Research Article

Home Range and Resource Selection by GPS-Monitored Adult Golden Eagles in the Columbia Plateau Ecoregion: Implications for Wind Power Development

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ABSTRACT Recent national interest in golden eagle (*Aquila chrysaetos*) conservation and wind energy development prompted us to investigate golden eagle home range and resource use in the Columbia Plateau Ecoregion (CPE) in Washington and Oregon. From 2004 to 2013, we deployed satellite transmitters on adult eagles ($n = 17$) and monitored their movements for up to 7 years. We used the Brownian bridge movement model (BBMM) to estimate range characteristics from global position system (GPS) fixes and flight paths of 10 eagles, and modeled resource selection probability functions (RSPFs). Multi-year home ranges of resident eagles were large (99% volume contour; $\bar{x} = 245.7$ km^2, SD $= 370.2$ km^2) but were one-third the size ($\bar{x} = 82.3$ km^2, SD $= 94.6$ km^2) and contained half as many contours when defined by 95% isopleths. Annual ranges accounted for 66% of multi-year range size. During the breeding season (16 Jan– 15 Aug), eagles occupied ranges that were less fragmented, about half as large, and largely contained within ranges they used outside the breeding season ($\bar{x}$ overlap $= 82.5\%$, SD $= 19.0$). Eagles selected upper slopes, rugged terrain, and ridge tops that appear to reflect underlying influences of prey, deflective wind currents, and proximity to nests. Fix distribution predicted by our resource selection model and that of 4 eagles monitored independently in the CPE were highly correlated ($r_s = 0.992$). Our findings suggest conservative landscape management strategies addressing development in lower-elevation montane and shrub-steppe/ grassland ecosystems can best define golden eagle ranges using exclusive 12.8-km buffers around nests. Less conservative strategies based on 9.6-km buffers must include identification and management of upper slopes, ridge-tops, and areas of varied terrain defined by predictive models or GPS telemetry. For both strategies, high, year-round intensity of eagle flight and perch use within 50% volume contours (average 3.2 km from nests) due to nest centricity may dramatically increase the probability of eagle conflict with wind turbines in core areas as evidenced by eagle turbine strikes that studies have documented within and beyond this zone. © 2014 The Wildlife Society.

Evidence for regional declines in North American golden eagle (*Aquila chrysaetos*) populations (Kochert and Steenhof 2002, Hoffman and Smith 2003, Boal et al. 2008, Millsap et al. 2013) has focused recent national attention on understanding eagle ecology and conservation, particularly with regard to establishing consistent inventory and monitoring protocols (Pagel et al. 2010) and the implications of energy development on populations (Fielding et al. 2006, Johnston 2011, United States Fish and Wildlife Service [USFWS] 2011). Golden eagles have been shown to be susceptible to turbine blade strikes (Hunt 2002, Thelander

and Smallwood 2007, Chamberlain et al. 2006, Noguera et al. 2010, Pagel et al. 2013) and turbine construction has been suggested, but not fully demonstrated, to be a cause of displacement of nesting eagles (Walker et al. 2005, Martínez et al. 2010). Accordingly, the United States Fish and Wildlife Service recommends an adaptive management approach for delineating potential conflict zones between golden eagles and wind turbines by integrating information on eagle range use as it becomes available (USFWS 2011). Information needs specific to resident, adult golden eagles include estimation of home range size, assessment of annual changes in range size, overlap, and eagle fidelity, and determination of habitat features selected by eagles within home ranges. Application of this information to unstudied eagle ranges, such as through predictive modeling, may be useful to inform turbine siting and establish protective

buffers. Temporal range characteristics will help to better identify when regulation of operational turbines can best avoid conflict with eagles, to determine the timing and utility of eagle monitoring in pre-project planning, and to understand the long-term implications of wind project construction on eagle territories in the context of home range dynamics (USFWS 2011).

In the northwest, nesting ecology of the golden eagle has been documented in the shrub-steppe desert of the Snake River Plain, Idaho (Beecham and Kochert 1975, Collopy and Edwards 1989) where black-tailed jackrabbits (*Lepus californicus*) exert a strong influence on home range and resource use (Marzluff et al. 1997). Little has been documented about eagle range use in the Columbia Plateau Ecoregion (CPE; Knight et al. 1982) where wind energy development is increasing (Conley et al. 2010).

The advent of global position system (GPS) satellite telemetry during the past decade, advancement of geographic information systems (GIS) and resource-selection analysis (Millspaugh et al. 2006, Lele and Keim 2006, Lele 2009, Northrup et al. 2013), and the development of home range analytical methods like the Brownian bridge movement model (BBMM; Horne et al. 2007, Walter et al. 2011) have improved our ability to understand and model range use of many raptors, including golden eagles. Transmitters with GPS capability and service-life up to 8 years (J. W. Watson, Washington Department of Fish and Wildlife [WDFW], unpublished data) can provide for long-term monitoring of long-lived species like golden eagles, resulting in a more accurate picture of lifetime home-range use than obtained through short-term studies.

We assessed home range and resource selection of resident, adult golden eagles captured in eastern Washington and Oregon and monitored with GPS telemetry. Our objectives were to 1) describe home range size and fragmentation, annual and seasonal range dynamics, and eagle fidelity to ranges; 2) determine terrain features selected by eagles and evaluate reliability of findings on unstudied eagle ranges; and 3) provide recommendations to reduce the potential for golden eagle collisions with turbines.

STUDY AREA

The Columbia River is one of several major rivers that are important influences on terrain and habitat in the CPE (Washington Wildlife Habitat Connectivity Working Group 2012). Canyon walls along the tributaries and the adjacent foothills provide cliff and tree nest sites for golden eagles. Most eagle nests are located below 1,000 m elevation. Nesting ranges included treeless to sparsely timbered hillsides, dominated by Douglas fir (*Pseudotsuga menziesii*) and ponderosa pine (*Pinus ponderosa*), with a shrub overstory of sagebrush (*Artemesia tridentata and A. tripartita*), and grass understory of bluebunch wheatgrass (*Agropyron spicatum*). Concurrent diet studies in the Columbia Basin suggest golden eagle prey is predominated by yellow-bellied marmots (*Marmota flaviventris*), carrion and young of deer (*Odocoileus* spp.) and coyotes (*Canis latrans*), and upland game birds (J. W. Watson, unpublished data).

Human activity commonly occurring near or within golden eagle home ranges in the Columbia Basin includes cattle ranching, farming, and recreation, especially rock climbing and hiking in late spring and game bird and deer hunting in the fall. Wind energy development has increased in the past decade on golden eagle home ranges in the CPE, particularly in south-central Washington and north-central Oregon (Conley et al. 2010).

METHODS

We selected 17 territories in the CPE where we captured adult (4+ yr) golden eagles. Most territories were in Washington where 60–80 territories have been used regularly by golden eagles in recent years (WDFW, Wildlife Resource Data System). Final territory selection was based on trespass permission and accessibility. Beginning in 2004, we captured eagles in January through the early breeding season using remote-control bow nets baited with deer carcasses (Jackman et al. 1994). We emphasized capturing males to obtain better information on ranging behavior during the breeding season because they tend to spend less time in nest maintenance activities (Collopy 1984), but we also telemetered females. In 2004, we fitted eagles with 100-g ARGOS transmitters (Microwave Telemetry, Inc., Columbia, MD) that provided non-GPS fixes calculated from low-orbiting satellites and the Doppler-effect. After 2005, we fitted all eagles with 70-g solar transmitters with GPS capability and data downloading via either ARGOS satellite or the digital cellular network. The former transmitters were pre-programmed to collect hourly GPS fixes for 21 hours (spring and summer) or 17 hours (fall and winter) daily; the latter transmitters collected GPS fixes at a 1-minute interval when solar charging was above a minimal threshold. Transmitters with GPS capability had built-in speed and activity sensors. To evaluate eagle residency, we included locations of all telemetered eagles but used only GPS data for analyses of home range and resource use. The manufacturer specified error for GPS fixes was ±22 m compared with ±150 m for the most accurate non-GPS fixes (T. Rollins, Microwave Telemetry, Inc., personal communication).

Home Range

We estimated multi-year ranges, annual ranges, breeding ranges (16 Jan–15 Aug), and non-breeding ranges (16 Aug–15 Jan) of eagles from flight locations (i.e., speed sensor >0 kph) and perch locations (i.e., speed sensor = 0 kph). We defined the breeding season as the period from increased intensity of courtship activity through fledging of young, although nest building will occur throughout the year and fledged young may not disperse from adult ranges until winter (Watson 2010). We considered mated eagles engaged in 1 or more breeding behaviors (e.g., courtship, egg laying, brood-rearing) as breeding. Small samples precluded testing effects of specific breeding behaviors and nest success on range characteristics.

We used the Brownian bridge movement model (BBMM) to delineate ranges (Horne et al. 2007). This method allowed

us to estimate utilization distributions (UDs) that included eagle flight paths in range estimation because it involved the probability of the bird being at any point between 2 locations based on elapsed time between fixes. Eagle use of airspace was relevant to our evaluation of potential conflicts with wind turbine siting. We calculated UDs and 99%, 95%, and 50% isopleths from consecutive locations separated by ≤2 hours using the R statistical package (R Version 2.15.1, www.r-project.org, accessed 7 Jul 2012) and the ADEHABITAT package (http://cran.r-project.org/package=adehabitat, accessed 7 Jul 2012). We chose this interval to include the minimal transmission time for programmed transmitters (e.g., 1-hr) and exclude longer periods of missed fixes. Plotting of ranges and movements was accomplished in GIS (ArcGIS 10.0, Environmental Systems Research Institute [ESRI], Redlands, CA).

For eagles monitored ≥2 seasons or ≥2 years, we assessed the variation between time periods to provide a measure of how informative 1 period of monitoring was to multiple periods of use. We compared range size and area overlap for BBMM ranges among respective years for individual eagles with complete annual data (e.g., years 1 to 2, years 2 to 3, and years 1 to 3, etc.). Similarly, we compared range size and overlap characteristics among consecutive breeding seasons, among consecutive non-breeding seasons, and among breeding and non-breeding seasons during the same year. The latter analyses provided information on the degree to which eagles shifted range use after nesting. We assessed shared range use using 2-dimensional (2-D) overlap between years or seasons for 99% isopleths and percentage of the total area of the base range (earliest season or year) represented by the overlap area. We measured 3-dimensional (3-D) overlap of UD volumes, that reflected eagle intensity of use with the volume-of-intersection statistic (VI; Seidel 1992) and Bhattacharyya's affinity (BA; Bhattacharyya 1943) for each pair-wise comparison. Both VI and BA increased from 0 to 1 as intensity of use became more similar.

We overlaid circular buffers, centered at nests and with radii 1.6, 3.2, 6.4, 9.6, 12.8, and 16.0 km, to measure overlap with 99%, 95%, and 50% isopleths for annual ranges. Nesting activity for all eagles, including those monitored multiple years, was centered at the same nest on each territory during data collection.

Covariate Selection

We generated 5 landscape-scale GIS variables (resolution = 30 m) within 99% home range contours that we hypothesized would be important for predicting golden eagle range selection that potentially related to flight and foraging conditions from previously published literature (Rosenberg and McKelvey 1999, McGrady et al. 2002, McLeod et al. 2002, Bögel and Eberhardt 2004, Tapia et al. 2007). Variables included terrain ruggedness, topographic position, thermal efficiency, distance-to-ridge, and distance-to-nest. We developed terrain ruggedness and topographic position using digital elevation models (DEMs) obtained from the 1 arcs National Elevation Dataset (http://ned.usgs.gov/, accessed 1 Jun 2010). We calculated ruggedness using the

terrain ruggedness index (TRI) with high values indicative of areas with large amounts of topographic variation (Riley et al. 1999). We identified topographic position using the topographic position index (TPI), which classified terrain into slope position (ridge, upper slope, flat and mid-slope, lower slope, and valley; Weiss 2001). We developed both TRI and TPI using Map Algebra, Python, and the Spatial Analyst extension to ArcGIS 10.0. In the absence of microsite wind data, we used 2 covariates that predicted favorable flight conditions on eagle ranges resulting from thermals (potential thermal efficiency) and surface winds (distance-to-ridge). We developed potential thermal efficiency after the model of Bögel and Eberhardt (2004), which consolidates effects of habitat features that generate solar radiation (insolation). We calculated potential thermal efficiency by multiplying potential ground warming by the annual global radiation proxy. We estimated potential ground warming from aggregated land cover classes with 30-m resolution using the 2006 update to the National Land Cover Database (NLCD; http://www.mrlc.gov/nlcd2006.php, accessed 1 Jun 2010; Table 1). We estimated annual global radiation using the "area solar radiation" tool and TimeSpecialDays parameter in the Spatial Analyst extension for ArcGIS 10.0. We calculated distance-to-ridge by identifying ridgeline features and calculating the Euclidean distance to these features. We used TPI to develop a binary slope position classification (1 = ridge or upper slope, 0 = remaining landscape), and vectorization routines available in the ArcScan extension for ArcGIS 10.0 to derive ridgelines. The final covariate we used was distance-to-nest. Because golden eagles typically return to a central place (nest) within the home range, we included this covariate to capture the expectation of declining use as distance to the central place increased (Rosenberg and McKelvey 1999). By including distance-to-nest as an explanatory variable, we avoided the risk of introducing positive bias into selection

Table 1. National Land Cover Database (NLCD) land cover classes (after Fry et al. 2011) and potential thermal efficiency (K) ratings used in development of the thermal efficiency model for golden eagles (after Bögel and Eberhardt 2004) based on distribution of 105,003 global positioning system fixes obtained in the Columbia Plateau Ecoregion, 2005–2013.

NLCD 2006 class	Aggregated land cover type	$K_{habitat}$	% of fixes
11—Open Water	Open Water	0.0	1.1
12—Perennial Ice/Snow	Snow	0.1	0.0
21—Developed, Open Space	Settlements	1.0	0.3
22—Developed, Low Intensity	Settlements	1.0	0.1
23—Developed, Medium Intensity	Settlements	1.0	0.0
24—Developed High Intensity	Settlements	1.0	0.0
31—Barren Land (Rock/Sand/Clay)	Rock	0.9	1.3
41—Deciduous Forest	Forest	0.6	0.3
42—Evergreen Forest	Forest	0.6	18.8
43—Mixed Forest	Forest	0.6	0.0
52—Shrub/Scrub	Shrub/Scrub	0.7	60.7
71—Grassland/Herbaceous	Grasslands	0.8	16.3
81—Pasture/Hay	Grasslands	0.8	0.0
82—Cultivated Crops	Grasslands	0.8	0.9
90—Woody Wetlands	Forest	0.6	0.1
95—Emergent Herbaceous Wetlands	Grasslands	0.8	0.1

coefficients for habitat features near the nest. We used the Euclidean distance to the nest location in each territory to define distance-to-nest.

Prior to their inclusion in selection analysis, we tested for multicollinearity between our 5 explanatory variables using the Spearman's correlation matrix available in the STATS package of R. None of our variables were correlated at $|r| > 0.50$. For analysis of range characteristics and resource selection we pooled data for female eagles (2 of 10 birds in final analysis) with males after examining the confidence intervals on coefficient estimates for habitat covariates of individual eagles. Variability between females and males was no less than that within individuals from year to year, and among individuals overall for all model variables (J. W. Watson, unpublished data).

Resource Selection

We used resource selection probability functions (RSPFs; Lele 2009) to obtain maximum likelihood estimates of golden eagle habitat selection for covariates in a logistic model (R Version 3.0.1, www.r-project.org, accessed 1 Sep 2013 and the RESOURCESELECTION package http:// cran.r-project.org/package=ResourceSelection, accessed 1 Sep 2013). We assessed third-order resource selection (Johnson 1980) and used the 99% home range contour to define the spatial extent of available resources. Prior to modeling, we conducted several confirmatory steps and sensitivity analyses. First, we tested several identical models using log and logit links to confirm that an exponential model did not outperform the logistic model (Lele 2009, Lele et al. 2013). Secondly, we tested several use-to-availability ratios (1:1 through 1:5) to ensure that logistic regression approximated the point process model as intended (Northrup et al. 2013). This analysis reduced or eliminated any potential effects resulting from serial location of fixes (Northrup et al. 2013); potential effects of serial correlation were also reduced because of flight mobility of golden eagles that provided them the capability to visit any area within their home ranges in <15 minutes, well within our 1-hour sampling interval. Finally, we tested the number of bootstrap samples (99–2,999) needed to ensure a stable result, that is, mean and variance of the bootstrap distribution did not fluctuate given the number of bootstrap samples used. Following these preliminary analyses, we used Akaike's Information Criterion (AIC) to identify the best RSPF based upon model parsimony (e.g., $\Delta AIC < 2$) and ecological relevance. In the best RSPF, we considered independent variables with confidence intervals that did not include 0 informative predictors of resource selection. We used standard partial regression coefficients to show the relative standardized strengths of the effects of the independent variables on selection (Sokal and Rohlf 1995) and log–odds ratios to determine the odds of a resource unit being selected versus not selected when that unit is encountered by an eagle on the landscape (Lele et al. 2013).

Model Evaluation

To evaluate our population-level RSPF, we used boot-strapped coefficients from 10 sampled eagles to predict eagle probability of selection (Lele et al. 2013) at 4 independent golden eagle territories in the CPE. Evaluation data were from eagles with GPS transmitters ranging from 4 months to 1 year. We applied our most parsimonious model to the ArcGIS spatial extent of our eagle evaluation fixes to calculate the probability of selection for each resource unit (30-m pixel) within the use area. We then classified probabilities of selection at each resource unit into 20 bins using a Jenks classification (ESRI 2011) ranging from 1 = low, to 20 = high. We counted the number of eagle locations in each bin and evaluated our model based on the assumption that we would find a larger number of eagle locations in higher probability bins when normalized by bin area. We used Spearman's rank correlation coefficient (Sokal and Rohlf 1995) to test the relationship between bin rank and number of observed eagle locations normalized by bin area.

RESULTS

Home Range

We monitored 12 adult male and 5 female golden eagles from 2004 to 2013 (Fig. 1). Success rate of GPS fix acquisition was high (85%). Eagles did not migrate, and movements were localized with the exception of periodic, 1- to 4-day excursions <75 km from ranges from July through November. For analysis of annual home ranges, we excluded eagle 28017 in 2007 because this bird did not nest and drifted extensively, resulting in an unusually large range (1,304 km^2 and 2,878 km^2 95% and 99% volume contours, respectively).

Mean range size and fragmentation for the 10 eagles with GPS transmitters (8 males, 2 females) varied with focal period and among isopleths (Table 2). Comprehensive home ranges of golden eagles defined by multi-year 99% isopleths were expansive ($\bar{x} = 245.7$ km^2, SD = 370.2 km^2) and typically fragmented into 7 islands. On average, when defined by 95% isopleths, home ranges were 66% smaller and
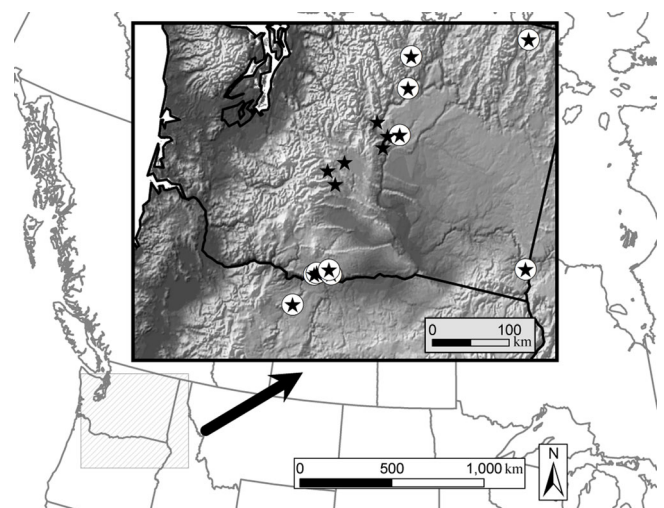

Figure 1. Capture locations (stars) of adult golden eagles monitored with satellite telemetry in the Columbia Plateau Ecoregion, 2004–2013. Circles identify eagles monitored with global positioning system telemetry.

Table 2. Home range size (km²) and frequency of volume contours estimated by the Brownian bridge movement model for 10 nesting golden eagles in the Columbia Basin Ecoregion of Washington and Oregon, 2005–2013.

| Range type | n | 50% Isopleth | | | | 95% Isopleth | | | | 99% Isopleth | | | |
| | | Size | | No. contours | | Size | | No. contours | | Size | | No. contours | |
		Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Multi-year	10	6.4	2.8	1.3	0.7	82.3	94.6	3.0	3.4	245.7	370.2	7.1	7.8
Annual	23	6.5	2.5	1.5	0.9	69.2	67.7	3.6	3.2	169.3	252.6	5.6	5.8
Breeding[a]	20	4.9	2.0	1.3	0.6	42.1	21.2	2.7	1.7	91.1	49.6	4.5	2.8
Non-breeding[a]	20	15.0	10.9	2.8	2.4	87.0	63.0	4.0	2.7	159.7	120.8	4.0	3.5

[a] Breeding season defined as 16 January–15 August, and non-breeding season 16 August–15 January.

half as fragmented. In a given year, eagles used ranges (99% isopleths) that were collectively 31% smaller and 22% less fragmented compared to multi-year ranges. On average, successive annual ranges of individual eagles (99% isopleths) overlapped 70.7% (SD = 20.0), shared an area of 100.0 km² (SD = 45.9), and displayed relatively high indices of 3-D overlap (Table 3). Thus, golden eagle space use for 1 year typically defined over 66% of the home range area used by that eagle during a subsequent year. Intuitively, year-to-year dynamics of eagle space use provided progressively better definition of lifetime ranges, illustrated for 2 birds monitored >4 years (Fig. S1, available online at www.onlinelibrary.wiley.com).

Core areas of ranges, defined as 50% isopleths, typically consisted of 1 contour that encompassed the used nest and 3–9% of the 95% or 99% home range area (Table 2). Size of core areas used by eagles increased substantially during the non-breeding season with decreased nest-centricity.

Differences in golden eagle home range characteristics were pronounced between seasonal periods. Average breeding season ranges were one-third to one-half the size of non-breeding ranges and less fragmented for every isopleth (Table 2). Successive breeding ranges (99% isopleths) of individual eagles displayed relatively high indices of 3-D overlap, whereas non-breeding ranges occupied by eagles in consecutive years had lower overlap (Table 3). This was not unexpected because all eagles used the same nests in successive years. Overlap of breeding and non-breeding ranges was highest among 2-D comparisons, but lowest for 3-D comparisons (Table 3). This reflected the fact that although eagles visited the nest during the non-breeding

period, birds shifted away from the nest, partly because of reduced nest attentiveness (Fig. S2, available online at www.onlinelibrary.wiley.com).

We assessed overlap of circular buffers from 20 annual ranges of 10 eagles that were monitored >75% of a given year ($\bar{x}$ = 306, SE = 48 days). Greater than 88% of the areas contained in golden eagle ranges defined by 50%, 95%, and 99% volume contours were encompassed by circular buffers centered on the nest with 3.2-km (2-mile), 9.6-km (6-mile), and 12.8-km (8-mile) radii, respectively (Fig. 2).

Resource Selection

We determined selection of terrain features by golden eagles from 105,003 GPS fixes ($\bar{x}$ = 10,500 fixes/individual, SD = 8,276; range = 2,200–22,000). Sensitivity analyses indicated our results stabilized prior to a 1:5 use-to-availability ratio, and 2,999 bootstrap samples. Assessment of likelihoods and AIC values for our 17 models indicated that the top-ranked model included terrain ruggedness, topographic position, distance-to-ridge, and distance-to-nest as variables most strongly associated with eagle selection of resource units within home ranges (ΔAIC = 10.2 for the second best model). Eagle habitat selection was most strongly influenced by distance-to-nest, followed by terrain ruggedness, topographic position, and distance-to-ridge and all variables were informative (95% CI did not overlap 0; Table 4). The log–odds ratio for distance-to-nest indicated that for a given resource unit, the odds of selection was expected to decrease by 0.023% for every 1-m increase in distance-to-nest out to a maximum of 87.2 km. The log–odds ratio for terrain ruggedness indicated that for every 1-unit

Table 3. Annual and seasonal home range dynamics of adult golden eagles in the Columbia Basin Ecoregion of Washington and Oregon, 2005–2013, described by overlap of 99% isopleths, which we estimated with the Brownian bridge movement model.

| Range comparison[a] | n | 2-dimensional overlap | | | | 3-dimensional overlap | | | |
| | | Area (km²) | | % | | BA index[b] | | VI index[b] | |
		Mean	SD	Mean	SD	Mean	SD	Mean	SD
Annual	18	100.0	45.9	70.7	20.0	0.93	0.07	0.79	0.07
Breeding season	23	74.5	22.7	69.7	20.0	0.95	0.02	0.79	0.06
Non-breeding season	23	118.7	64.3	72.0	19.0	0.87	0.06	0.66	0.11
Breeding vs. non-breeding	20	88.8	86.5	82.5	19.0	0.87	0.09	0.65	0.17

[a] Each range for an individual eagle compared to every other range for the same eagle for the identified seasonal period (e.g., annual ranges of eagle 33241 for year 1 compared to year 2, year 3, etc.). Breeding season defined as 16 January–15 August, and non-breeding season 16 August–15 January.
[b] BA Index = Bhattacharyya's affinity (Bhattacharyya 1943); VI Index = volume of intersection statistic (Seidel 1992).
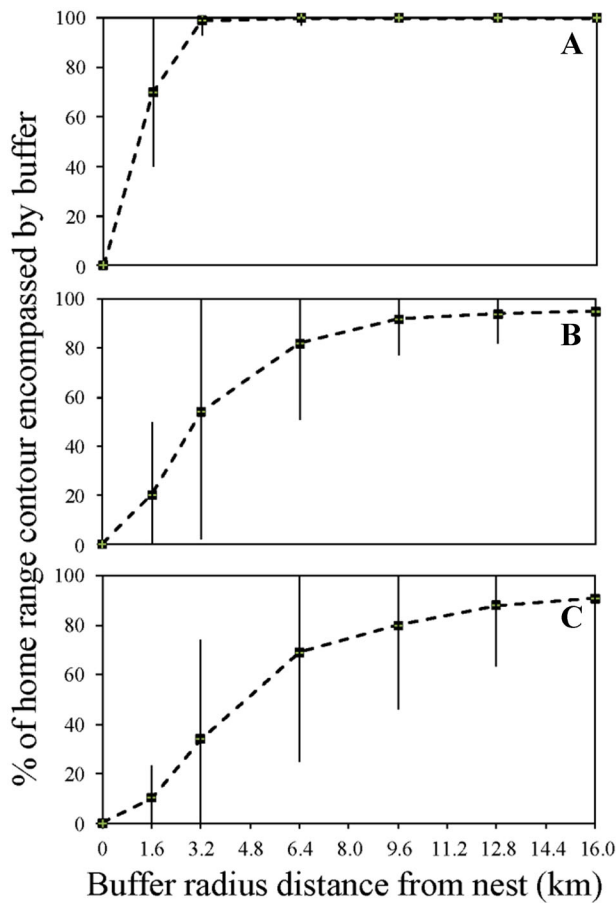
Figure 2. Percentage of annual golden eagle home ranges ($n = 20$) encompassed by circular buffers surrounding the used nest in the Columbia Plateau Ecoregion, 2005–2013. We estimated home ranges with the Brownian bridge movement model for (A) 50%, (B) 95%, and (C) 99% isopleths. Mean percentages (boxes) and associated 95% confidence intervals (bars) are shown at each increment and connected by the hashed line.
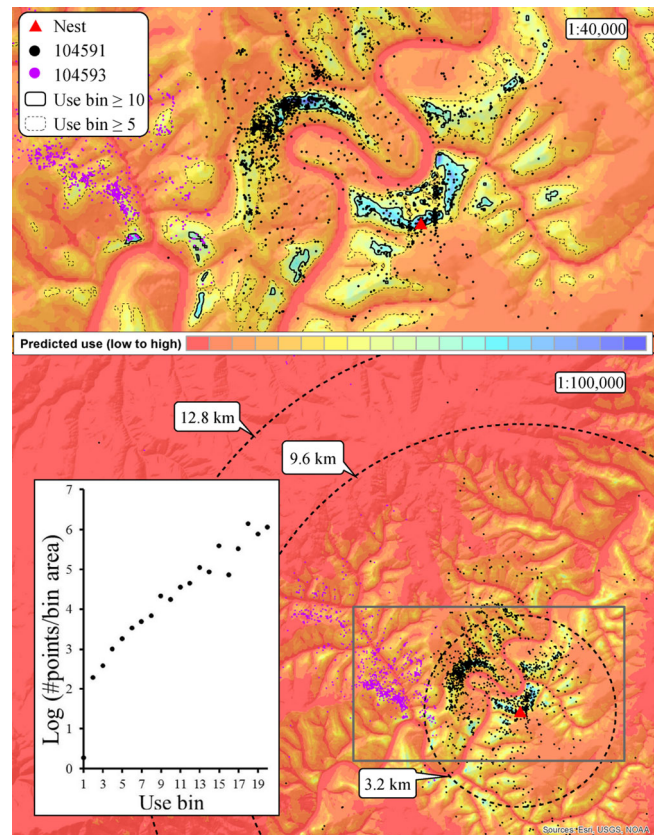

Figure 3. Predicted and actual range use of adult male golden eagle 104591 in 2011 at a large scale (top and inset) and small scale (bottom). Predicted use was based on terrain variables identified in resource selection probability functions for 10 eagles, derived by applying unstandardized coefficients of significant terrain variables to the landscape using ArcMap's raster calculator, and classifying resource units into 20 predicted use bins. Actual use was identified by global positioning system (GPS) fix locations ($n = 3,465$) recorded for 1 year. Dashed lines indicate mean nest buffers encompassing 50%, 95%, and 99% of home range contours for the sampled eagle population. The GPS fix locations in maroon ($n = 1,659$) of juvenile eagle 104593 from the adjacent nesting range illustrate potential for territoriality to affect fit of predictive model.

increase in TRI from 0 to 1,783, the odds of eagle selection increased by 0.553%. Log–odds ratios for topographic position indicated that every 1-unit increase in TPI from −112 to 142, the odds of eagle selection increased by 2.54%. The log–odds ratio for distance-to-ridge indicated that for every 1-m increase in distance-to-ridge out to a maximum of 4.3 km, the odds of eagle selection decreased by 0.011%.

The population-wide RSPF developed using both flight and perch locations (flight: transmitter speed sensor ≥ 0) accurately predicted golden eagle fix locations on evaluation ranges (Fig. 3). Collectively, 73.4% of all evaluation fixes were contained within 2 groups of bins that represented only 1.4% of the RSPF prediction area. Bins 10–20 defined areas

Table 4. Estimated coefficients (β), standard errors (SE), 95% confidence intervals (CI), and log–odds ratios (%) of terrain features selected for by adult golden eagles in the Columbia Plateau Ecoregion, 2005–2013. We determined habitat selection by modeling resource selection probability functions for 10 eagles within 99% home range contours that were estimated from global positioning system fixes and Brownian bridge home range models. We estimated coefficients and standard errors for terrain ruggedness (TRI), slope position (TPI), distance-to-ridge (DTR), and distance-to-nest (DTN) by bootstrapping ($B = 2,999$). We considered independent variables with confidence intervals that did not include 0 informative predictors of resource selection.

	Unstandardized estimates				Standardized estimates		
Covariate	β	SE	95% CI	Log–odds ratio (%)	β	SE	95% CI
Intercept	$-5.782e^0$	$3.284e^{-3}$	$-5.789e^0$ to $-5.774e^0$	$-9.9692e^{-1}$	$-6.130e^0$	$1.010e^{-2}$	$6.188e^0$ to $-6.072e^0$
TRI	$5.514e^{-3}$	$1.014e^{-6}$	$5.510e^{-3}$ to $5.520e^{-3}$	$5.530e^{-1}$	$9.780198e^{-1}$	$2.190e^{-4}$	$9.780187e^{-1}$ to $9.780211e^{-1}$
TPI	$2.508e^{-2}$	$5.370e^{-6}$	$2.507e^{-2}$ to $2.509e^{-2}$	$2.540e^0$	$5.50856e^{-1}$	$1.454e^{-4}$	$5.50853e^{-1}$ to $5.50860e^{-1}$
DTR	$-1.130e^{-4}$	$6.089e^{-6}$	$-1.270e^{-4}$ to $-9.900e^{-5}$	$-1.130e^{-2}$	$-2.94390e^{-2}$	$2.042e^{-3}$	$-2.94401e^{-2}$ to $-2.94397e^{-2}$
DTN	$-2.305e^{-4}$	$1.728e^{-6}$	$-2.345e^{-4}$ to $-2.265e^{-4}$	$-2.304e^{-2}$	$-1.871300e^0$	$1.130e^{-2}$	$-1.871304e^0$ to $-1.871299e^0$

with high probability of selection and represented only 0.06% of the RSPF prediction area but contained 34.7% of fixes across all 4 evaluation territories. Bins 5–9 defined areas with intermediate probability of selection and represented 1.3% of the RSPF prediction area but contained an average of 38.6% of fixes. Model performance was exceptional across all 4 evaluation territories based on the correlation of bin rank and number of fixes ($r_s = 0.992$).

DISCUSSION

Proximity to nests and location of specific terrain features were key underlying influences on golden eagle focal use, and resulted in multi-year ranges that were comparatively large (Kochert et al. 2002), relatively stable, yet individually and seasonally dynamic. Influence of the location of the used nest was particularly important because intensity of perch and flight behaviors was constant and high <3.2 km from nests throughout the year. This use pattern was maintained by eagles monitored multiple years and resulted in home range boundaries that changed little over multiple years; Marzluff et al. (1997) observed the same stability for golden eagle ranges in Idaho over a 20-year period. Consistency of eagle spatial use provided a template that is useful to predict eagle range use: the used nest as a centroid surrounded by a zone of intense activity (e.g., 3.2-km radius), with peripheral range use out to 12.8 km and dictated by the location of selected landscape features. Over time, as eagles build new nests or use alternative nests on ranges, core use may shift, depending on durability of available nest structures (cliff vs. tree) and how far nests are separated, but golden eagle nest use is often static even for decades with mated pairs and their subsequent replacements reusing the same nest or nests in close proximity (McGahan 1968, Kochert and Steenhof 2012). Cliff-nesting eagles showed high nest fidelity during a 45-year period in the Snake River Canyon in Idaho where 88% of nests ($n = 42$) were occupied multiple years and 90% of alternate nests on a territory were built <500 m away (Kochert and Steenhof 2012). The 1 nest switch during our study that occurred in the fifth year of monitoring was 2.1 km from the original cliff nest to a new cliff site that eagles used consistently within the 50% volume contour, suggesting the importance of alternate nest locations on eagle focal use. In addition, nests influence other patterns of eagle home range use, including effects of season (i.e., less intense use at nest during non-breeding; Haworth et al. 2010), breeding status (i.e., less intense use at nest for birds that fail during nesting or do not nest; Haworth et al. 2010), and parental behavior (i.e., females more closely allied with nests during incubation and brood-rearing, whereas males forage widely; Ellis 1979, Collopy 1984). These effects are important to recognize when developing monitoring and sampling protocols (Marzluff et al. 1997, McGrady et al. 1997, McLeod et al. 2002).

Elevated terrain features eagles selected were essential to flight behavior and relate to prey distribution on eagle ranges. Lift created by deflective currents from ridge tops and upper slopes are vital for flying golden eagles to locate and acquire food (McLeod et al. 2002, Bögel and Eberhardt 2004), patrol

territories (i.e., aggression and display; Harmata 1982, Collopy and Edwards 1989), and migrate (Johnston 2011, Katzner et al. 2012). Golden eagles are relatively heavy-bodied raptors with broad wings and low wing-loading that are energetically efficient in low-speed soaring flight but not high-speed flight (Bildstein 2006). The typical pattern we observed in the field during nesting was for male eagles roosting on leeward hillsides to initiate morning hunting flights at dawn when surface wind was steady but remained perched in dead-air until mid-morning to minimize their reliance on powered flight. When terrain warmed, they sought out thermal-rich areas on their ranges. We did not find an association between eagles and thermal-rich areas based on potential thermal efficiency; this suggests either thermals were not one of the most important factors driving eagle resource selection or this variable needed to be refined, and preferentially ground-truthed, to better reflect conditions promoting thermals. Not surprisingly, eagles did not favor perches on lower elevation slopes, probably because of poor airflow and other unsuitable habitat conditions (McLeod et al. 2002), but sought higher elevations near ridge tops when they could attain flight altitude more easily.

The relatively high success rate of GPS acquisition (85%) was aided by elevated perching and flight as compared to mammal tracking where canopy often inhibits reception (Nielson et al. 2009). Failed GPS acquisition was at least partly related to overcast conditions and consequent reduced solar charging. We suspect that some missed fixes resulted from reduced reception when eagles were perched in particularly rugged habitats because 2-D fixes, that we included in resource analysis, had proportionally greater representation in rugged habitats than 3-D fixes. Any bias resulting from this effect would have underestimated eagle use of rugged habitat. However, in the same habitats in Washington, prediction models for mountain goats (*Oreamnos americanus*) were improved by only 1–2% after inclusion of correction bias due to 35% missed GPS fixes (Wells et al. 2011), and habitat selection for mule deer (*O. hemionus*) was generally unbiased for GPS data sets missing up to 50% of fixes (Nielson et al. 2009).

Evidence suggests eagle use of rugged terrain on upper slopes was due in part to prey distribution. Prey availability is a primary factor governing habitat selection of *Aquila* eagles (Marzluff et al. 1997, Hunt 2002, Fernández et al. 2009) and therefore range size (Collopy and Edwards 1989, Marzluff et al. 1997). The breeding season range of an adult male golden eagle in the San Juan Islands of western Washington that fed extensively on a concentration of European hares (*Lepus europaeus*) was only 3 km^2 (J. W. Watson, unpublished data), compared to 225 km^2 for a male eagle we studied in native arid habitat that fed on yellow-bellied marmots, coyote pups, and mule deer fawns (J. W. Watson, unpublished data). Marmots were the most important prey by frequency (40%) and biomass (73%) of golden eagles nesting in eastern Washington and were closely allied with variable terrain and dens in rocky outcrops and talus (Van Vuren 2001). Chukar partridge (*Alectoris chukar*), that

reside in talus and hilly terrain (Lindbloom et al. 2004) were the most important upland bird in diets (4%). A dietary shift from small mammals to more widely distributed carrion for golden eagles in eastern Washington (Marr and Knight 1983) explained the seasonal range expansion of our study eagles during the non-breeding season. In our study area, large expanses of agriculture that were devoid of eagle prey but interspersed with native vegetation increased the size of some eagle home ranges, similar to stands of closed-canopy forest that were avoided by golden eagles in other regions (McGrady et al. 1997).

Intensity of golden eagle use, dictated by nest proximity and location of elevated terrain features, has direct relevance to potential short- and long-term impacts from wind power development. The intensity of golden eagle flights we documented during multiple years within core areas (e.g., <3.2 km from nests) dramatically increases the probability of conflict when development, such as wind power, is proposed in this zone, especially when associated with upper slopes and ridge tops, and increasingly varied topography (i.e., ruggedness). Little evidence indicates that territorial golden eagles are displaced by new operational wind turbines (see review, Madders and Whitfield 2006), implying that eagles will often continue to use the same focal areas of ranges before and after turbine construction. If exposure risk of nesting eagles to turbines is not reduced by an eagle's displacement from the area, an eagle's ability to avoid a moving rotor when on a path of potential collision (i.e., avoidance behavior; Band et al. 2007) will ultimately dictate collision risk (Madders and Whitfield 2006). In that case, emphasis for reducing collision risk of golden eagles should include application of buffers and avoiding development overlap with preferred terrain features. These pro-active management measures need to be emphasized to avoid drastic actions such as prey or nest removal, or operational curtailment or removal of turbines where eagle kill is excessive from turbines previously sited in risk zones.

We argue that eagle airspace must be managed as habitat throughout the entire home range (e.g., analysis based on the BBMM), with regularly used flight paths considered in conjunction with perch locations to assess potential for conflict with development. Significantly, collision risk of soaring raptors and vultures with turbines may be greatest when poor wind conditions exist at locations where these birds regularly seek lift (Barrios and Rodríguez 2004, Smallwood et al. 2009). Nine adult golden eagles that collided with wind turbines in Washington and Oregon from 2010 to 2012 were an average of 4.7 km (range 0.7–9.8 km) from the closest known golden eagle nest and were recovered at turbines located atop ridges, on flats above slopes, or on upper slopes (J. W. Watson, unpublished data, and M. Meyer, Fish and Wildlife Service, personal communication). Distant ridgelines away from nests that create eagle viewsheds may be significant focal locations for interactions with adjacent nesting eagles (e.g., undulating flight displays, sentinel perching, tail chases), dictate the shape of territories (Fig. 3), and act as density-dependent constraints on range size (Watson 2010).

Our model creates a template for predicting spatial selection of terrain by non-migratory golden eagles nesting in shrub-steppe grasslands to moderately forested montane ecosystems that vary topographically. Characteristics of golden eagle ranges in heavily forested or desert ecosystems may differ because of differences in topographic relief and prey density or type (Marzluff et al. 1997, Watson 2010). To test appropriateness of model application and to detect hidden extrapolations outside the range of observations, we recommend initial examination of leverage values (e.g., Neter et al. 1996:377–378).

MANAGEMENT IMPLICATIONS

Our study provides a method for managers to predict golden eagle range use as an alternative to site-specific field investigations that can be labor intensive and relatively expensive. Application of management buffers to protect home ranges (Fig. 2) can be used in combination with identification of important resource components (e.g., slope position, ruggedness, and distance to ridge) and GIS analysis to predict areas of critical eagle use and potential conflict with development (e.g., wind power). Managers seeking to define and protect comprehensive home ranges of golden eagles can apply 12.8-km (8-mile) nest buffers based on our estimate for 99% contours. Less-conservative strategies that attempt to either avoid or minimize impacts of habitat alterations within eagle ranges can apply 9.6-km (6-mile) nest buffers (e.g., 95% contours) and terrain modeling to identify key upper slopes, ridge tops, and areas of varied terrain 9.6–12.8 km (6–8 miles) from nests. Either approach must emphasize protecting the integrity of the core area <3.2 km (2 miles) from nests. Predicted eagle range use can be refined by on-site documentation of unusual prey concentrations, unique habitat features (e.g., transmission towers), and significant areas of eagle non-use. When biologists need site-specific documentation of eagle range use via telemetry, we recommend they preferentially track adult males and simultaneously collect wind speed and direction information to best understand peripheral range use patterns. Monitoring should be conducted for a minimum of 2 complete years to capture seasonal and annual dynamics for this species that lives up to 30 years in the wild (Harmata 2012).

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