the area could potentially be used by nesting Golden Eagles (Sergio et al. 2006). To estimate suitable nesting habitat, we used a 30-m-resolution land-cover layer obtained from the Wildlife Spatial Analysis Lab at the University of Montana in ArcGIS 10.0 (ESRI Inc., Redlands, California, U.S.A.). We collapsed the land-cover types from 77 very specific categories to 13 more general categories to create more biologically relevant categories. To create our nesting habitat layer, we used only the land-cover types present at Golden Eagle nest sites. We then projected random points into our potential nesting habitat layer to represent the centers of available core areas and home ranges. We projected a number of random locations equal to the number of used locations for the core area and home-range scale, with a minimum distance apart equal to the minimum nearest neighbor distance of documented nests to account for territoriality of the species (Sergio et al. 2006). We projected a unique set of random home-range centers equal to the number of used home-range centers for the core-area scale and home-range scale. If radii surrounding random sites overlapped, we used the same methodology for delineating home ranges (i.e., bisection between home-range centers).

After used and random core-area and home-range estimates were finalized, we extracted covariate information. We used measures of primary prey habitat that we predicted to be the primary factor influencing selection by breeding Golden Eagles. In our study area, 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 live in open areas of mixed sagebrush and grassland (Yeaton 1972, Hansen and Gold 1977, Johnson and Hansen 1979, Rogowitz 1992, Knick and Dyer 1997), a habitat that we included as a covariate (Table 2). As part of the habitat-based prediction, we also included mean terrain ruggedness, which has been positively associated

Table 2. All landscape 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 aspect covariate was categorical; the reference category was north. For territory selection and daily nest survival portions, covariates were tested from the home range and core home range (i.e., core area).

Model	Variable Abbreviation	Description	Predicted Relationship
Territory selection	% 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	−
	TRd	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	−
Daily nest survival	% Shrub	Percent of nesting territory composed of shrubs	+
	% Grassland	Percent of nesting territory composed of grassland	+
	TRI	Mean terrain ruggedness index value	+
	LowSHB	Percent of nesting territory with shrub canopy cover from 0–30%	−
	IntSHB	Percent of nesting territory with shrub canopy cover from 30–70%	+
	HighSHB	Percent of nesting territory with shrub canopy cover from 70–100%	−
	LowHERB	Percent of nesting territory with herbaceous canopy cover from 0–30%	−
	IntHERB	Percent of nesting territory with herbaceous canopy cover from 30–70%	+
	HighHERB	Percent of nesting territory with herbaceous canopy cover from 70–100%	−
	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	−

with the presence of breeding Golden Eagles (McLeod et al. 2002, Sergio et al. 2006, Taipia et al. 2007). We estimated terrain ruggedness using a 10-m-resolution digital elevation model layer. We calculated the terrain ruggedness index (Riley et al. 1999) using the raster package in program R (Version 3.0.2, R Development Core Team 2013). A primary alternative prediction that we tested was that Golden Eagles' resource selection is negatively associated with the presence of anthropogenic disturbance on the landscape, which we accounted for with multiple covariates (Table 2). All land-cover covariates that we used were taken from the collapsed land-cover layer and total linear distance of roads in each estimated home range was taken from a layer created by the Montana Department of Transportation (M.D.O.T. 2010).

After we obtained covariate values, we used Spearman's correlation coefficients to check for collinearity among covariates with $|r| = 0.60$ as the acceptable threshold (Green 1979). In cases where collinearity occurred, we kept the variable that was more biologically relevant to Golden Eagles. We then created an *a priori* candidate model set for both scales, with each model representing one of our predictions. We used logistic regression to assess the probability of use based on covariates of interest and we used Akaike Information Criteria adjusted for small sample size (ΔAIC*c*) for model selection (Manly et al. 2002). We considered all models $\leq$2 ΔAIC*c* of the top model as competitive, with the exception of models with uninformative parameters (Burnham and Anderson 2002, Arnold 2010). Uninformative parameters exist when models are $\leq$2 AIC units of the best model, but include only one additional parameter based on the penalty given to each parameter in AIC and the inability of that single parameter to sufficiently reduce model deviance (Arnold 2010). In these cases, the additional parameter does not explain enough variation in the model to warrant its inclusion in the model. Arnold (2010) recommends five potential methods for dealing with models containing uninformative parameters, including dismissing the model or models with uninformative parameters. For all analyses, we also included a null model to compare the ability of covariates to explain each response variable.

To analyze which scale (core area vs. home range) was better at predicting the probability of use by breeding Golden Eagles, we used the area under the receiver operator characteristics curve, or AUC. The AUC values provided a comparison of the performance and predictive ability of each top model (Hosmer et al. 2013). We defined the scale with the higher AUC value as the better scale at predicting second-order habitat selection and used the best model associated with that scale for inference (Squires et al. 2008). We also used the AUC value from the best model at the appropriate scale to assess goodness-of-fit of the best model (Hosmer et al. 2013).

Within-home-range Resource Selection. We were also interested in determining which factors were important at the within-home-range scale, or third order of habitat selection (Johnson 1980). We used locations from the same 10 tagged breeding males and two breeding females to assess resource selection at this scale. We used 95% kernel home-range estimates (KDE) to define boundaries with which to project random points representing available locations. By limiting our projected random points to a home range that did not include spurious areas, we were able to make a more robust estimate of resource selection in the third order. Kernel utilization distributions were estimated using the adehabitatHR package in R (Version 3.0.2, R Development Core Team 2013). We used the default smoothing value when estimating the utilization distributions in the adehabitatHR package. Within each 95% KDE for all 12 Golden Eagles, we projected a number of random points equal to the number of tracked locations for each individual to represent available locations. Initially, we separated males and females to allow for differences in within-home-range resource selection, but the results did not differ, so we grouped all birds together for the analysis. We grouped nesting season locations for each bird together when there were multiple years of tracking data for an individual (n = 2).

We tested covariates that we predicted would have the greatest influence on use by Golden Eagles within the third order of habitat selection. We included landscape covariates representing prey habitat, human disturbance, aspect, terrain ruggedness, and distance to nest (Table 2). We used distance to land-cover type instead of the land-cover type directly associated with the location, which differs from most other resource selection studies. Using distance was more appropriate, as Golden Eagles often soar or perch while hunting and their hunting grounds are often not directly under the individual. We also used distance to nest to account for the breeding eagles' frequent returns to their nest site (Rosenberg and McKelvey 1999, Irwin et al. 2007, Watson et al. 2014).

We used logistic regression in an information-theoretic framework to assess the probability of use within-home-range by breeding Golden Eagles. We used individual as a random effect in our models to account for an unbalanced number of locations for each individual tracked and spatial autocorrelation (Gillies et al. 2006, Fieberg et al. 2010). All covariates were checked for collinearity prior to being used in the modeling process. To aid in model convergence, we standardized covariates to have a mean = 0 and unit variance. We used AIC for model selection and considered all models $\leq$2 ΔAIC units of the top model as competitive. We used *k*-fold cross validation with five folds to assess model performance of the top model (Boyce et al. 2002). We 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). All analyses were done using R (Version 3.0.2, R Development Core Team 2013).

Factors Influencing Nest Survival. We also examined which environmental factors influenced DSR of Golden Eagles breeding within the study area. We assessed DSR to avoid overestimating nest survival rates and to make a more robust attempt at identifying factors that may influence Golden Eagle nest survival in our study area (Mayfield 1961, 1975, Brown et al. 2013). We considered covariates that included year, structural habitat, and disturbance that we predicted may influence DSR at both the core area and home-range scales (Table 2). Our chosen landscape covariates were from the same layers we used for the second-order habitat selection analysis, with the addition of shrub and herbaceous canopy cover, which we derived from 30-m-resolution LANDFIRE layers (U.S.G.S. 2012). We used hierarchical models in a Bayesian framework to test the influence of our covariates on DSR (Royle and Dorazio 2008, Schmidt et al. 2010, Brown and Collopy 2012). DSR was expressed as independent Bernoulli trials each day, for each nest over the course of the nesting season. We used information on (1) the day the nest was located, (2) the last day the nest was seen occupied, and (3) the last day the nest was checked to build our capture history (Schmidt et al. 2010). We used an information-theoretic approach for model selection in which we ranked competing models using the Deviance Information Criteria (DIC; Spiegelhalter et al. 2002). We used a modeling approach similar to Brown and Collopy (2012) in which we first separated the models into three categories: (1) Year, (2) Landscape, and (3) Disturbance. We tested year first to see whether differences existed between years in the estimated DSR and whether we need to consider such differences in subsequent models. For landscape and disturbance models, we tested covariates from the core area separately from those of the home range to see which scale was more influential on DSR based on DIC values. We used variables from the top-ranked model from each category, if the model was ≥10 DIC units less than the null, to build a smaller subset of models with the most influential variables. The coefficient estimates from the model with the lowest DIC value were used to explain relationship between our chosen covariates and DSR. All models included a random effect of territory to account for repeated observations of nest survival at nesting territories. We also tested our best model without the random effect of territory to assess the importance of its inclusion and the influence of the random effect on the parameter estimates (Schmidt et al. 2010, Brown and Collopy 2012). We used DIC to assess the importance of the random effect (Schmidt et al. 2010). We used uninformative priors with uniform distributions in the interval −10 to 10 for the intercept and coefficient estimates and a range of 0 to 7 for the standard deviation of the random effect. We ran 25,000 to 100,000 iterations for each model with a burn-in period ≥5000 depending on the complexity of the model. We assessed convergence of the Markov Chain Monte Carlo runs with Gelman-Rubin diagnostics and visual inspection of the chains using the coda package in R (Gelman and Rubin 1992, Plummer et al. 2006, Schmidt et al. 2010). We measured goodness-of-fit of our top-ranked model using the Bayesian *P*-value (Schmidt et al. 2010, Brown and Collopy 2012). A well performing model will result in a Bayesian *P*-value close to 0.5, whereas a poorly performing model will result in a Bayesian *P*-value closer to 0 or 1 (Gelman et al. 2004). We used R (Version 3.0.2, R Development Core Team 2013) to connect with WinBUGS via the R package R2WinBUGS for the DSR analysis (Spiegelhalter et al. 2004, Sturtz et al. 2005). We used our best model to estimate DSR and annual nest survival based on a 101-d nesting period for Golden Eagles and mean values of covariates (Schmidt et al. 2010, Brown et al. 2013).

RESULTS

Selection of Home Range. We identified 45 Golden Eagle nesting territories within the study area during the 2010–2013 nesting seasons. The average MCP estimate of the core area of tracked individuals in our study was equal to 2.28 km^2 (SD = 1.83) and the mean estimate of the home range was equal to 16.73 km^2 (SD = 5.87). Based on our estimated core area and home-range sizes, we used a 1000-m radius (3.14 km^2) area surrounding used and random points for the core-area scale and a 2500-m radius (19.63 km^2) area for our home-range scale. We increased the estimated areas slightly for both the core area and home range given the large variation of estimates at both spatial scales. The top model describing home-range selection by Golden Eagles in our study area at the core-area scale included the percentage of prey habitat and an additive effect of ruggedness (Table 3). At the home-range scale, the best model included only proportion of prey habitat and the second-best model included proportion of pasture (Table 3). We did not consider the second-best model competitive because it only offered an uninformative parameter (Arnold 2010). The better scale for predicting home-range selection was the core area. The

Table 3. Model selection results describing second order habitat selection by breeding Golden Eagles at the core home range (i.e., core area, 1000-m radius) and home range (2500-m radius) scales. Models are ranked by Akaike weights (w_i) and only the top five models for both scales are shown. The number of parameters in each model (K) and the difference in estimated Akiake Information Criteria, adjusted for small sample size ($\Delta AICc$), are also provided. See Table 2 for variable definitions.

SCALE	MODEL	K	$\Delta AICc$	w_i
Core area (1000 m)	% Shrub-Grassland + TRI	3	0.00	0.94
	% Shrub-Grassland	2	6.30	0.04
	% Shrub-Grassland + % Pasture	3	7.91	0.02
	% Shrub-Grassland + % Developed	4	9.92	0.00
	Null	1	34.66	0.00
Home range (2500 m)	% Shrub-Grassland	2	0.00	0.45
	% Shrub-Grassland + % Pasture	3	1.72	0.19
	% Shrub-Grassland + TRI	3	2.06	0.16
	% Shrub-Grassland + % Developed	4	3.52	0.08
	% Cultivation + % Developed	3	5.03	0.04

AUC value for the core area was 0.85 compared to 0.66 at the home-range scale. With an AUC value of 0.85, the fit of the best model from the core-area scale was considered excellent (Hosmer et al. 2013). Using the top model from the core area, our results suggest Golden Eagles were selecting locations for their breeding season home ranges with more 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-home-range Resource Selection. We collected a mean of 1265 locations per individual (SD = 465.5, range = 582–1950) and used 15,182 GPS locations collected from the 12 breeding Golden Eagles to assess third-order habitat selection during the nesting season. Estimated 95% KDE homeranges varied from 3.14 km^2 to 27.27 km^2 (mean = 15.75 km^2, SD = 7.15) and 50% KDE's varied from 0.06 km^2 to 4.70 km^2 (mean = 2.08, SD = 1.55). The top model for the third order, or within-home-range resource selection, included main effects of terrain ruggedness, distance to prey habitat, aspect, distance to nest, and an interaction between terrain

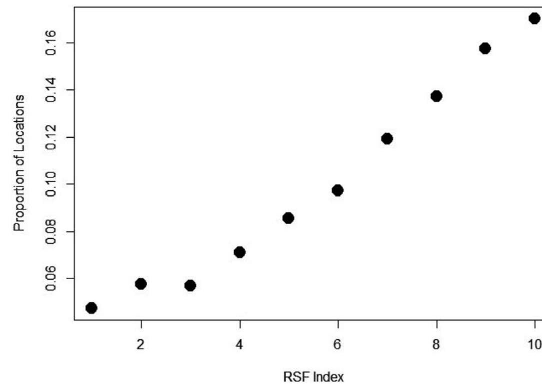

Figure 2. Proportion of breeding Golden Eagle locations that were classified into each RSF bin. A RSF score of 10 represents a high probability of use, whereas 1 represents a low probability of use.

ruggedness and distance to prey habitat (Table 4). Terrain ruggedness was the most important variable describing selection by Golden Eagles (Table 5). Our best model was the only competitive model and held 100% of the model weight (Table 4). Based on the support for the interaction term, Golden Eagles selected areas with high terrain ruggedness in close proximity to prey habitat (Table 5). If ruggedness was high, but the location was farther away from prey habitat, then the probability of use by Golden Eagles declined. Golden Eagles also selected areas closer to their nests and facing the west (Table 5), which is the primary wind direction on the study area (Western Regional Climate Center 2002). The average Spearman's ρ from the k-fold cross validation was 0.99 ($P < 0.0001$), indicating the model was effective at predicting resource selection by breeding Golden Eagles. In addition, 76.4% of locations were estimated to be in the RSF bin category of 5–10, with 17.3% of all locations in the top bin further supporting the predictive capacity of our best model (Fig. 2).

Daily Nest Survival Rate. We documented 115 apparent nest initiations during the 2010–2013 nesting seasons and 74 nests with young that reached the minimum acceptable age of fledging during our study period. We removed one nest from our DSR analysis because it was only checked one time during the breeding season, so data were inadequate. All other nests were visited at least twice, with most nests visited 2–4 additional times. We found no support for the influence of year on DSR based on the proximity of DIC values to the null model; therefore, we grouped all years together for the remainder of our

Table 4. Model selection results showing top models for third-order habitat selection by breeding Golden Eagles. Models are ranked by Akaike weights (w_i). The number of parameters in each model (K) and the difference in estimated Akiake Information Criteria (ΔAIC) is also provided. Top five models are shown. See Table 2 for variable definitions; "*" represents an interaction between covariates.

MODEL	K	ΔAIC	w_i
TRI + DSG + W_ASP + TRI * DSG + DNest	7	0.00	1.00
TRI + DSG + W_ASP + DNest	6	146.46	0.00
TRI + W_ASP + TRI * W_ASP + DNest	5	209.66	0.00
TRI + W_ASP + DNest	6	219.02	0.00
TRI + DSG + DNest	5	227.05	0.00

Table 5. Standardized coefficient estimates, SE's, and 95% confidence intervals (CI) for covariates describing third-order resource selection by breeding Golden Eagles. See Table 2 for variable definitions; "*" represents an interaction between covariates. Negative coefficient estimates for distance covariates represent selection for that covariate (i.e., probability of use decreases as distance increases).

			95% CI	
VARIABLE	β	SE	LOW	HIGH
Intercept	−0.09	0.18	−0.45	0.27
TRI	1.13	0.02	1.10	1.17
DSG	−0.17	0.01	−0.20	−0.15
W_ASP	0.29	0.03	0.23	0.35
TRI * DSG	−0.16	0.01	−0.18	−0.13
DNest	−0.21	0.02	−0.24	−0.18

analyses (Table 6). Initially, we had planned on integrating the best supported covariates from the landscape-only models and the disturbance-only models to create a small model subset that may best describe factors influencing DSR of breeding Golden Eagles in our study area. However, all models in the disturbance-only category had little to no support as judged by the small difference in the DIC values from the null model (Table 6). Therefore, we considered the best supported model for our DSR analysis the top model in the landscape-only category, which consisted of mean terrain ruggedness measured at the area, proportion of core area composed of shrub habitat, and distance from nest site to shrub habitat (Table 6). In our best supported model, only mean terrain ruggedness measured at the core area had a 95% credible interval (CRI) that did not overlap zero, suggesting the directionality of the relationship of the other covariates in our best supported model were unclear (Table 7). We found the relationship between mean terrain ruggedness and DSR was negative, suggesting the more rugged territories were less likely to successfully fledge young. The Bayesian *P*-value of our best model was equal to 0.450, which suggests the model fit was adequate.

We found the DIC value for the fixed-effects model was equal to 143.9, which was 3.9 units higher than the mixed-effects model, suggesting the random effect of nesting territory was marginally important to include in the models. The relationship between the covariates and DSR in the fixed-effects model was very similar to the mixed-effects model, although credible intervals were small for mean terrain ruggedness measured at the core-area scale in the fixed-effects model and the proportion of the core area composed of shrubs and greater for the influence of distance from nest site to shrub habitat; however, all still overlapped zero. The Bayesian *P*-value from the fixed-effects model was equal to 0.493, which suggests the goodness-of-fit from the model was adequate.

The estimated DSR during the 2010–2013 nesting seasons using the parameter estimates from our best model, including the random effect of territory, was 0.995 (95% CRI = 0.888–1.000) and the annual nest survival rate based on a 101-d nesting period was 0.634 (95% CRI = 0.000–0.986).

DISCUSSION

With our multiscaled approach, we identified important factors for Golden Eagles' selection of breeding-season home ranges and their selection of habitat within their territories. We found that Golden Eagle habitat selection, both in the second and third order, was best explained by covariates associated with prey habitat and prey acquisition. Our results from the DSR analysis showed nest survival was not influenced by two of our three chosen covariates, but the 95% CRI describing the influence of mean terrain ruggedness was negative and did not overlap zero. This result suggested an inverse relationship between terrain ruggedness and nest survival, which was counter to our prediction.

Resource Selection. As with many top predators, the presence of Golden Eagles on the landscape was highly correlated with prey habitat. For this study, we were unable to measure diet, specific

Table 6. Model selection results describing the daily nest survival rate of Golden Eagles breeding in south-central Montana from 2010–2013. See Table 2 for variable definitions; "*" represents an interaction between covariates. The addition of *_Core* to the end of the name represents the value was taken from the estimated core home range (i.e., core area).

Type of Model	Model	K	DIC	ΔDIC
Time	Year	2	149.2	0.0
	Null	1	149.7	0.5
Landscape	TRI_Core + % Shrub_Core + DistSHB	4	140.0	0.0
	TRI_Core + % Grassland_Core	3	141.6	1.6
	TRI_Core + % Shrub_Core + % Grassland_Core + TRI_Core * % Shrub_Core	5	141.6	1.6
	TRI + % Shrub + DistSHB	4	143.2	3.2
	TRI + % Shrub + % Grassland + TRI * % Shrub	5	143.3	3.3
	TRI + % Grassland	3	143.6	3.6
	% Shrub	2	146.4	6.4
	IntSHB	2	146.7	6.7
	IntSHB + IntHERB	3	147.8	7.8
	% Shrub_Core	2	148.4	8.4
	Null	1	149.7	9.7
	HighSHB	2	150.0	10.0
	LowSHB + IntSHB	3	151.1	10.1
Disturbance	TOTSTR	2	147.6	0.0
	% Developed_Core + % Cultivation_Core	3	147.4	0.2
	% Developed_Core	2	148.0	0.4
	TOTRDS + TOTSTR	3	148.9	1.3
	Null	1	149.7	2.1
	% Developed + % Culitvation	3	150.0	2.4
	TOTRDS	2	151.3	3.7
	% Developed	2	151.6	4.0

characteristics of prey habitat, or variation in prey densities. Based on previous work, we know which prey items Golden Eagles in our area are most likely to hunt (McGahan 1966, 1968, Reynolds 1969), which justified an investigation into the relationship between Golden Eagle selection and prey habitat. We were able to identify the clear importance of prey habitat, which consisted of intermixed shrub and grassland, to help understand and rank the significance of varying environmental factors on selection by breeding Golden Eagles. In a conservation context, determining the most important factors for Golden Eagles (e.g., prey habitat) and focusing primary protection, enhancement, or mitigation efforts on those factors is an integral aspect of building an effective and comprehensive management plan. Our study has obvious limitations in applicability due to our focus on one relatively small area, but identifying trends of habitat selection from multiple locations will help build a better understanding of habitat needs for this species.

Table 7. Coefficient estimates describing daily nest survival of Golden Eagles from our top supported model in the landscape category in Table 6. See Table 2 for variable definitions. Mean coefficient estimates are given in addition to the estimated Bayesian *P*-value and the lower and upper bounds of the 95% credible interval (LCRI and UCRI, respectively).

Variable	Mean	LCRI	UCRI
Intercept	7.092	5.744	8.640
TRI_Core	−0.320	−0.525	−0.140
% Shrub_Core	−0.689	−2.457	1.154
DistSHB	0.003	−0.007	0.014
Territory (SD)	0.461	0.011	1.745
P	0.450		

Golden Eagle selection for topography and aspect combined suggest the birds in our study area were selecting locations based on the ability to exploit orographic uplift. Orographic uplift is created by the deflection of horizontal winds by sloping terrain and its importance to raptor migration is well documented and is the reason we tested the importance of topography and aspect in our study (Bildstein 2006, Bohrer et al. 2012). In addition to migration, Golden Eagles established nesting territories based in part on terrain ruggedness, which was likely related to orographic uplift (McLeod et al. 2002, Sergio et al. 2006, McIntyre et al. 2006). However, the importance of topography for nesting-season movements by individuals is less well documented (but see Watson et al. 2014). Katzner et al. (2012) noted that migratory Golden Eagles in the eastern United States flew at relatively low altitudes over steep slopes and cliffs during local movements in winter. Based on that information, we could assume that breeding-season movements are similar to local movements made by overwintering migrants, which is supported by our results showing selection for terrain ruggedness and western aspects by our tracked individuals and the results of Watson et al. (2014). Regardless, consideration of the influence of topography may be important in minimizing the risk to Golden Eagles from potential threats such as wind energy development, because many of the same landscape features that maximize wind energy yield may also be preferred by migratory and nonmigratory Golden Eagles.

We were surprised by the apparent lack of avoidance by Golden Eagles in our study area to sources of potential anthropogenic disturbance. The human population in our study area has increased by at least 55% since the 1960s (Hansen et al. 2002). In addition, the amount of land developed in Park County, Montana, has increased approximately 293% since 1970 and development has occurred primarily in the rural areas where nesting Golden Eagles are found (Park County Planning Department 2013). Unlike most intensively monitored Golden Eagle populations in the region, the breeding eagles in our study area have increased in population density by approximately 50% since the 1960s despite these changes (Crandall 2013). Nesting Golden Eagles in other locations are negatively influenced by factors such as distance from nest sites to roads and trails and all-terrain vehicle use (Martin et al. 2009, Steenhof et al. 2014). However, the studies describing these relationships focused on breeding performance, rather than avoidance by eagles of probable sources of anthropogenic disturbance on the landscape. Our GPS location data allowed fine-scale and accurate movement-based analyses for breeding Golden Eagles. Using these fine-scale data, we found no apparent avoidance of our chosen measures of anthropogenic disturbance, which may help explain why, despite the increase in human presence, the study area supports a higher number of breeding Golden Eagles than in past decades. As caveats, we note that we did not assess the influence of acute disturbance events, which may be more likely to negatively influence breeding eagles, and it is possible we chose poor measures of human disturbance. We selected disturbance measures known to negatively influence Golden Eagles and other raptors, but it is certainly possible the birds in our study area may respond to other disturbances that we did not measure. Nevertheless, it is encouraging that Golden Eagles in our study area may be tolerant of humans in the landscape to some degree.

Daily Nest Survival Rate. The only variable that we tested in our DSR analysis for which we could confidently report a directional relationship was terrain ruggedness measured at the core-area scale. We predicted a positive relationship between DSR and terrain ruggedness assuming that higher mean ruggedness would improve the ability of the adults to hunt and capture prey if, in addition, there was also adequate prey habitat, but our results were counter to that prediction. The best model from our DSR analysis included both mean percent shrub cover and distance from nest site to prey habitat, but credible intervals overlapping zero prevented us from determining relationships between those covariates and DSR. A negative relationship between terrain ruggedness and nest survival may be difficult to interpret, although some possible explanations exist. For example, one aspect of terrain ruggedness that we did not consider was the thermoregulatory component. Golden Eagle nestlings located in nests in rugged terrain may be more susceptible to heat or cold stress if the nest is exposed. We had no way of explicitly testing this in our study but it may potentially explain the relationship we documented. Another possibility is that the nesting territories with higher ruggedness were in the more mountainous terrain of our study area and had less available prey habitat. There were no significant correlations between terrain ruggedness and proportion of land-cover types for our estimated home ranges, so this explanation seems unlikely. Although the reason for the negative relationship between DSR and topography and the importance of topography alone to explain DSR is unclear, this apparent relationship warrants future attention.

Summary. Our results suggested that rugged topography and aspect may be important to breeding Golden Eagles. Much of the concern over Golden Eagle populations currently is due to the perceived threat from an increase in the development of wind energy in the western United States due to the species' susceptibility to turbine blade strikes (Hunt 2002, Chamberlain et al. 2006, Smallwood and Thelander 2008, Pagel et al. 2013). Currently, managers are tasked with permitting the legal take of Golden Eagles, which must not result in a population-level decline in abundance (U.S.F.W.S. 2013). The many facets of preventing population-level declines include assessing the current status of the population for comparisons in the future and ensuring future developments are installed in locations that minimize the potential for mortalities (Millsap et al. 2013). The techniques we describe here to assess third-order habitat selection could be used on a local scale to predict the locations most likely to be used by Golden Eagles where wind energy development is expected. When siting a wind farm, managers could use a spatially projected RSF similar to the one we have created for our study area as a guide to avoid areas with the highest probability of use on the landscape (Fig. 3) and on a micro-site level to help adjust the location of wind turbines to

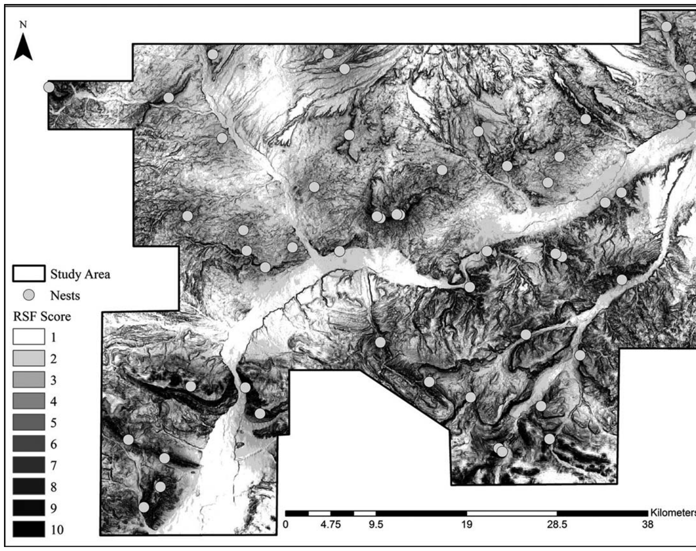

Figure 3. Predictive surface based on best model from third-order resource selection function (RSF) analysis seen at the study-area scale. A RSF score of 10 represents a high probability of use, whereas 1 represents a low probability of use.

an area with the lowest probability of use by breeding eagles (Fig. 4). By avoiding areas with highest probability of use at those two scales, managers may minimize the potential for conflict between wind energy development and Golden Eagles and the potential for population-level declines. Conservation practitioners should not overextend the applicability of spatially explicit models, but estimating the usefulness of models created in ecologically similar areas may provide information on how to effectively use limited resources to protect important areas for Golden Eagles.

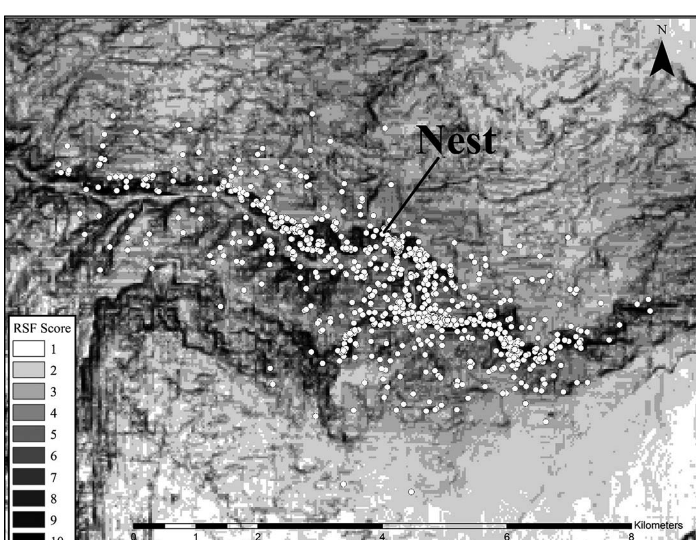

Figure 4. Predictive surface with locations from one Golden Eagle during the nesting season. A resource selection function (RSF) score of 10 represents a high probability of use, whereas 1 represents a low probability of use. White dots represent one Golden Eagle location.

However, if the goal of management actions is to promote breeding success, simply identifying factors that explain habitat selection may not be sufficient. Our results showed that Golden Eagles in our study area select for terrain ruggedness, but ruggedness was negatively related to nest survival, which certainly could influence management actions. Our results highlight the importance of assessing factors influencing selection and breeding success when adequate data exist to do so. For Golden Eagles specifically, identifying the factors that influence nest survival will remain difficult, especially on a broad geographic scale. Nevertheless, clear management objectives and integrated information on resource selection and factors influencing breeding success will be important to the creation of effective conservation strategies for Golden Eagles in North America.

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