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PATTERNS OF SPATIAL DISTRIBUTION OF GOLDEN EAGLES ACROSS NORTH AMERICA: HOW DO THEY FIT INTO EXISTING LANDSCAPE-SCALE MAPPING SYSTEMS?

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ABSTRACT.—Conserving wide-ranging animals requires knowledge about their year-round movements and resource use. Golden Eagles (*Aquila chrysaetos*) exhibit a wide range of movement patterns across North America. We combined tracking data from 571 Golden Eagles from multiple independent satellite-telemetry projects from North America to provide a comprehensive look at the magnitude and extent of these movements on a continental scale. We compared patterns of use relative to four alternative administrative and ecological mapping systems, namely Bird Conservation Regions (BCRs), U.S. administrative migratory bird flyways, Migratory Bird Joint Ventures, and Landscape Conservation Cooperatives. Our analyses suggested that eagles initially captured in eastern North America used space differently than those captured in western North America. Other groups of eagles that exhibited distinct patterns in space use included long-distance migrants from northern latitudes, and southwestern and Californian desert residents. There were also several groupings of eagles in the Intermountain West. Using this collaborative approach, we have identified large-scale movement patterns that may not have been possible with individual studies. These results will support landscape-scale conservation measures for Golden Eagles across North America.

KEY WORDS: *Golden Eagle*; Aquila chrysaetos; *hierarchical clustering*; *landscape-scale movements*; *satellite telemetry*.

PATRONES DE DISTRIBUCIÓN ESPACIAL DE *AQUILA CHRYSAETOS* A TRAVÉS DE AMÉRICA DEL NORTE: ¿DE QUÉ MANERA SE INCLUYEN EN LOS SISTEMAS ACTUALES DE MAPEO A ESCALA DE PAISAJE?

RESUMEN.—La conservación de animales de distribución amplia requiere conocer sus movimientos a lo largo del ciclo anual y su uso de recursos. *Aquila chrysaetos* presenta un amplio rango de patrones de movimiento a través de América del Norte. Combinamos datos de seguimiento de 571 ejemplares de *A. chrysaetos* de múltiples proyectos independientes de telemetría satelital de América del Norte para proporcionar un

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análisis completo sobre la magnitud y el alcance de estos movimientos a escala continental. Comparamos los patrones de uso en relación a cuatro sistemas de mapeo administrativos y ecológicos, específicamente las Regiones para la Conservación de Aves (RCAs), las rutas administrativas de aves migratorias de Estados Unidos, los Emprendimientos Mixtos de Aves Migratorias y las Cooperativas para la Conservación de Paisajes. Nuestros análisis sugieren que las águilas capturadas inicialmente en el este de América del Norte utilizaron el espacio de una manera diferente a las capturadas en el oeste de América del Norte. Otros grupos de águilas que exhibieron patrones distintos de uso del espacio incluyeron individuos migradores de larga distancia provenientes de latitudes septentrionales e individuos residentes de California y provenientes del sur. También hubo numerosas agrupaciones de águilas en el oeste inter-montano. Utilizando este enfoque colaborativo, identificamos patrones de movimientos a gran escala que no hubieran sido posibles a partir de estudios individuales. Estos resultados apoyan las medidas de conservación a escala de paisaje para *A. chrysaetos* a lo largo y ancho de América del Norte.

[Traducción del equipo editorial]

Conservation of a single species is most effectively achieved when considered within landscapes of appropriate biological relevance (Fedy et al. 2014). Such an approach requires data-driven planning that incorporates the different requirements exhibited by individuals at various stages of their life cycle. However, developing effective conservation plans can be challenging for wide-ranging species that exhibit a diversity of movement patterns across multiple jurisdictional boundaries throughout their lives (Marra et al. 2011).

The Golden Eagle (*Aquila chrysaetos*) is a highly mobile and long-lived species that exhibits delayed sexual maturity (Kochert et al. 2002, Watson 2010). Golden Eagles occur across North America and exhibit a wide range of movement patterns. On one end of the movement spectrum are sedentary or resident eagles that may spend their entire lives within a relatively small geographic area (Steenhof et al. 1984). On the other end of the spectrum are the long-distance migrants that travel tens of thousands of kilometers across a continent during their lives (Brodeur et al. 1996, McIntyre et al. 2008, Miller et al. 2014). However, even Golden Eagles that are considered residents may exhibit a wide range of movements that vary interannually and by season (Watson et al. 2014, Poessel et al. 2016). Overall, the movement patterns of Golden Eagles, regardless of their migratory status, may vary by age, breeding status, and resource availability (Steenhof et al. 1984, Watson 2010, Braham et al. 2015, Poessel et al. 2016). Such diversity of movement behaviors and patterns defies simple classification of landscape use, which in turn creates challenges to establishing wide-ranging conservation measures across the species' vast North American range.

In addition to informing overall conservation planning, improved understanding of Golden Eagle movements may have direct application to management of the species. The Golden Eagle's high mobility and diversity of movement patterns carry individuals across multiple political, administrative, and ecological boundaries (Brodeur et al. 1996, McIntyre et al. 2008, Braham et al. 2015, Poessel et al. 2016). Variation in regulatory and land-management priorities among various administrative units may have consequences for Golden Eagles. For example, an administrative unit may be disproportionately used by eagles migrating from their breeding locations in another, possibly distant, unit. In contrast, a unit may contain the majority of movements by a resident population. Within the U.S.A., the Bald and Golden Eagle Protection Act (16 United States Code 668–668d; hereafter Act) and subsequent rules authorize the U.S. Fish and Wildlife Service (Service) to permit take (defined by regulations as disturbance, injury, or death of eagles, or destruction of nests and eggs), after a quantitative determination that the permitted take is "... compatible with the goal of stable or increasing populations" within population management units (Eagle Management Units [EMU]; U.S. Fish and Wildlife Service 2009). Lacking definitive ecological information to delineate Golden Eagle populations in the western U.S.A., the Service used North American Bird Conservation Regions (BCRs; U.S. North American Bird Conservation Initiative Monitoring Subcommittee 2007) to define EMUs for the species when it created a permitting process for incidental take in 2009 (Babcock et al. 1998, U.S. Fish and Wildlife Service 2009). In May 2016, the Service released a draft Programmatic Environmental Impact Statement proposing to adopt the U.S. administrative migratory bird flyways (hereafter, Flyways; U.S. Fish and Wildlife Service 2014) as EMUs for Golden Eagles, based on an analysis of

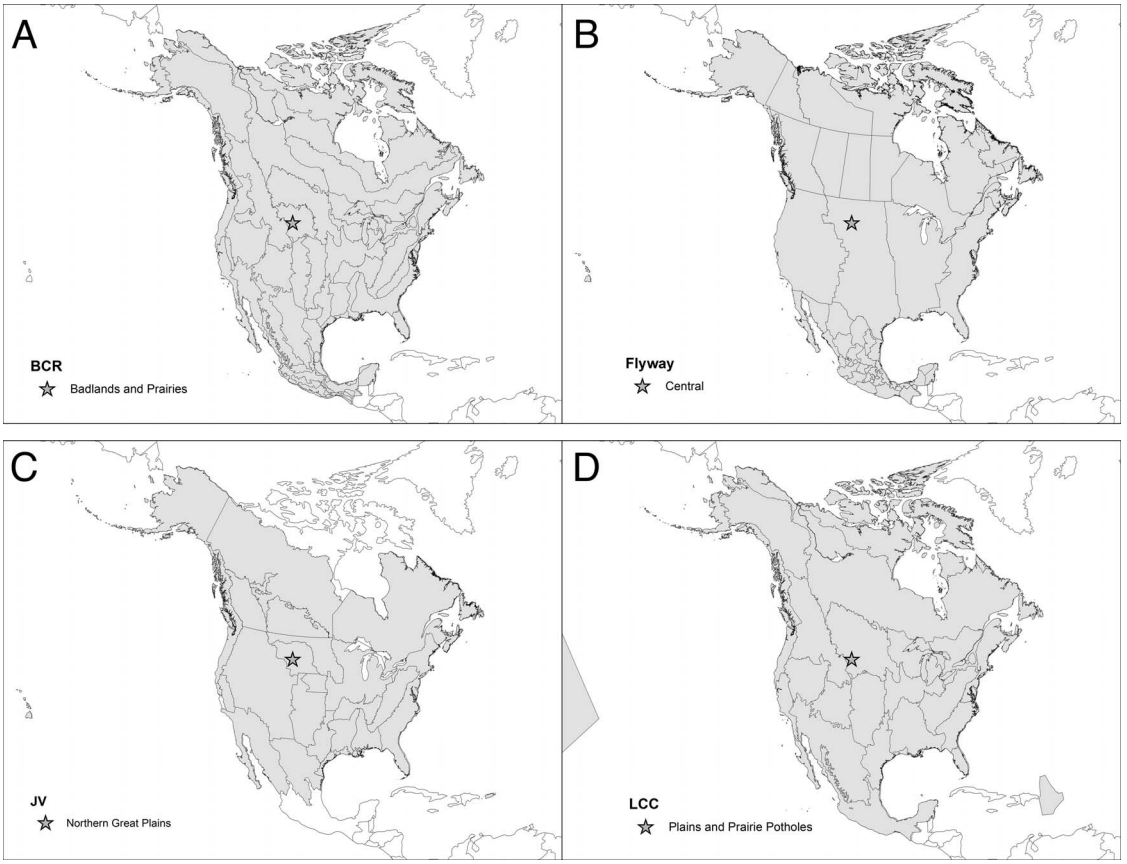

Figure 1. Boundaries of (A) Bird Conservation Regions (BCR), (B) Flyways, (C) Joint Ventures (JV), and (D) Landscape Conservation Cooperatives (LCC) in North America.

banding locations and subsequent locations of mortality recoveries (U.S. Fish and Wildlife Service 2016). This analysis demonstrated that 84% of recoveries of banded Golden Eagles were confined within the same Flyway unit in which the birds originated, whereas only 73% of recoveries were within the same BCR (U.S. Fish and Wildlife Service 2016). This in part led the Service to propose using the Flyways as management units for regulating take. Although Flyways may be an appropriate management unit for regulating take over broad geographic regions, alternative administrative and ecological mapping systems also may have utility for regional conservation planning purposes.

In this study, we combined tracking data from 571 Golden Eagles from 34 studies in North America to evaluate the distribution of Golden Eagle movements relative to four administrative mapping systems that focus on avian conservation and management: Flyways, BCRs, Landscape Conservation Cooperatives (LCCs), and Migratory Bird Joint Ventures (JVs; Fig. 1). Our research addresses the following eagle management research questions: (1) Do movements of Golden Eagles align with any of the preexisting mapping systems described above, such that the movements of identifiable subpopulations of eagles are confined to specific, definable locations/regions, and the extent of those regions are well-described by the boundaries of the preexisting mapping systems? and (2) How does an eagle's migratory behavior affect conformity to these systems? Possible outcomes included determining that (a) eagle movements were adequately represented by one or more mapping systems; (b) eagle movements were not well represented by any of the assessed systems, but results suggested an alternative

classification (e.g., perhaps combinations of existing units from single or multiple mapping systems that could be adopted for eagle management); or (c) eagle movements were too complex or diverse for all populations or age-classes to conform to a common geography. Given the migratory nature of some North American Golden Eagle populations, and the high degree of mobility of many eagles, we predicted that the most appropriate systems would be either the Flyways, because they were intended for management of a migratory group of birds, or the JVs, because they integrate and synthesize landscape attributes over continental and regional scales. In contrast, the BCRs and LCCs tend to be small in area relative to known eagle ranging behavior, and were generally developed for conservation of a wide range of species with varying life histories and characteristics.

METHODS

History of Mapping Systems. The boundaries for each of the relevant mapping systems were delineated considering various applications, leading to some marked differences in geography among units. The Flyways (i.e., Atlantic, Mississippi, Central, and Pacific) were devised primarily by the Service to help coordinate management of waterfowl populations across state and national boundaries (U.S. Fish and Wildlife Service 2014, 2015). We could find no direct accounts of the procedures followed to designate the boundaries of Flyway units, which follow political boundaries (sometimes at the county level). Given that the first use of administrative Flyways dates to 1947, we suspect the decisions were informed primarily by band returns of hunter-killed waterfowl (U.S. Fish and Wildlife Service 1984). Unlike Flyways that focused on waterfowl populations, habitat JVs were originally envisioned to help conserve waterfowl habitat (U.S. Fish and Wildlife Service 1986). The 11 habitat JVs that were established before 1999 considered only waterfowl habitat, whereas the nine JVs established later included all birds in their initial planning processes (Migratory Bird Joint Ventures 2016). Several JV boundaries were influenced by, or directly followed, BCR boundaries (see description below) or ecoregional boundaries that informed the development of BCR boundaries. Currently, all the JVs consider all bird species for their conservation planning and implementation efforts.

In contrast to Flyways and the first JVs that focused on a single non-raptor taxonomic group, the BCRs were developed by an international team in 1998 to reflect the current understanding of bird species distributions and requirements, as well as conservation challenges (Babcock et al. 1998). The BCR boundaries were derived from Commission for Environmental Cooperation (1997) level II, III, and IV ecoregions that were intended to map ecological regions of North America based on "enduring" components of ecosystems such as soil, landform, and major vegetation types. The stated purposes of BCRs included facilitating communication among bird conservation initiatives; systematically apportioning North America into conservation units; facilitating a regional approach to bird conservation; promoting new, expanded, or restructured partnerships; and identifying overlapping or conflicting conservation priorities. Lastly, the LCC Geographic Areas were formed in 2010 by considering BCRs, Omernik ecoregions, Freshwater Ecoregions, and existing national planning partnerships such as the JVs (U.S. Fish and Wildlife Service 2010). The goal for use of the LCC mapping system was conservation of both terrestrial and aquatic species, so some BCRs were split or combined to accommodate important watersheds.

Field Protocols. Golden Eagles were captured and tracked for various studies (Table 1). All eagles were fitted with transmitters mounted on custom-made backpacks and standard United States Geological Survey (U.S.G.S.) leg bands; some were also fitted with unique colored visual ID bands or patagial tags. Transmitters included Argos-only Platform Transmitting Terminals (PTTs), Global Positioning System (GPS)/Argos PTTs, and GPS/Global System for Mobile Communications (GSM) units from various manufacturers, which varied in shape, size, and mass (Table 1). Most transmitters were attached via variations of the "Y-harness" constructed of Teflon ribbon (Buehler et al. 1995). With harness material attached, transmitters typically weighed between 55 and 100 g, amounting to $\leq$3% of the mass of tagged eagles (Stahlecker et al. 2015). For additional details on methods specific to each study, see references in Table 1.

Initial Post-processing of Fixes. Argos fixes represented only those in location classes 3, 2, and 1 (estimated error radii of $<$250 m, 250–500 m, and 500–1500 m respectively), unless the researcher had already screened the points and decided to retain lower-quality location classes (CLS [Collecte Localisation Satellites] 2011, McIntyre et al. 2008). If the Argos fixes had not been previously screened before

Table 1. Sources of data on Golden Eagle fixes.

STUDY	CONTRIBUTOR(S)	*n*	START	FINISH	PLATFORM	MASS	REFERENCES
WGET (USFWS)	B. Woodbridge	70	4 May 2014	4 December 2015	GPS/Argos	45	B. Woodbridge unpubl. data
Harmata GOEA study	A. Harmata	20	2 March 2011	23 September 2014	Argos	32	A. Harmata unpubl. data
PG&E GOEA study	B. Wymore	9	3 December 2010	5 January 2015	GPS/Argos	70	B. Wymore unpubl. data
Region 6 FWS GOEA WYCONE	B. Smith, K. Kritz, M. Lockhart, D. Stahlecker, J. Jorgensen, A. Dwyer, L. Snyder, B. Millsap, R. Murphy	32	14 May 2014	11 March 2015	GPS/Argos	45	B. Smith unpubl. data
Quebec Golden Eagle movement study	S. Brodeur and M. Fuller	6	1 August 1992	9 August 1993	Argos	95	Brodeur et al. 1996
Livingston, Montana Golden Eagle Movement Study	R. Crandall, B. Bedrosian, D. Craighead	30	25 March 2011	9 February 2015	GPS/Argos	30, 45, 70	Crandall et al. 2015, R. Crandall et al. unpubl. data
Denali Golden Eagle Movement Study, Phase 1	C. McIntyre, M. Collopy, D. Douglas	48	24 July 1997	17 May 2002	Argos	95	McIntyre et al. 2008
BLM GOEA study	C. Hummel	7	13 June 2014	18 November 2015	GPS/Argos	70	C. Hummel unpubl. data
Golden Eagles in the Altamont Pass WRA and Diablo Range, California	D. Bell, J. DiDonato, H. Wilson, C. Nowell, R. Culver, S. Smallwood, F. Garland, C. Richardson, D. Driscoll, B. Latta, A. Fateman, D. Seever, M. Taylor, H. Beeler, C. Battistone, M. Lanzone, A. McGann, T. Katzner, C. Lenihan	10	19 December 2012	22 June 2015	GPS/Argos, GPS/GSM	70	D. Bell unpubl. data
HawkWatch International Migratory Golden Eagle Tracking Study 1999–2009	J. Smith, J. DeLong, K. Donohue, R. Gerhardt, L. Greenwood, D. Hengstenberg, Z. Hurst, K. Jacobson, W. Lehman, M. McCaustland, N. McNett, M. Neal, C. Neri, S. Page, A. Peterson, D. Sandack, D. Sherman, M. Vekasy, J. Watson, K. Woodruff	33	5 October 1999	27 October 2009	Argos, GPS/Argos	65, 100	Smith 2002, 2010, Smith et al. 2002, Goodrich and Smith 2008

Table 1. Continued.

Study	Contributor(s)	*n*	Start	Finish	Platform	Mass	References
WA Adult Eagle Movements 2004–2014	J. Watson	6	8 March 2004	18 October 2008	Argos	95	Watson et al. 2014
WA Adult Eagle Movements 2004–2014	J. Watson	7	23 February 2005	12 October 2014	GPS/Argos	70	
Kentucky GOEA study	K. Slankard	1	10 February 2015	25 May 2015	GPS/Argos	?	K. Slankard unpubl. data
CCB Mid-Atlantic Golden Eagles	E. Mojica	3	7 March 2008	4 August 2014	GPS/Argos	70	E. Mojica and B. Watts unpubl. data
Midwest Golden Eagle Project	M. Martell, K. Hall, S. Mehus	6	25 March 2009	23 April 2015	GPS/Argos	70	M. Martell unpubl. data
EarthSpan GOEA study	M. Fuller, E. Craig, M. Yates	21	1 September 1992	14 November 1996	Argos	?	M. Fuller and E. Craig unpubl. data
NYSDEC GOEA tracking	NYSDEC	1	20 January 2008	30 March 2010	GPS/Argos	?	C. McIntyre unpubl. data
Gerhardt GOEA study	R. Gerhardt	4	9 February 2011	29 December 2014	GPS/Argos	70	R. Gerhardt unpubl. data
RVRI Adult Migratory GOEA Study	R. Domenech, A. Shreading, B. Bedrosian	15	29 March 2007	19 February 2015	Argos (4), GPS/Argos (22), GPS/GSM (1)	30, 45, 70, 90	RVRI unpubl. data
RVRI/MPG Ranch Adult Wintering GOEA Study	R. Domenech, A. Shreading	12	28 February 2014	18 February 2015	GPS/Argos	45, 70	RVRI unpubl. data
Four Corners Golden Eagle Study	R. Murphy	69	3 July 2010	28 July 2015	GPS/Argos	30, 45, 70	B. Millsap unpubl. data; R. Murphy unpubl. data
Eastern Montana GOEA Study	B. Bedrosian	39	8 July 2012	1 May 2015	Argos, GPS/Argos	45, 65	B. Bedrosian unpubl. data
HawkWatch International and U.S. DoD	S. Slater	31	25 June 2013	21 November 2014	GPS/Argos	45	S. Slater and R. Knight, unpubl. data
ADFG Golden Eagles	T. Booms, C. Barger, S. Lewis, C. McIntyre	30	24 March 2014	9 March 2016	GPS/Argos	45	T. Booms unpubl. data

Table 1. Continued.

STUDY	CONTRIBUTOR(S)	*n*	START	FINISH	PLATFORM	MASS	REFERENCES
AL DCNR / Friends of TNF - Katzner Lab Grp	Soehren, Threadgill, Stober, Miller, Lanzone	3	31 January 2014	21 January 2015	GPS/GSM	78.5, 95	Bohrer et al. 2012, Miller 2012, Duerr et al. 2012, 2014, Katzner et al. 2012b, 2012a, 2015a, 2015b, Lanzone et al. 2012, Miller et al. 2014, 2016, Dennhardt et al. 2015a, Morneau et al. 2015, Nelson et al. 2015, Dennhardt et al. 2015b, Jachowski et al. 2015
DOAS - Katzner Lab Grp	Van Arsdale, Salo, Lanzone	3	8 February 2014	9 April 2014	GPS/GSM	80	
Miller et al. - Katzner Lab Grp	Miller, Lanzone, Katzner, O'Malley	12	16 February 2009	31 December 2014	GPS/GSM	95	
TWRA - Katzner Lab Grp	Somershoe, Kelly, Miller, Lanzone	6	5 February 2013	25 January 2015	GPS/GSM	95	
USFWS - Katzner Lab Grp	Koppie, Lanzone	2	20 March 2012	11 November 2014	GPS/GSM	95	
VDGIF - Katzner Lab Grp	Miller, Lanzone, Cooper, Katzner	14	7 February 2012	24 March 2014	GPS/GSM	95	
VDGIF - Katzner Lab Grp	Miller, Lanzone, Cooper, Katzner	19	16 March 2011	11 April 2011	GPS/GSM	95	
BLM-2010 - Katzner Lab Grp	Bloom, Miller, Lanzone, Katzner, Duerr, Braham, Driscoll	18	13 January 2012	10 February 2015	GPS/GSM	85	Braham et al. 2015, Duerr et al. 2015, Poessel et al. 2016
CDFW-2012 - Katzner Lab Grp	Bloom	25	15 November 2012	11 February 2015	GPS/GSM	80, 85	

submission to this study, we passed the higher-quality location class fixes through the Douglas Argos-filter algorithm (Douglas et al. 2012). Spikes with angles smaller than 15° and 25° were removed if their extension was farther than 2500 and 5000 m, respectively. We then passed fixes through several different velocity filters (20, 27.8, and 40 m/s), generated tracks for each filtered set, and selected which threshold to use based on visual inspection. At a minimum, we visually screened GPS fixes for obvious outliers, but some data sets received additional filtering and quality checks before being analyzed. To scale all observations to the same spatial scale, we then transferred both forms of eagle location data to a common, continent-wide 3-km grid and reported each fix as the center coordinates of a grid cell. Because datasets included fixes collected at various temporal scales (e.g., temporal frequencies from every 30 sec to $\geq$4 hr), we subsampled the data by selecting the first hourly fix per bird. Therefore, each dataset contributed no more than one fix per eagle per hour.

We assigned each fix to the relevant mapping unit in each of the four alternative administrative and ecological mapping systems. These four mapping systems divide North America into non-overlapping geographic regions, but the Flyways, JVs, and LCCs do not include all of North America. Our analytical approach required classification of all fixes to units. Therefore, for portions of North America not classified into a particular unit, we assigned fixes to either the appropriate Canadian province or Mexican state (for Flyways, because some provinces and states are assigned to unique Flyways), or to a combined unclassified Canada/Mexico. For example, a fix at coordinates of 45°12.405′N 105°46.722′W (NAD 83) would be assigned to the Badlands and Prairies BCR, the Central Flyway, Northern Great Plains JV, and Plains and Prairie Potholes LCC (Fig. 1). For each eagle, we then counted the subsampled fixes within each mapping system unit. The resulting four matrices (one for each mapping system) became the basis for further analyses, with each matrix having one row for each eagle, one column for each mapping unit, and the number of eagle fixes reported in each cell.

Cluster Analysis of Eagle Presence in Mapping System Units. We performed a cluster analysis to determine how the patterns of mapping-unit use by individual eagles conformed to preexisting administrative or ecological mapping systems. Individual eagles that used mapping units in similar proportions were grouped together regardless of total number of fixes per eagle because we transformed the data using a dissimilarity index that is unbiased by raw abundances (Legendre and De Cáceres 2013). For example, eagles that used the Atlantic Flyway exclusively would likely form one cluster, whereas eagles that used the Pacific and Central Flyways in similar proportions would form another cluster. We used a hierarchical clustering algorithm and performed separate analyses for each mapping system. Only counts of fixes per eagle within units informed the cluster analysis: the analyses did not consider the explicit spatial relationships among units (e.g., inter-unit distances and adjacency metrics). We transformed the summed eagle fixes per unit to a dissimilarity matrix using the Chao-Jaccard dissimilarity index (*CommEcol* package; Melo 2016) using R 3.2.2 (R Core Team 2015). The resulting dissimilarity matrix then formed the basis for a hierarchical agglomerative cluster using the flexible-beta linkage method, which sought to balance the development of compact, spherical clusters with optimizing similarity among cluster members (*cluster* package; Legendre and Legendre 1998, Maechler et al. 2015). Because cluster membership can be assigned to any number of clusters between one and the sample size, we determined the optimal number of clusters by visually inspecting plots of measures of cluster quality (average silhouette width or ASW, Hubert's gamma or HG, and point biserial correlation or PBC) and looking for the point(s) at which additional numbers of clusters failed to greatly improve clustering quality (*WeightedCluster* package; Studer 2013). After assigning each eagle to a movement cluster, we interpreted each cluster by examining which units were used by eagles in that cluster as well as by viewing maps of unit use by cluster. We also sought meaningful aggregations of mapping units. If multiple mapping units were represented in one cluster, or if several clusters were spatially contiguous and clearly nested within another cluster, we interpreted this as a suggestion that the mapping units could be combined into a single functional unit.

RESULTS

Summary of Data. We analyzed tracking data from 571 Golden Eagles, tracked for various periods between 1 August 1992 and 9 March 2016 (Fig. 2). Most of the data were from eagles tracked after 2010, although at least one eagle was being tracked at any given date during the study period, except for gaps from 10 May 1994 to 10 December 1995, 30 August

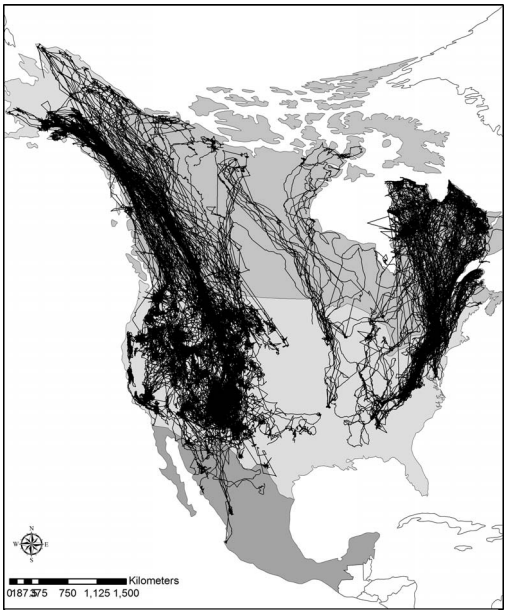

Figure 2. Telemetry fixes of 571 Golden Eagles tracked in North America between 1992 and 2016. Lines indicate unobserved straight-line paths between consecutive telemetry fixes.

1996 to 24 July 1997, and 16 January 1999 to 21 July 1999. We considered data only from eagles tracked for 22 d or longer, which was sufficient time for at least one eagle to have crossed boundaries in each mapping system. Of these, we tagged 212 eagles (37%) in their nests as flightless young, 72 as fledged hatch-year eagles (13%), and 255 as after-hatch-year eagles (45%), and the age of 32 tagged eagles was reported as unknown (6%). Minimum distance moved by eagles in these four age classes averaged 10,409 km, 7846 km, 14,860 km, and 10,058 km respectively. Mean tracking duration per eagle was 419 d (95% CI: 387–451 d), with the longest tracking duration 3131 d. Eagle locations were as far south as 20.22°N and as far north as 70.48°N.

Spatial Patterns Identified Through Cluster Analysis. The optimal number of clusters per mapping system varied from as few as five for Flyways to as many as eight for LCCs, implying that eagles could be classified into groups that shared distinctive movement behaviors based on their telemetry fixes (Table 2, Fig. 3). Distinguishing clusters representing migratory eagles from clusters containing mostly nonmigratory eagles was straightforward, because the higher maximum latitudes (i.e., most northerly locations) used by migratory eagles led to greater

Table 2. Suggested optimal number of clusters and interpretation of cluster meanings by administrative or ecological mapping system.

	Bird Conservation Regions (BCR)	Flyways	Joint Ventures (JV)	Landscape Conservation Cooperatives (LCC)
Optimal cluster number	6	5	7	8
Eastern group (units used exclusively)	Yes (8, 12, 13, 14, 22, 23, 26, 27, 28, 29, 30)	Yes (Atlantic)	Yes (Atlantic Coast, East Gulf Coastal Plain)	Yes (Appalachian, Eastern Tallgrass Prairie & Big Rivers, North Atlantic, South Atlantic, Upper Midwest & Great Lakes)
Great Basin/Intermountain West	Yes	No	Yes	Yes
California Coastal/Central	Yes	No	Yes	Yes
Southern Rockies/Four Corners	Yes	No	No	Yes
Northern Rockies	Yes	No	No	Yes
Northern Rockies and Badlands/Prairies	Yes	No	No	Yes
Badlands/Prairies	No	No	Yes	Yes
Midwestern/Central	No	Yes	No	No
Mojave and Sonoran deserts	No	No	Yes	No
Alaskan migrants to Intermountain West	No	No	Yes	No
Canadian migrants throughout west	No	No	Yes	No
Appalachian only (short-term tracking)	No	No	Yes	No
Deserts and Southern Rockies	No	No	No	Yes

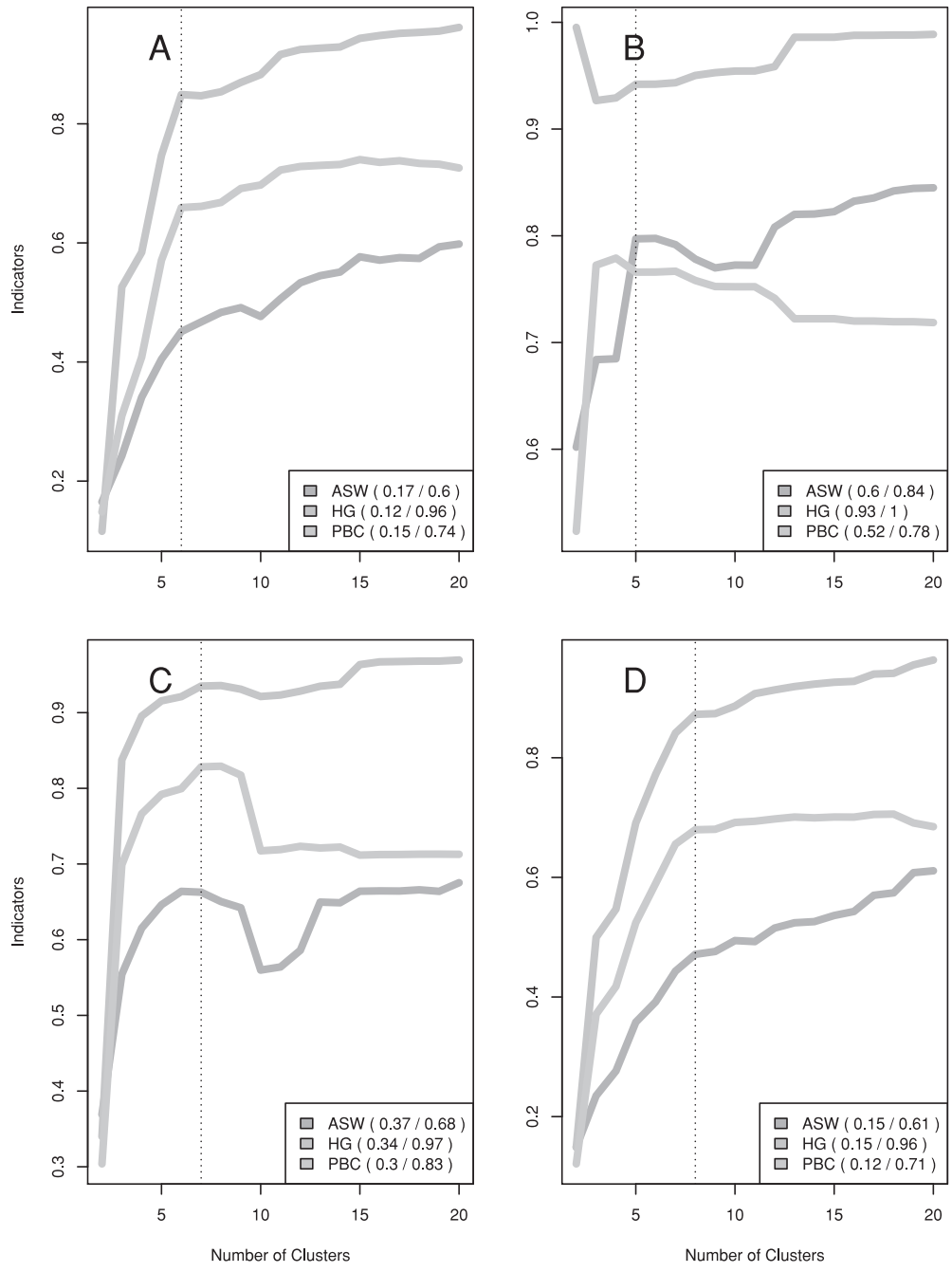

Figure 3. Example of quality statistics for clustering solutions (x-axis indicates number of clusters) for (A) Bird Conservation Regions (BCR), (B) Flyways, (C) Joint Ventures (JV), and (D) Landscape Conservation Cooperatives (LCC). Average silhouette width is ASW, Hubert's Gamma is HG, and PBC is Point Biserial Correlation. The peak or point of inflection of each curve suggests a number of clusters that balances cluster quality with cluster number, indicated by dashed vertical lines.

proportions of fixes in more northern mapping units. Mapping the percentage of fixes in each unit for each cluster provided additional clarification into the different uses of space by each group of eagles (see Fig. 4 for the example of the LCC mapping system).

For all four systems considered, cluster analyses effectively separated the easternmost Golden Eagles (initially captured in winter or on migration in the Appalachians or Atlantic coastal regions) from their more western counterparts (Table 2). A second cluster of eastern eagles was identified in the JV system, which consisted of a few eagles tracked only briefly (<58 d) and therefore not observed to migrate north. Three of the remaining clusters in the Flyways were characterized by overlapping use of the Pacific, Central, and Mississippi Flyways as well as much of Canada, but a fifth cluster identified eagles that used only the Central Flyway, the Canadian provinces to the north, and the Mexican state of Coahuila. We found two additional clusters with similar geography in the BCR, JV, and LCC systems (Table 2). Each of these mapping systems contained a cluster of predominantly Great Basin or Intermountain West sedentary eagles, and another cluster of eagles that stayed primarily within the Coast Ranges or Central Valley of California. The BCR and LCC systems contained a Southern Rockies/Colorado Plateau/Four Corners regional cluster, a cluster combining the Northern Rockies with the Badlands/Prairie region, and a Northern Rockies/Alaskan migrant cluster. We found a Badlands/Prairie cluster in both the LCCs and JVs. The JV system further contained clusters of eagles that migrated from Alaska to the Intermountain West, those that migrated mostly from Arctic Canada throughout the western U.S.A., and sedentary eagles in the Mojave and Sonoran deserts. In contrast, in the LCC system, eagles using the Mojave and Sonoran deserts clustered with others using the Southern Rockies.

DISCUSSION

Adequacy of Administrative and Ecological Mapping Systems to Partition Eagle Fixes Among Units. Our set of eagle data did not conform well to any of the four mapping systems examined here, because eagles that were grouped into different clusters used many of the same geographic units. We could not devise a better grouping of units, primarily because only some eagles exhibited seasonal migratory behavior. However, our analysis highlighted several specific administrative units of relatively greater importance for conservation of Golden Eagles. For example, when considering LCCs, 92% of eagle fixes in the Northern Rockies cluster were within the Great Northern LCC, suggesting the presence of a resident population of Golden Eagles (Fig. 4). Additionally, the Great Northern LCC was the unit used second-most often by eagles in the Far Northern Migrant cluster, Plains and Prairies Potholes cluster, Southern Rockies cluster, and Great Basin cluster, containing 16%, 11%, 10%, and 6% respectively, of their fixes. Although Golden Eagles are not among the species currently designated as Target Species in the LCC's Strategic Conservation Framework (Chambers et al. 2013), conservation goals and targets for sage steppe and Rocky Mountain landscapes may potentially be expanded to incorporate this species, particularly with regard to wildlife habitat connectivity and energy development.

For some systems, the clustering exercise succeeded in illustrating logical groupings of eagles by combining their use of geography and migratory movements. Using all four mapping systems considered here, we could distinguish the group of eagles initially captured in the Appalachians and Atlantic coastal regions from all other groups, with several units used almost exclusively by eagles in that single Eastern cluster (Table 2). Most of the systems considered contained several clusters consistent with long-distance seasonal migrants, and other clusters that represented eagles that were more sedentary within a limited number of units. For example, the optimal clusters of LCC fixes identified a cluster of eastern long-distance migrants (Fig. 4E), two clusters of western long-distance migrants with different wintering areas (Fig. 4B, C), and five regionally focused clusters in the Great Basin, Northern Rockies, California, Desert, and Southern Rockies LCCs (Fig. 4A, D, F, G, H). The eagles in the five regional clusters appeared to be primarily sedentary or short-distance migrants. For each system, additional clusters of long-distance migrants may be identifiable by visualizing a larger number of clusters than the number suggested as a parsimonious solution.

Our analytical approach did not always depict the actual use of space by Golden Eagles, possibly because of the use of geographic boundaries that did not adequately demarcate Golden Eagle movements. For example, many eagles appeared to concentrate movements along the continental di-

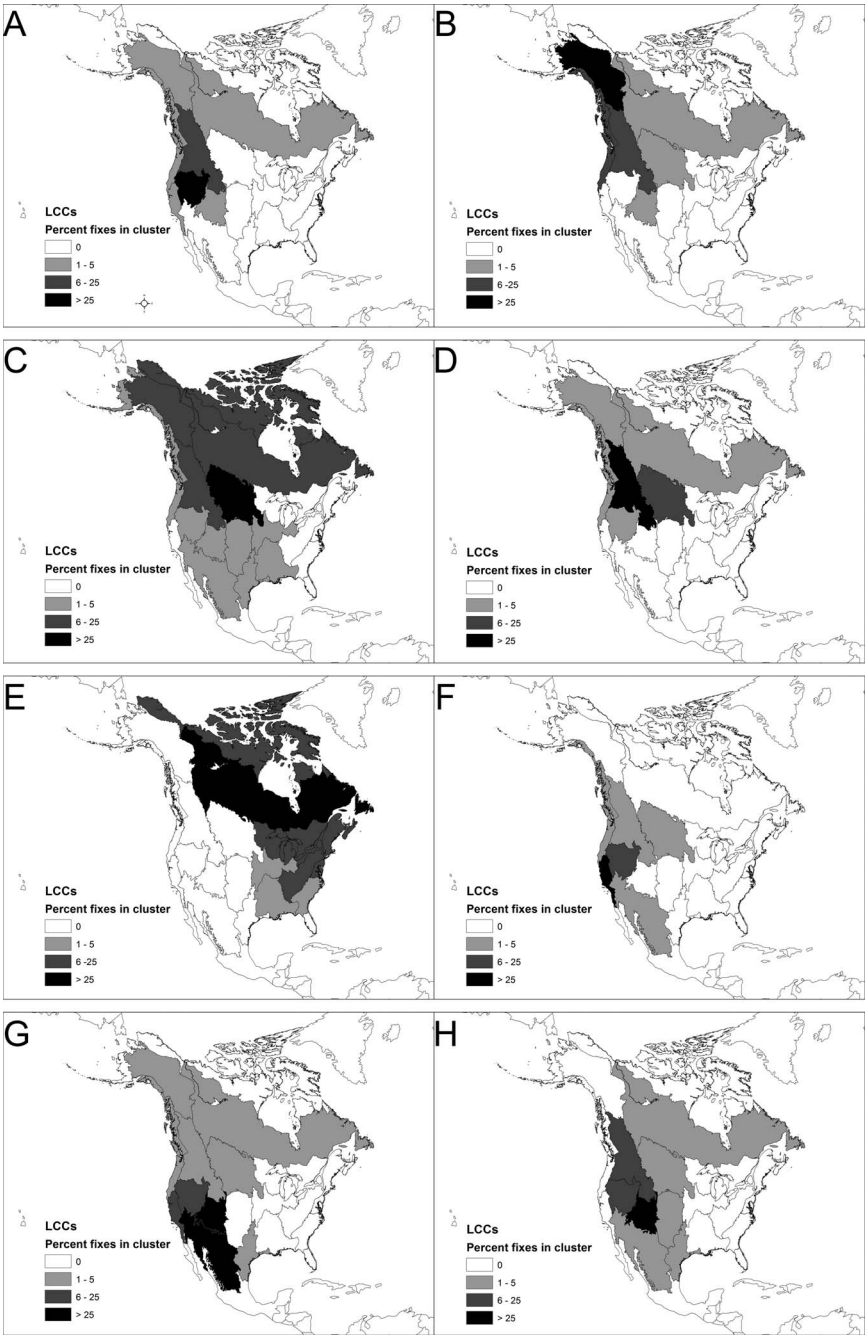

Figure 4. Percent of Golden Eagle telemetry fixes in relation to U.S. Fish and Wildlife Service Landscape Conservation Cooperative (LCC) units within movement clusters.

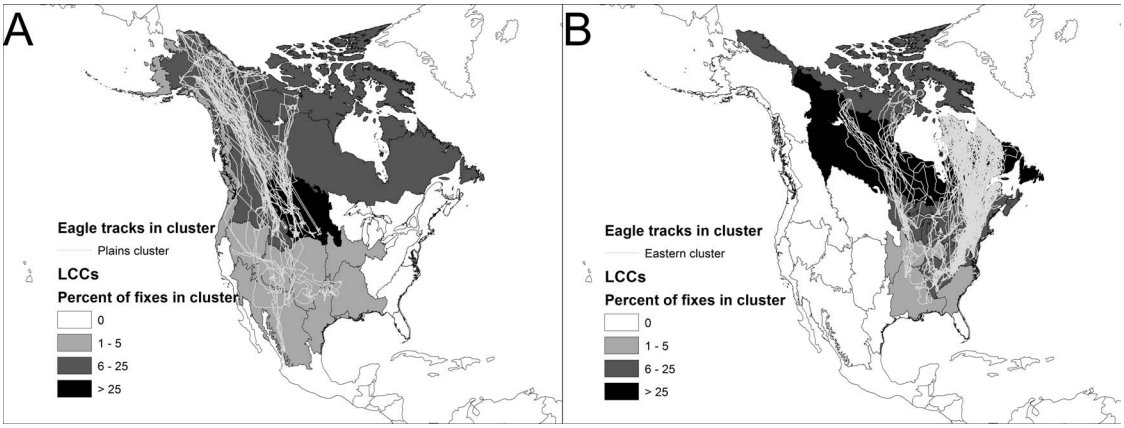

Figure 5. Inferred paths of Golden Eagles (gray lines) overlying the number of telemetry fixes of eagles within classified movement clusters in relation to U.S. Fish and Wildlife Service Landscape Conservation Cooperative (LCC) units.

vide, a feature that forms part of the boundary between the Pacific and Central flyways. As a consequence, this likely reduces the effectiveness of this administrative boundary for conservation planning for eagles. Overlaying eagle tracks on cluster maps revealed other instances where eagles moved along or crossed boundaries, or where new boundaries might be useful. In the northern portion of the continent, eagle movements and space use tended to be directed along north-south vectors. This is not surprising, because many eagles depart northern-latitude ecosystems and overwinter in southern areas (Kochert et al. 2002). For example, eagles in both the Plains and Prairie Potholes Cluster and the Eastern Cluster used the Arctic LCC extensively, but the eagles in the western cluster were restricted to the Alaskan, Yukon, and Northwest Territories portion of the Arctic LCC (Fig. 5). Thus, alternative boundaries in the northern portions of the Golden Eagle's range may improve separation of eagle movement clusters into more mutually exclusive groups.

Synthesis and Recommendations for Future Work. Our retrospective analyses allowed us to address our research questions with a level of rigor not possible before, but even with a large sample of tagged eagles, some age classes and capture locations were not well-represented by our data. We pooled data from 34 different studies, most of which deployed their transmitters in one to a few locations within a specific region. Furthermore, many studies focused on eagles of a particular age class, or deployed transmitters only during migration or winter. This resulted in initial uneven distributions of monitored eagles across the landscape (Fig. 6). Such data limitations may consequently limit our scope of inference for discerning continent-wide patterns of space use, especially if other groups of eagles not yet studied are as sedentary as those inhabiting the Californian Coastal Ranges and Central Valley, or as migratory as those in the east or Alaska. Therefore, our results will be helpful for directing strategic deployment of future survey and tracking efforts in underemphasized geographic regions, such as northwestern and north-central Canada, Mexico, and the central and midwestern U.S.A.

Regardless of biases in initial transmitter deployment locations, our analyses identified groups of both long-distant migrants and more sedentary eagles, as well as a consistent separation of eastern (and perhaps midwestern) from western Golden Eagles. Our results were consistent with a recent analysis of the genetic structure of North American Golden Eagles, which detected genetic differences between eastern and western Golden Eagles, and additional yet still unresolved population structure for eagles throughout the west (Doyle et al. 2016). Contrary to our expectations that eagle fixes would be best depicted by either the Flyways or the JVs, clusters of recognizable migrant or resident eagles were also detected when using the generalist bird- or ecoregion-focused systems of BCRs and LCCs. This suggests that an ecoregional mapping approach may be most useful when seeking to understand the space use and movements of a highly mobile and adaptable species such as the Golden Eagle. Further analyses of

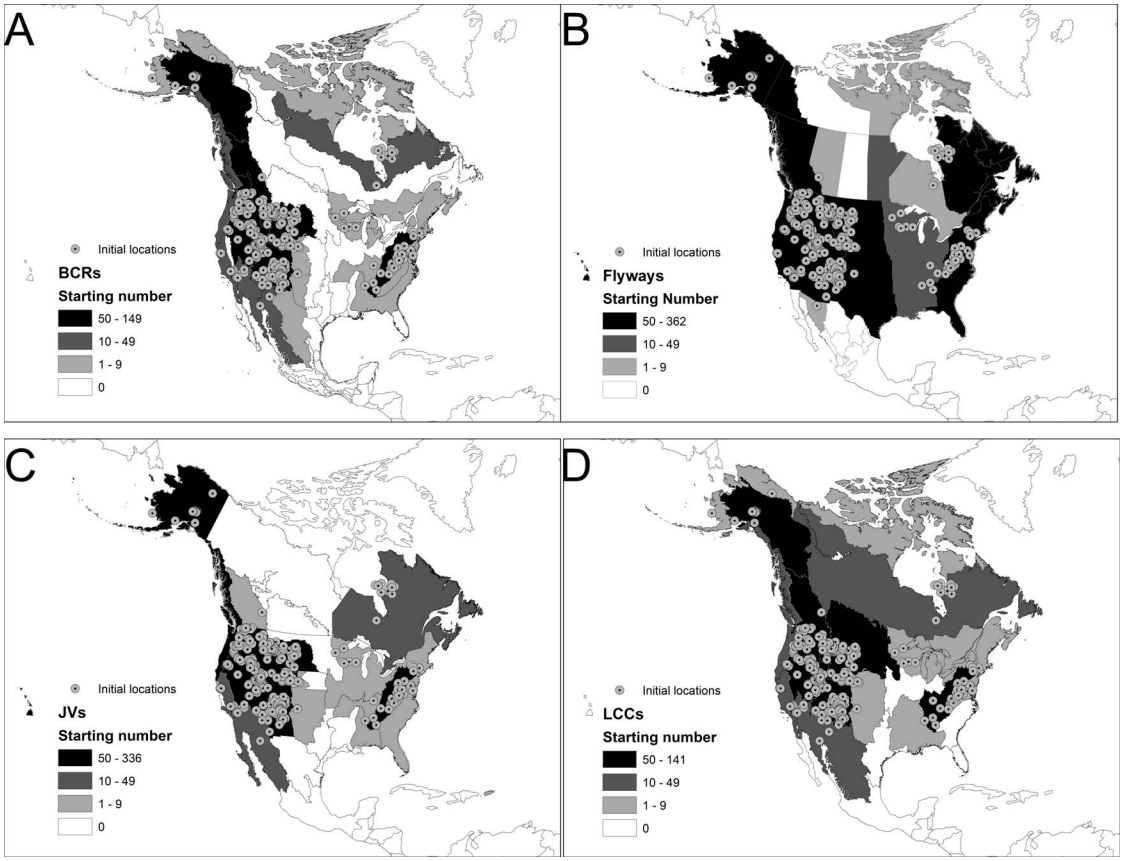

Figure 6. Numbers of Golden Eagles captured within geographic units for (A) Bird Conservation Regions (BCR), (B) Flyways, (C) Joint Ventures (JV), and (D) Landscape Conservation Cooperatives (LCC).

these data as spatially and temporally explicit eagle movement paths will bring greater insight into migration behavior, especially by identifying migration corridors and wintering areas, as well as factors influencing the timing and location of movements.

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Appendix. Funding sources for Golden Eagle movement studies

FUNDER	STUDY(IES)
Alabama Department of Conservation and Natural Resources	AL DCNR / Friends of TNF - Katzner Lab Grp
Alaska Department of Fish and Game, Threatened, Endangered, and Diversity Program through the State Wildlife Grant Program	ADFG
Altria Group Incorporated	Livingston, MT, Golden Eagles
California Department of Fish and Wildlife	CDFW-2012 - Katzner Lab Grp
Charles A. and Anne Morrow Lindbergh Foundation	Miller et al. - Katzner Lab Grp
Charles Engelhard Foundation	Livingston, MT, Golden Eagles
Cinnabar Foundation	Livingston, MT, Golden Eagles; RVRI Adult Migratory GOEA Study
Contra Costa Water District	Altamont Pass and Diablo Range Study
Delaware-Otsego Audubon Society	DOAS - Katzner Lab Grp
Dr. Ezekiel R. and Edna Wattis Dumke Foundation	HawkWatch International Migratory Golden Eagle Tracking Study 1999–2009
Dumke Foundation	RVRI Adult Migratory GOEA Study
East Bay Regional Park District	Altamont Pass and Diablo Range Study
East Contra Costa County Habitat Conservancy	Altamont Pass and Diablo Range Study
Friends of the Talladega National Forest	AL DCNR / Friends of TNF - Katzner Lab Grp
Highland County Golden Eagle Chase	CCB Mid-Atlantic Golden Eagles
JEPS Foundation	HawkWatch International Migratory Golden Eagle Tracking Study 1999–2009
Jerry Metcalf Foundation	RVRI Adult Migratory GOEA Study
Katherine W. Dumke and Ezekiel R. Dumke Jr. Foundation	HawkWatch International Migratory Golden Eagle Tracking Study 1999–2009
LaSalle Adams Fund	HawkWatch International Migratory Golden Eagle Tracking Study 1999–2009
LCAO Foundation	RVRI Adult Migratory GOEA Study
M.J. Murdock Foundation	RVRI Adult Migratory GOEA Study, HawkWatch International Migratory Golden Eagle Tracking Study 1999–2009
Maki Foundation	RVRI Adult Migratory GOEA Study
Mountaineers Foundation	RVRI Adult Migratory GOEA Study, HawkWatch International Migratory Golden Eagle Tracking Study 1999–2009
National Fish and Wildlife Foundation	HawkWatch International Migratory Golden Eagle Tracking Study 1999–2009
National Geographic Foundation	Livingston, MT, Golden Eagles
National Science Foundation	Eastern Montana GOEA Study
Nebraska Game and Parks Commission	USFWS Region 6 GOEA WYCONE
New Mexico Game and Fish	HawKwatch International Migratory Golden Eagle Tracking Study 1999–2009
NextEra Energy, Inc.	Altamont Pass and Diablo Range Study
Norcross Wildlife Fund	RVRI Adult Migratory GOEA Study
North Star Science and Technology	HawkWatch International Migratory Golden Eagle Tracking Study 1999–2009
Okanogan/Wenatchee, Mt. Hood, and Cibola National Forests and U.S. Forest Service, Region 3	HawkWatch International Migratory Golden Eagle Tracking Study 1999–2009
Oregon Department of Fish and Wildlife	HawkWatch International Migratory Golden Eagle Tracking Study 1999–2009
Patagonia Foundation	RVRI Adult Migratory GOEA Study
Penn State Earth and Environmental Institute Fellowship	Miller et al. - Katzner Lab Grp

Appendix. Continued.

Funder	Study(ies)
Pennsylvania Game Commission	Miller et al. - Katzner Lab Grp
Signals of Spring	HawkWatch International Migratory Golden Eagle Tracking Study 1999–2009
State Wildlife Fund, Washington Dept. of Fish and Wildlife	WA Adult Golden Eagle Study
Tennessee Wildlife Resources Agency	TWRA - Katzner Lab Grp
The Center for Conservation Biology	CCB Mid-Atlantic Golden Eagles
The Gordon and Betty Moore Foundation	Altamont Pass and Diablo Range Study
The Louis L. Borick Foundation	RVRI Adult Migratory GOEA Study
The MPG Ranch	RVRI/MPG Ranch Adult Wintering GOEA Study
U.S. Army Aberdeen Proving Ground	CCB Mid-Atlantic Golden Eagles
U.S. Army Dugway Proving Ground	HawkWatch International and U.S. DoD
U.S. Bureau of Land Management	BLM-2010 - Katzner Lab Grp; Livingston, MT, Golden Eagles; RVRI Adult Migratory GOEA Study; USFWS Region 6 GOEA WYCONE; Eastern Montana GOEA Study; HawkWatch International Migratory Golden Eagle Tracking Study 1999–2009 (Elko NV and Kemmerer WY Field Offices)
U.S. Bureau of Reclamation, Upper Colorado Regional Office	HawkWatch International Migratory Golden Eagle Tracking Study 1999–2009
U.S. Department of Defense Legacy Program	HawkWatch International and U.S. DoD
U.S. Department of Energy	Miller et al. - Katzner Lab Grp
U.S. Fish and Wildlife Service	USFWS - Katzner Lab Grp; Livingston, MT, Golden Eagles; USFWS Region 6 GOEA WYCONE; Eastern Montana GOEA Study; HawkWatch International Migratory Golden Eagle Tracking Study 1999–2009 (Region 2)
U.S. Geological Survey	Denali NPS (Forest and Rangeland Ecosystem Science Center); HawkWatch International Migratory Golden Eagle Tracking Study 1999–2009 (Biological Resources Division, Patuxent Wildlife Research Center)
U.S. National Park Service, Denali National Park and Preserve	Denali NPS
Various private donors	Livingston, MT, Golden Eagles; RVRI Adult Migratory GOEA Study
Virginia Department of Game and Inland Fisheries	VDGIF - Katzner Lab Grp
Virginia Society of Ornithology	CCB Mid-Atlantic Golden Eagles
Washington Department of Fish and Wildlife	HawkWatch International Migratory Golden Eagle Tracking Study 1999–2009
Western Bird Banding Association	Livingston, MT, Golden Eagles
Yellowstone to Yukon	RVRI Adult Migratory GOEA Study