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FIRST-YEAR DISPERSAL OF GOLDEN EAGLES FROM NATAL AREAS IN THE SOUTHWESTERN UNITED STATES AND IMPLICATIONS FOR SECOND-YEAR SETTLING

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Abstract.—Knowledge of dispersal from natal areas by pre-breeding-age Golden Eagles (*Aquila chrysaetos*) in North America is sparse, though crucial for conservation planning. During 2010–2015, we used satellite telemetry to document movement behavior of pre-breeding-age Golden Eagles from the Colorado Plateau and Southern Rocky Mountains of the southwestern U.S.A. Here we report on (1) 1st-yr dispersal timing, distances, strategies, and survival; (2) influences of age, sex, nest-mates, and area of origin; and (3) progressive distancing from natal nests and coinciding space use, including overlap between individuals' home ranges at the end of their 1st and 2nd yr. Our dataset included 293,960 GPS fixes from 66 Golden Eagles monitored through at least the onset of dispersal. All dispersed at age <1 yr. Most (66.7%) initiated dispersal during 16 September–21 November (median = 22 October, 191 d after median hatch date). We could assign each of 60 eagles to one of four 1st-yr dispersal categories based on maximum distance traveled from natal nests: short-distance (SD), generally <120 km (66.7% of eagles); moderate-distance (MD), 120–500 km (16.7%); long-distance (LD) >500 km (13.3%); and Other (3.3%). LDs dispersed at younger ages than SDs and were more likely to be from the arid half of our study area. First-year survival was significantly lower for LDs. Overlap of 95% kernel density home ranges at ages 12 and 24 mo was 42.2% (±6.4 SE) for 26 SDs and 26.5% (±9.5) for eight MDs. Our data indicate that, during at least their 1st and 2nd yr of life, most Golden Eagles from the Colorado Plateau and Southern Rocky Mountains remain within 120 km of their nests, where they experience high survival and are relatively settled by the end of their 1st yr. As such, these landscapes are key habitat for at least 1st- and 2nd-yr eagles as well as breeding pairs.

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KEY WORDS: *Golden Eagle*; Aquila chrysaetos; *dispersal*; *movement behavior*; *spatial use*; *survival*; *southwestern United States*.

RESUMEN.—El conocimiento de la dispersión de individuos en edad pre-reproductiva desde sus áreas natales en América del Norte es escaso, pero es crucial para planificar la conservación. Durante 2010-2015 utilizamos telemetría satelital para documentar el comportamiento de movimientos de individuos en edad pre-reproductiva de *Aquila chrysaetos* en la Planicie de Colorado y en el sur de las Montañas Rocosas en el suroeste de los Estados Unidos. En este trabajo informamos sobre (1) tiempos, distancias, estrategias y supervivencia de la dispersión de individuos durante su primer año de vida; (2) la influencia de la edad, el sexo, las parejas y el área de origen y (3) el distanciamiento progresivo desde los nidos de nacimiento y el uso coincidente del espacio, incluyendo la superposición entre áreas de campeo hacia el final del primer y segundo año. Nuestros datos incluyeron 293,960 localizaciones GPS de 66 individuos de *A. chrysaetos* seguidos al menos durante el inicio de la dispersión. Todos los individuos se dispersaron a la edad de <1 año. La mayoría (66.7%) inició la dispersión entre el 16 de septiembre y el 21 de noviembre (mediana = 22 de octubre, 191 días después de la fecha mediana de eclosión). Pudimos asignar cada una de las 60 águilas a una de cuatro categorías de dispersión de primer año, basados en la distancia máxima viajada desde los nidos de nacimiento: de corta distancia (CD), generalmente <120 km (66.7% de las águilas); de distancia moderada (DM), 120–500 km (16,7%); de larga distancia (LD) >500 km (13.3%); y otra (3.3%). Los individuos LD se dispersaron a una edad menor que los individuos CD y tuvieron mayor probabilidad de provenir de la porción árida de nuestro área de estudio. La supervivencia del primer año fue significativamente menor para los individuos LD. La superposición de las áreas de campeo de acuerdo con el kernel del 95% a las edades de 12 y 24 meses fue del 42.2% (±6.4 EE) para 26 individuos CD y de 26.5% (±9.5) para ocho individuos DM. Nuestros datos indican que, durante por lo menos el primer y segundo año de vida, la mayoría de los individuos de *A. chrysaetos* de la Planicie de Colorado y del sur de las Montañas Rocosas permanecen a menos de 120 km de sus nidos, donde exhiben una supervivencia elevada y donde están relativamente establecidos hacia finales de su primer año. De esta manera, estos paisajes son un hábitat clave por lo menos para las águilas del primer y segundo año así como para las parejas reproductoras.

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Dispersal is among key underpinnings of population ecology due to its influence on: (1) survival; (2) gene flow and genetic structuring; (3) range expansion, colonization, and rescue effect; (4) metapopulation dynamics and connectivity; and (5) source-sink dynamics (Greenwood 1980, Pulliam 1988, Clobert 2012). Pre-breeding-age dispersal primarily influences the spatial distribution of a bird population (Greenwood and Harvey 1982, Soutullo et al. 2013). Dispersal generally is thought to include three sequential phases: (1) departure or the onset of dispersal, coinciding with end of parental dependency; (2) transience, in which dispersing individuals move away from their natal areas and "sample" other areas in search of a suitable location to settle; and (3) settlement, where a territory or home range is established and ultimately breeding may be attempted (Gonzalez et al. 1989, Bowler and Benton 2005, Weston et al. 2013). During initial dispersal, movement and learning are linked; as an individual's movement patterns develop, its knowledge of the surroundings increases and it is presumably influenced both by habitat selection as well as biotic interactions, including predators, prey, and conspecific territory owners which interfere with access to resources (Vuilleumier and Perrin 2006, Delgado et al. 2009). An evolving awareness is likely critical to subsequent decisions that directly affect fitness.

As a *K*-strategist, Golden Eagles (*Aquila chrysaetos*) have a lengthy period of pre-breeding-age dispersal, typically with a 4-yr lapse between departure from the natal area during the 1st yr and sexual maturity in the 5th yr. Soutullo et al. (2006a) characterized this long period for Golden Eagles as consisting of a wandering phase, then an exploratory or nomadic phase driven mainly by foraging opportunity, followed by a return to somewhere near the natal area. Some individuals might have multiple transient and settlement phases before reaching breeding age, as

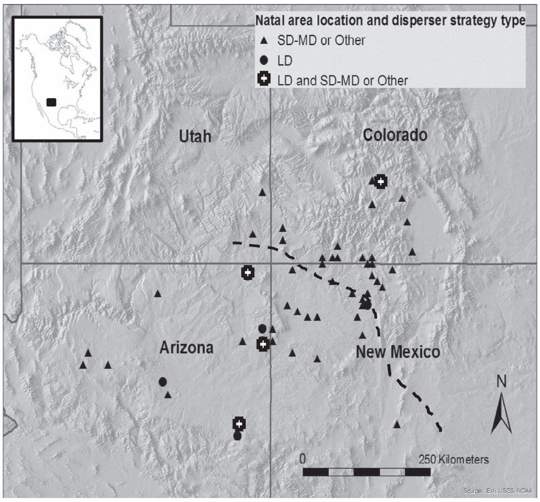

Figure 1. Fifty-three Golden Eagle breeding areas in the Colorado Plateau and Southern Rocky Mountains of the southwestern U.S.A, where 66 Golden Eagle nestlings were tagged with PTTs during 2010–2014 and monitored during dispersal from natal areas. Dashed line approximates the boundary between breeding areas in the arid, lower-elevation (1700–2700 masl) part of the study area and those in the relatively less arid, higher-elevation (2100–3600 masl) part of the study area. Disperser strategy type of eagles from different natal areas, as described in text, include: (1) SD – short-distance disperser, (2) MD – moderate-distance disperser, (3) LD – long-distance disperser, and (4) Other – individually unique dispersal strategy. At some natal areas, more than one eagle was tagged; individuals from some such sites exhibited different strategies, as indicated. Natal area locations on lands of Native American tribes are obfuscated (±50 km) for purposes of confidentiality.

do congeneric Bonelli's Eagles (*A. fasciata*; Balbontín and Ferrer 2009). Comprehensive knowledge of this pre-breeding-age period is vital to the species' conservation, as roughly three-fourths of the Golden Eagle's mortality and perhaps that of other *Aquila* species occurs during this period (Harmata 2002, Caro et al. 2011).

Knowledge of pre-breeding-age dispersal is vital to defining populations of Golden Eagles and evaluating the suitability of management units. Other than an annual, late-summer survey of Golden Eagles of all age classes (Millsap et al. 2013, Nielson et al. 2014) and an associated distribution model (Nielson et al. 2016), conservation planning for Golden Eagles in the western U.S.A. stems mainly from data on breeding adults and nests, e.g., resource selection, landscape-scale movement, and distribution (Phillips et al. 1984, Marzluff et al. 1997, Braham et al. 2015, Tack and Fedy 2015; but see Brown et al. 2017). A coarse-level assessment of natal dispersal distances by Golden Eagles, based largely on band encounter data for the western U.S.A. (Millsap et al. 2014), is the only published broad-scale, quantitative assessment of any aspect of its dispersal in North America. Dispersal by Golden Eagles during their 1st yr has been studied in several regions of Europe (Soutullo et al. 2006a, 2006b, 2013, Weston 2014, Nygård et al. 2016), but inference of these studies for understanding dispersal behavior of North American Golden Eagles is uncertain. For example, it is not known whether landscapes used by breeding Golden Eagles in North America might be ecological traps for pre-breeding-age individuals. Temporal and spatial dynamics of settlement through pre-breeding-age dispersal may influence survival, but, again, little is known. Pre-breeding-age Golden Eagles from one regional population may emigrate to other populations, but the extent of this behavior is unstudied.

The goal of our study was to document 1st-yr dispersal by Golden Eagles from natal areas across much of the Colorado Plateau and Southern Rocky Mountains of the southwestern U.S.A. and to assess its influence on settling in the subsequent year. Specific objectives were to quantify (1) 1st-yr dispersal timing, distances, strategies, and survival; (2) influences of age, sex, nest-mates, and area of origin; and (3) progressive distancing from natal nests and coinciding space use including overlap between individuals' home ranges at the end of their 1st and 2nd yr.

METHODS

Study Area. We studied Golden Eagles that originated from natal areas across the southern half of the Colorado Plateau physiographic province (Patton et al. 1991) and adjacent (to the east) parts of the Rocky Mountains' southern terminus in southwestern North America (37°N, 109°W). This area included far southeastern Utah, northeastern Arizona, northwestern New Mexico, and southwestern Colorado (Fig. 1), though some eagles we tracked moved far beyond this area. The southwestern half of the study area was arid to semiarid land (mean annual precipitation 25–35 cm), with sparse to moderate plant cover dominated by perennial grasses and low (<3 m high) shrubs. The northeastern half was slightly less arid (annual precipitation

35–40 cm) and was dominated by big sagebrush (*Artemisia tridentata*) shrub-steppe and conifer woodland (*Pinus edulis*, *P. ponderosa*, *Juniperus* spp.). Parts of the latter area included irrigated pastureland, hayland, and cropland. Small mountain ranges and sandstone ridges, mesas, and outcrops occurred across most of the study area; elevations of these typically were 1700–2700 m in the southwest to 2100–3600 m in the northeast. Land use was mainly livestock ranching, recreation, and gas and oil extraction. Main prey of Golden Eagles on the study area, at least during the eagle breeding season, included black-tailed jackrabbits (*Lepus californicus*), cottontail rabbits (*Sylvilagus* spp.), and Gunnison's prairie dogs (*Cynomys gunnisoni*; Stahlecker et al. 2009). About 90% of nests of Golden Eagles were on cliffs and the rest were in ponderosa pine.

Telemetry. During late May through early July each year, we entered Golden Eagle nests when nestlings were 7- to 8-wk old (i.e., near fledging age) and fitted nestlings with platform terminal transmitters (PTTs; Solar Argos/GPS models PTT-45 and PTT-70; Microwave Telemetry, Inc., Columbia, MD U.S.A.) that produced GPS-based fixes with $\pm$20-m accuracy. PTTs were attached via "Y-harness" (Buehler et al. 1995) made with 0.64-cm wide Teflon ribbon (Bally Ribbon Mills, Bally, PA U.S.A.). With harnesses attached, PTT-45 and PTT-70 units weighed approximately 55 g and 90–100 g, respectively (Stahlecker et al. 2015), <3% of the mass of nestlings. Our dataset included GPS fixes (n = 293,960) collected hourly each day during 0900–1600 H.

Dispersal Timing, Distance, and Strategies. We used "Method 7" from Weston et al. (2013) as one of two criteria that best defined the onset of dispersal for Scottish Golden Eagles. Their approach, based on patterns of space use around nests by territorial adults as delineated by McGrady et al. (2002), determined that a pre-breeding-age eagle initiated dispersal when it ventured >9 km from its natal nest and stayed >6 km from the nest for the next 10 d. Initially, we estimated this 10-d distance for each of 35 unique breeding areas where we tagged nestling Golden Eagles with PTTs by measuring the distance from a nest at which we tagged a nestling to the nearest nest occupied by a territorial pair of Golden Eagles. One-half of that mean inter-nest distance was 4.0 km (SE = 0.4). Because this nearest-neighbor distance was derived from the less arid half of our study area where breeding density was comparatively high (D. Stahlecker unpubl. data), our result likely was biased downward. Thus, we adopted the 6-km criterion of Weston et al. (2013) and considered the area $\leq$6 km from the natal nest to be the natal area.

To characterize 1st-yr dispersal strategies, we considered hatch date for all eagles to be 15 April because this approximated the median hatch date (14 April) and individual hatch dates diverged little from this (SE = 1.2 d; n = 66). Next we considered 1 yr from 15 April to be the end of each eagle's 1st yr of life, with 16 March–15 April representing the early spring period ending the 1st yr. We plotted the maximum distance from the natal nest for each eagle each day through the 1st yr and visually examined these distance graphs for evidence of distinct temporal-spatial patterns possibly representing various dispersal strategies. We then assigned each eagle to one of four 1st-yr dispersal strategy categories: (1) short-distance dispersers (SD) remained <120 km from natal nest; (2) moderate-distance dispersers (MD) dispersed 120–500 km from natal nest; (3) long-distance dispersers (LD) dispersed >500 km; or (4) Other individuals, which demonstrated unique dispersal patterns. Exceptions included some SDs that made brief excursions up to 192 km from natal nests and some MDs that made brief excursions to as close as 12 km from natal nests. Individuals that made excursions typically did so only one to three times, with each excursion lasting 1–4 d.

Influence of Area of Origin. We considered that 1st-yr dispersal strategies of Golden Eagles could be driven by prey availability via positive linkages with precipitation and primary productivity (e.g., leporids in western North America: McKay and Verts 1978, Ernest et al. 2000, but see Lightfoot et al. 2011). Specifically, we hypothesized that eagles from natal areas in arid landscapes would disperse farther than those from natal areas in moister landscapes; assuming that prey would be more abundant in the latter. To test this, we calculated total precipitation within 120 km of the natal nest in the year each eagle was tagged as a nestling, plus total precipitation from the previous year. Daily precipitation records were extracted from Oak Ridge National Laboratory's Daymet service (Thornton et al. 2014) for each 1-km $\times$ 1-km grid cell covering the 120-km-radius area. We used 120 km because it was the upper limit of 1st-yr dispersal distance for SDs.

First-year Survival. We estimated 1st-yr survival rate for Golden Eagles that lived >3 wk after the onset of dispersal, which we deemed long enough to reveal their dispersal strategy. To analyze survival by dispersal strategy type with minimal bias, we combined data from three eagles that died approximately 4 mo after the onset of dispersal with those surviving longer and dispersing relatively short distances because all exhibited roughly similar early dispersal movement, especially distance from natal nest. We also combined data from two eagles classified as Other with those that dispersed moderate distances because all moved within the same range of distance from respective natal nests through the 1st yr. Results of the survival analysis were unchanged if data from these five individuals were excluded.

All eagles in the overall sample retained functional PTTs through death or age 1 yr, such that we could estimate true annual survival (*S*) directly from the data. We generated estimates in program R (R Core Team 2015), using a logit-link generalized linear model (GLM) in a Bayesian framework (Kéry 2010), with the binary response variable alive (1) or not (0) at age 1 yr and with fixed categorical effects for dispersal strategy. We compared GLMs that estimated 1st-yr survival of (1) SDs, MDs, and LDs separately; (2) pooled SDs and MDs (SDs–MDs) versus LDs; (3) pooled MDs and LDs (MDs–LDs) versus SDs; and (4) an intercept-only (null) model. We used the Markov chain Monte Carlo method implemented in program WinBUGS (Lunn et al. 2012) to estimate posterior distributions of annual survival probabilities. For all models we ran three chains for 60,000 iterations each with a burn-in of 10,000 iterations per chain. We inspected history plots and used $\hat{R}$ to estimate convergence; models with values of $\hat{R} < 1.1$ were considered to have converged (Gelman and Hill 2006). We compared models based on their deviance information criterion (DIC) scores (Burnham and Anderson 1998, Hooten and Hobbs 2014). We considered models within two DIC units of each other as having equal support (Burnham and Anderson 1998), in which case we selected the model with the fewest estimated parameters as the preferred model. We also examined the relationship between 1st-yr survival of Golden Eagles and maximum distance from natal nests by (1) arranging maximum distances of individual eagles from shortest to longest and (2) calculating the percentage of eagles that survived to 1 yr and had maximum distances greater than each focal eagle's maximum distance. Eagles that moved ≥800 km were placed in one group.

Progressive Distancing and Space Use. We generated 95% kernel density estimates of home ranges by using a 0.7 proportional modifier in place of least-squares cross-validation for bandwidth (Worton 1989). These home ranges, hereafter termed HRs, were estimated in AnimalMovement tools for ArcGIS (https://github.com/regan-sarwas/AnimalMovement). The centroid of a given HR was derived from all polygons and represented the kernel density area's center of mass. We explored evidence of 1st-yr settling by measuring (1) the distance from each eagle's natal nest to centroids of successive monthly HRs; (2) month-by-month cumulative HR size, corresponding with total area explored over time; and (3) percentage overlap between successive monthly HRs. A horizontal asymptotic trend in any of these cases would suggest settling. We began with November, as most dispersal was initiated by the end of this month. Eagles that died before the end of the 1st yr were excluded from the dataset. Next, we conjectured that if an eagle shifted among temporary HRs or wandered randomly before reaching breeding age, there would be little or no overlap between its 1st- and 2nd-yr HRs. Thus, we measured overlap between HRs of individuals at approximately 12 mo and 24 mo of age. For 1st-yr eagles, this 1-mo, early spring period of comparison was the interval between the last dispersals from natal areas and the first northward summer migrations by about one-third of the eagles, starting at the beginning of their 2nd yr (R. Murphy and D. Stahlecker unpubl. data). To convey simple examples of 1st- and 2nd-yr home range overlap and support comparisons among studies, we also estimated home ranges by using 95% minimum convex polygons.

Statistical Analyses. Our dataset included several pairs of nest-mates. We considered members of individual pairs independent of one another in our analyses because we did not observe consistent, paired links in either dispersal timing, strategy, or distance and direction from natal nests at the end of the 1st yr; however, we acknowledge that nest-mates' shared genetic and environmental histories may engender some nonindependence. Throughout, we convey central tendency as means ± SEs and medians. We used unequal variance, unpaired or paired *t*-tests for simple univariate comparisons after checking data for normality. The *t*-tests were one-tailed when we had an *a priori* notion about the direction of a relationship as conveyed in this Methods section; otherwise tests were two-tailed. We used the nonparametric Mann-Whitney *U*-test for unpaired, univariate comparisons if data were

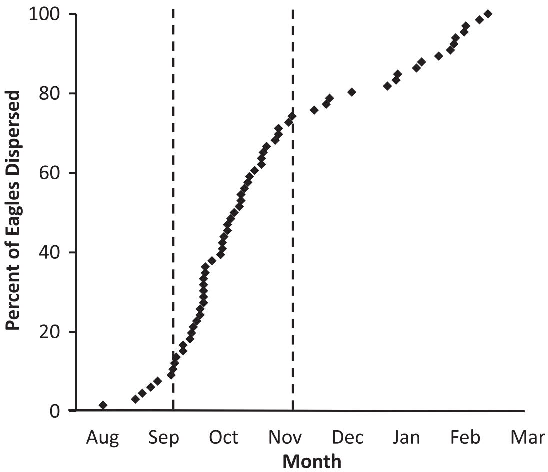

Figure 2. Date of onset of dispersal from natal areas for 66 juvenile Golden Eagles tagged as nestlings with PTTs. Dates were determined by using Method 7 in Weston et al. (2013). Forty-four (66.7%) of the eagles dispersed during the 10-wk period bounded by dashed lines. All eagles dispersed by age 1 yr.

not normally distributed and to test for differences in dispersal timing where the median was the most appropriate metric of central tendency. We used Pearson's r to evaluate correlation between age and dispersal date, and survival and maximum distance traveled from natal nest. We considered $\alpha = 0.05$ to indicate statistical significance.

Results

Dispersal Timing, Distance, Direction, and Strategies. Sixty-six Golden Eagle nestlings tagged with PTTs during 2010–2014 (4, 10, 14, 23, and 15 eagles respectively; total $n = 40$ males and 26 females, including seven pairs of nest-mates) survived at least until the onset of dispersal from their natal areas. All were represented in our analyses of dispersal timing and survival. Three of the eagles died <3 wk after dispersing; data for these were omitted in other analyses.

All eagles dispersed from natal areas before age 1 yr. Onset of dispersal by individual eagles spanned 32 wk (4 August–18 March) but was concentrated (66.7% of individuals) during 16 September through 21 November (Fig. 2). Median date for the onset of dispersal was 22 October (mean ± SE = 8 November ± 7.1 d). Annual median dates were congruent in 3 of the 4 yr with ≥10 dispersal records (17, 13, and 15 October in 2011, 2013, and 2014) and about 3 wk later in the other year (8 November in 2012). Before dispersing, 78.8% of eagles made one to five brief (1–4 d) excursions up to 150 km from the natal nest (Fig. 3a); others remained <9 km from the natal nest until dispersing or made an excursion immediately before dispersing (Fig. 3b). Only six eagles that we classified as dispersed returned to natal areas during their 1st yr. All such returns were temporary: (1) two eagles returned for <1 d each; (2) three returned six, seven, and nine times, respectively, each return visit lasting <1–4 d; and (3) one eagle returned 10 times during a 6-wk period that began 2 wk after dispersing, with three returns of <1 d each to <3 km of its natal nest and the rest 5–6 km from the natal nest for parts of 1- to 9-d periods.

Maximum straight-line distances of Golden Eagles from natal nests during their 1st yr of life ranged from 55 km to 1379 km ($n = 63$). These were highly skewed toward shorter distances (Fig. 4); thus, the mean maximum distance (279 ± 39 km) was nearly twice that of the median (151 km). Included were three eagles that died approximately 2 mo after the onset of dispersal. Maximum distances <350 km were in relatively random directions from natal nests (Fig. 5). Greater distances were mostly (71.4%; $n = 14$) south or southeast or east, to Mexico, east-central and southeastern New Mexico, and west central Texas. Most distant (>900 km) points reached by the eagles extended from northern Sinaloa to western Nuevo Leon, Mexico (southernmost latitude 25°45′N; $n = 4$), plus far western Arkansas (easternmost longitude 94°05′W; $n = 1$).

First-year dispersal strategies of 60 Golden Eagles were 66.7% SD, 16.7% MD, 13.3% LD (Fig. 6), and 3.3% Other. The latter included one eagle that alternated between short- and moderate-distance movements through its 1st yr and another that moved back and forth between an area 150–200 km from its natal nest and an area approximately 375 km away. MDs–LDs ($n = 18$) dispersed earlier than SDs (medians = 1 October and 29 November respectively; $U = 155$, $P < 0.001$; means = 4 October ± 5.4 d and 29 November ± 10.1 d respectively). All MDs–LDs, but only 57.5% of SDs dispersed by 23 November.

Influences of Age, Sex, Nest-mates, and Area of Origin. The eagles' median hatch date was 14 April (mean = 13 April ± 1.2 d; interquartile range = 6–19 April; range = 16 March–13 May). Thus, 4.3 mo lapsed between median dates of fledging and dispersal onset (22 October), assuming a fledging

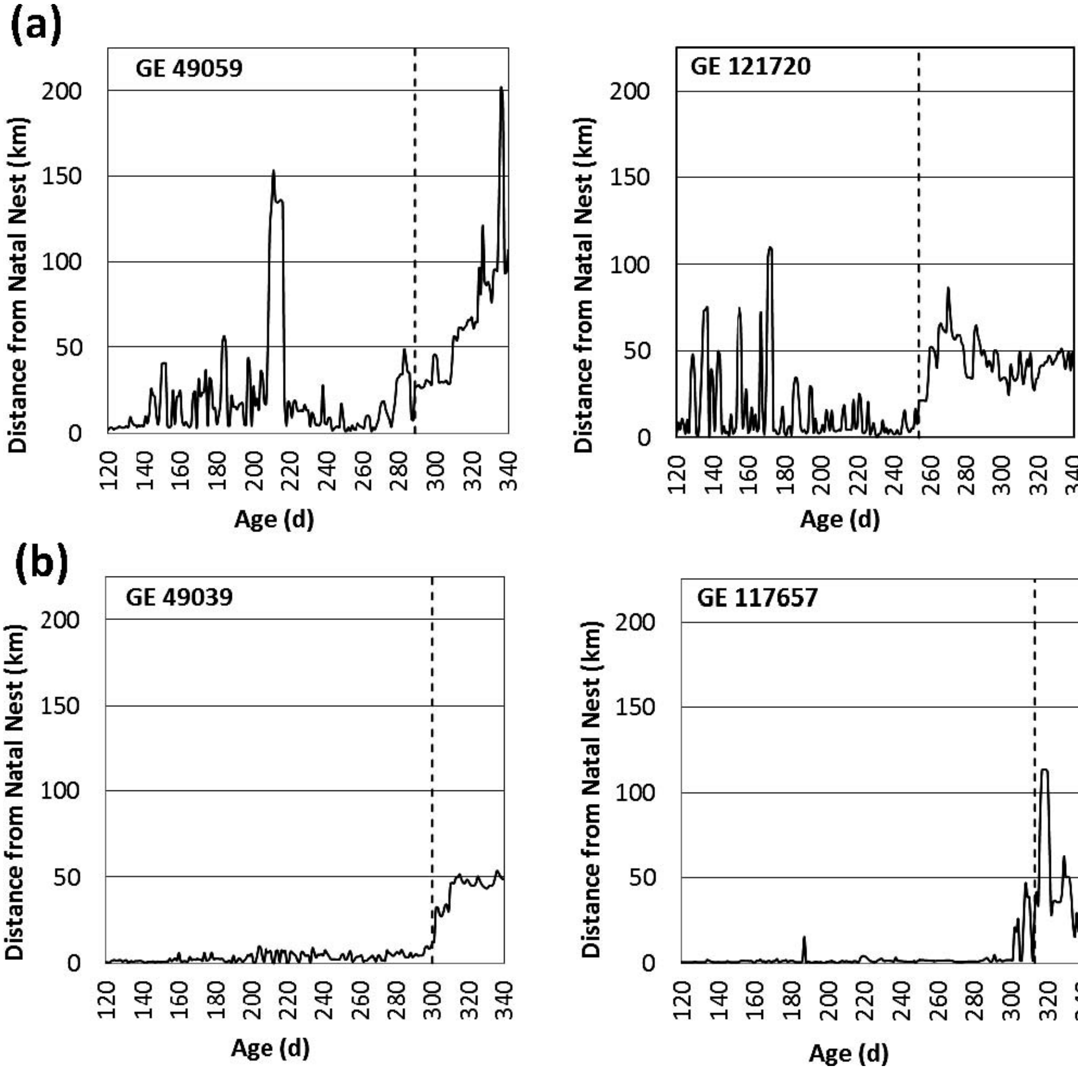

Figure 3. Movement patterns of Golden Eagles before and just after onset of dispersal from natal nests: (a) typical pre-dispersal pattern including multiple, 1- to 4-d excursions to 20–150 km from natal nest; (b) less common pattern, with no excursions before dispersing or just one to two excursions 2–12 d before dispersing. Vertical dashed lines represent date of the onset of dispersal, determined by using Method 7 in Weston et al. (2013).

age of approximately 10 wk (O'Toole et al. 1999, Watson 2010). All eagles dispersed before age 1 yr. We found no overall relationship between age and date of the onset of dispersal ($r = 0.040$, $P = 0.37$, $n = 66$). However, MDs–LDs dispersed at younger ages than SDs (174.2 ± 6.4 d and 230.2 ± 10.2 d respectively; df = 56, $t = 3.54$, $P < 0.001$). All MDs–LDs, but only 65.0% of SDs dispersed by 250 d of age.

We detected no overall sex bias in timing of dispersal onset (median = 14 October and 11 November for males and females respectively; $U = 443$, $P = 0.29$, $n = 40$ and 26; mean = 27 October ± 8.0 d and 26 November ± 12.6 d). Among SDs, however, onset of dispersal was earlier for males than females (median = 24 October and 3 January respectively; $U = 116$, $P = 0.04$, $n = 24$ and 16; mean = 12 November ± 12.1 d and 25 Dec ± 15.5 d). Sex

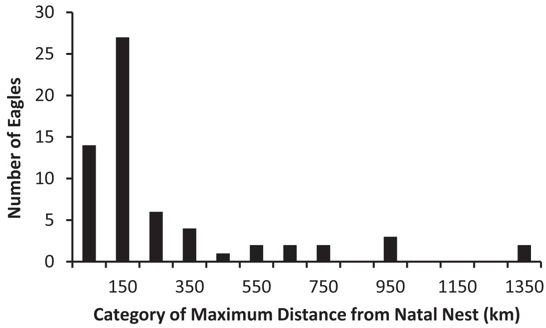

Figure 4. Maximum distance (km) from natal nest during 1st-yr dispersal for 63 Golden Eagles tagged with PTTs as nestlings in the Colorado Plateau and Southern Rocky Mountains of the southwestern U.S.A. during 2010–2014. Each distance category value (x-axis label) is ±50 km.

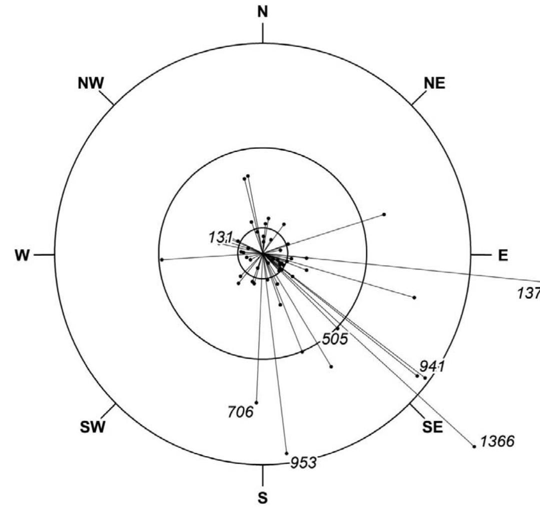

Figure 5. Maximum distances (km) moved and direction to point of maximum distance moved by 63 Golden Eagles from the Colorado Plateau and Southern Rocky Mountains during their 1st yr of life. Each eagle is represented by a line extending from the central point; maximum distances of eagles that died before 1 yr of age are indicated by numeric values at ends of their respective lines. Radii of inner to outer circles are 120 km, 500 km, and 1000 km.

bias in dispersal timing was not evident among MDs–LDs, but the sample was small ($n = 10$ males and eight females). We found no overall sex bias in maximum distance traveled from the natal nest during the 1st yr (276.7 ± 53.9 km for males and 283.6 ± 53.3 km for females, respectively; $n = 37$ and 26; df = 61, $t = 0.08$, $P = 0.93$). Males composed nearly identical proportions of SDs and MDs–LDs (0.60 and 0.56 respectively; $n = 40$ and 18 total eagles, sexes combined).

Golden Eagles we monitored included seven pairs of nest-mates. The difference in dispersal date between individuals of nest-mate pairs ranged from 3 d to approximately 3–5 mo (Table 1). Of four nest-mate pairs that survived through age 1 yr, two (nest locations named "Angus" and "Chama") included SDs that remained closely associated through early spring despite initiating dispersal approximately 3.5 and 1 mo apart, respectively. Another pair of SD nest-mates ("Grapevine") occupied early spring HRs in opposite directions of their common natal nest. The fourth nest-mate pair monitored through age 1 yr ("Kittyhawk") included a LD eagle that by early spring had returned close to its natal area and thus nearer to its SD nest-mate.

Golden Eagles from the more arid, southwestern half of our study area were more likely to be MDs–LDs; seven of eight LDs originated there (Fig. 1). Mean annual precipitation within 120 km of the natal nest during the hatch year plus previous year for individual eagles was lower among MDs–LDs (325.9 ± 26.5 mm) than SDs (381.8 ± 14.7 mm; $n =$ 18 and 40, df = 23, one-tailed $t = 1.85$, $P = 0.04$). Moreover, the coefficient of variation in annual precipitation within 120 km of natal nests during the same respective 2-yr periods was lower among MDs–LDs (mean = 31.1 and 41.0 respectively; df = 27, one-tailed $t = 4.13$, $P < 0.001$).

First-year Survival. Fifty-two of 66 Golden Eagles survived the period between the onset of dispersal and end of the 1st yr of life. Causes of mortality included electrocution and/or collision with electrical distribution lines (five); shooting (two); starvation/disease in winter (two); killed by mountain lion at deer carcass (one); unrecoverable (due to human safety concerns) but presumed dead based on circumstances associated with data record (three); and unknown cause (one). Overall survival rate between the onset of dispersal and end of the 1st yr of life was 78.8% (95% CI = 68.2%–87.6%). Only four of 43 eagles and none of 12 eagles categorized for this survival analysis as SDs and MDs (respectively) died before the end of their 1st yr, but seven of eight LDs died. The most competitive model grouped SDs and MDs and separated LDs (Table 2). First-year survival was 92.6% (84.4%–97.9%) for the SD–MD group and 13.2% (5.0%–42.0%) for LDs (P difference $\neq 0 = 1.0$). We plotted 1st-yr survival rate against maximum distance moved from natal

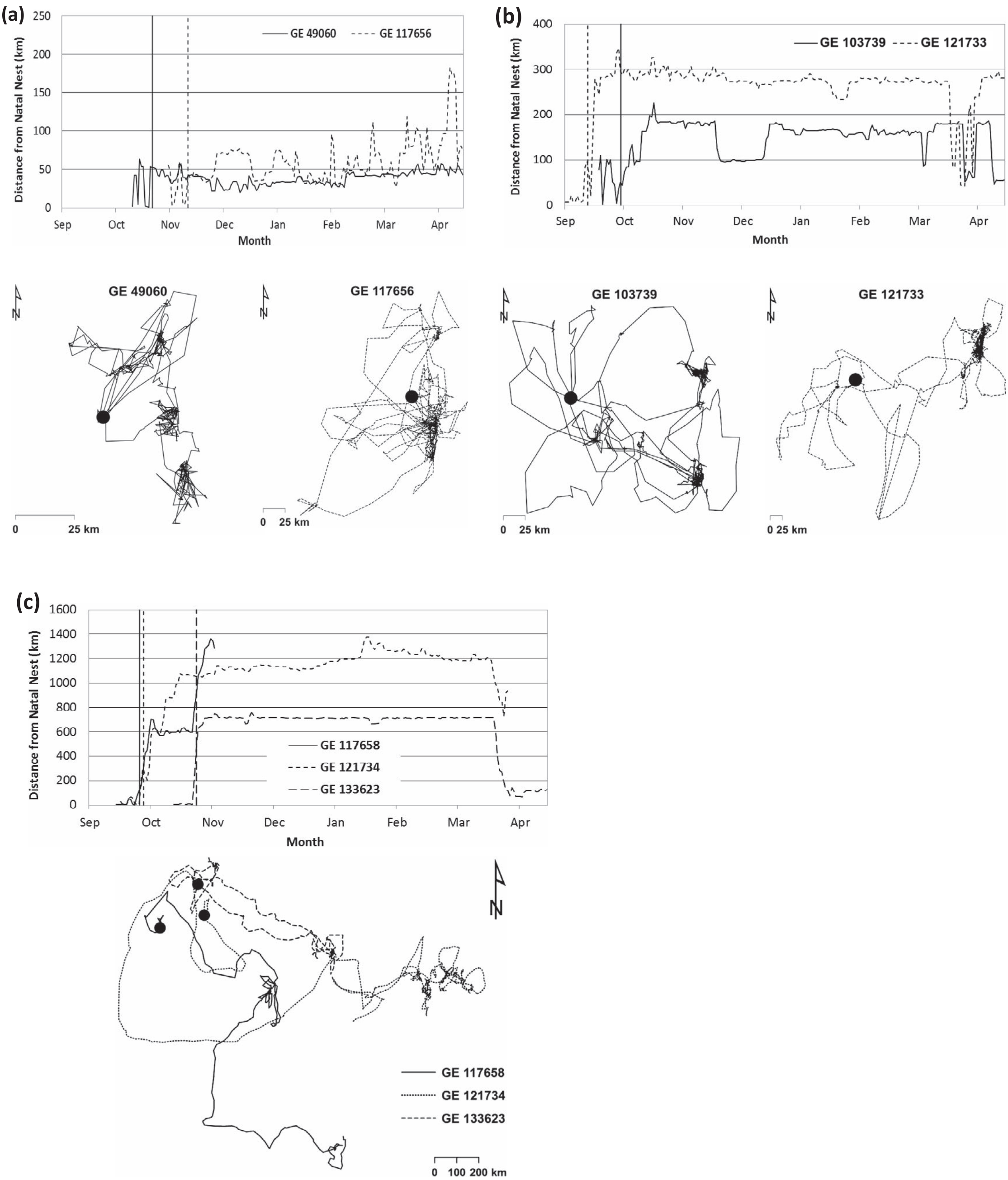

Figure 6. Examples of dispersal onset and subsequent movement through ca. the 1st yr of life for Golden Eagles exhibiting three dispersal strategies, based on maximum daily distances from the natal nest: (a) two short-distance dispersers, (b) two moderate-distance dispersers, and (c) three long-distance dispersers. For each strategy type, time-distance graphs are accompanied by movement tracks of the respective individual eagles to provide spatial context; black dots represent natal nests. Onset of dispersal (vertical lines) is based on changes in distance from natal nest per Method 7 in Weston et al. (2013). Maximum daily distance is derived from GPS locations collected hourly during 0900–1600 H.

Table 1. Characteristics of 1st-yr dispersal by Golden Eagle nestmates from natal areas in the Colorado Plateau and Southern Rocky Mountains of the southwestern U.S.A., monitored via satellite telemetry during 2010–2015.

Natal Area Name	Eagle Number	Sex	Dispersal Date	Nest-mate Difference in Date of Dispersal (d)	No. of Days Alive 1st Yr	Dispersal[a] Strategy	Early Spring Distance[b] from Natal Nest (km)	Early Spring Distance Between Nest-mates (km)
Angus	121729	male	3 Oct	71	365	SD	17.6	49.0
	121730	female	13 Dec		365	SD	56.7	
Chama	117644	male	27 Feb	104	365	SD	75.1	26.6
	117645	male	15 Nov		365	SD	56.0	
Grapevine	133618	male	14 Sep	30	365	SD	91.5	118.6
	133619	male	14 Oct		365	SD	45.0	
Kittyhawk	133622	male	26 Oct	43	365	SD	112.5	60.0
	133623	female	13 Sep		365	LD	83.3	
Sal	103735	female	2 Oct	162	365	SD	32.9	-[c]
	133620	male	13 Mar		209	unknown	-	
Stubbs	117643	male	16 Oct	3	365	SD	104.6	-
	133615	male	13 Oct		290	LD	-	
Dutch	117661	female	23 Nov	88	264	LD	-	-
	117662	female	27 Aug		365	other	144.0	

[a] SD, MD, LD = short-, moderate-, and long-distance disperser, respectively.
[b] Early spring = 16 March–15 April; distance measured to centroid of 95% kernel density estimate home ranges.
[c] All dashes indicate no data due to mortality before early spring, i.e., before 1 yr of age.

nest and found an inverse relationship between the two ($r = 0.98$, $P < 0.001$, $n = 66$; Fig. 7).

Progressive Distancing and Space Use. SDs appeared to settle by November–December, on average, based on constant to slightly increasing distance from natal nests from then through March (Fig. 8a); distance increased in April, however, compared with November (55 ± 5 km and 33 ± 6 km, respectively).

Table 2. Models evaluated to explain variation in the probability of survival to age 1 yr by dispersal strategy for Golden Eagles from natal nests in the Colorado Plateau and Southern Rocky Mountains of the southwestern U.S.A., monitored via satellite telemetry during 2010–2015. Survival probabilities were estimated using a generalized linear model with a logit-link function in a Bayesian framework (see Methods for more details on the modeling approach). Model ranking was based on deviance information criterion (DIC).

Model	pD[a]	DIC	ΔDIC[b]
SD + MD + LD [c]	2.4	37.7	0
SD − MD + LD	2	38.8	1.1
SD + MD-LD	2	56.6	18.9
NULL	1	60.4	22.7

[a] Effective number of parameters in the model.
[b] Difference in DIC relative to the lowest-scoring model.
[c] SD, MD, LD = short-, moderate-, and long-distance disperser, respectively ($n = 43$, 12, and 8).

Correspondingly little change occurred in month-to-month, cumulative HR size (Fig. 8b). MDs exhibited a roughly similar pattern for both metrics albeit with much individual variation (Fig. 8a, b). Successive monthly HRs of SDs overlapped, on average, by roughly one-half during February–April while those of MDs increased to about three-fourths by April (Fig. 8c). Relatively high overlap between October and November by SDs reflects the fact that many initiated dispersal during those months. Month-to-month comparisons based on minimum convex polygon estimates of home ranges (Appendix) generally showed parallel patterns, especially in distance from nest and cumulative home-range size, albeit with much greater within-month variation.

Distances from natal nests to centroids of 1st- and 2nd-year, early spring HRs did not differ in a paired between-year comparison for individuals tracked through at least their 2nd year, both for 34 SD–MDs (1st year 76.4 ± 15.6 km, median = 43.2 km; 2nd year 66.4 ± 16.9, median = 33.4; paired $t = 0.96$, df = 33, $P = 0.33$) and for 26 SDs (1st year 42.2 ± 4.8, median = 34.5; 2nd year 35.1 ± 4.8, median = 32.7; $t = 1.48$, df = 25, $P = 0.15$); between-year distances for 16 (61.5%) of the SDs differed by only 0.8–24.3 km. Between-year distances of the eight MDs tracked through their 2nd year varied more (1st year 187.5.0 ±48.2, median = 158.0; 2nd year 168.1 ± 59.4,

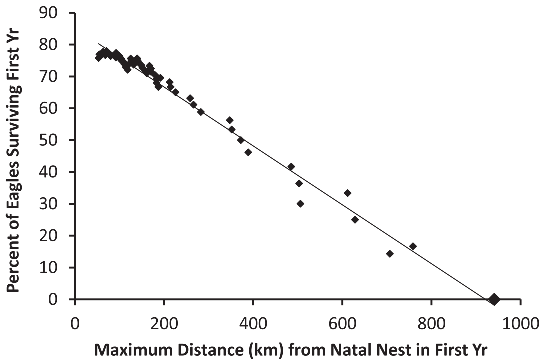

Figure 7. Relationship between percentage of 66 Golden Eagles surviving through their 1st yr of life and "greater than" maximum distance traveled from the natal nest. This distance includes all eagles that moved farther than any particular x-axis value, e.g., 12 eagles moved >400 km, and six (50%; y-axis) of these survived through the end of their 1st yr of life. Data are truncated at 800 km to simplify the illustration; five individuals had maximum distances of 941 to 1379 km and none of these survived to age 1 yr.

median = 90.7), including one eagle with a three-fold decrease and another with a five-fold increase.

Average overlap of 1st- and 2nd-year, early spring HRs was 31.8% (±4.8; median = 25.2%, n = 34). Half of SDs exhibited >40% overlap versus only one of eight MDs, though overall HR overlap did not differ strongly between the two groups, due in part to the relatively small number of MDs; we had predicted greater overlap for SDs (SDs 42.2% ± 6.4%, median = 37.2%, n = 26; MDs 26.5% ± 9.5%, median = 21.9%, n = 8; one-tailed t = 1.22, df = 32, P = 0.12). Based on 95% minimum convex polygon estimates, 2nd-year, early spring home ranges of SDs typically were smaller than and often nested entirely within 1st-year home ranges, although size and spatial configuration of the home ranges varied extensively among individuals and between years for individuals (Fig. 9).

DISCUSSION

Ours is the first comprehensive documentation of dispersal by 1st-yr Golden Eagles from a population in North America that does not exhibit southward winter migration, and it may be the only such study in the ca. southern one-third (ca. south of 39°N latitude) of the species' global breeding range. Overlap of dispersal and migration periods (McIntyre et al. 2008, Nygård et al. 2016) make it difficult to distinguish and describe the eagle's pre-breeding-age dispersal movement behavior. Compared with other *Aquila* spp., particularly Bonelli's Eagle (*A. fasciatus*; Balbontín and Ferrer 2009, Cadahía et al. 2010) and Spanish Imperial Eagle (*A. adalberti*; Ferrer 1993a, Muriel et al. 2015), 1st-yr Golden Eagles are believed to range much more widely while dispersing instead of being limited to a few "temporary settlement areas" with relatively high prey densities and few breeding eagles (Ferrer and Calderón 1990, Soutullo et al. 2008, Balbontín and Ferrer 2009), though Weston (2014) recently documented routine use of such areas by 1st-yr Golden Eagles in Scotland. The Golden Eagle's dispersal is less constrained than that of other *Aquila* spp. because the eagle can use a broader range of prey types and can fast much longer due to its relatively greater mass, lower metabolic rate, and ability to accumulate more fat reserves (Soutullo et al. 2008).

We were able to characterize distinct 1st-yr dispersal strategies of Golden Eagles, in contrast with the common notion that the eagle is "... notorious for its high inter-individual variation in dispersal strategy" (Weston et al. 2013), though we acknowledge that spatial scales at which dispersal strategies operated in our study area likely differ from those in other regions. We found that two-thirds of Golden Eagles dispersing from natal areas in the Colorado Plateau and Southern Rocky Mountains were relatively settled within approximately 120 km of natal nests by late winter to early spring of their 1st yr and tended to be in about the same respective settlement areas at the end of their 2nd yr. Nearly all the rest either dispersed up to approximately 500 km away (MDs) or to 500–1379 km away (LDs). Some key demographic differences were that MDs–LDs dispersed at younger ages than SDs, MDs–LDs were more likely to be from the arid half of our study area, and LDs experienced much lower survival than other eagles. Given the latter, natural selection likely does not favor LDs in most settings though the strategy may represent a high-risk trait that occasionally enhances genetic connectivity and population expansion (Trakhtenbrot et al. 2005).

About two-thirds of the Golden Eagles we studied initiated dispersal from natal areas during an approximately 2-mo period in fall, though timing of dispersal onset varied much among individuals, similar to other nonmigratory populations of the species (Soutullo et al. 2006b, Weston et al. 2013). Also, the range of dispersal dates we documented (4

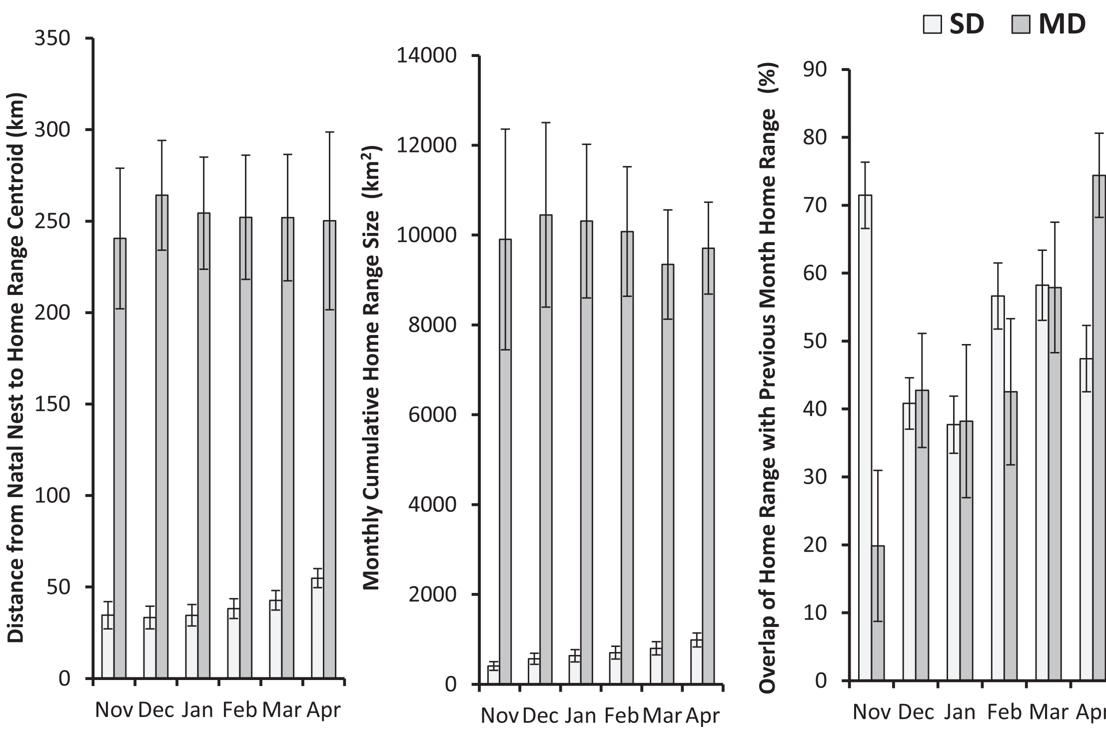

Figure 8. Progressive distancing and spatial use by 1st-yr Golden Eagles exhibiting short-distance (SD; $n = 38$) or moderate-distance (MD; $n = 10$) strategies for dispersing from natal nests through the end of their 1st yr (April): (a) mean distance between natal nests and centroids of monthly home ranges (95% kernel density estimates); (b) mean month-to-month, cumulative home-range size; (c) percentage overlap between successive monthly home ranges. Only individuals that survived $\geq$1 yr are included. Error bars are $\pm$SE.

August–18 March, approximately 7.5 mo) was remarkably broad. Soutullo et al. (2006a) noted that reports of dispersal date ranges of Golden Eagles can be exaggerated if early exploratory movements are inadequately distinguished from "true independence." This was not the case in our study, however, as graphs of maximum daily distances from natal nests consistently showed that the approach we used was biologically valid. Moreover, no eagle in our study failed to disperse in its 1st yr of life.

Prey availability may have influenced the timing of dispersal onset among Golden Eagles we studied. In populations that migrate from the most northerly regions of the species' range, decreased prey availability due to the arrival of winter weather indirectly hastens departure from natal areas (McIntyre and Collopy 2006, McIntyre et al. 2008, Nygård et al. 2016). For example, McIntyre and Collopy (2006) reported that for Golden Eagles in interior Alaska, post-fledging dependence lasted 50 d on average (versus 4 mo in our study), nest-mates left natal areas only 1–13 d apart (versus 3 d to >120 d in our study), and departure from natal areas occurred during 15 September to 5 October (versus 4 August–18 March in our study). Where 1st-yr movement does not include migration, as in our study, dispersal timing may still be influenced by prey availability; some species of raptors disperse from natal areas earlier in years when prey are scarce and vice versa (Kenward et al. 1993, Kennedy and Ward 2003). Median date of dispersal onset in our study was similar ($\pm$2 d) during 3 yr and was only 3 wk later in another year, suggesting no substantial changes in prey abundance occurred as per the above premise. However, wide dietary breadth of Golden Eagles (Kochert et al. 2002) could obscure a relationship between dispersal timing and prey abundance.

Moreover, we suspect that eagles from the arid half of our study area tended to disperse earlier because they could not find sufficient prey during pre-dispersal exploratory excursions. This may explain why many MDs–LDs, especially LDs, departed

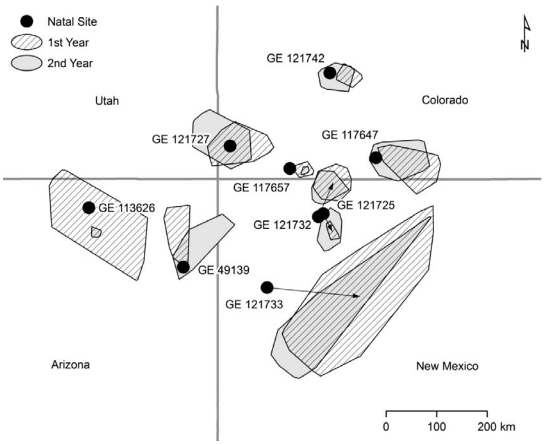

Figure 9. Spatial overlap between 1st-yr and 2nd-yr, early-spring home ranges of eight Golden Eagles classified as short-distance dispersers and one (GE 121733) classified as a moderate-distance disperser, and relationship to their respective natal nest locations. For simplicity, home ranges are estimated by 95% minimum convex polygons. Arrows link natal nests of three eagles to their respective home ranges. Early spring is 16 March–15 April, corresponding roughly to age 12 mo in the 1st yr and 24 mo in the 2nd yr. Some natal nest locations are intentionally inexact to protect sensitive areas.

abruptly from natal areas and traveled hundreds of km in <1 wk. Eagles from the arid part of the study area also may have dispersed earlier if their parents' physical condition, and thus provisioning rates, waned due to prey scarcity; declining condition of breeding Spanish Imperial Eagles led to a reduced period of parental dependency (Ferrer 1992a). Conversely, there is some evidence that well-provisioned 1st-yr *Aquila* spp. depart natal areas earlier and thus have the opportunity to move greater distances (e.g., Spanish Imperial Eagle; Ferrer 1992b, 1993a). Early, more distant dispersal may confer advantages, e.g., promptly gaining familiarity with relatively high quality areas before other 1st-yr conspecifics. Nonetheless, breeding pairs of Golden Eagles in much of the arid part of our study area often experience low annual productivity (Stahlecker et al. 2017), likely due to low prey abundance, supporting the idea that prey scarcity may have contributed to early dispersal from the arid landscape. Early dispersal onset in general may be related to high breeding density (Greenwood and Harvey 1982), but surveys of breeding Golden Eagles across most of our study area and during overlapping years with our study indicated a lower breeding density in the more arid half of the study area (D. Stahlecker unpubl. data).

Golden Eagles often move briefly (approximately 1–4 d) from, and return to, natal areas before showing distinct, relatively permanent dispersal, e.g., Weston et al. (2013) reported pre-dispersal excursions for 91.7% of 24 Golden Eagles studied in Scotland compared to 78.8% in our study. Nine of 13 Golden Eagles from a migratory population in Norway made such moves (Nygård et al. 2016). This transitional, pre-dispersal period and its characteristic movement patterns among some *Aquila* spp. have been referred to as "exploratory" (Gonzalez et al. 1989); "preliminary dispersal" (versus subsequent "permanent dispersal"); "preliminary excursion" (Nygård et al. 2016); and "restricted pre-dispersal movement around natal nest" (Soutullo et al. 2006a). Pre-dispersal excursions away from natal areas before the onset of dispersal probably serve as a "prospecting mechanism" for assessing foraging opportunities and competition (i.e., from breeding pairs or other older-age conspecifics) in the surrounding landscape, to help decide when and where to disperse (Weston et al. 2013). Some prospecting may be done to learn about potential future breeding sites (Weston 2014).

Based on graphs of maximum daily distances from natal nests through the 1st yr, all but six Golden Eagles in our study demonstrated permanent departure from the natal area that was distinguished clearly from pre-dispersal movement, regardless of the extent of travel after dispersal onset. We largely attribute this clear depiction of the onset of dispersal to methods developed specifically for Golden Eagles by Weston et al. (2013). Eagles that returned to natal areas during their 1st yr generally visited briefly (<1–4 d). Brevity of these return visits might suggest breeding pairs were present and aggressive toward the young eagles (*sensu* Trivers 1974), but territorial adult Golden Eagles seem tolerant of conspecifics with the distinct juvenal plumage, identifying the latter as non-competitors for breeding areas (Ellis and Lish 2006).

Maximum dispersal distances >350 km by 14 1st-yr Golden Eagles were mainly in southeasterly directions from natal nests, into parts of states overlapping the Sonoran Desert, Chihuahuan Desert, and Shortgrass Prairie regions. These landscapes generally are open and less mountainous than those encompassing the eagles' natal areas. We are unsure why the eagles dispersed far to these regions, except that breeding Golden Eagles may be sparsely distributed there, reducing competition for space and prey resources. Weather conditions at the time of dispersal may play some role in dispersal direction; weather patterns—especially wind direction—influence general dispersal direction of Spanish Imperial Eagles (Ferrer 1993b) and other raptor species (Common Buzzard [*Buteo buteo*]; Walls et al. 2005). Regardless, not all eagles in our study area with substantial maximum distances reached such points directly.

We found no evidence of sex-biased dispersal distance. Dispersal distance in Class Aves tends to be female-biased at least in monogamous systems, with the male's dominant role in defending resources prompting stronger philopatry compared to the female (Greenwood 1980). In raptors, sex-biased dispersal behavior may reduce competition between sexes for food and space resources; females generally disperse farther than males (Newton 1979, Soutullo et al. 2006a). Maximum 1st-yr dispersal distances of seven female Golden Eagles in Spain averaged twice as great as six males (138.5 and 70.5 km; Soutullo et al. 2006b). Although Ferrer (1993a) found no difference in maximum distances between male and female Spanish Imperial Eagles, females remained longer in the most distant areas before moving back closer to natal areas. First-year eagles in our study may have reduced competition for food and space simply through each sex using multiple dispersal strategies instead of sexes moving different distances.

Management Implications

Our findings of two general dispersal strategies among 1st-yr Golden Eagles indicates that conservation to benefit the species in the southwestern U.S.A. needs to be considered at two very different scales. First, most eagles that we studied remained within approximately 120 km of natal areas during their 1st yr, where they displayed relatively stable spatial use through at least their 2nd yr with high survival. Moreover, a high proportion of space use by most of the eagles occurred within considerably shorter distances. Higher survival of eagles exhibiting the SD strategy may confer increased likelihood of local recruitment. Indeed, five Golden Eagles that we fitted with PTTs as nestlings in 2010 and 2011 and that were included among SDs in this study have remained (as of summer 2016) within approximately 120 km of their natal nests through attainment of breeding age (R. Murphy and B. Millsap unpubl. data). Thus, conservation actions (e.g., improving range condition and habitat heterogeneity to sustain prey populations) focused in areas of the southwestern U.S.A. with aggregated suitable breeding habitat or that are known to support breeding pairs likely will also benefit nonbreeding eagles. In particular, prioritization of risk reduction measures (e.g., retrofitting of hazardous electrical distribution lines, discouraging wind energy development) in this zone will improve survival of both breeding and nonbreeding members of this population.

Secondly, we predict that LDs will increase in proportion among 1st-yr Golden Eagles in the southwestern U.S.A. due to effects of increased aridity of landscapes associated with climate change (Seager et al. 2007). Because LDs displayed the lowest 1st-yr survival in our study, such effects could have negative population consequences. In a recent review of the population status of Golden Eagles in the U.S.A. (United States Fish and Wildlife Service 2016), starvation or a combination of starvation and disease accounted for an estimated 605–1205 (95% credible interval) deaths of 1st-yr Golden Eagles annually, more than half of that cohort's total mortality. However, survival increased markedly after the 1st yr (estimated at 0.7) to 0.77, 0.84, and 0.87 in 2nd, 3rd, and 4th/after 4th yr respectively. This implies that successful initial dispersal is highly important for both individual fitness and population stability. Consequently, conservation actions to maintain or improve the survival of LDs in the southwestern U.S.A. should include interregional and international cooperation to safeguard potentially prey-rich landscapes from northern Mexico to the southern Shortgrass Prairie Region, areas which also support overwintering Golden Eagles from as far north as Alaska (McIntyre et al. 2008).

Acknowledgments

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Appendix. Progressive distancing from natal nests and progressive use of space by Golden Eagles monitored via satellite telemetry while dispersing from natal areas in the Colorado Plateau and Southern Rocky Mountains of the southwestern U.S.A. during 2010–2015, based on 95% minimum convex polygon home ranges: (1) straight-line distances from natal nests to centroids of monthly home ranges; (2) percentage overlap of monthly home range with the previous month's home range; (3) cumulative monthly home range size. Eagles are grouped by two dispersal strategies: (1) short-distance dispersers (SDs; $n = 38$) and (2) moderate-distance dispersers (MDs; $n = 10$). Includes only data from individuals that survived ≥1 yr of age (i.e., until approximately 15 April); eagles were about 7 mo of age in November. Data are presented as mean ± SE and (median).

Measurement	Dispersal Strategy	Month					
		November [a]	December	January	February	March	April
Distance from nest to home range centroid (km)	SDs	34.4 ± 5.7 (23.3)	35.8 ± 5.6 (21.9)	32.6 ± 5.6 (19.4)	36.8 ± 5.0 (34.2)	36.6 ± 4.0 (31.3)	50.7 ± 4.5 (44.1)
	MDs	240.3 ± 34.4 (216.6)	256.7 ± 33.0 (247.8)	248.0 ± 32.2 (233.5)	246.0 ± 33.8 (243.5)	239.3 ± 39.6 (257.4)	205.7 ± 44.7 (166.4)
Cumulative monthly home range size (km^2)	SDs	407 ± 97 (149)	566 ± 122 (229)	635 ± 137 (287)	702 ± 142 (309)	800 ± 147 (470)	987 ± 156 (612)
	MDs	9903 ± 2455 (8746)	10,450 ± 2053 (10,254)	10,311 ± 1712 (10,322)	10,080 ± 1439 (11,484)	9,346 ± 1215 (10,332)	9,709 ± 1024 (10,318)
Overlap of monthly home range with previous month's home range (%)	SDs	53.3 ± 4.7 (58.4)	42.7 ± 4.9 (35.8)	40.1 ± 4.6 (35.8)	67.1 ± 5.1 (76.1)	63.8 ± 5.5 (57.1)	57.5 ± 5.3 (60.7)
	MDs	20.4 ± 10.7 (3.5)	40.7 ± 10.0 (23.5)	27.9 ± 8.3 (24.3)	44.7 ± 13.2 (32.2)	50.3 ± 9.2 (52.9)	83.0 ± 5.2 (87.4)

[a] Eighteen (47.4%) SD eagles and nine (90.0%) MD eagles dispersed from natal areas before November; all eagles dispersed by 18 March.