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SPACE USE AND HABITAT SELECTION BY ADULT MIGRANT GOLDEN EAGLES WINTERING IN THE WESTERN UNITED STATES

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Abstract.—Recently, there has been an increase in concern for Golden Eagle populations in the western United States, stemming from a marked decrease in the number of migrants and an increase in future threats from a variety of factors including, but not limited to, energy development. Part of an effective conservation strategy for Golden Eagles involves understanding basic requirements of the eagles during both the breeding and nonbreeding seasons. We used PTT and GPS/PTT transmitter data from 14 adult, migratory Golden Eagles captured near the Rocky Mountain Front in Montana to determine the location and size of winter ranges and habitat use and selection within chosen winter ranges. We found large variability in location and size of winter ranges in the western United States. Eagles showed high fidelity to core wintering areas but plasticity in annual range sizes. Adult, migrant Golden Eagles used habitat types associated with perches and primary prey species. Golden Eagles chose areas within winter ranges that were close to prey habitat, within conifer forests and riparian areas, in relatively low elevations, and in areas conducive to orographic uplift. Golden Eagles appeared to avoid urban areas, grassland, agriculture, and non-sagebrush-steppe habitat types. Our results suggest that an effective conservation strategy for migrant Golden Eagles wintering in the western United States should include a large geographic area with heterogeneous habitat allowing for adequate hunting perches and prey habitat, with little urban development or anthropogenic habitat conversion.

Key Words: *Golden Eagle*; Aquila chrysaetos; *habitat selection*; *home range*; *satellite telemetry*; *winter range.*

USO DEL ESPACIO Y SELECCIÓN DE HÁBITAT POR ADULTOS MIGRATORIOS DE *AQUILA CHRYSAETOS* QUE INVERNAN EN EL OESTE DE LOS ESTADOS UNIDOS

Resumen.—Recientemente ha aumentado el interés por las poblaciones de *Aquila chrysaetos* en el oeste de los Estados Unidos. Dicho interés proviene de una marcada disminución en el número de migrantes y en un aumento en las amenazas a futuro derivadas de una variedad de factores, que incluyen el desarrollo energético, pero que no están limitados por éste. Parte de una estrategia de conservación efectiva para *A. chrysaetos* incluye el entendimiento de los requerimientos básicos de las águilas durante las épocas reproductiva y no reproductiva. Utilizamos datos recogidos mediante transmisores PTT y GPS/PTT de 14 individuos adultos migrantes de *A. chrysaetos* capturados cerca del Rocky Mountain Front en Montana para determinar la localización y el tamaño de las áreas de invernada y el uso y selección de hábitat dentro de las áreas de invernada escogidas. Encontramos una amplia variabilidad en la localización y tamaño de las áreas de invernada en el oeste de los Estados Unidos. Las águilas evidenciaron una elevada fidelidad a las áreas de invernada núcleo, pero una mayor plasticidad en los tamaños de las áreas de distribución anuales. Los individuos adultos migrantes de *A. chrysaetos* utilizaron tipos de hábitat asociados con los posaderos y las

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principales especies de presa. *A. chrysaetos* eligió zonas dentro de las áreas de invernada que estaban cerca del hábitat de sus presas, dentro de bosques de coníferas y áreas ribereñas, en elevaciones relativamente bajas y en áreas propicias para ganar altura gracias al empuje orográfico. Aparentemente, la especie evitó áreas urbanas, pastizales, tierras agrícolas y tipos de hábitat distintos a la estepa de *Artemisa.* Nuestros resultados sugieren que una estrategia efectiva de conservación para individuos migrantes de *A. chrysaetos* que invernan en el oeste de los Estados Unidos debe incluir una amplia área geográfica con hábitats heterogéneos que permitan la existencia de posaderos para la caza y hábitats para las presas adecuados, con poco desarrollo urbanístico o transformaciones de hábitat de origen antrópico.

[Traducción del equipo editorial]

There has been recent concern and debate about the status of some Golden Eagle (*Aquila chrysaetos*) populations in the western United States. There has been evidence of declining migration counts (e.g., Hoffman and Smith 2003, Smith et al. 2008, but see McCaffery and McIntyre 2005) and breeding territory occupancy and productivity rates appear to be declining in some areas (Kochert and Steenhof 2002, Nielson et al. 2014), while range-wide population trends appear to be stable (Millsap et al. 2013). The Golden Eagle in western North America is considered a partial migrant and productivity is often dependent on cyclical prey populations (Hoffman and Smith 2003, Watson 2010, McIntyre and Schmidt 2012), making inferences about the population status of Golden Eagles difficult. Golden Eagles that breed in the northern latitudes of Canada and Alaska annually migrate south to winter ranges, whereas eagles that breed in the continental United States (hereafter referred to as the western United States) are considered nonmigratory, typically remaining near their breeding territory year-round (Marzluff et al. 1997, Kochert and Steenhof 2002, McIntyre et al. 2008). There are a host of reasons for apparent population trends, including habitat loss, declining prey base, increased mortalities, and the interaction of these factors. Alternatively, declines in numbers of migrating eagles could result from changing migration strategies toward more sedentary patterns resulting from large-scale changes in climate or prey availability patterns (Newton 2008).

There are likely different selective pressures operating on the resident versus migratory populations of eagles. Resident, breeding eagles typically occupy territories year-round (Marzluff et al. 1997, Watson et al. 2014) and do not encounter the increased risk of mortality typically associated with migration (Newton 2008). Migrants encounter novel, high-risk anthropogenic hazards at a greater rate while on migration than eagles with knowledge of their territories. Migrants also must find winter ranges among territorial residents, and factors shaping their habitat selection may differ from those of year-round residents. With the increasing anthropogenic conversion of landscapes and associated human presence in the western United States, it is important to understand the habitat and space use of migrants to maintain adequate wintering habitat in the future.

There remain several important and currently undocumented ecological aspects related to adult, migratory Golden Eagles in North America. These include important migratory pathways, overwintering areas, space-use, and habitat requirements during the nonbreeding season. Gathering data concerning these aspects of eagle biology has been historically difficult due to extreme distances travelled by migrating eagles, low densities of eagles, and difficulty in capturing known long-distance migrants. However, the increasing availability of satellite tracking devices, long-term migratory banding studies, and easily accessible moderate-resolution vegetation data has made it possible to assess movements, survival, and habitat selection of migratory Golden Eagles year-round and across the continent.

Our goal was to improve the understanding of spatial and habitat requirements of migrant Golden Eagles that overwinter in the western United States to help develop management and conservation strategies. Specifically, we investigated how migrant, adult Golden Eagles use the landscape during the nonbreeding season. Our objectives were to determine (1) where Golden Eagles that migrate along the Rocky Mountains spend the nonbreeding season, (2) the size of the nonbreeding season territories, (3) the habitat types used and selected by Golden Eagles in wintering areas and (4) whether migratory Golden Eagles show fidelity to wintering areas.

METHODS

Trapping and Tracking. We captured adult Golden Eagles while on fall migration using bow-nets

(Hull and Bloom 2001) at the Nora Ridge raptor migration and banding station, 22 km east of Lincoln, MT (47°1.2′N, 112°24.2′W). Wintering eagles were captured in the northern Bitterroot Valley of western Montana (46°41.8′N, 114°2.3′W) and the Shields River Valley of central Montana (45°48.1′N, 110°29.6′W) using road-killed carrion and net launchers (Trapping Innovations, LLC, Kelly, Wyoming, U.S.A.). Eagles were fitted with battery-powered Argos Platform Terminal Transmitters (PTT) or solar-powered GPS/PTTs using a cross-chest Teflon ribbon harness (Bedrosian and Craighead 2007). Argos PTT models used were manufactured by Northstar Science and Technology, LLC, (80 g; King George, Virginia, U.S.A.) and Wildlife Computers (65 g; Redmond, Washington, U.S.A.) and GPS/PTTs (70 g or 30 g) were manufactured by Microwave Telemetry, Inc. (Columbia, Maryland, U.S.A.). Morphometric measurements were taken to aid in sex identification (Bortolotti 1984, Edwards et al. 1988).

We deployed six Argos PTTs from 2007–2010. Argos PTTs were configured with different duty cycles depending on the manufacturer and the year of deployment. Each unit transmitted to the Argos satellite system (CLS America, Lanham, Maryland, U.S.A.) for 4 hr every day ($n = 3$) or every other day ($n = 3$) during the winter. In 2011, we deployed seven GPS/PTTs, programmed to gather hourly GPS locations during 0700–2000 H, MDT with an additional location at 00:00 H. Data were post-processed using the manufacturer's software which allowed for PTT location class filtering by individuals and dates. Estimated errors associated with Argos/Doppler locations were calculated by Argos during the satellite pass and are classified, ranked highest to lowest, as location classes (LC) 3, 2, 1, 0, A, B, and Z. Estimated errors associated with each LC are <250 m, 250–500 m, 500–1500 m, >1500 m for LC 3–0, respectively (CLS America 2014). Argos PTT data were reduced to location classes 0–3, plotted in Arc 10 (ESRI, Redlands, California, U.S.A.) for visual inspection of outliers and data analysis. We also deployed one Global Systems for Mobil Communication network (GSM) GPS transmitter that uploaded locations via the cell phone network (55 g, Vektortek, LLC, Reston, Virginia, U.S.A.).

Analysis. We defined wintering areas of Golden Eagles based on Mandernack et al. (2012); concentrated local movement preceded by autumn migration and before spring migration. Localized movements were visually estimated from the locations after plotting them in Arc10. Each eagle's home-range size within its wintering area was measured post-hoc using 50% and 95% minimum convex polygon (MCP) estimates for all birds (Hayne 1949). We also measured home-range size estimates using the kernel density estimator (KDE; Worton 1989; PLUGIN bandwidth) at the 50% and 95% levels. We measured home-range sizes using both estimators for comparative purposes. Minimum convex polygon home ranges were estimated using the adehabitatHR package in program R (R Core Development Team 2013) and KDE home-range estimates were done using Geospatial Modeling Environment (Beyer 2012). We chose 50% home ranges to represent core home ranges and 95% home ranges to represent primary winter home ranges. Argos PTTs datasets were reduced to one location/day of the highest quality possible ≥0. Class 0 locations may overestimate home-range sizes due to errors associated with the location estimate but were included in the dataset because these locations often were the highest quality available for a given day. Furthermore, excluding them would have resulted in inadequate sample sizes. We estimated wintering area fidelity by calculating the percentage of overlap between 50% and 95% MCPs for eagles with data for at least two consecutive winters.

To assess habitat use and selection, we only used locations from GPS/PTT transmitters due to error associated with Argos PTT transmitters and the resolution of our land-cover layer. Unlike our analysis of home-range estimates, we used all locations from all years, including those from birds captured during the winter. We assumed habitat associations were not influenced by length of tracking on winter range. Land-cover characteristics were extracted from the 2010 30-m resolution Gap Analysis land-cover layer (U.S.G.S. 2012) in ArcGIS. Initially, there were 93 land-cover types, but we collapsed those into 17 land-cover types to increase accuracy of the remote sensing data because more general categories result in a greater number of correct classifications (e.g., classifying coniferous forest is more likely to be accurate than classifying forest by species composition). The final land-cover categories included wetland, sagebrush (*Artemesia* spp.) steppe, riparian, Pinyon (*Pinus edulis*)-Juniper (*Juniperus* spp.), non-sagebrush shrub, logged, grassland, urban, deciduous forest, coniferous forest, mixed coniferous/deciduous, alpine, cultivated agriculture, pasture and hay, burned, coastal, desert/dune, and water. The land-cover types were defined when the layer was created (2011); therefore, changes may have occurred between layer creation and our data analysis and may not be represented. We estimated habitat use for all birds with GPS transmitters by assessing the percentage of all used points in each habitat type.

We used a resource selection function framework to assess the influence of our selected covariates on resource selection by wintering Golden Eagles (Manly et al. 2002). For this analysis, we excluded data from the one GPS/GSM transmitter because it provided only 72 locations for the entire nonbreeding season. We excluded GPS/PTT data that were collected during pre-dawn, post-dusk and at 00:00 H to avoid roosting locations in our analysis because we were focused on determining diurnal habitat selection, not roost site selection. We projected 1000 points randomly within each 95% MCP home range for each bird to represent available locations. We then extracted covariate values to each used and available location. Covariates included distance to shrubs, which included sagebrush, non-sagebrush shrubs and pinyon-juniper, distance to grassland, a measure of topographic ruggedness, categorical land-cover covariates, elevation (both in the linear and quadratic form), and a categorical measure of aspect which included north, south, east, and west. We included the pinyon-juniper habitat type in our distance to shrub covariate because it is most likely similar to shrub habitat for Golden Eagles on their wintering range in terms of its importance for prey acquisition. The distance to shrub and distance to grassland covariates were created by collapsing all shrub and grassland layers and then determining the Euclidean distance from each point to the created layer. The primary prey species of Golden Eagles in the Rocky Mountains typically use areas dominated by shrubs and grasslands, which is why we tested the importance of Golden Eagle selection in proximity to those habitat types (McGahan 1968, Marzluff et al. 1997, Steenhof et al. 1997, Kochert et al. 1999, Crandall 2013). We determined distance to shrubs and grasslands was appropriate in addition to the categorical land-cover type, because the exact location of the bird may have represented a perch and not necessarily the area the bird was hunting. Using these covariates, we assumed all shrub and grassland habitat types were potentially prey habitat. Watson et al. (2014) found eagle presence was positively correlated to the distance to ridges for perching and soaring. Therefore, we predicted that habitat selection would be negatively associated with distance to shrub or grassland cover types because the eagle would be more likely to choose perches close to prey. We used the terrain ruggedness index (TRI) as our measure of topographic variation (Riley et al. 1999). We created a TRI raster layer based on a 30-m resolution digital elevation model raster layer. We included categorical land-cover types that previous studies indicated were most likely to influence probability of use by wintering eagles; these included coniferous, non-sagebrush shrub, grassland, sagebrush steppe, urban, and pinyon-juniper (Marzluff et al. 1997, Pedrini and Sergio 2001, Crandall 2013). We used elevation to test whether eagles were selecting wintering areas based on elevation. We used the quadratic form of elevation to allow for the possibility of a nonlinear relationship between Golden Eagle selection and elevation, and included the linear form of elevation in all models that contained elevation in the quadratic form. We predicted Golden Eagles would select low- to mid-elevation areas, which are likely more valuable for hunting because high-elevation areas are likely covered in deep snow and low-elevation areas may not be acceptable Golden Eagle habitat. We also included categorical measure of aspect (north, south, east, and west) in our resource selection analysis. We predicted that if Golden Eagles were selecting for certain aspects, these aspects would be associated with prevailing wind direction to assist with orographic uplift, or simply the uplift generated from wind hitting a slope. Golden Eagles use orographic uplift for migration, hunting, and soaring (Watson 2010, Bohrer et al. 2012, Katzner et al. 2012). All covariates were screened prior to inclusion in the modeling process using Pearson's correlation coefficient with $|r| < 0.6$ defined as the threshold (Hosmer and Lemeshow 2000).

We used generalized linear mixed models to test the strength of our chosen covariates on the probability of use, using a random effect of individual to account for differences in sample sizes among tracked eagles (Gillies et al. 2006). The response variable in our models was binary, with 0 representing an available location and 1 representing a used location. We used a manual backwards-stepwise model selection process described by Hosmer and Lemeshow (2000) to choose the best model. As Hosmer and Lemeshow (2000) recommend, we first screened all covariates prior to inclusion in the modeling process in a univariate logistic regression model to assess the importance of each covariate independently; they recommend only retaining variables to be used in multiple regression models when the variables' *P*-value is <0.25 (Hosmer and Lemeshow 2000). After we had determined the variables that were significant in a univariate model, we built a full model that included all covariates, followed by reduced models until we had a model where all terms were significant at the traditional level ($P \leq 0.05$; Hosmer and Lemeshow 2000). To test the predictive ability of our top model, we conducted *k*-fold ($k = 5$) internal cross-validation (Boyce et al. 2002). All analyses were done using R statistical software (R Development Core Team 2013).

RESULTS

We deployed transmitters on a total of 14 adult, migrant Golden Eagles during 2007–2012 (Table 1). We deployed six Argos PTTs on eagles from 2007–2010 (Table 1), with an average of 76 locations/bird/year after filtering for accuracy (SD = 45). From 2011–2012, we fit eagles with GPS/PTTs (Table 1), with 1061 average locations/eagle/winter (SD = 561). We also fit one eagle with a GPS/GSM transmitter in 2012 that gathered a total of 669 locations.

Our marked Golden Eagles wintered in areas across the western United States, from west-central Montana to Texas (Fig. 1). We gathered data from 13 eagles for at least one entire winter season and four eagles (two Argos PTT and two GPS/PTT) for two winter seasons (Table 1). Argos PTTs stopped transmitting before spring migration and two eagles with GPS/PTTs were captured after they had settled on their wintering grounds; information from these four eagles was not used in our analysis (Table 1). One bird either died or its transmitter fell off during late winter. We assumed we had accurately documented its wintering area and included the data in our analysis because the event happened shortly before the typical onset of spring migration.

We found large variation within and between migratory adult Golden Eagles in winter home-range size and duration of winter range use (Table 1). Individual eagles exhibited high fidelity to their wintering areas as evidenced by the overlap in home ranges among years (Table 2) but were inconsistent in range sizes between years (Fig. 1, Table 1).

Habitat use by Golden Eagles with GPS/PTT transmitters also varied among individuals. The primary habitat type used by Golden Eagles was coniferous forest, followed by pinyon-juniper and then grassland (Fig. 2). The top model describing habitat selection by wintering Golden Eagles included the covariates distance to grassland, the linear elevation term, TRI, east and south aspects, and eight categorical land-cover types. Based on our best model, Golden Eagles selected for rugged areas, lower elevations, south and east aspects, coniferous forests, pinyon-juniper, and riparian areas (Table 3). Golden Eagles avoided urban areas, non-sagebrush shrub, grasslands, cultivated agriculture, and pasture (Table 3). *K*-fold internal cross validation showed that our top model was effective at predicting selection by Golden Eagles with average Spearman's ρ equal to 0.71 ($P = 0.03$).

DISCUSSION

We found high variation in geographic location and space use of Golden Eagle wintering in the western United States. Low migratory connectivity (i.e., dispersed wintering locales) is not uncommon in generalist species (Newton 2008). McIntyre et al. (2008) found similar dispersion of overwintering areas for migrant juvenile Golden Eagles originating from the same breeding area in Denali National Park. Low connectivity and large variation in wintering home ranges, however, has pertinent management implications. Many eagle hazard assessments for new developments (e.g., wind farms) are based on surveys to estimate concentrations of wintering birds (assessment methodology based on U.S. Fish and Wildlife Service 2012). Our data, like those of Watson et al. (2014), indicate eagles may alter the size of winter ranges annually. Although migrant eagles show fidelity to core wintering areas, in some years they may respond to variation in local prey availability (Steenhof et al. 1997, McIntyre and Adams 1999) and range over broader areas. Therefore, single-year assessments of eagle distribution and abundance for energy development projects may not capture such variability.

No comparisons exist for winter-range size and habitat use among juvenile, subadult, and adult Golden Eagles, but information from other raptors typically indicates that adults generally have more constricted home ranges than their younger conspecifics (e.g., owls; Belthoff et al. 1993). This is likely a result of adults having previously established winter ranges and juveniles/subadults exploring larger areas to find adequate space and prey resources. Consequently, adults typically exhibit high fidelity to their wintering areas, as documented for Bald Eagles (*Haliaeetus leucocephalus*; Harmata and Stahlecker 1993, McClelland et al. 1994, Mandernack et al. 2012). When returning to core wintering areas, the eagles

Table 1. Summary table of home-range size and other information on tracked birds. Birds without durations and home-range estimates were tracked for partial seasons. MCP is minimum convex polygon and KDE is kernel density estimator.

ID	Sex	Transmitter Type	Duty Cycle	Capture Date	Capture Location	Begin Winter Range	End Winter Range
542[a]	Male	PTT	1 loc/d	15 Oct 2007	Nora Ridge	6 Nov 2007	21 Dec 2007
869	Female	PTT	1 loc/d	24 Oct 2007	Nora Ridge	8 Nov 2007	14 Mar 2008
869[a]						4 Nov 2008	22 Dec 2008
877	Male	PTT	1 loc/2 d	29 Sep 2008	Nora Ridge	15 Nov 2008	4 Feb 2009
878	Male	PTT	1 loc/2 d	29 Sep 2008	Nora Ridge	8 Oct 2008	5 Apr 2009
305	Female	PTT	1 loc/d	1 Oct 2008	Nora Ridge	6 Nov 2008	11 Mar 2009
305						4 Nov 2009	7 Feb 2010
321	Female	PTT	1 loc/3 d	21 Oct 2010	Nora Ridge	14 Nov 2010	21 Feb 2011
321						29 Nov 2011	28 Jan 2012
852	Male	GPS/PTT	15 locs/d	3 Oct 2011	Nora Ridge	28 Nov 2011	9 Mar 2012
852[b]						21 Oct 2012	12 Mar 2013
856	Male	GPS/PTT	15 locs/d	10 Oct 2011	Nora Ridge	15 Oct 2011	3 Jan 2012
858	Male	GPS/PTT	15 locs/d	10 Oct 2011	Nora Ridge	20 Nov 2011	22 Feb 2012
858						24 Oct 2012	27 Feb 2013
867	Male	GPS/PTT	15 locs/d	20 Oct 2011	Nora Ridge	16 Nov 2011	11 Mar 2012
870[c]	Male	GPS/PTT	15 locs/d	9 Dec 2011	Bitterroot Valley	10 Dec 2011	18 Feb 2012
870						6 Nov 2012	16 Mar 2013
025	Female	GPS/PTT	15 locs/d	22 Feb 2012	Shields Valley	2 Oct 2012	31 Mar 2013
357[c]	Female	GPS/PTT	15 locs/d	12 Dec 2011	Bitterroot Valley	13 Dec 2011	23 Feb 2012
357						4 Nov 2012	21 Feb 2013
363	Male	GPS/PTT	1-5 locs/d	13 Oct 2012	Nora Ridge	6 Dec 2012	21 Feb 2013
Average							
SD							

need to show plasticity to adapt to local food and conditions and potential competition from conspecifics and other species (Mandernack et al. 2012). Our data support this supposition, in that the six eagles we tracked for consecutive years returned to the same core areas, but altered their home-range sizes (Table 1, Fig. 1), likely as a result of local food availability and distribution.

Breeding Golden Eagles also similarly alter their winter ranges to account for changes in food resources (Watson et al. 2014), but the winter range sizes of migratory eagles measured in this study were drastically larger than winter home ranges of nonmigratory eagles (e.g., Marzluff et al. 1997, Haworth et al. 2006, Watson et al. 2014). This difference is not novel in migratory raptors, but it creates difficulty for managers trying to identify and protect important wintering habitat. Conservation and management of breeding habitats may effectively protect local populations, but may fall short on protecting overwintering eagles due to differences in habitat selection.

Another factor influencing space use by wintering birds is the presence of locally breeding conspecifics that may be defending resources within their territories. Resident Golden Eagles typically occupy their territories year-round, but defense lessens during the winter months, especially outside of the core home range directly surrounding the nest site (R. Domenech unpubl. data). However, in many portions of the western United States, breeding commences in January, and wintering eagles need to navigate between territorial residents or find areas with adequate prey that are not occupied by or defended by resident eagles.

Our habitat selection results indicate that the wintering adult Golden Eagles in this study avoided urban areas, grasslands, non-sagebrush shrub habitats, cultivated agriculture, and pasture or hay fields (Table 3). Wintering Golden Eagles preferred coniferous forests, pinyon-juniper habitats, riparian areas, rugged terrain, lower elevations, and east- and south-facing aspects (Table 3). Like Crandall (2013) and Watson et al. (2014), we found terrain ruggedness was an important factor in predicting eagle habitat selection. High ruggedness allows for elevated perches, open viewsheds, and orographic

Table 1. Extended.

Duration (d)	Number of Locations	Location (State)	MCP (km²) 50%	MCP (km²) 95%	KDE (km²) 50%	KDE (km²) 95%
–	46	TX	–	–	–	–
127	131	NM	347.5	1303.0	280.4	1593.2
–	40	NM	–	–	–	–
81	50	TX	55.0	1916.3	219.8	1820.9
179	134	WY	14,881.1	36,143.3	4514.1	26,830.6
125	124	CO/NM	669.5	2715.0	897.4	4102.4
95	96	CO/NM	2312.4	10,610.0	915.2	6037.9
99	44	MT	209.9	814.1	443.8	1728.2
60	22	MT	546.2	942.5	405.8	1682.9
102	1435	CO	2737.0	16,185.0	3180.0	17,827.0
–	1887	CO	5279.3	15,639.7	1128.5	6504.7
80	1179	CO	181.0	2065.0	208.0	1901.0
94	1334	NM	1474.0	9921.0	1331.0	9079.0
126	1636	NM	15,509.6	19,796.1	2284.3	118,864.9
116	1678	NM	1722.0	4972.0	920.0	6257.0
–	723	MT	–	–	–	–
130	824	MT/ID	5273.7	20,717.7	1552.1	9279.4
180	319	MT/WY	27,137.3	46,648.2	5420.5	30,727.9
–	714	MT	–	–	–	–
109	936	MT	1892.5	5104.2	590.0	3262.3
77	72	NM	1007.3	3030.1	1131.2	4755.5
107	639		5222.0	12,693.0	1495.0	48,838.0
31	651		7856.0	13,752.0	1606.0	29,824.0

[a] Individuals that either dropped their transmitter or died early on the winter range; thus, we did not estimate home ranges.
[b] Individual that lost his transmitter toward the end of his time on winter range; thus, we did not estimate total duration on winter range, but we did estimate winter-range sizes.
[c] Individuals captured on their winter ranges; thus, we did not estimate home-range sizes for that year.

updrafts for both general movements and efficient hunting (Watson et al. 2014). Crandall (2013) found that breeding Golden Eagles in south-central Montana preferred rugged areas adjacent to foraging habitats, but were not associated with coniferous land-cover types. Similarly, McGrady et al. (2002) found breeding Golden Eagles in Scotland avoided coniferous forests.

In an effort to understand the significance of our data as compared to previous findings, we further investigated the association between terrain ruggedness and coniferous habitat to assess whether the selection of coniferous habitat was simply due to the occurrence of coniferous habitat in more rugged terrain. We compared terrain ruggedness values across land-cover types and found that ruggedness values were highest in alpine, coniferous, deciduous, burned, and logged habitat types. If selection of coniferous habitat was simply a result of higher terrain ruggedness in coniferous habitat, we would have expected our tracked Golden Eagles to also select the other habitat types with high ruggedness values, which was not the case. Even so, we explored the relationship between terrain ruggedness and coniferous habitat further.

Both variables, terrain ruggedness and coniferous habitat, were significant in univariate models, which was necessary for their inclusion in the full model. To test which variable was more influential in our best model and whether each variable was significant without the inclusion of the other variable, we removed each independently and compared the resulting *P*-value from the variable still included in the model and the Akaike Information Criteria (AIC) values from the reduced models to our best model. We considered the reduced model with the largest discrepancy in AIC value to contain the more influential variable. When we removed coniferous habitat from the full model, terrain ruggedness was still significant in the reduced model and difference in AIC values was

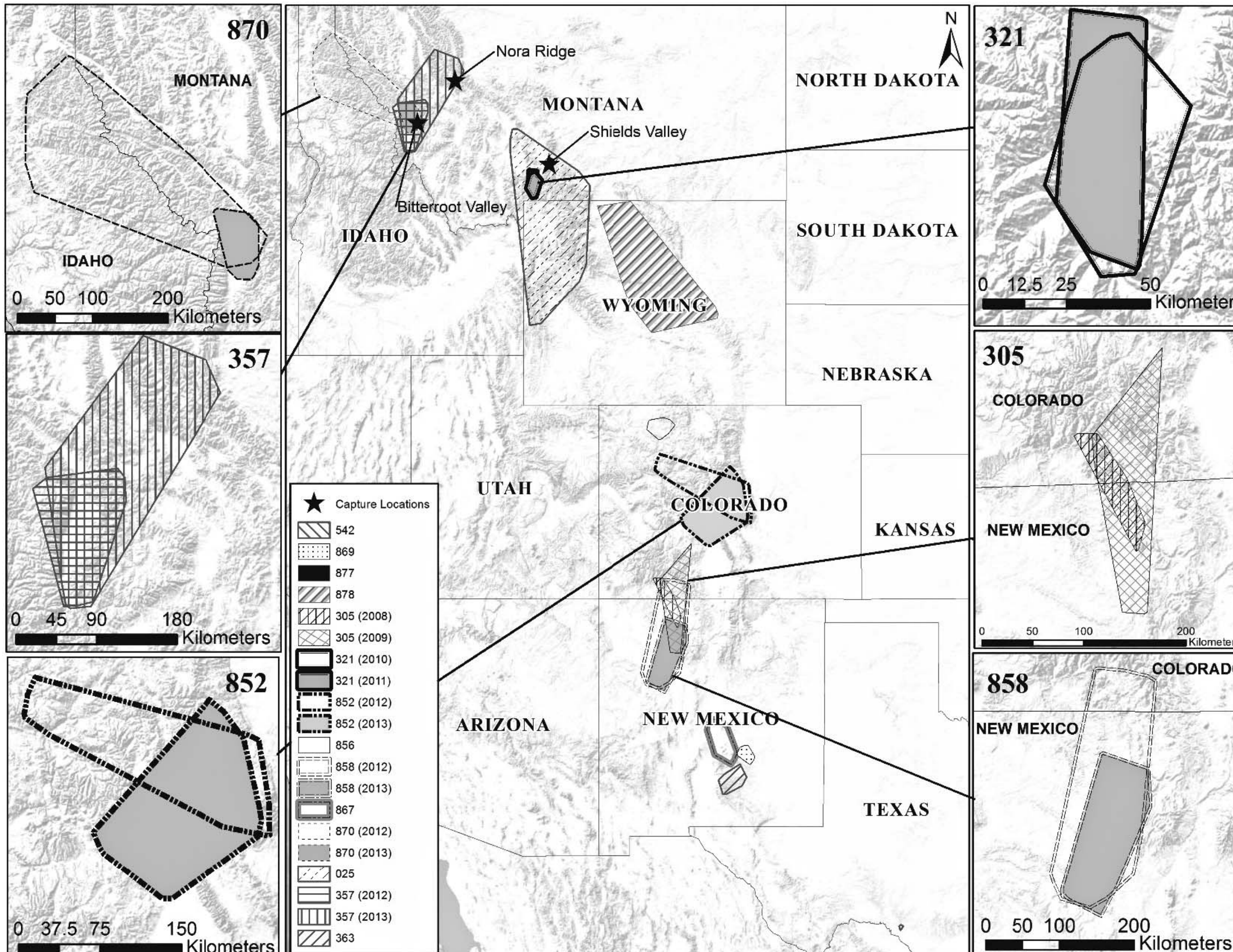

Figure 1. 95% MCP home-range estimates representing winter range for all Golden Eagles tracked for all years. The inset maps show the 95% MCP home-range estimates for the six birds tracked for two consecutive nonbreeding seasons.

Table 2. Territory overlap (%) for birds tracked in consecutive years. Overlap was estimated by percent of MCP from year t +1 that overlapped the MCP from year t.

ID	SEX	TRANSMITTER TYPE	% OVERLAP	
			50% MCP	95% MCP
305	Female	PTT	58.1	85.4
321	Female	PTT	97.4	84.4
852	Male	GPS/PTT	73.5	45.6
858	Male	GPS/PTT	100	95.3
870	Male	GPS/PTT	59.3	82.5
357	Female	GPS/PTT	100	31.3

142 points ($AIC_{reduced}$ = 29,473, AIC_{best} = 29,331). We then removed terrain ruggedness from the best model and found that coniferous habitat was still significant in the reduced model and the difference in AIC values was 831 points ($AIC_{reduced}$ = 30,162, AIC_{best} = 29,331). These comparisons suggest terrain ruggedness was contributing more to the best model; however, both variables remain independently significant without the influence of the other. The independent importance of each variable in the reduced models in addition to the lack of selection for other land-cover types based on the importance of terrain ruggedness in our best model supports the differentiation of selection for coniferous habitat and terrain ruggedness. Because breeding Golden Eagles do not select coniferous habitat, our results suggest an important role of coniferous habitats for wintering eagles. The selection of coniferous habitat by our transmittered eagles may be indicative of niche partitioning among adult migrants and breeding eagles, differential resource allocation, thermal regulation, or some combination of factors. More detailed studies are needed to determine if this relationship holds in other regions and to determine the driving force behind conifer selection in wintering Golden Eagles.

Table 3. Coefficient estimates from top model describing habitat selection of adult Golden Eagles on winter range in western United States. All habitat types were categorical and we used alpine cover type as the reference category. Our covariate for aspect, which included north, south, east, and west, was also categorical with north as the reference category. TRI is terrain ruggedness index. The negative coefficient estimate representing distance to prey habitat indicates selection for this covariate (i.e., probability of use decreases as distance from prey habitat increases).

MODEL COVARIATE	β	SE	*P*
Intercept	−0.32	0.34	0.3428
Distance to grassland	0.14	0.02	<0.0001
Elevation	−0.48	0.03	<0.0001
TRI	0.50	0.02	<0.0001
East aspect	0.42	0.03	<0.0001
South aspect	0.12	0.04	0.0009
Coniferous	0.57	0.05	<0.0001
Urban	−1.96	0.40	<0.0001
Non-sagebrush shrub	−0.59	0.07	<0.0001
Pinyon-juniper	0.15	0.07	0.0205
Grassland	−0.18	0.06	0.0018
Riparian	1.17	0.10	<0.0001
Cultivated agriculture	−0.47	0.10	<0.0001
Pasture	−0.60	0.18	0.0010

As in our study, adult resident Golden Eagles in Idaho avoided grassland habitats while preferring sagebrush during the nonbreeding season (Marzluff et al. 1997). As grass cover dissipates over the autumn, hares move from areas of high grass cover into areas of higher brush cover for the winter (Knick and Dyer 1997). Movement of prey into sagebrush and native shrub habitats likely alters Golden Eagle foraging behaviors to account for their preference for these habitats during the winter months. Habitat heterogeneity surrounding these foraging areas is important for eagles, so they can adequately hunt using either perches or updrafts in areas with high terrain ruggedness. Hence, Golden Eagles would likely greatly benefit from conservation and management of local prey species in areas of high terrain ruggedness.

In addition to live prey, Golden Eagles also rely on carrion as a food source in the winter (Watson et al. 2014), making alternative habitats and ranging behaviors important during the winter months. Reliance on carrion likely explains the use of lower elevation and riparian habitats by wintering eagles, as large mammals typically move to these habitats in the winter to access better forage. Use of coniferous forests may also be linked to the use of carrion in some areas, particularly in the late fall months when increased numbers of gut piles from hunting may become available.

Conservation plans and management strategies for Golden Eagle populations in the United States should encompass habitat needs for both residents and overwintering eagles. It is essential to preserve and restore foraging habitat for both local and migrant eagles and efforts should be directed toward such habitats in heterogeneous landscapes with high terrain ruggedness and low levels of urban development or cultivation. Specifically, relatively low elevation sagebrush steppe, native shrubland, riparian areas, and even coniferous habitats in rugged

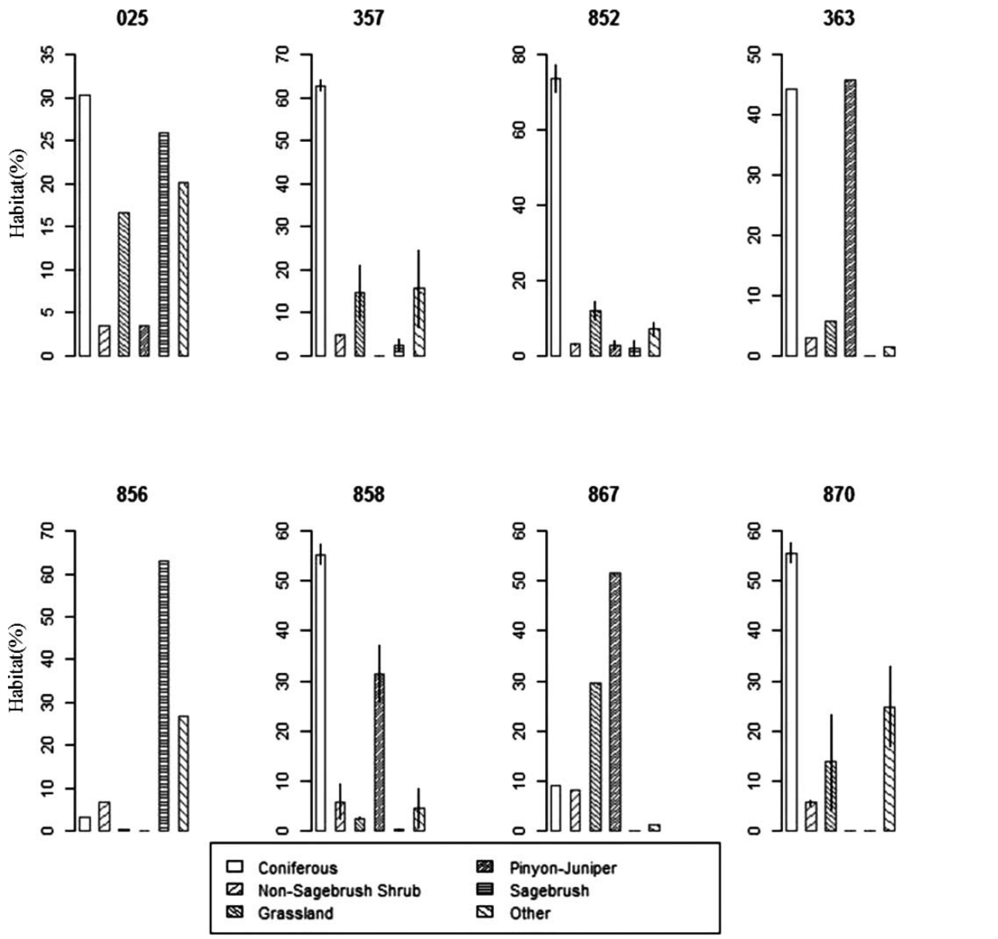

Figure 2. Major habitat types (%) used by each individual tracked with a GPS/PTT transmitter. For eagles tracked two consecutive years, the percent of each habitat type used is the mean with error bars representing the standard deviation. Individual ID numbers listed above graphs.

landscapes should be identified as important wintering areas.

Plasticity in winter home-range sizes is both a challenge to and benefit for conservation planners. Although adult Golden Eagles tend to return to core areas, they also winter over large areas and alter space use annually. This is likely in response to changes in prey availability and distribution. Low migratory connectivity is a benefit to Golden Eagle migratory populations, as local perturbations to winter habitat can likely be overcome by shifting wintering areas to avoid the disturbance or negative change. However, the threshold of cumulative habitat loss that negatively affects wintering Golden Eagles remains unknown and occurs at different levels for different individuals because of the difference in home-range sizes. Our results suggest that wintering eagles may occupy habitats avoided by resident breeding Golden Eagles and reduction in those habitats may significantly increase intraspecific competition and reduce overwinter survival of migrants.

Watson et al. (2014) recommend a minimum of two complete years of monitoring for site-specific investigations to understand potential conflicts between eagles and development (e.g., wind power). Our data corroborate that recommendation because of the changes in winter home-range sizes and suggest that longer durations may be necessary to capture the variability. We suggest that more detailed studies of habitat and space use among wintering Golden Eagles of all age classes utilizing GPS telemetry and interactions among adult wintering migrants and residents is warranted, given the limitation of our sample sizes within the large geographic distribution of wintering Golden Eagles. We also urge caution in utilizing habitat use and utilization distribution models built from data collected from resident eagles to delineate important areas for migrant Golden Eagles due to differences in habitat preference.

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