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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 CHRYSÆTOS* 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

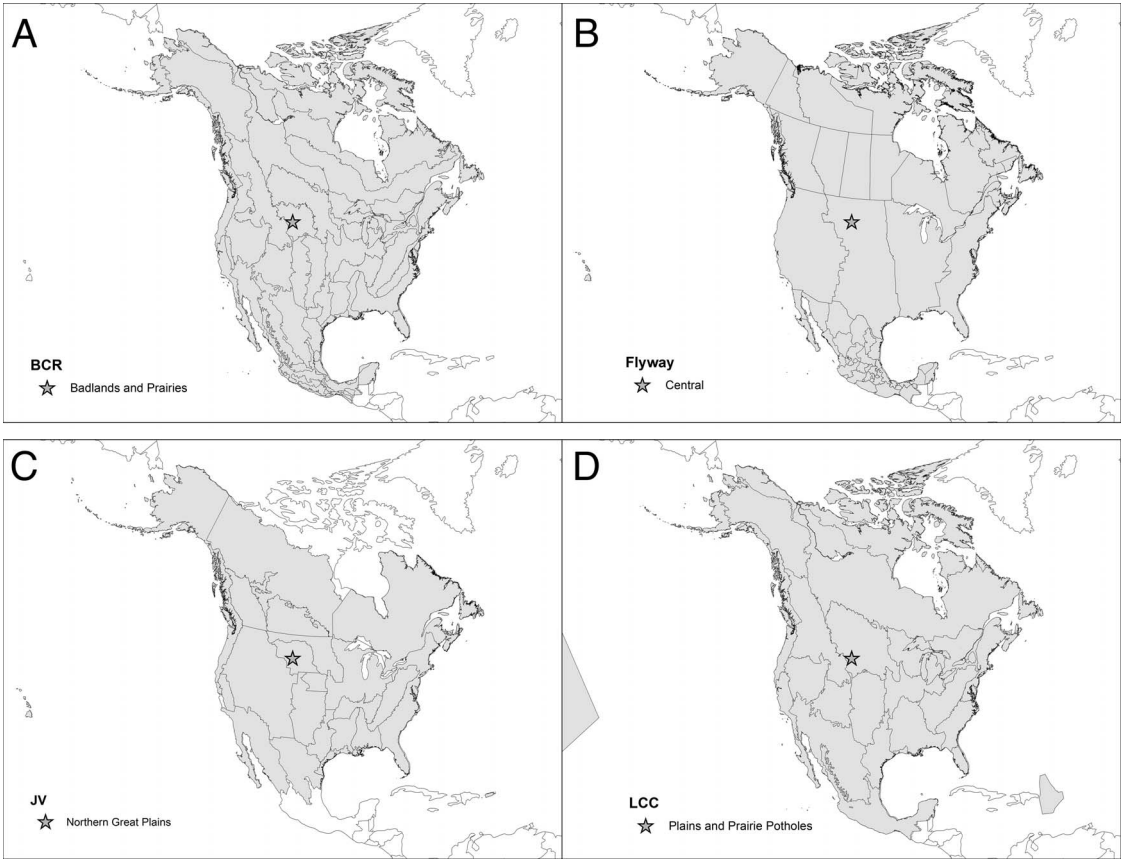


Figure 1. Boundaries of (A) Bird Conservation Regions (BCR), (B) Flyways, (C) Joint Ventures (JV), and (D) Landscape Conservation Cooperatives (LCC) in North America.

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. Kritiz, 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. McCann, 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 study | NYSDEC | 1 | 20 January 2008 | 30 March 2010 | GPS/Argos | ? | C. McIntyre unpubl. data |
| RVRI Adult Migratory 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. |
| DOAS - Katzner Lab Grp | Van Arsdale, Salo, Lanzone | 3 | 8 February 2014 | 9 April 2014 | GPS/GSM | 80 | 2012b, 2012a, 2015a, 2015b, Lanzone et al. |
| Miller et al. - Katzner Lab Grp | Miller, Lanzone, Katzner, O'Malley | 12 | 16 February 2009 | 31 December 2014 | GPS/GSM | 95 | 2012, Miller et al. 2014, 2016, Denhardt et al. 2015a, Morneau et al. |
| TWRA - Katzner Lab Grp | Somershoe, Kelly, Miller, Lanzone | 6 | 5 February 2013 | 25 January 2015 | GPS/GSM | 95 | 2015, Nelson et al. 2015, Denhardt et al. 2015b, Jachowski et al. 2015 |
| USFWS - Katzner Lab Grp | Koppie, Lanzone | 2 | 20 March 2012 | 11 November 2014 | GPS/GSM | 95 | Braham et al. 2015, Duerr et al. 2015, Poessel et al. 2016 |
| 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 | |
| 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 ≥ 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 $45^\circ 12.405' \text{N}$ $105^\circ 46.722' \text{W}$ (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 propor-

tions 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

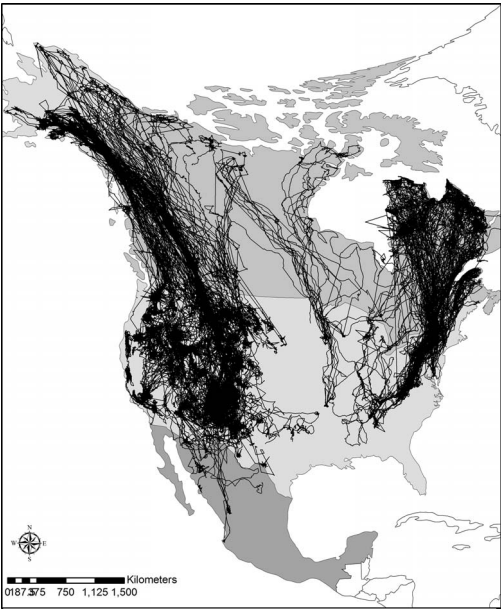


Figure 2. Telemetry fixes of 571 Golden Eagles tracked in North America between 1992 and 2016. Lines indicate unobserved straight-line paths between consecutive telemetry fixes.

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 |

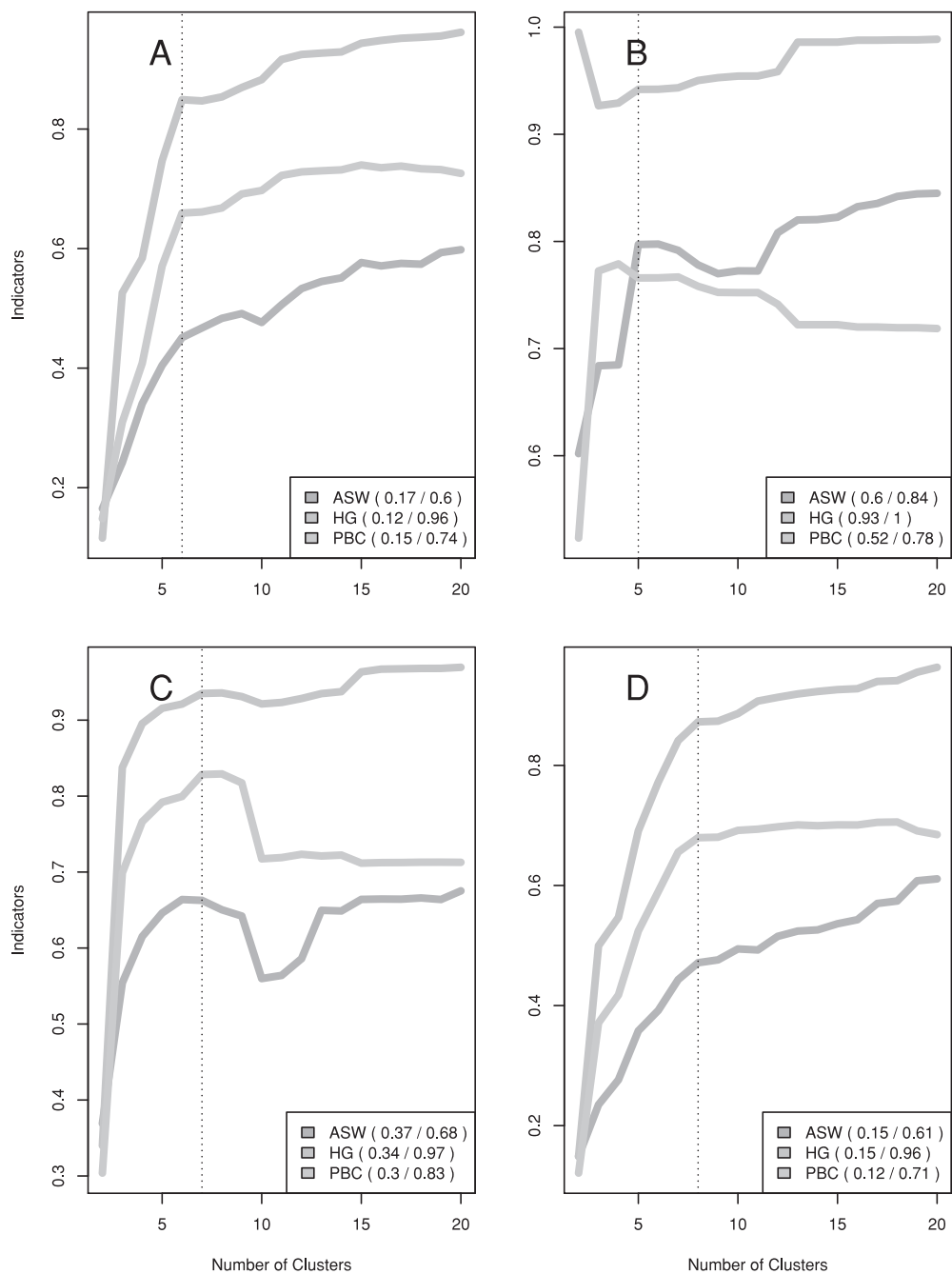


Figure 3. Example of quality statistics for clustering solutions (x-axis indicates number of clusters) for (A) Bird Conservation Regions (BCR), (B) Flyways, (C) Joint Ventures (JV), and (D) Landscape Conservation Cooperatives (LCC). Average silhouette width is ASW, Hubert's Gamma is HG, and PBC is Point 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 Pot-holes 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-

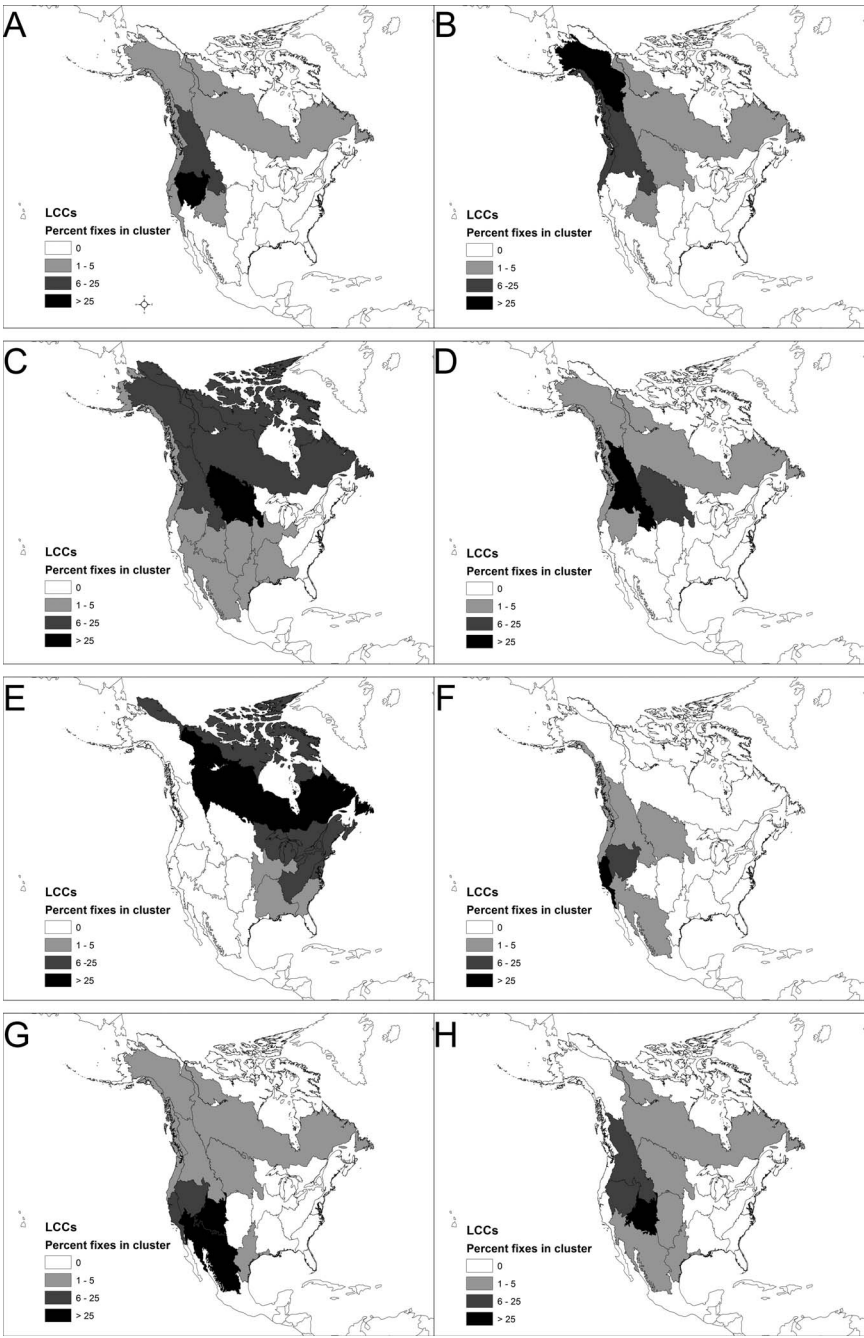


Figure 4. Percent of Golden Eagle telemetry fixes in relation to U.S. Fish and Wildlife Service Landscape Conservation Cooperative (LCC) units within movement clusters.

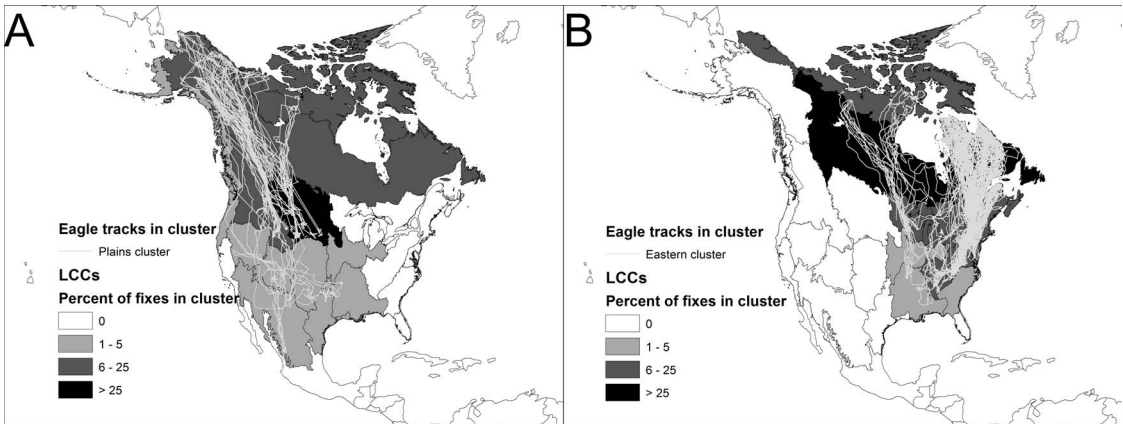


Figure 5. Inferred paths of Golden Eagles (gray lines) overlying the number of telemetry fixes of eagles within classified movement clusters in relation to U.S. Fish and Wildlife Service Landscape Conservation Cooperative (LCC) units.

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

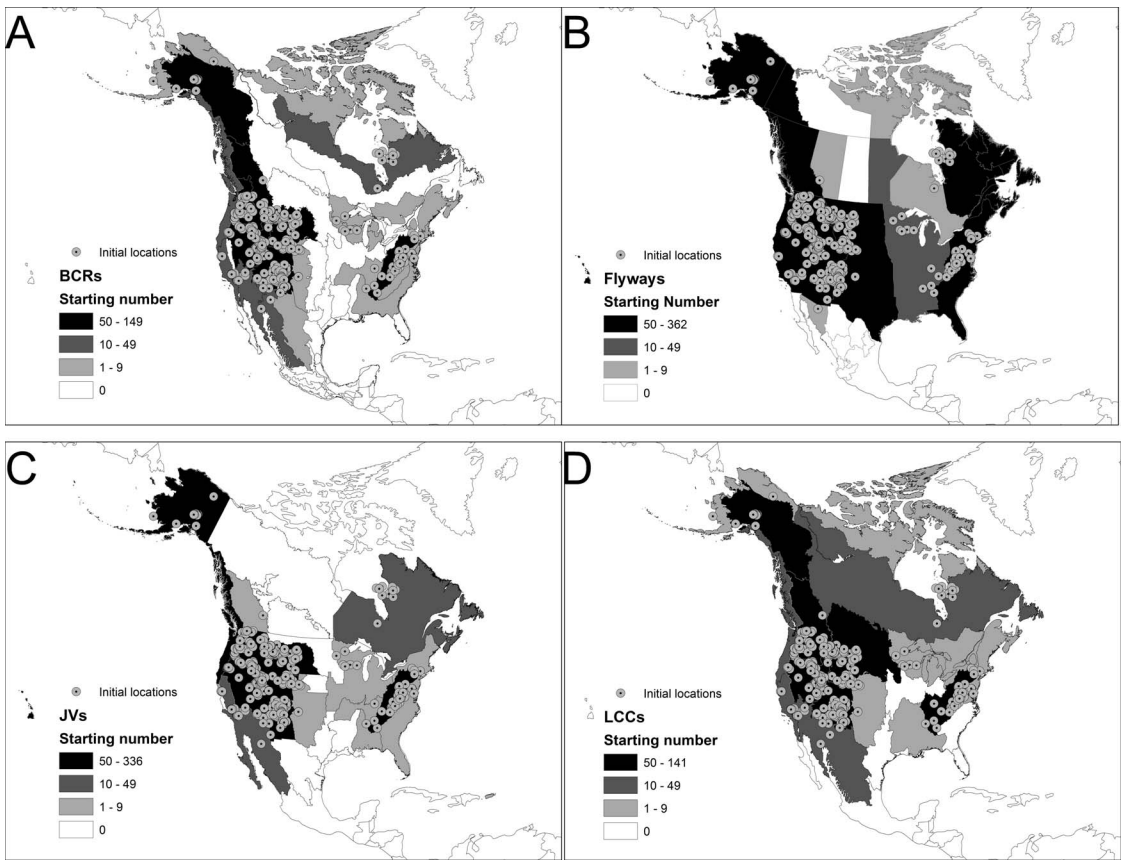


Figure 6. Numbers of Golden Eagles captured within geographic units for (A) Bird Conservation Regions (BCR), (B) Flyways, (C) Joint Ventures (JV), and (D) Landscape Conservation Cooperatives (LCC).

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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firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government. We additionally thank the many sources of funding for the eagle tracking studies (Appendix). This paper is based on a presentation given at the Golden Eagles in a Changing World symposium held at the 2015 Raptor Research Foundation Annual Meeting in Sacramento, CA. We thank the Academy for the Environment, University of Nevada, Reno, for providing financial support for publication costs. We also thank the U.S. Fish and Wildlife Service, especially the Western Golden Eagle Team, for their financial and logistical support of this work.

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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 | HawkKwatch 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 Signals of Spring | Miller et al. - Katzner Lab Grp 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 |