



Home in the heat: Dramatic seasonal variation in home range of desert golden eagles informs management for renewable energy development



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ABSTRACT

Renewable energy is expanding quickly with sometimes dramatic impacts to species and ecosystems. To understand the degree to which sensitive species may be impacted by renewable energy projects, it is informative to know how much space individuals use and how that space may overlap with planned development. We used global positioning system–global system for mobile communications (GPS–GSM) telemetry to measure year-round movements of golden eagles (*Aquila chrysaetos*) from the Mojave Desert of California, USA. We estimated monthly space use with adaptive local convex hulls to identify the temporal and spatial scales at which eagles may encounter renewable energy projects in the Desert Renewable Energy Conservation Plan area. Mean size of home ranges was lowest and least variable from November through January and greatest in February–March and May–August. These monthly home range patterns coincided with seasonal variation in breeding ecology, habitat associations, and temperature. The expanded home ranges in hot summer months included movements to cooler, prey-dense, mountainous areas characterized by forest, grasslands, and scrublands. Breeding-season home ranges (October–May) included more lowland semi-desert and rock vegetation. Overlap of eagle home ranges and focus areas for renewable energy development was greatest when eagle home ranges were smallest, during the breeding season. Golden eagles in the Mojave Desert used more space and a wider range of habitat types than expected and renewable energy projects could affect a larger section of the regional population than was previously thought.

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1. Introduction

Renewable energy development is occurring globally at a rapid pace (AWEA, 2013; EWEA, 2013). This process can have both positive and negative consequences to species and ecosystems (Katzner et al., 2013). For example, renewable energy development has the potential to reduce fossil fuel emissions and ameliorate global climate change and its effects on wildlife globally (AWEA, 2013; EWEA, 2013). However, renewable energy may also harm

wildlife locally, most often directly via mortality (collision), or indirectly, through habitat alteration or through increased physiological costs due to behavioral responses (Katzner et al., 2013).

Managing the effects of renewable energy development on wildlife is improved by assessment of its potential impacts (Miller et al., 2014). When development is planned, overlap of its location with use of space by individual animals may be an important proxy to understand this risk. It is therefore important to understand space use by species potentially affected by renewable energy. The use of space by an animal changes over time, by age and by sex (Aebischer et al., 1993), and understanding these drivers can aid assessment of the impacts of development and for eventual mitigation of costs (Langston and Pulan, 2003; Marques et al., 2014).

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The Mojave Desert of southern California supports many renewable energy projects and the region is targeted for substantial increases in energy development. New development is needed to reach California's goal of providing 33% of retail electricity sales through renewable sources by 2020 (CA Senate Bill No. 2, 2011). To mitigate potential impacts of future renewable energy installations, the California Energy Commission, partnering with other government agencies, initiated the Desert Renewable Energy Conservation Plan (DRECP; CEC, 2014, 2011). This conservation plan is intended to identify areas well suited for energy development (Development Focus Areas or DFAs) and to identify areas of high biodiversity better suited for conservation.

The golden eagle (*Aquila chrysaetos*) is a primary target for conservation in the DRECP area (~91,406 km²). A small population of breeding golden eagles nests within the DRECP (Latta and Thelander, 2013), and large numbers of eagles elsewhere have been affected both directly (killed; Smallwood and Thelander, 2008) and indirectly (Johnston et al., 2014) by renewable energy development. Eagles are long-lived species that produce few offspring and occur at low densities throughout their range (Watson, 2010); therefore, understanding potential impacts to these birds is a high priority for management agencies (USFWS, 2013).

We evaluated use of space by Mojave golden eagles as a proxy for risk (e.g., wind turbine blade strikes, solar flux or incineration, loss of foraging habitat, reduction in prey populations) from renewable energy development in and near the DRECP. We focused on 4 objectives to illuminate basic elements of golden eagle ecology and identify the temporal and spatial scales at which eagles may be affected by renewable energy. We (1) measured the size and monthly variation in size of golden eagle home ranges; (2) described extrinsic (vegetative class, elevation) and intrinsic (sex and age) characteristics of golden eagle monthly home ranges; and then (3) determined which biologically relevant extrinsic variables influenced temporal size patterns in home ranges. Finally, (4) we interpret these patterns in the context of planned renewable energy development within the DRECP.

2. Methods

2.1. Study area and focal species

We tracked eagles within the DRECP and surrounding Mojave Desert areas (for details see online Appendix A and Fig. B.1). Golden eagle nests in the Mojave Desert are sparsely distributed, with approximately 74 occupied territories in ~4.5 million hectares of public lands within the DRECP area (Latta and Thelander, 2013; see online Appendix A for details).

2.2. The Desert Renewable Energy Conservation Plan

The DRECP is designed to “provide for the protection and conservation of California desert ecosystems while providing streamlining of permitting for appropriate renewable energy projects” (CEC, 2011; www.drecp.org). It is intended to serve as a programmatic Habitat Conservation Plan under section 10 of the US Endangered Species Act (ESA), with coverage intended to include golden eagles and other species not otherwise listed under the ESA. The DRECP was developed by a group of collaborating agencies responsible for energy development and land management, including the California Energy Commission, the California Department of Fish and Wildlife, the U.S. Bureau of Land Management and the U.S. Fish and Wildlife Service. The plan identifies areas of high suitability for renewable energy (Renewable Energy Study Areas and DFAs) and areas of high conservation value

that are less suited to renewable energy development (i.e., it identifies areas of avoidance for mitigation purposes; Marques et al., 2014). To minimize effects of renewable energy development and provide for the long-term conservation and management of species and their habitats, the DRECP aims to maximize conservation lands, maintain connectivity across the landscape, minimize edges, and represent the ecoregions, watersheds, and ecological communities across the environmental gradients of the desert region. Because of its adaptive nature, the draft DRECP identified a range of DFA alternatives that could meet the renewable energy needs of the state and the conservation needs of species and habitats managed by the cooperating agencies. The sizes and locations of renewable energy development varied among DFA alternatives of the DRECP. The agency version of the plan has been drafted; it is currently undergoing public review and is expected to become finalized in 2016.

2.3. Data collection

We captured and telemetered territorial golden eagles within the DRECP area (see online Appendix A for details on eagle selection and capture). Birds were outfitted with CTT-1070 global positioning system–global system for mobile communications (GPS–GSM) telemetry systems (Cellular Tracking Technologies, Somerset, PA, USA) attached as backpacks with a Teflon ribbon harness (Bally Ribbon Mills, Bally, PA) in an X configuration. These telemetry systems (<3% of body weight, per BBL standards) collect GPS data at 15-min intervals for 9 days and every 10th day at 30-s intervals and send them over the GSM network to data servers (Lanzone et al., 2012). We removed poor-quality GPS locations (i.e., 2D fixes and altitude above ground levels of <–50 m; Katzner et al., 2012) and, to be consistent in data analysis among days, we subsampled the 30-s data to 15-min intervals.

2.4. Data analysis

2.4.1. Home range and core range estimation

We estimated home ranges separately for each month of the two-year study period with adaptive Local Convex Hulls (aLoCoH; Getz et al., 2007) using package *adehabitatHR* (Calenge, 2006) within R (R Core Team, 2013). We used 95% and 50% isopleths to estimate overall monthly home range size (hereafter “home range”) and monthly core home range size (hereafter “core range”), respectively (Getz et al., 2007; Kie et al., 2010; Powell, 2000; online Appendix A and Table A.1).

2.4.2. Extrinsic and intrinsic characteristics

Within the boundary of each monthly home range and core range we extracted GAP vegetation classes (USGS, 2011) and 10-m resolution elevation from the National Elevation Dataset (Gesch et al., 2002; ArcGIS 10.1, ESRI, Redlands CA). For our analysis, we used the four most common vegetation classes found in the study area (Forest & Woodland, Nonvascular & Sparse Vascular Rock Vegetation, Semi-desert, and Shrubland & Grassland) and combined all other classes that occurred with low frequency (Agriculture Vegetation, Aquatic Vegetation, Developed & Other Human Use, Open Water, and Recently Disturbed or Modified). We then calculated the proportion of area for each of the five classes in each monthly home range and core range.

We described the topographic characteristics of the home ranges and core ranges using three measurements. The first was the range of elevation (maximum–minimum elevation) within each home range. The second was a roughness ratio (DEM Surface Tools; Jenness, 2013) that accounts for areas with large (high values) or small (low values) amounts of topographic heterogeneity (online Appendix A). We used the standard deviation of

those roughness ratios to characterize the amount of topographic variation throughout each home range. The third was a measurement of slope position (Land Facet Corridor Designer; Jenness et al., 2013) estimated with a topographic position index (TPI). We used the TPI to classify the home range landscape into four slope position categories (canyon, gentle slope, steep slope, and ridge) and estimated the proportion of each position category that made up each home range.

We compared the monthly range size between the two calendar years and according to a more biologically relevant breeding year. Our breeding year cycle (created post hoc) started with the initiation of breeding behavior in September, included fledging in May, and ended with post-fledging in August. We considered eagles to be breeding when they were exhibiting (as determined from observation of birds or of GPS telemetry data) territorial behaviors or had chicks or eggs in the nest. We considered eagles to be non-breeding when they did not produce chicks or when nesting was not successful. Post-breeding behavior occurred after nests failed or chicks fledged.

2.4.3. Statistical analysis

To address our first research objective, focused on size and monthly variation of eagle home ranges, we used two linear mixed-effects models (LMM; package *nlme*; Pinheiro et al., 2013; R Core Team, 2013) to evaluate how size (response variable) of monthly home ranges (first model) and core ranges (second model) were related to month (explanatory variable). We included bird identification in the model structure via a random effects component to account for autocorrelation from repeated measures of the same individual. To more closely meet assumptions of homogeneity of variances and normality of the data, we log-transformed the home range and core range sizes. We used restricted maximum likelihood methods for model estimation.

To address our second objective, describing extrinsic and intrinsic characteristics of golden eagle ranges, we estimated monthly means and variation for each extrinsic characteristic (proportion of vegetation class, topographic characteristics, breeding year) and intrinsic categories (age, sex) within home ranges and core ranges.

To address our third research objective, how extrinsic variables influence temporal patterns in size of home range and core range, we first identified explanatory variables that are biologically relevant. We chose particular variables because we expected them to be linked to eagle ecology. For example, the slope positions “canyon” and “gentle slope,” are typical environments where eagles hunt (updraft and prey are available in these areas; Watson, 2010). Likewise, roughness and elevation both describe features that aid generation of thermal or orographic updraft (Brandes and Ombalski, 2004) and thus we interpreted these terms as especially relevant to eagle flight. We included number of days above 32.2 °C (reported as days >90°F; Lawrimore et al., 2011) as a measure of thermal stress to desert eagles. Finally, we interpreted breeding year effects as relevant to eagle nesting behavior.

We developed two sets of LMMs to determine which combinations of these 6 biologically relevant variables (canyon, elevation, gentle slope, number of days above 32.2 °C, topographic roughness, and breeding year) explained variation in monthly home and core range sizes (log-transformed response variables; Pinheiro and Bates, 2000). In these LMMs, we included bird and month as random effects. We then used Akaike information criterion with small sample size correction (AICc) to rank the models in each model set and estimate model weights (Burnham and Anderson, 2002). Using a weight of evidence approach, we calculated relative variable importance (summing the model weights across all models that included the parameter of interest)

and model averaged parameters to incorporate model selection uncertainty (Buckland et al., 1997).

To address our final objective, assess overlap of DFAs within the DRECP and eagle home ranges, we calculated monthly overlap of DFA with home ranges (proportion of home ranges composed of DFA). There were six different alternative DFA plans considered (CBI, 2013), we present overlap of eagle home ranges with each of the six alternatives. We used the 6 draft DFA integrated alternatives described as (1) Disturbed Lands/Low Resource Conflict, (2) Geo Balanced/Transmission Aligned B, (3) West Mojave Emphasis Alternative, (4) Geo Balanced/Transmission Aligned A, (5) Increased Geologic/Technology Flexibility, and (6) Geo Balanced Alt C with Variance Lands (CBI, 2013).

3. Results

We captured and telemetered nine golden eagles from nine territories, seven in 2012 and two in 2013 (5 male, 4 female, 7 adults, 2 sub-adults holding territories and apparently parts of breeding trios; e.g., Watson, 2010, p. 190). We did not include data from one adult male's telemetry unit that lasted ~20 days. Over the study period (Jan 2012–Dec 2013), we collected 419,605 GPS locations. After removal of poor GPS fixes and subsampling the 30-s data, we used 121,802 locations. We generated home range or core range size estimates in cases where there were ≥100 data points in a single month (details on sample sizes by month are provided in online Appendix A and Table B.1).

In breeding year 1 all birds telemetered initiated breeding and most produced chicks ($n=6$ total), as did a large proportion of non-telemetered eagles in the DRECP (Smallwood and Thelander, 2008). Year 2 of our study was dramatically different. We know of no eagles within the DRECP, telemetered or non-telemetered, that fledged chicks. Nesting status was not known for year 3. Of the 6 birds we monitored over multiple breeding years, one sub-adult did not return to its previous territory and one sub-adult returned in year 2 but not year 3.

3.1. Size and monthly variation of golden eagle home ranges

The monthly home range (95% aLoCoH) size of golden eagles in the Mojave Desert ranged from 4.5 km² to 3547.3 km² and averaged 307.8 km² (SE ± 66.4; $n=8$ eagles and 117 months, reported as grand mean). Core ranges (50% aLoCoH) ranged from 0.1 km² to 484.1 km² and averaged 16.1 (±5.0) km² ($n=115$). Home range sizes differed among months ($F_{11,98}=2.29$, $P=0.02$), but core ranges did not ($F_{11,96}=1.61$, $P=0.11$, online Appendix Table B.2).

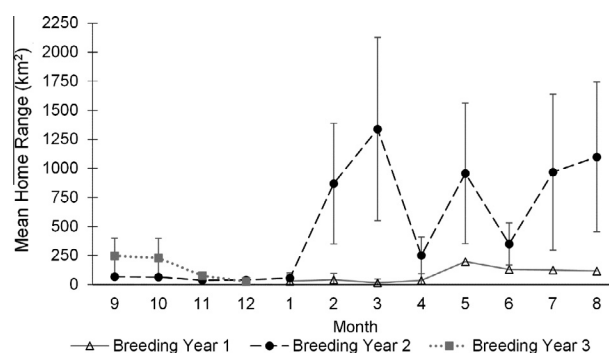


Fig. 1. Mean monthly home range size (95% aLoCoH (adaptive local convex hull), $n=8$ eagles and 117 eagle months) of golden eagles in the Mojave Desert of southern California, 2012–2013. Breeding years start in month 9 (September) and continue through month 8 (August).

Golden eagles used the smallest and least variable amount of space from November through January ($\bar{x} = 47.2 \pm 7.6$, range = 9.0–178.0 km², $n = 28$ eagle months, Fig. 1, online Appendix Fig. B.2), likely coinciding with initiation of the breeding cycle. Golden eagle space use was the most extensive and most variable in March ($\bar{x} = 751.2 \pm 476.0$, range = 4.5–3440.1 km², $n = 9$). We observed similar patterns in February ($\bar{x} = 502.2 \pm 309.7$, range = 10.5–2579.8 km², $n = 9$), May ($\bar{x} = 501.8 \pm 256.7$, range = 26.5–2604.1 km², $n = 10$), July ($\bar{x} = 508.8 \pm 315.6$, range = 34.9–3547.3 km², $n = 11$) and August ($\bar{x} = 607.8 \pm 346.5$, range = 23.4–3246.1 km², $n = 10$).

3.2. Description of intrinsic and extrinsic variables for monthly home ranges

In months when golden eagles used relatively more space, their use of that additional space was not random. The range of elevation within home ranges was highest in July ($\bar{x} = 1751.9 \pm 244.1$ m), August ($\bar{x} = 1368.5 \pm 278.6$ m), May ($\bar{x} = 1296.2 \pm 236.8$ m), and June ($\bar{x} = 1270.2 \pm 264.0$ m). These months coincided generally with both the months with greatest number of days above 32.2 °C and larger home range sizes. As an example, temperatures were >32.2 °C for ≥ 30 days/month in July and August of 2012 and 2013 (online Appendix Fig. B.2). Likewise, the range of elevation within a home range was positively but weakly correlated with the number of days above 32.2 °C ($r = 0.354$). The months when home ranges were of relatively small size and variability (November–January) were also months when eagles used the lowest range of elevation ($\bar{x} = 652.2 \pm 75.0$ m) and there were zero days above 32.2 °C. The duration and frequency of long distance movements to cooler, higher elevation sites, was greatest during post-breeding months. Our study eagles traveled to higher elevation sites on trips of 2–10 days and then returned to desert nesting habitat for a similar amount of time. All birds made trips from the desert to the higher elevation sites. The monthly variance of roughness throughout home ranges seemed unrelated to the amount of space used by the birds ($\bar{x} = 1.1 \pm 0.002$, range = 1.0–1.1 km²).

The other topographical features of the home range landscape changed only slightly with the amount of space used. On average, canyon landscapes made up 60% ± 0.6% of the mean home range (range = 37–71%). Ridges were the next most abundant topographic feature ($\bar{x} = 34\% \pm 0.5\%$, range = 21–46%), followed by gentle ($\bar{x} = 5\% \pm 0.5\%$, range = 0.2–42%), and steep slopes ($\bar{x} = 2\% \pm 0.04\%$, range = 0.4–3%).

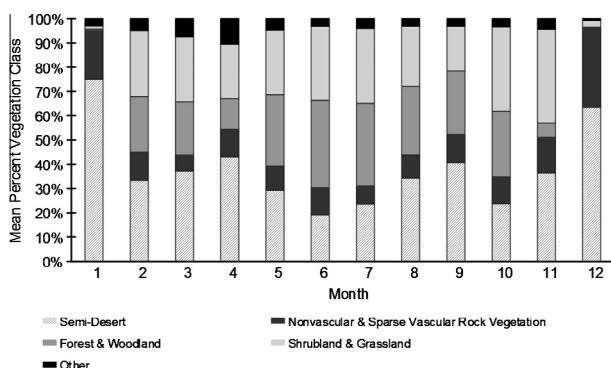


Fig. 2. The mean percent of GAP vegetation classes found within the home ranges (95% adaptive local convex hull, aLoCoH) of eight golden eagles in the Mojave Desert of southern California, 2012–2013 (calendar years). The “other” category includes the following low frequency vegetation classes: agricultural vegetation, aquatic vegetation, developed & other human use, open water, and recently disturbed or modified.

Differences in monthly home range size and space use patterns were reflected in use of vegetation classes (Fig. 2). Vegetation within golden eagle home ranges was predominantly semi-desert; that cover type was used most in January (75% of cover within home ranges) and December (64%), when birds were at lower elevations. Nonvascular & sparse vascular rock vegetation occurred at highest proportions in December (32%), January (20%), and November (15%). When birds used higher elevation habitat types during May, June, and July, forest and woodland was the dominant vegetation type (30%, 36%, 34%, respectively), closely followed by shrubland and grassland (27%, 30%, 31%). Monthly patterns of vegetative composition of core ranges were similar to home ranges (online Appendix Fig. B.3).

Golden eagle use of space varied among the breeding years and was smallest in year 1 (Fig. 1; $\bar{x} = 5.1 \pm 0.8$, range = 0.3–15.9 km², $n = 38$ eagle months), when all eagles attempted to nest. Average space use and variation of space use was largest in year 2 ($\bar{x} = 23.2 \pm 9.3$, range = 0.1–484.2 km², $n = 60$) when none of our telemetered eagles successfully nested. Space used during the first 4 months of breeding year 3 was large ($\bar{x} = 14.2 \pm 7.2$, range = 0.5–140.6 km², $n = 19$) and consistent with a more typical year with few nesting attempts. Similar trends were visible when we organized the home ranges according to calendar, rather than biological, year (2012, $\bar{x} = 4.4 \pm 0.5$; range = 0.2–15.9 km², $n = 59$; 2013, $\bar{x} = 27.5 \pm 9.7$, range = 0.1–484.2 km², $n = 58$).

The sub-adult golden eagles we tracked used more space (home range size $\bar{x} = 841.61 \pm 194.70$, range = 4.5–3547.3 km², $n = 2$ eagles, 35 eagle months) than the adults ($\bar{x} = 79.9 \pm 9.2$, range = 8.8–411.6 km², $n = 6, 82$; because of the small sample sizes for different age and sex, we perform no statistical tests and only report means and ranges for these comparisons). In contrast, the amount of space used by the male ($\bar{x} = 257.0 \pm 74.5$, range = 8.8–3440.1 km², $n = 4, 60$) and female ($\bar{x} = 361.2 \pm 111.9$, range = 4.5–3547.3 km², $n = 4, 57$) eagles differed only slightly. These patterns were also reflected in core range, such that sub-adult core range size ($\bar{x} = 42.9 \pm 16.2$, range = 0.3–484.2 km², $n = 2, 34$) was larger than that of adults ($\bar{x} = 4.8 \pm 0.5$, range = 0.1–24.1 km², $n = 6, 81$). Likewise, core ranges of males ($\bar{x} = 14.0 \pm 5.2$, range = 0.4–276.9 km², $n = 4, 60$) were only slightly different from those of females ($\bar{x} = 18.2 \pm 8.9$, range = 0.1–484.2 km², $n = 4, 55$). However, when we consider only adults, male home ranges were smaller than those of females (males: $\bar{x} = 53.0 \pm 6.2$, range = 8.8–303.2 km², $n = 3, 49$; females: $\bar{x} = 119.9 \pm 19.0$, range = 9.0–411.6 km², $n = 3, 33$). A similar effect was also seen in the core range size of adult males ($\bar{x} = 3.5 \pm 0.4$, range = 0.4–15.9 km², $n = 3, 49$) and adult females ($\bar{x} = 6.8 \pm 0.9$, range = 0.1–24.1 km², $n = 3, 32$).

3.3. Covariation between extrinsic and intrinsic variables and monthly home range size

Models with support in the data (AICc weight > 0.01) confirmed that patterns in space use by our eight eagles corresponded with breeding year and elevation variability within monthly home ranges. Although the best model containing only these 2 variables did not have overwhelming support in the data (AICc weight = 0.19), it did include the only variables whose importance showed support in the data (importance = 1.00; Table 1). Breeding year (and thus breeding status) and elevation variability were positively associated with and highly important in determining size of the home range. All other models with support in the data included these two variables and combinations of other variables that were otherwise unimportant (online Appendix Table B.4).

Core range size was positively associated with proportion of canyon, proportion of gentle slope, elevation variability, and number of days > 32.2 °C (Table 1; online Appendix Table B.5). The best

Table 1

Model-averaged coefficients, from Akaike's information criteria (AICc) of linear mixed effects models^a, to explain variable influences on temporal size patterns of home range (95% adaptive localized convex hull (aLoCoH, $n = 8$ eagles and 117 eagle months) or core range (50% aLoCoH, $n = 8$ eagles and 115 eagle months) for golden eagles in the Mojave Desert of southern California, 2012–2013.

	Variable	Estimate	Adjusted SE	Importance
Monthly home range (95% aLoCoH)	(Intercept)	0.567	4.712	
	Breeding Year 2	0.708	0.154	1.00 ^c
	Breeding Year 3	0.743	0.240	
	Canyon	1.688	1.959	0.35
	Gentle Slope	1.944	1.958	0.38
	Elevation	1.669	0.125	1.00
	Variability			
	Roughness	3.854	6.474	0.3
	Variability			
	Temp > 32.2 ^b	0.004	0.008	0.25
Monthly core range (50% aLoCoH)	(Intercept)	−3.362	0.920	
	Breeding Year 2	0.372	0.225	0.32 ^c
	Breeding Year 3	0.480	0.310	
	Canyon	5.869	1.561	1.00
	Gentle Slope	9.588	2.558	1.00
	Elevation	1.940	0.293	1.00
	Variability			
	Roughness	3.510	3.386	0.36
	Variability			
	Temp > 32.2 ^b	0.018	0.008	0.85

^a Results are based on variables from objective 3, the log transformation of range sizes, and the random effects month and individual bird.

^b Number of days above 32.2 °C (The data were from NOAA's National Climatic Data Center, Global Historical Climatology Network- monthly, version 3; was reported as 90 °F; equal to ~32.2 °C).

^c Importance score for breeding year is based on the inclusion of the categorical variable as a whole.

model for core home range included all variables for which variable importance showed support (importance > 0.85; Table 1). All other models included breeding year (variable importance = 0.32) or included a subset of important variables (see online Appendix B, Table B.5).

3.4. Overlap of eagle home ranges and development focal areas

Monthly home ranges of the eight golden eagles we monitored contained from 0 to 483.9 km² of DFA land. The amount of overlap depended on the DFA alternative (Figs. 3 and 4) and month (Fig. 4). DFA alternative 1 (the smallest DFA) overlapped the least (generally < 1%) with telemetered eagle home ranges. The other DFA alternatives showed similar patterns of overlap, except for the month of January.

The most overlap occurred with DFA alternative 5 (24%) in the month of January (Fig. 4E). January overlap was slightly less with DFA alternative 3 (23%), alternative 4 (21%), and alternative 2 (20%). The remaining months had overlaps often well below 10% for each of the DFA alternatives.

4. Discussion

Golden eagles in the Mojave Desert showed seasonal variation in home range size and in use of vegetation classes that was tied to breeding status and environmental variation. These eagles also would have encountered focal areas for desert renewable energy development especially during the beginning of the breeding cycle (Fig. 4). This new information has important implications for understanding eagle biology and for management of this species in the face of rapid growth of renewable energy development.

4.1. Eagle ecology

Home range size of non-migratory golden eagles varies between breeding and non-breeding seasons (Marzluff et al., 1997; Moss et al., 2014; Watson et al., 2014) and migratory golden eagles move long distances seasonally (Miller et al., 2014). However, the constancy and extent of the temporal variation in movements we report is unprecedented for a putatively sedentary (non-migratory) population. This is true in spite of the relatively small number of eagles we telemetered (our sample size is similar to that of the three other studies noted above; home range estimation for $n = 9$ territories in Marzluff et al., 1997; $n = 9$ territories, Moss et al., 2014; $n = 10$ territories Watson et al., 2014).

The temporal variation we recorded is almost certainly linked to two primary factors – eagle breeding ecology and seasonal variation in weather and prey availability. Previously it had been assumed that golden eagles in the Mojave begin to display breeding behavior in December (LL, personal observations). Our analyses suggest that this behavior may begin much earlier, in September or October (Fig. 1). When eagles nested, as the majority did in breeding year 1, home ranges stayed small through April. In contrast, when they did not nest (year 2), eagles were not tied to a nest and moved long distances in February and March. This high variability of space use, especially in February through May, likely is due to the inter-annual and inter-individual variation in nest success among individual eagle pairs (in year 1 some nests failed ($n = 3$), others fledged chicks ($n = 5$)) and the concomitant change in behavior that accompanied nest failure.

The monthly variation in movement we recorded also was tied to habitat features, such that specific vegetation types and topographies were associated with larger home ranges (Fig. 2; Table 1; online Appendix Table B.3). Eagles did not expand their small home ranges equally in all directions (i.e., they did not go from a small circular home range to a larger circular home range). Instead, during movements away from the nest eagles predictably went uphill, from the desert to the mountains. When this happened, the proportion of the home range composed of desert and desert rock vegetation declined and the proportion of the home range composed of mountainous cover types – forest and mid-elevation grasslands – increased.

Desert dwellers, whether they be human or animal, prefer to find refugia from the heat of the summer sun. Seasonally migrant human retirees (appropriately called “snowbirds”) escape the summer heat by retreating north. Desert dwelling mammals avoid the heat by restricting activity to nocturnal and crepuscular hours and are almost never diurnal (Hoffmeister, 1986). Even reptiles and many insects are only seasonally active during the desert day (Casey, 1976; Davis and DeNardo, 2010). Thus, it should come as no surprise that Mojave-nesting eagles also chose to desert the desert during the hottest periods of the year, when they did not have chicks in the nest and when diurnally accessible food would be least available.

Migration theory suggests an alternate hypothesis of the origin of movement patterns that we observed. Neotropical migrants are thought to have evolved in the tropics and moved to higher latitudes to nest because of intense competition in the tropics and unfilled niches at temperate latitudes (Newton, 2008). Similarly, although we propose that desert eagles are summering in the mountains, the patterns we observed may be alternately explained by mountain eagles that move to the desert to nest. Life in the desert is difficult; success rates and productivity are low compared to those just outside the desert, but cliffs for nesting are abundant. If this alternative hypothesis is correct, then desert eagles could be subordinate mountain eagles that cannot successfully compete for (presumably) higher quality territories found in the prey-rich mountains and higher elevation grasslands. Their

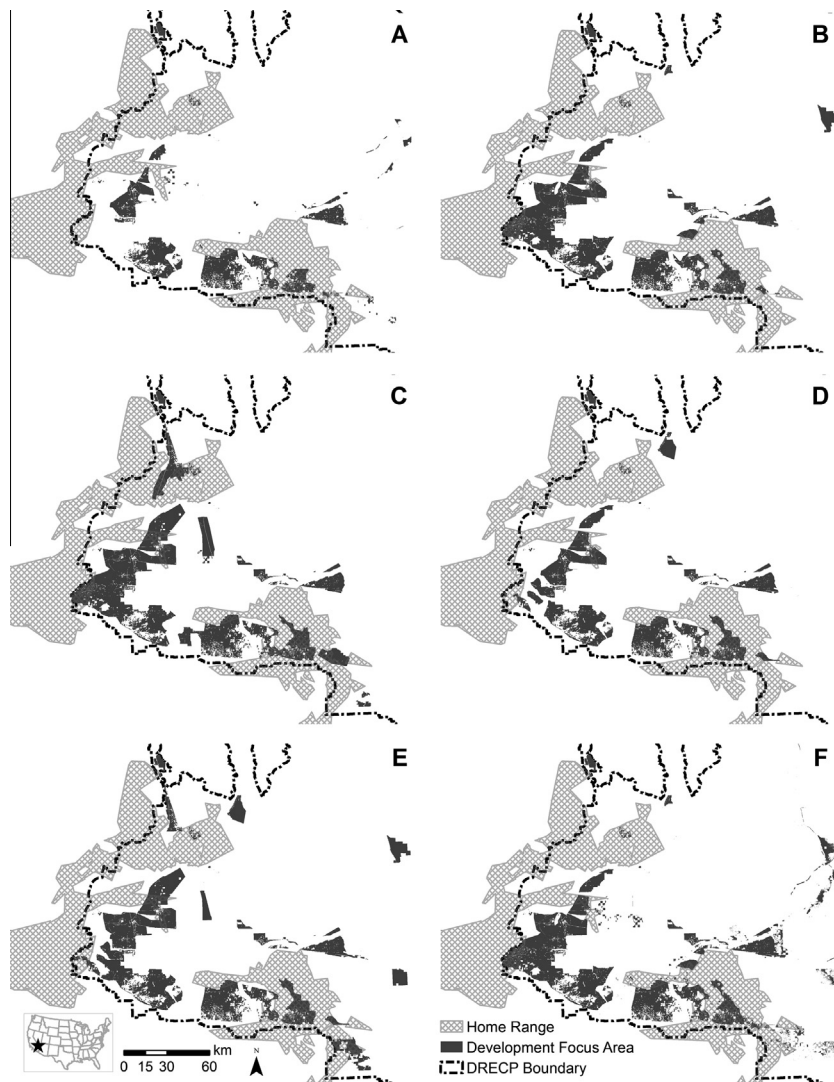


Fig. 3. Overlap of 95% aLoCoH (adaptive local convex hull) monthly home ranges ($n = 8$ eagles, 117 eagle months) of golden eagles with six different alternative Development Focus Areas (DFA) of the Desert Renewable Energy Conservation Plan (DRECP) for southern California, 2012–2013. (A) Represents DFA alternative 1, (B) represents DFA alternative 2, (C) represents DFA alternative 3, (D) represents DFA alternative 4, (E) represents DFA alternative 5, and (F) represents DFA alternative 6. The DFA data layers came from Conservation Biology Institute, Alternative - DFAs, DRECP (December 2012 version). Eagles telemetered are only a small portion of those actually nesting within the DRECP, this figure is provided as an example of potential impacts not as a comprehensive survey of impacts.

use of desert nesting sites would thus be a tactic that gives them more opportunity to reproduce than they would gain by waiting for a preferred territory in the mountains to become available. These two theses are not mutually exclusive. However identifying which best fits the patterns we observed does have implications for the origins, and thus conservation, of these desert-nesting eagles.

4.2. Management of desert eagles and renewable energy development

The conceptual framework for our work is predicated on space use being a reasonable proxy of risk to eagles from renewable energy development. Because untelemetered eagles almost certainly used different space than telemetered ones, the overlap analyses we presented show potential overlap between eagle home ranges and DFAs rather than comprehensively evaluating all overlap. Nevertheless, our analyses support a logical conclusion – the more space that an individual eagle uses, the more likely it is to encounter renewable energy projects.

The DRECP is intended to provide effective protection and conservation of desert ecosystems while allowing for the development

of renewable energy projects. Our analysis suggests that conservation of DRECP area golden eagles will be most effective if it includes management of habitat outside of the plan area, where eagles encounter both risk and habitat types beyond those typically associated with deserts. For example, conservation measures proposed in the Draft DRECP focus on protecting nests and a 1-mile buffer around nests. As is demonstrated in this study, eagle habitat use is complex and likely not fully captured with a 1-mile buffer. Managers planning for the DRECP's adaptive approaches to habitat conservation may wish to consider these desert golden eagles' seasonal changes in behavior and reliance on habitat outside the DRECP boundary.

Our data provide important perspective on the design of surveys for highly mobile species. Golden eagles are a high priority for management in arid ecosystems, and substantial effort has been expended towards surveys for them. However, some of these surveys have been conducted when our data suggest that territorial golden eagles were irregularly present in the desert. Surveys designed to count territorial eagles would be best conducted when eagles are present in the desert, are holding

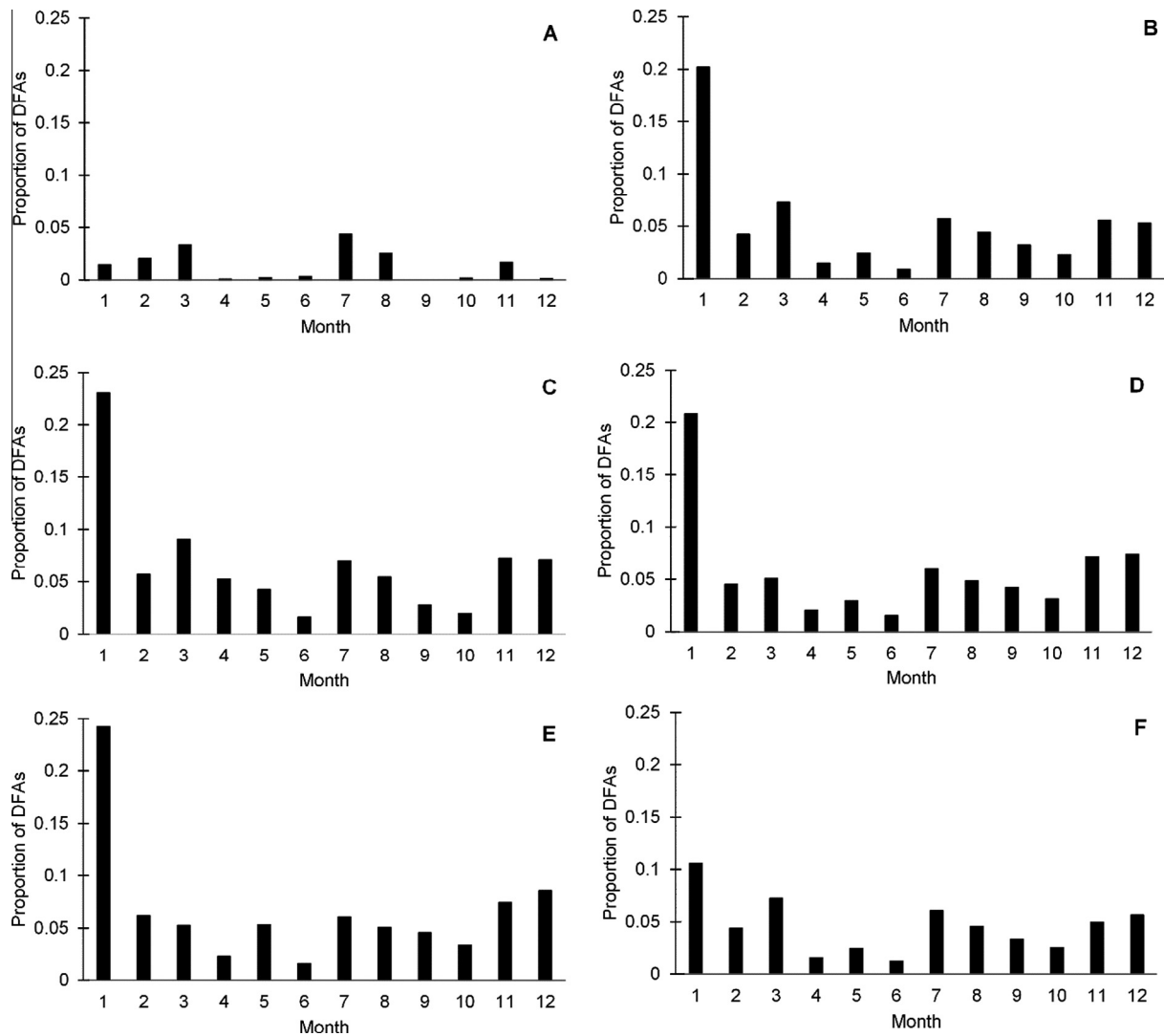


Fig. 4. The proportion of DFA lands that overlap the monthly home ranges (95% aLoCoH (adaptive local convex hull)) of golden eagles in the Mojave Desert of southern California, 2012–2013 (calendar years; $n = 8$ eagles, 117 eagle months). (A) Represents DFA alternative 1, (B) represents DFA alternative 2, (C) represents DFA alternative 3, (D) represents DFA alternative 4, (E) represents DFA alternative 5, and (F) represents DFA alternative 6.

territories, and are most likely to be detected – specifically when home ranges are smallest (from November through January). Surveys completed during early summer, May–July, may capture productivity, but are likely to miss adult eagles during years of limited nesting. Thus results of surveys conducted during summer (post-fledging) may be comparatively uninformative, and possibly erroneous, with regards to eagle demography and territory occupancy. Likewise, our data suggest that surveys designed to estimate the size of the breeding component of the population may produce estimates that are highly dependent on the proportion of territorial breeders attending nests in any given year. For example, surveys for territory occupancy conducted in year 1 of our study would provide a dramatically different result than similar surveys in year 2 of our study.

5. Conclusions

Space use by golden eagles appears to provide a reasonable proxy for pre-construction evaluation of potential influences to birds from renewable energy development. In the case of eagles in California deserts, renewable energy is being developed under a management plan (the DRECP) that only has responsibility for

a subset of lands that these birds use throughout the year. Management for species with movements that take them outside of areas of local control (e.g., Neotropical migrants, migratory waterfowl and waders) has been improved through incorporation of range-wide conservation actions. Similarly, management for golden eagles within the DRECP and other conservation areas likely will be most effective if it includes recognition of and mitigation for eagles that use space beyond jurisdictional boundaries.

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Appendices: Supplementary material

Detailed information on methods and some results, including the comparison of 95% and 50% aLoCoH, minimum convex polygons, and kernel density estimators of the monthly home ranges (Appendix A), and golden eagle data descriptions and summaries (Appendix B) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author. Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocon.2015.03.020>.

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