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Research

Seasonal variation in resource selection by subadult golden eagles in the Great Basin Desert

Kathy M. Hixson, Steven J. Slater, Robert N. Knight and Robert C. Lonsinger

K. M. Hixson and R. C. Lonsinger (https://orcid.org/0000-0002-1040-7299) ✉ (robert.lonsinger@okstate.edu), Dept of Natural Resource Management, South Dakota State Univ., Brookings, SD, USA. RCL also at: U.S. Geological Survey, Oklahoma Cooperative Fish and Wildlife Research Unit, Oklahoma State Univ., Stillwater, OK, USA. – S. J. Slater, HawkWatch International, Salt Lake City, UT, USA. – R. N. Knight, U.S. Army Dugway Proving Ground, Natural Resource Program, Dugway, UT, USA.

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Golden eagles *Aquila chrysaetos* are a long-lived and wide-ranging species believed to be stable or in slight decline across North America. Golden eagles have an extended subadult stage (4–5 years) that is critical to maintaining recruitment into the breeding population and population viability. Compared to adult golden eagles, the ecology of subadult golden eagles (hereafter, subadults) has received little attention. We investigated patterns of resource selection for subadults in the Great Basin Desert of the western United States during summer and winter, 2013–2019. We monitored 46 subadults with GPS transmitters and related locations ($n = 99\ 037$) with predictors hypothesized to influence seasonal patterns of space use with mixed-effects logistic regression. Subadults selected for ridges and upper slopes in summer and winter, but higher elevations in summer. Subadults showed weak selection for lower ridge density in summer, which was likely facilitated by selection for areas with greater thermal wind current potential. In contrast, subadults showed strong selection for higher ridge density in winter. Subadults selected areas further from roads in summer and closer to roads and electrical transmission lines in winter, which may be related to winter scavenging of road-killed ungulates. Resource selection functions suggested subadults selected for shrublands and woodlands in both seasons, but odds ratios revealed that during winter subadults avoided shrublands and increased selection of woodlands relative to summer. Subadults selected for areas with infrequent fires in both seasons; areas with frequent fires were avoided in summer but selected for in winter. Seasonal changes in resource selection suggested that subadults used woodlands more than expected, potentially reflecting spatial partitioning by subadults to lower-quality habitats to minimize competition with breeding adults during winter when energetic demands for thermoregulation were presumably higher and prey more limited.

Keywords: *Aquila chrysaetos*, golden eagle, GPS, Great Basin Desert, habitat use, resource selection, seasonal habitat, subadults

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Introduction

Understanding how species select habitat features is critical to making informed land management decisions for species conservation (Johnson 1980, Manly et al. 2002). Habitat selection by a species may change over time, owing to anthropogenic disturbances (Whitfield et al. 2007), shifting resource availability (Crandall et al. 2015), environmental conditions (e.g. seasonal temperatures; Marzluff et al. 1997, Braham et al. 2015) or life-stage requirements (Webber et al. 2013). For widespread species, patterns of habitat use may vary among ecoregions and it is important for managers to evaluate patterns of selection at spatial scales that reflect management (Crandall et al. 2015).

Golden eagles *Aquila chrysaetos* are long-lived, wide-ranging apex predators that occur throughout a Holarctic distribution (Kochert and Steenhof 2002, Watson 2010). Golden eagles exhibit delayed reproductive maturity, typically not breeding until their fourth or fifth year (Steenhof et al. 1984). A clutch of two eggs is common for golden eagles in North America (Kochert and Steenhof 2002, Watson 2010), but variation in prey availability, habitat conditions for nesting and hunting, and weather can limit population-level productivity (Steenhof et al. 1997); collectively, these patterns potentially limit the ability of populations to respond rapidly to population declines (McIntyre and Schmidt 2012). Subadult golden eagles (hereafter, subadults) may attempt to nest when intraspecific competition is reduced (e.g. prey is abundant or adult eagle population is low), but their egg production and nest success (< 5%) rates are generally lower than adults (Steenhof et al. 1983, McIntyre and Schmidt 2012).

Maintaining populations of subadults is critical for ensuring recruitment into the reproductive (adult) class (Katzner et al. 2006, Soutullo et al. 2008, Tack et al. 2017). Reduced subadult survival could lead to changes in population age structure, decreased nesting and population declines (McIntyre and Schmidt 2012). Despite the importance of subadults, golden eagle habitat or nest-site selection studies in North America have focused primarily on breeding adults (Marzluff et al. 1997, McIntyre and Schmidt 2012, Watson et al. 2014, Braham et al. 2015, Crandall et al. 2015). During breeding season, nest locations facilitate monitoring of adults (Watson et al. 2014, LeBeau et al. 2015). In contrast, subadults may roam extensively, sometimes moving thousands of kilometers from their natal nest, and their movements are not constrained by breeding or territorial behaviors (O'Toole et al. 1999, Soutullo et al. 2006, 2013, Murphy et al. 2017). Once they reach sexual maturity, they generally return to the vicinity of their natal site to breed (Steenhof et al. 1984, Millsap et al. 2014). Although the subadult period is critical for honing flight and hunting skills, it has been among the least understood aspects of golden eagle ecology (Watson 2010). Murphy et al. (2017) investigated natal dispersal of golden eagles, revealing that among 16 telemetered eagles the mean distance between their natal site and adult territory was 55.3 km (± 29.7 SD), though they did not report movement distances prior to selection of the adult territory.

Advancements in satellite tracking have facilitated the study of subadults, providing new insights into natal dispersal (Soutullo et al. 2006, 2013, Murphy et al. 2017, 2019), migration (McIntyre et al. 2008) and survival (McIntyre et al. 2006). Subadult habitat use has also been studied, but these investigations have been restricted spatially to within natal territories (Sandgren et al. 2014), limited temporally to within an animal's first year (Soutullo et al. 2008), or only considered topographical features (i.e. slope, aspect, altitude and distance to ridge) as predictors of space use (Fielding et al. 2019). Other studies of habitat selection have included subadults, but only in combination with adults (Nielson et al. 2016, Poessel et al. 2016, Miller et al. 2017).

In the United States, golden eagle populations are stable or in slight decline (Millsap et al. 2013, Nielson et al. 2014, U.S. Fish and Wildlife Service 2016). In portions of the Great Basin Desert (hereafter, Great Basin), though, occupied territories have decreased by almost half since 2007 (Slater et al. 2013). Golden eagle declines in this region are likely driven primarily by changes in native habitat caused by cheatgrass *Bromus tectorum* invasion (Knapp 1996, Kochert and Steenhof 2002, Slater et al. 2013), which limits important leporid prey populations (Knick and Dyer 1997, Bedrosian et al. 2017). We investigated resource selection of subadults prior to recruitment into the breeding population, with a focus on informing natural resource management in the Great Basin. Our objectives were to use locational data (fixes) from tagged, free-ranging subadults within the Great Basin to 1) investigate second-order selection of topographic, climatic, land cover and anthropogenic variables and 2) compare selection between summer and winter. Golden eagles have been associated with steep slopes, cliffs and areas with high-class winds, all of which may contribute to generating orographic uplift (Katzner et al. 2012, 2015). Golden eagles may also improve flight efficiency by subsidizing flight with thermal uplift (Katzner et al. 2015). Wildfires impact land cover and the availability of prey; golden eagles may be particularly impacted by fires reducing shrublands, which support leporid populations in the Great Basin and have long recovery periods (Knick and Dyer 1997, Pellant et al. 2004, Bedrosian et al. 2017). Wildfires have resulted in lower reproductive success and abandonment of territories for breeding golden eagles (Kochert et al. 1999, Slater et al. 2013), and may also influence subadult space use. Golden eagles generally avoid areas with human disturbance, but are attracted to some infrastructure features that may provide perching or scavenging opportunities (Lehman et al. 2007, Lonsdorf et al. 2018, Tack et al. 2020). We predicted that subadult space use would be positively associated with topographic relief, shrublands and thermal efficiency (a predictor of thermal wind currents; Watson et al. 2014), and negatively associated with anthropogenic land-cover types (e.g. urban and agricultural lands). We predicted that habitat use would vary by season, and that cooler habitats (e.g. higher elevation, more woodland habitats) would be selected for more strongly in summer (Braham et al. 2015).

Methods

Study area

We conducted our study in the Great Basin of western North America (Fig. 1). This semi-arid ecosystem was characterized by cold, wet winters and hot, dry summers with < 305 mm of precipitation annually (Pellant et al. 2004). Topography was characterized by mountain ranges with elevations < 3000 m separated by large, flat valleys. Lower elevations were characterized by sagebrush (*Artemisia* spp.) steppe and greasewood *Sarcobatus vermiculatus* shrublands, grasslands and salt playas, whereas open pinyon *Pinus edulis* and juniper (*Juniperus* spp.) woodlands dominated higher elevations (Pellant et al. 2004). Invasive grasses (e.g. cheatgrass) have increased the extent and frequency of wildfires, reducing native shrubs and increasing invasive grasses (Pellant et al. 2004).

Data collection and processing

Telemetered golden eagles in this study fledged from nests in the vicinity of the US Army's Dugway Proving Ground (hereafter, Dugway) in western Utah, where golden eagle nest monitoring and inventory has been ongoing since 2007 (Knight 2016). From 2013 to 2018, we entered golden eagle nests and hand-captured nestlings that were 7–8 weeks old. We sought to maximize the geographic distribution of deployments around Dugway, but some territories were sampled in multiple years due to limited availability of nestlings each year. Nestlings were fitted with 45-g solar-powered Argos/GPS Platform Transmitter Terminals (PTTs, Microwave Telemetry, Inc., Columbia, MD; horizontal accuracy was ± 18 m) as a backpack using Teflon ribbon. Transmitters were programmed to take hourly fixes between 07:00 and 19:00 h, a midnight roost location, and transmit data to a satellite every three days. Nestlings were returned to the nest after processing.

We were interested in the independent life stage that occurs after parental dependency and before breeding; we refer to this period as the subadult stage. Length of dependency on parental care can vary depending on prey availability and breeding density (Murphy et al. 2017), but based on eagle monitoring in our study region, most hatch-year golden eagles were independent by late summer. Thus, we excluded GPS fixes collected before September of each individual's hatch year. Breeding may begin the fourth year, so we also excluded GPS fixes collected after February following each individual's third year. Additionally, to minimize the influence of antagonistic behavior from territorial adults on subadult habitat selection and to avoid periods of migration, we examined selection during two annual periods: summer (8 July–14 September) and winter (16 November–31 January). Although some telemetered individuals ranged outside of the Great Basin, we were interested in resource selection within the Great Basin and, therefore, we excluded locations collected outside of the Great Basin from subsequent analyses.

We identified five broad categories of predictors (covariates) hypothesized to influence subadult space use including topography, climate-related wind patterns, land cover, wildfire disturbance and linear anthropogenic features (Table 1). We acquired spatial data characterizing covariates from publicly available datasets and processed data using ArcGIS Desktop 10.6. We derived five topographic covariates expected to influence orographic lift from 30-m-resolution US Geological Survey 3D Elevation Program Digital Elevation Models (Table 1, Fig. 2): elevation, slope, topographic position index (TPI), ridge density and topographic

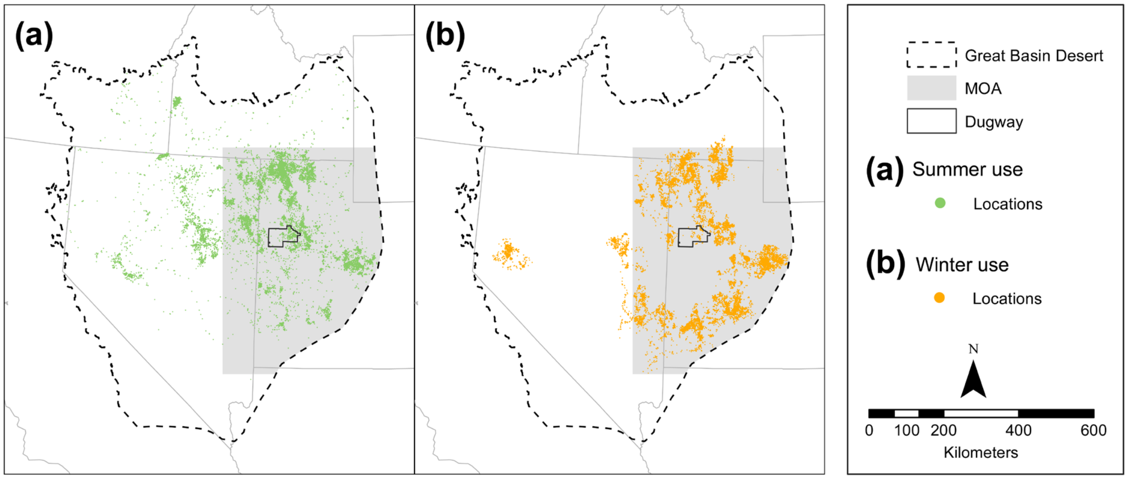

Figure 1. Subadult golden eagle *Aquila chrysaetos* locations (fixes) within the Great Basin Desert during (a) summer and (b) winter; subadults were captured and tagged as nestlings within the Military Operational Area (MOA) around the U.S. Army's Dugway Proving Ground (Dugway).

Table 1. Covariates considered for resource selection functions used to assess patterns of use for subadult golden eagles *Aquila chrysaetos* in the Great Basin Desert during summer and winter (2013–2019). Positive (+) and negative (−) predictions indicated these covariates were expected to be positively and negatively associated with use, respectively, whereas 0 indicated that we expected these covariates may influence use but could have positive or negative associations.

Category	Covariate	Prediction	Unit
Topography	Elevation[1]	+	30 m
	Slope[1]	+	
	Topographic position index (TPI)[1]	+	
	Ridge density[1]	+	
	Topographic roughness index[1]	+	
Climate	Wind speed[2]		
	Distance to high-class winds	−	m
	Wind class	+	m s^{-1}
	Median wind class	+	m s^{-1}
	Thermal efficiency[1]	+	30 m
Land cover	Categorical land cover[3]		
	Agriculture	−	30 m
	Barren	−	
	Developed	−	
	Grassland (including herbaceous)	+	
	Shrubland (including scrubland)	+	
	Vegetated wetland	−	
	Woodland	+	
	Shrubland and woodland cover[3]		
	Proportion of shrubland and woodland cover	+	
	Majority shrubland and woodland	+	
Wildfire	Fire-return cycles[1]		
	Short (<10 years)	−	30 m
	Intermediate (11–20 years)	−	
	Long (>20 years)	+	
	Non-burnable	−	
	Indeterminate	NA	
Anthropogenic features	Distance to primary or secondary road[4]	0	m
	Distance to electrical transmission line[5]	0	m

[1] LANDFIRE 2010 (<http://landfire.cr.usgs.gov/>), [2] National Renewable Energy Lab (<https://data.nrel.gov/>), [3] 2011 National Land Cover Database (<www.mrlc.gov/>), [4] US Census Bureau (<www.census.gov/programs-surveys/geography.html>), [5] Homeland Infrastructure Foundation-level Data (<https://hifld-geoplatform.opendata.arcgis.com/>).

roughness. We calculated both TPI and ridge density using the relief analysis toolbox (Weiss 2001, Miller and Schaetzl 2015). The TPI compared each location to the mean elevation of a circular neighborhood within 500 m. Ridge density estimated the proportion of area within 500 m characterized by TPI as ridge or upper slope (Watson et al. 2014). We estimated the topographic roughness index using digital elevation model surface tools for ArcGIS 10 (Jenness 2013). We characterized wind speed in three ways: wind class, median wind class and distance to high-class winds (Table 1). Wind class was obtained from National Renewable Energy Lab (<https://data.nrel.gov/>; Fig. 2). Wind classes ranged from 1 to 7 with the maximum mean wind speed (m s^{-1}) at 50 m above ground for each class being 5.6, 6.4, 7.0, 7.5, 8.0, 8.8 and 11.9, respectively. We calculated median wind class within 500 m. Finally, we measured the distance to the closest area with high wind potential by reclassifying the wind classes into low (1–2) and high (3–7) classes (sensu Katzner et al. 2012); high-class winds represented those considered viable for wind energy. As acknowledged by Katzner et al. (2012), wind speeds were variable (both spatially and temporally) and therefore patterns of use associated with measures of wind should be interpreted as relative trends. We used the spatial analyst area solar radiation tool in ArcGIS 10 to estimate seasonal solar radiation and multiplied solar radiation by potential land cover ground warming ratings to estimate season-specific potential thermal efficiency (Watson et al. 2014; Fig. 2).

We used 2011 National Land Cover Database to characterize land cover (Fig. 2). We reclassified land cover into eight categories: agriculture, barren, developed, grassland and herbaceous (hereafter, grassland), open water, shrubland and scrubland (hereafter, shrubland), vegetated wetland and woodland (sensu Nielson et al. 2016; Table 1). Land-cover types vary in prey availability, thermal conditions and human disturbance (Marzluff et al. 1997, Whitfield et al. 2007, Braham et al. 2015), and these factors likely vary seasonally within each land-cover type. In the Great Basin of western Utah, shrubland and woodland habitats have been associated with higher leporid abundances (Arjo et al. 2007). Consequently, we also characterized land cover within 500 m as 1) a continuous predictor representing the proportion of land cover that was shrubland or woodland (%SW), and 2) as a binary predictor indicating if > 50% of the land cover was

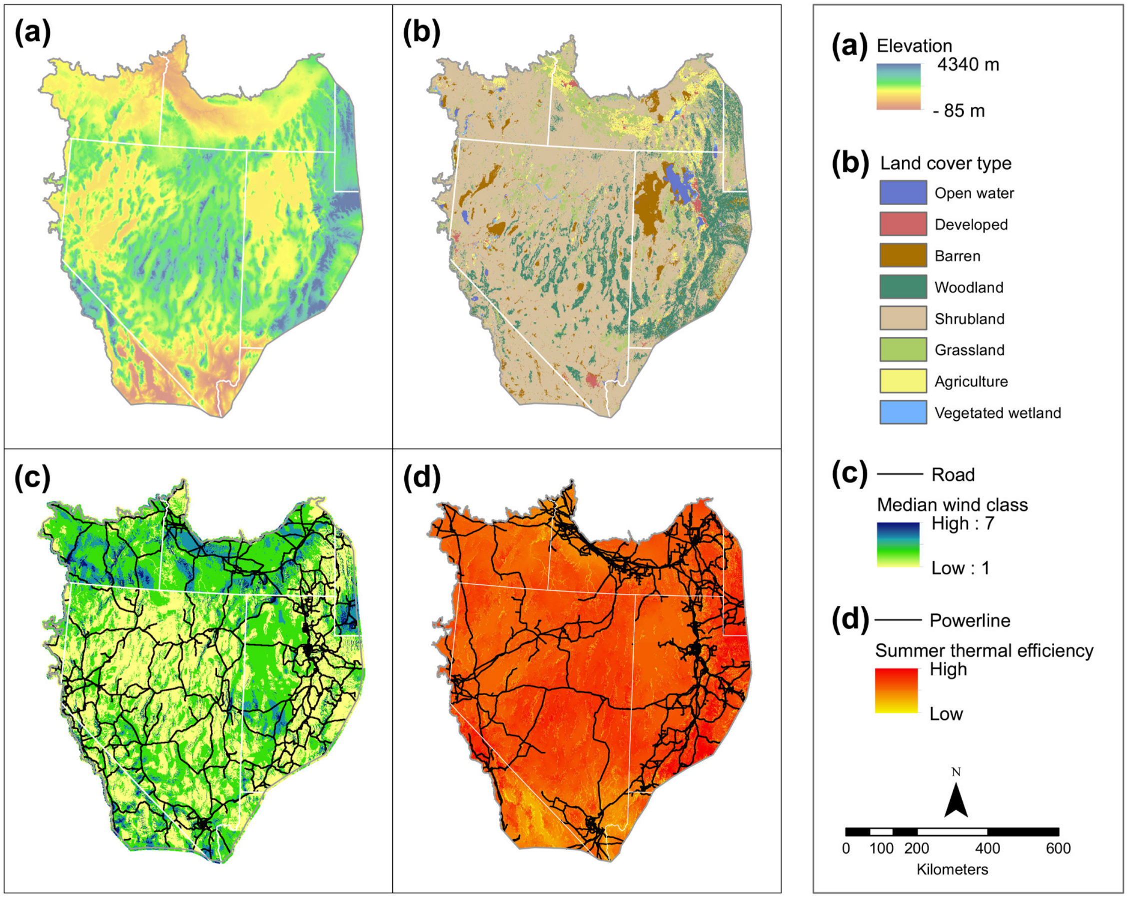

Figure 2. Distribution of select covariates in the most-supported models of seasonal resource selection by subadult golden eagles *Aquila chrysaetos* in the Great Basin Desert during summer and winter seasons (2013–2019).

either shrubland or woodland (majority SW). We obtained data from LANDFIRE 2010 that represented the mean period between fires. We classified fire-return intervals into short (< 10 years), intermediate (11–20 years) and long (> 20 years) periods. Two additional classes defined locations that were non-burnable or had insufficient data to classify (indeterminate). We obtained data from US Census Topologically Integrated Geographic Encoding and Referencing Product (<www.census.gov/programs-surveys/geography.html>) to determine distance to the nearest primary or secondary road. We used the US Department of Homeland Security's Homeland Infrastructure Foundation-level Data (<https://hifld-geoplatform.opendata.arcgis.com>) to estimate the distance to the nearest electrical transmission line.

Resource selection analyses

We standardized continuous covariates by subtracting the mean and dividing by the standard deviation. We randomly split fixes using 75% for model training and 25% for model validation. For each season, we generated random available points within our spatial extent equivalent to the number of training fixes. Open water is not considered habitat for golden eagles, but GPS fixes may be acquired over open water due to eagles crossing water bodies or precision of GPS fixes. Consequently, we excluded fixes over open water from used and available data points.

For each season, we used the training dataset and resource selection functions (RSFs) to relate probability of use by subadults to candidate models (Manly et al. 2002, Gillies et al. 2006, Long et al. 2009). We included a random effect for individual golden eagles to account for unbalanced samples sizes and pseudoreplication from multiple fixes per individual (Gillies et al. 2006). We fit mixed-effects logistic regression models and estimated coefficients for RSFs using lme4 in R (Bates et al. 2015, <www.r-project.org>). We evaluated relative model fit based on Akaike's information criterion (AIC; Burnham and Anderson 2002).

To refine our covariate set and develop a candidate model set, we employed a modified stepwise approach. We tested for correlations among continuous covariates using Pearson's correlation coefficients (r) with corrplot in R (<www.r-project.org>). For covariates having $|r| \geq 0.6$ (Crandall et al. 2015), we fit single-predictor models for each season and retained only the most-supported covariate for subsequent season-specific analyses. For covariates that were characterized in multiple ways (i.e. wind speed and shrubland and woodland cover), we fit single-predictor models for each season and retained only the most-supported characterization for subsequent season-specific analyses. Nielson et al. (2016) found a quadratic effect for elevation to be an important predictor of eagle space use, so we also compared elevation with a quadratic effect for elevation (i.e. elevation + elevation^2) in each season and retained the most-supported season-specific characterizations.

We expected that categorical land-cover and fire-return cycle predictors were not independent of elevation (and potentially slope). Including covariates that are not independent in the same model may result in inflated p-values and inconsistent coefficients (i.e. coefficient estimates can vary substantially, including an artificial change in sign; Lonsinger et al. 2019). Thus, for each season we first compared the single-predictor model of land cover to additive models with land cover and either slope, elevation (in a quadratic form) or both. We repeated this process for fire-return cycle. In both seasons, additive models containing the categorical predictors with elevation, slope or both resulted in inconsistencies in the coefficient estimates, including changes in the direction of effect (i.e. change in sign). For example, when considering only land cover in summer, the coefficient suggested that woodland was positively (and strongly) associated with subadult space use (this was supported by resource selection ratios). But when slope, elevation or both were included with land cover, the association between subadult space use and woodlands was reportedly negative. Consequently, for each season we compared single-predictor models for land cover and fire-return cycle to models with the additive combination of slope and elevation (in a quadratic form); these comparisons led to the exclusion of land cover and fire-return cycle as categorical predictors in the mixed-effects logistic regression models).

After refining the covariate set to uncorrelated predictors potentially influencing subadult space use, any combination of covariates could represent an appropriate model of resource selection. When a priori combinations of predictors cannot be identified to reduce a model set, evaluating all possible combinations of predictors has been suggested (Doherty et al. 2012, Morin et al. 2020), as stepwise selection procedures may result in spurious model selection results (Burnham and Anderson 2002, Calcagno and de Mazancourt 2010). Consequently, our candidate model set for each season included all possible additive combinations of our refined covariate set and the null model. We excluded models that failed to converge from subsequent comparisons. After identifying the most-supported model in each season, we tested if previously excluded characterizations of predictors in the model were more supported than the retained characterizations when considered in concert with the other predictors found in the most-supported season-specific models.

Although the categorical land-cover and fire-return cycle predictors were excluded from the mixed-effects logistic regression models, these were important to managers. Consequently, we used a χ^2 test to evaluate if the proportion of used points within a category (e.g. a land-cover type) was different from the proportion of random available points, and calculated odds ratios with 95% confidence intervals. Odds ratios > 1 suggested selection for a particular feature, whereas ratios < 1 suggested avoidance.

Model validation

We used the most-supported season-specific models to predict patterns of subadult space use based on:

$$\text{Predicted use} = \text{Exp}\left(\sum_{i=1}^{p} \beta_i x_i\right)$$

where β represented the RSF coefficient, *x* represented the value of the associated covariate at a given point, and *p* was the total number of covariates in the model. Within our area of management interest (i.e. the Military Operational Area around Dugway; Fig. 1), each 30-m cell was assigned a predicted use value. We scaled these values to a range of 0–1 by dividing each predicted use value by the maximum predicted use value and classified predicted use into 10 bins (with 10 being the highest) using equal-area rank bins (Nielson et al. 2016). In each season, we summed the number of validation points within each bin, expected higher ranked areas to be used disproportionately more, and used Spearman's rank coefficients to evaluate these relationships and assess model performance.

Results

Capture, tracking and covariate refinement

We outfitted 76 eagle nestlings from 72 nests with GPS transmitters; 46 transmitted data from within our study extent from September of their hatch year through January 2019 and were included in the analysis (Table 2). Fifteen individuals survived long enough to age out of the subadult class, whereas eight individuals were still subadults at the end of the study (Table 2). Telemetered subadults produced a total of 453 711 fixes from 2013 to 2019, including 99 037 fixes (excluding open water fixes) distributed between summer (47 773) and winter (51 264) within the Great Basin (Table 3). Although more individual subadults contributed data during summer than winter, individuals in winter contributed more fixes within the Great Basin Desert than those in summer (Table 3). The variation in predictors within the random available points was comparable to the variation in predictors across the Great Basin Desert (Supporting information).

Among spatial covariates, only slope and topographic roughness were correlated (r = 0.86) and in both seasons slope (AIC: summer = 95 072; winter = 102 033) received greater support than topographic roughness (AIC: summer = 95

Table 2. Temporal distribution of 76 nestling golden eagles *Aquila chrysaetos* GPS-tagged in the Great Basin Desert from 2013 to 2018 and the number of individuals surviving to the subadult stage and transmitting data from each annual cohort during each of six subsequent summer (8 July–14 September) and winter (16 November–31 January) seasons.

Life stage	Season[1]	2013	2014	2015	2016	2017	2018
Nestlings		19	24	8	8	9	8
Subadults	Summer 2013	11	–	–	–	–	–
	Winter 2013	7	–	–	–	–	–
	Summer 2014	6	18	–	–	–	–
	Winter 2014	6	14	–	–	–	–
	Summer 2015	6	12	3	–	–	–
	Winter 2015	5	9	2	–	–	–
	Summer 2016	–	9	2	6	–	–
	Winter 2016	–	9	1	6	–	–
	Summer 2017	–	–	1	6	4	–
	Winter 2017	–	–	1	6	3	–
	Summer 2018	–	–	–	5	3	3
	Winter 2018	–	–	–	3	2	3

[1] Year for each season indicates the season start date.

878; winter = 103 515). In both seasons, the quadratic effect for elevation (AIC: summer = 94 436; winter = 99 636) was more supported than elevation (AIC: summer = 95 441; winter = 102 676). In summer, wind class (AIC = 98 892) was more supported than median wind class (AIC = 99 090) or distance to high-class winds (AIC = 99 135). In contrast, median wind class (AIC = 105 931) was more supported in winter than wind class (AIC = 106 288) or distance to high-class winds (AIC = 106 593). In both seasons, majority SW (AIC: summer = 98 551; winter = 105 079) was more supported than %SW (AIC: summer = 99 042; winter = 105 179). As expected, models of subadult use containing land cover with slope, elevation or both resulted in inconsistent patterns in the direction of effect for beta coefficients of land-cover categories. Similarly, models containing fire-return cycle with slope, elevation or both produced inconsistencies for beta coefficients associated with fire-return cycle categories. These inconsistencies (and change in direction of effect) suggested underlying multicollinearities between each categorical predictors and slope and elevation. In both seasons, the additive model of slope and elevation in a quadratic form (AIC: summer = 92 590; winter = 97 477) was more supported than land cover (AIC: summer = 98 759; winter = 104 034) or fire-return cycle (AIC: summer = 98 312; winter = 105 129). Following comparisons of covariates, we retained nine predictors for each season including slope, quadratic form of elevation, TPI, ridge density, distance to primary or secondary roads, distance to transmission lines, majority SW, season-specific thermal efficiency and either wind class (summer) or median wind class (winter).

Resource selection analyses

Within each season, there were 512 possible models representing additive combinations of covariates or the null model. In both seasons, 2.1% of models failed to converge and were excluded from model selection. In summer, the most-supported model of resource selection by subadults included elevation (quadratic form), slope, distance to roads, majority SW, TPI, thermal efficiency and ridge density (Table 4, 5). Three additional models were competitive (within 4 ΔAIC), and each contained the same structure as the most-supported model but with the addition of wind class, distance to transmission lines or both (Table 4). Closer inspection of these models revealed that the additional parameters did not improve model fit relative to the most-supported model (Table 4) and 95% confidence intervals for their beta coefficients overlapped 0, indicating these covariates were uninformative (Arnold 2010, Leroux 2019). The cumulative Akaike weight of the top four models was 96% (Table 4). Subadult use in summer was positively associated with steeper slopes, thermal efficiency, distance from roads and land cover dominated by shrubland and woodland (Table 5, Fig. 3). Use was also associated with higher TPI (i.e. ridges), but negatively associated with ridge density (Table 5, Fig. 3). Subadult use was highest at intermediate elevations (Table 5, Fig. 3). For winter, the most-supported model of resource selection by subadults received 100% of the Akaike weight and included elevation (quadratic form), slope, distance to roads, majority SW, TPI, ridge density, distance to transmission lines and median wind class (Table 4, 5). The next closest model was

Table 3. Number of GPS-tagged subadult golden eagles *Aquila chrysaetos*, mean (± SD) number of GPS locations (fixes) per subadult, and total number of subadult locations used for model training and validation during summer (8 July–14 September) and winter (16 November–31 January) in the Great Basin Desert.

		Training fixes		Validation fixes	
Season	Subadults	Mean/subadult	Total	Mean/subadult	Total
Summer	46	779 (± 582)	35 829	260 (± 195)	11 944
Winter	36	1068 (± 677)	38 448	356 (± 226)	12 816

Table 4. Most-supported mixed-effects logistic regression model(s) of subadult golden eagle *Aquila chrysaetos* resource selection in the Great Basin Desert during summer and winter (2013–2019). Explanatory variables include elevation (Elev), slope, distance to road (DistR), distance to transmission lines (DistT), ridge density (Ridge), majority shrubland and woodland (SW), topographic position index (TPI), summer thermal efficiency (TE), wind class (Wind) and median wind class (MedWind). Each model is ranked based on ΔAIC, where K = number of model parameters, w_i = Akaike weight, Σw_i = cumulative Akaike model weights and LL = log-likelihood. For each season, only the model(s) required to achieve a $\Sigma w_i > 0.98$ are presented.

Model	K	AIC	ΔAIC	w_i	Σw_i	LL
Summer						
Elev + Elev^2 + Slope + DistR + SW + TPI + TE + Ridge	10	91 316.77	0.00	0.50	0.50	−45 647.9
Elev + Elev^2 + Slope + DistR + SW + TPI + TE + Ridge + DistT	11	91 317.59	1.82	0.20	0.70	−45 647.8
Elev + Elev^2 + Slope + DistR + SW + TPI + TE + Ridge + Wind	11	91 317.72	1.95	0.19	0.88	−45 647.9
Elev + Elev^2 + Slope + DistR + SW + TPI + TE + Ridge + DistT + Wind	12	91 319.55	3.78	0.07	0.96	−45 647.8
Elev + Elev^2 + Slope + DistR + SW + TPI + TE	9	91 322.00	6.23	0.02	0.98	−45 652.0
Winter						
Elev + Elev^2 + Slope + DistR + SW + TPI + Ridge + DistT + MedWind	11	93 234.67	0.00	1.00	1.00	−46 606.3

> 105 ΔAIC from the most-supported model. Subadult use in winter was positively associated with steeper slopes, TPI, ridge density and land cover dominated by shrubland and woodland cover (Table 5, Fig. 3). Use was negatively associated with median wind class, as well as distance from roads and transmission lines (Table 5, Fig. 3). Winter subadult use was highest at intermediate elevations (Table 5, Fig. 3). In both seasons, replacing predictors in the top model that were characterized in multiple ways with previously excluded alternative characterizations did not improve model fit.

Excluding grasslands in summer ($p = 0.1$), the proportion of used points within each land-cover class was significantly different from available points (all $p < 0.001$) in both seasons. Odds ratios suggested selection for woodlands in both seasons, contrasting patterns for shrublands (selection in summer; avoidance in winter) and grasslands (no selection in summer; avoidance in winter), and avoidance of all other land-cover classes (Fig. 4). For fire frequency, the proportion of used points within each class was significantly different from available points (all $p < 0.001$) in both seasons. Odds ratios suggested subadults selected for areas with long fire-return cycles (> 20 years) and avoided areas that were non-burnable or had intermediate fire-return cycles (11–20 years; Fig. 4). Odds ratios suggested areas with short fire-return cycles (< 10 years) were avoided in summer, but selected for in winter (Fig. 4).

Model validation

Restricting the model validation procedures to the Military Operational Area around Dugway resulted in 92% of validation points being considered for model validation. Validation points were disproportionately located in bins with higher predicted use relative to their availability. In summer, 73.5% and 21.2% of validation points were in the highest and second highest predicted use bins, respectively. In winter, 25.0% and 17% of validation points were in the highest and second highest predicted use bins, respectively. In both seasons, the proportion of validation points decreased with decreases in predicted use bins; no validation points were in the lowest predicted use bins in summer. Based on Spearman's rank correlations,

Table 5. Estimated beta coefficients (β), standard errors (SE) and p-values of the most-supported model structure of subadult golden eagle *Aquila chrysaetos* resource selection in the Great Basin Desert during summer and winter (2013–2019). A dash indicates that the covariate was not included in the most-supported model structure for that season.

	Summer			Winter		
	β	SE	p-value	β	SE	p-value
Intercept	−0.1247	0.036	< 0.001	−0.1554	0.054	0.004
Topography						
Slope	0.3832	0.011	< 0.001	0.3565	0.010	< 0.001
Elevation	1.8376	0.049	< 0.001	3.0636	0.061	< 0.001
Elevation^2	−1.5010	0.046	< 0.001	−2.8449	0.060	< 0.001
Topographic position index	0.2616	0.008	< 0.001	0.2933	0.009	< 0.001
Ridge density	−0.1102	0.038	0.004	0.3982	0.039	< 0.001
Climate						
Median wind class	–	–	–	−0.2859	0.011	< 0.001
Summer thermal efficiency	0.1138	0.010	< 0.001	–	–	–
Land cover						
Majority shrubland and woodland	0.1535	0.029	< 0.001	0.3664	0.028	< 0.001
Anthropogenic features						
Distance to primary and secondary road	0.0601	0.008	< 0.001	−0.1814	0.010	< 0.001
Distance to electrical transmission line	–	–	–	−0.3048	0.010	< 0.001

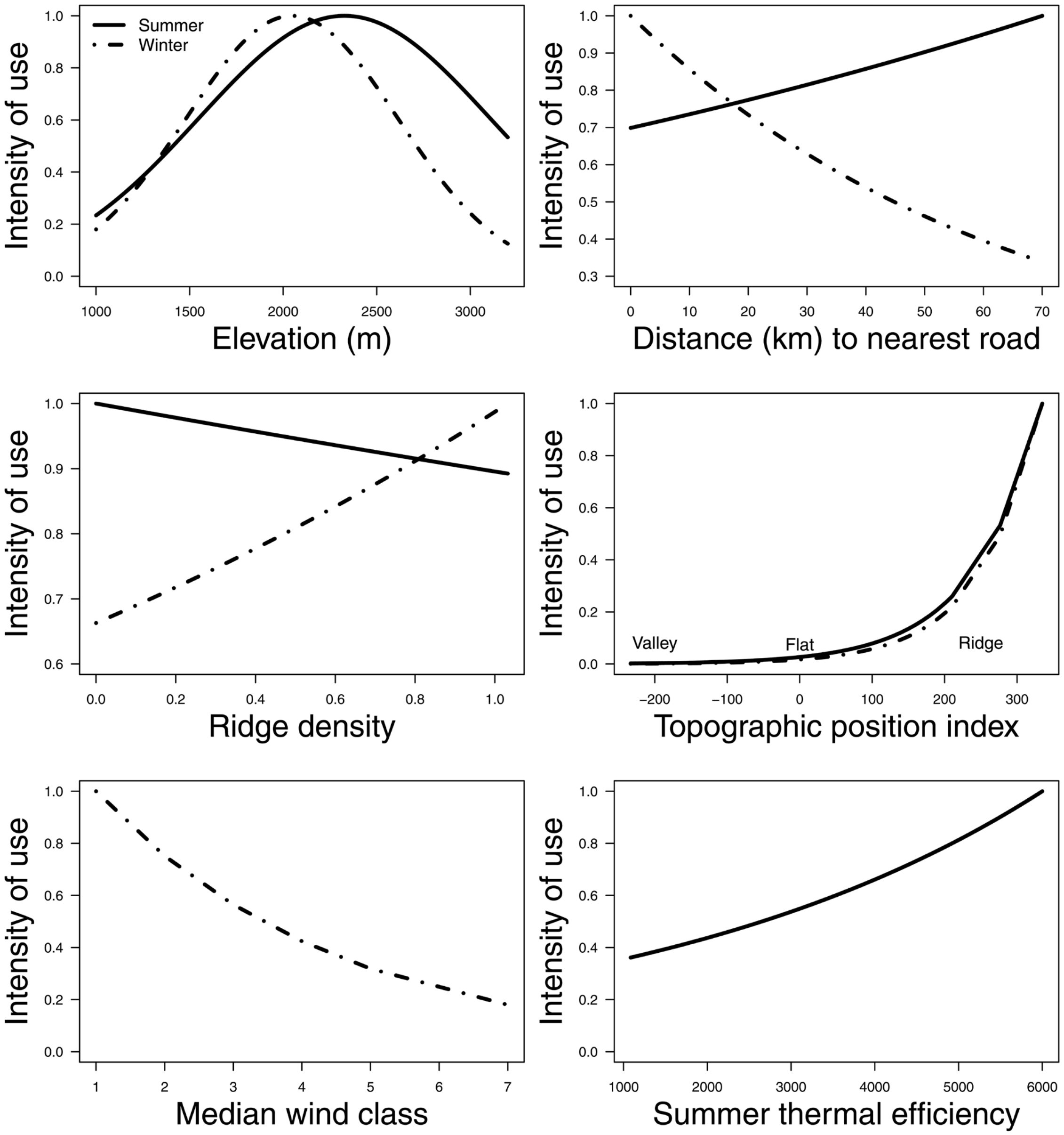

Figure 3. Intensity of use by subadult golden eagle *Aquila chrysaetos* as a function of select predictors in the most-supported model structures for resource selection in the Great Basin Desert during summer and winter (2013–2019). Use was scaled to a maximum value of 1 and plotted based on mean elevation (excluding the plot for elevation), median values for other numeric covariates, and for sites characterized as majority (> 50%) shrubland or woodland.

both summer ($r_s = 0.969$, p-value < 0.001) and winter ($r_s = 0.867$, p-value $= 0.002$) models performed well.

Discussion

There is a paucity of information on patterns of resource selection by subadult golden eagles, in part, because they are nomadic and do not maintain stable home ranges or territories, making them difficult to study (Watson 2010). In contrast, adult golden eagles often demonstrated space use patterns restricted to home ranges containing nest sites and foraging habitats (Marzluff et al. 1997, Watson 2010, McIntyre and Schmidt 2012). Previous resource selection studies for golden eagles have focused on adults and within home range selection (Watson et al. 2014, Braham et al. 2015, Crandall et al. 2015). Resource use by adults has been described as 'stable' over time (Marzluff et al. 1997, Watson et al. 2014), with use anchored by nests (Kochert and Steenhof 2012, Watson et al. 2014). Still, adults have demonstrated seasonally dynamic

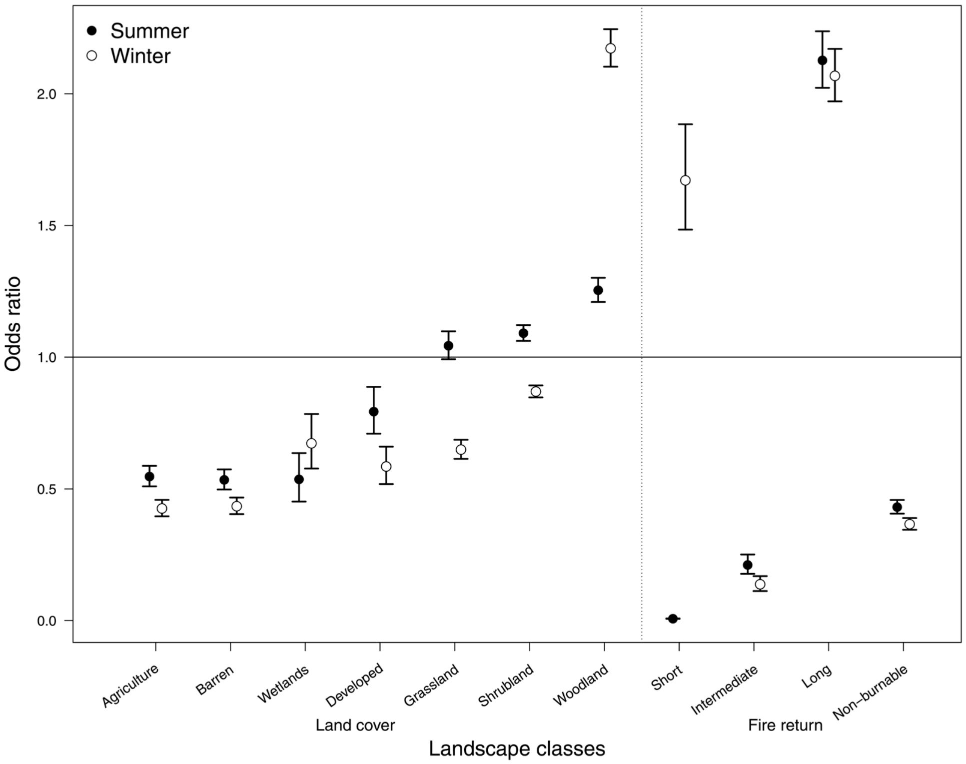

Figure 4. Odds ratios and 95% confidence intervals for subadult golden eagle *Aquila chrysaetos* resource selection of land-cover types and fire-return cycles in the Great Basin Desert during summer and winter (2013–2019). Fire-return cycles included short (< 10 years), intermediate (11–20 years), long (> 20 years) and non-burnable. Values > 1 indicated selection for a class, whereas values < 1 indicated avoidance. The vertical line separates land-cover types from fire-return cycles.

core use areas due to shifting resource availability and climatic conditions (Watson et al. 2014, Braham et al. 2015). While seasonal patterns in resource availability and conditions may be expected to influence subadult space use, they are not tethered to nests or territories and therefore may select resources differently than adults. Our results supported dynamic patterns of space use for subadults, with patterns of selection varying between summer and winter. We were interested in patterns of space use during the subadult stage and, therefore, assumed behavior related to space use patterns was more similar among subadults (regardless of their age) than between subadults and adults. Our sampling design of tagging nestlings resulted in more first-year subadults in our sample than second-year subadults, and more second-year than third-year subadults. Thus, if subadults change their behavior from their first to third year, our results likely reflect the patterns of younger subadults to a greater degree than older subadults.

Landscape characteristics have consistently been associated with golden eagle resource selection. Broad-scale modeling of adults in the western United States during summer found that space use increased with elevation up to a threshold of 3012 m (Nielson et al. 2016). Our results also suggested seasonal thresholds, with use increasing up to ~2330 m in summer and ~2050 m in winter. Adults in the Mojave Desert disproportinatly used higher elevations more during warmer months and made long-distance movements to cooler, higher elevation sites (Braham et al. 2015). The shift by subadults that we observed to higher elevations in summer, and lower elevations in winter, was likely related to behavioral thermoregulation, foraging opportunities or both. Subadult use of the highest elevations (those over the threshold elevation) was substantially higher in summer than winter; for example, intensity of use at 3200 m by subadults was > 4× higher in summer than winter, presumably due to avoidance of snow covered ridges and reduced prey availability during winter.

Golden eagles exploit orographic lift and rising convectional currents (i.e. thermals) to subsidize flight (Katzner et al. 2015). While subsidizing sustained flight is adventageous, subadults are less efficient than older eagles (Pirotta et al. 2018). Eagles may select for landscape features and conditions conducive to generating orographic lift or thermals (Watson et al. 2014, Nielson et al. 2016). Adults in the Rocky Mountains and Columbia Plateau tended to select rugged terrain and ridges with sufficient slope to produce orographic lift (Watson et al. 2014, Domenech et al. 2015). Subadults in the Great Basin demonstrated similar patterns, selecting greater slopes and ridges that likely generated lift and subsidized lower-altitude soaring (Katzner et al. 2012, 2015). Subadults used areas with greater ridge densities more in winter and lower ridge densities more in summer. These patterns likely reflected, at least in part, seasonal availability of thermals. In winter, shorter day length and lower angle of the sun limit the generation of thermals (Maransky et al. 1997). Consequently, subsidizing flight through orographic lift may have been more important in winter, whereas thermals may be important in summer to subsidize energetic demands of hunting over longer diurnal periods. Measures associated with thermals have been related to golden eagle space use in some studies (Nielson et al. 2016) but not others (Watson et al. 2014). Nielson et al. (2016) found that late-summer eagle use was influenced by solar radiation. We found evidence that thermals influenced subadult space use in summer as well, and thermals may facilitate use of lower ridge density areas. Golden eagles reportedly select for areas with higher wind speeds during spring and fall migration (Katzner et al. 2012) and late summer (Nielson et al. 2016). In contrast, we did not find an influence of wind speed on summer space use, and our results suggested that winter use was highest at low wind speeds. These conflicting results may be due to the scale of inquiry, high variability in wind speeds, quality of wind speed data or a combination of these factors. Notably, there was proportionally less high-class winds in our Great Basin spatial extent than in the broader western United States (Nielson et al. 2016). Temporal variation in wind speed may also influence differences in seasonal patterns of use by subadults; as one reviewer suggested, subadults may avoid areas where wind speeds are more variable. The wind speed data we used represented the annual average wind-power class, and we did not have season-specific estimates of wind speed or measures of wind speed variability at a scale and resolution necessary to address the influence of variation in wind speed.

During breeding and non-breeding seasons, adults in the Great Basin selected for core areas with shrublands (e.g. sagebrush, rabbitbrush (*Chysothamnus* spp.) and salt-desert scrub) and avoided grasslands (Marzluff et al. 1997). Similarly, the majority of adult locations in the Columbia Plateau region were in shrublands (60.7%), with fewer locations in forests (19.2%) or grasslands (17.3%; Watson et al. 2014). In the western United States, Nielson et al. (2016) reported a negative relationship between golden eagle space use and forests (or woodlands), but did not find a relationship between use and shrublands or grasslands; they suggested that these patterns implied selection for open landscapes. Marzluff et al. (1997) suggested that selection for shrublands was related to the availability of important prey (black-tailed jackrabbits *Lepus californicus*). Jackrabbit relative abundance has been positively associated with shrublands in other portions of the Great Basin, including in western Utah (Arjo et al. 2007). In contrast, subadults selected most strongly for woodlands in both seasons, selected for shrublands in summer, and avoided shrublands in winter. Eagles are less efficient at hunting in dense forests (Whitfield et al. 2007), but woodlands of the Great Basin are predominantly open pinyon–juniper so these differences may have reflected spatial partitioning by subadults to lower-quality (e.g. reduced prey, more difficult hunting) habitats to minimize competition with adults. Avoidance of shrublands during winter suggested spatial partitioning was stronger when energetic demands were higher and prey resources more limited (Halley and Gjershaug 1998). During summer, proportional use of grasslands by subadults may be facilitated by lower energetic requirements and seasonally higher prey availability. Subadults avoided agriculture, barren, wetland and developed cover types in both seasons. Avoidance of agriculture and developed lands has been documented among adults in the Rocky Mountains, Columbia Plateau, Mojave Desert and northern Great Basin (Marzluff et al. 1997, Watson et al. 2014, Braham et al. 2015, Domenech et al. 2015).

Inferred patterns of land-cover selection by subadults assume that land-cover data from 2011 adequately represented land cover during sampling. Fire is the primary driver of land-cover change in the Great Basin, and the distribution and frequency of fires is greatest in lower-elevation areas that are predominantly grasslands, where cheatgrass is more prevalent and land-cover is reestablished as grasslands (Kitchen 2012, Williamson et al. 2020). The Great Basin was characterized primarily (> 88%) by long fire-return cycles (> 20 years), with < 1% of the area having short fire-return cycles (< 10 years; Supporting information). Consequently, we expect only negligible change in land-cover types across the study area between the time the land-cover data was collected and the start of the study (2013). Still, severe fire disturbance in shrublands and woodlands was possible and would have been expected to produce directional land-cover change (i.e. land cover would transition to earlier successional grasslands). Over a 10-year period, Byerly et al. (2018) reported a mean decrease of only 2% for Great Basin land-cover types that were included in our shrubland and woodland categories. Considering the directional pattern of fire disturbance, if shrubland or woodlands did decrease substantially in the study area during our study, using land-cover data collected prior to our study period (relative to land-cover data from the middle or end of our study period) would have produced conservative estimates (i.e. odds ratios) of the strength of selection for shrublands and woodlands, and avoidance of grasslands.

Fires alter land cover and can influence prey availability. In the Great Basin, increased fire frequency has resulted in the loss of shrublands and increase in invasive grasslands (Pellant et al. 2004). Subadult selection for areas with long fire-return cycles aligns with selection for prey-rich shrubland and woodland habitats. We hypothesize that subadult selection for areas with short fire-return cycles in winter (which was avoided in summer) could be related to selection for areas near roads and transmission lines during winter. Areas within a 15-km radius of a road or transmission line were 4.6× more likely to have a short fire-return interval than areas that were further away, a pattern which may be related to the distribution of roads and transmission lines relative to fire-prone cheatgrass grasslands, increased human activity and human-caused fires in areas closer to roads, or both.

Securing food is a substantial challenge for golden eagles, especially hatch-year birds that lack hunting experience and may die of starvation (U.S. Fish and Wildlife Service 2016). In Scotland, winter diet of golden eagles was dominated by carrion, resulting from winter-killed ungulates (Watson et al. 1992). Carrion is an important source of food during winter when live prey is scarce (Marr and Knight 1983, Halley and Gjershaug 1998, Bedrosian et al. 2017) and subadults will visit carrion sites more frequently than adults (Halley and Gjershaug 1998, Watson 2010). Anecdotal observations suggested that golden eagles in the Great Basin may also rely heavily on carrion from road- and winter-killed ungulates. In the Great Basin, many roads traverse remote areas and have high speed limits, conditions that may increase the frequency of road-killed ungulates (Gunther et al. 1998). Our results suggested that in winter, subadults used areas closer to roads more frequently, and these patterns may be related to selection for areas that provided scavenging opportunities. In contrast, subadults selected for areas further from roads in summer, but this relationship was not as strong. Halley and Gjershaug (1998) found that golden eagles did not scavenge carcasses in summer, perhaps due to increased bacterial contamination and lower nutritional quality of carcasses, higher prey availability, lower energetic demands or a combination of factors.

Golden eagles used transmission lines more during winter than other seasons (Craig and Craig 1984, Slater and Smith 2010). Slater and Smith (2010) documented a surge in golden eagle activity along transmission lines in winter. Similarly, our results suggested that in winter, subadults selected for areas closer to transmission lines, which may have been related to winter communal roosting opportunities with thermoregulatory benefits (Craig and Craig 1984) or animals cueing off one another to locate carrion when resources were scarce.

Our goal was to test hypotheses related to seasonal variation in selection by subadults, not to develop a predictive model. Logistic regression-based models of space use can be useful for testing hypotheses about a priori predictors and interpreting individual regression coefficients, and still have poor predictive capabilities. Although the validation procedures suggested the summer and winter models performed well, we caution against using these models for predictive purposes. Model validation using a subset of data withheld from the sampled data (as we have done, and as is common in resource selection studies when independent data is not available) is fraught with issues and often appear to predict well, even when they have little (or no) predictive power (Copas 1983, Beutal et al. 1999). We restricted our validation to the Military Operational Area around Dugway due to computational limitations, and because managers in this region were interested in visualizing the spatial (predicted) distribution subadults in this area during the period of study.

Patterns of selection suggest that continued loss of shrublands due to increased spread of invasive grasslands and fire frequency (Pellant et al. 2004) may negatively influence subadults. Similarly, winter space use by subadults, when their spatial patterns are more aggregated, emphasize the importance of maintaining open woodland habitats. Our results provide complementary data to previous studies, identifying patterns of selection for subadults that are comparable, but not identical to patterns of selection by adults.

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Author contributions

Kathy M. Hixson: Data curation (equal); Formal analysis (equal); Methodology (equal); Writing – original draft (equal); Writing – review and editing (equal). **Steven J. Slater**: Conceptualization (equal); Funding acquisition (equal); Investigation (equal); Methodology (equal); Project administration (equal); Resources (equal); Writing – original draft (supporting); Writing – review and editing (supporting). **Robert N. Knight**: Conceptualization (equal); Data curation (equal); Project administration (equal); Resources (equal); Writing – original draft (supporting); Writing – review and editing (supporting). **Robert C. Lonsinger**: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Funding acquisition (equal); Investigation (equal); Methodology (equal); Project administration (equal); Writing – original draft (equal); Writing – review and editing (equal).

Data availability statement

Data are available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.xpnvx0kgm> (Hixson et al. 2021).

Supporting information

The supporting information associated with this article is available from the online version.

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