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Ectoparasitism and Energy Infrastructure Limit Survival of Preadult Golden Eagles in the Southern Great Plains

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ABSTRACT.—Much of the US Southern Great Plains (SGP) continues to undergo intensive energy development that could affect the region's Golden Eagles (*Aquila chrysaetos*), yet the species' population status there is unknown. During 2011–2020, we used satellite telemetry to assess annual survival rates and causes of mortality among 40 preadult (<3 yr of age) Golden Eagles in the SGP; 29 were monitored beginning at the late nestling stage and 11 immigrated into the SGP from western regions. For comparison we monitored 15 preadult Golden Eagles from nests in the Central Great Plains (CGP), where energy development was less extensive. We estimated survival rates by using a multi-state model in a Bayesian framework that accounted for probabilities of causes of death. Mean annual survival in the SGP during the preadult period was 0.060, versus 0.512 in the CGP and ~0.7–0.9 reported elsewhere in the coterminous western USA. Mexican chicken bugs (*Haematosiphon inodorus*) were implicated in deaths of at least seven Golden Eagles during the ~2-wk late nestling stage and in two deaths <3 mo after fledging. Energy infrastructure especially electrocutions accounted for 12 (57.1%) of 21 deaths of post-fledged preadults. Seven of 11 immigrant eagles died. Overall, probabilities of death of a Golden Eagle during the preadult period in the SGP due to Mexican chicken bugs and to electrocution were both 0.345. We estimated that the SGP population may be declining 9% annually due to poor recruitment; mitigation of underlying factors should be a priority for managing Golden Eagles in the western USA.

KEY WORDS: *electrocution*; *Great Plains*; Haematosiphon inodorus; *Mexican chicken bug*; *mortality*; *survival rate estimate.*

EL ECTOPARASITISMO Y LA INFRAESTRUCTURA ENERGÉTICA LIMITAN LA SUPERVIVENCIA DE LOS INDIVIDUOS PREADULTOS DE *AQUILA CHRYSAETOS* EN LAS GRANDES LLANURAS DEL SUR

RESUMEN.—Buena parte de las Grandes Llanuras del Sur (GLS) de EEUU continúan sometidas a un desarrollo energético intensivo que podría afectar a los individuos de *Aquila chrysaetos* de la región; sin embargo, el estado de la población de la especie en esta zona es desconocido. Durante 2011–2020, usamos telemetría satelital para evaluar las tasas de supervivencia anuales y las causas de mortalidad entre 40 águilas preadultas (<3 años de edad) de *A. chrysaetos* en las GLS; 29 fueron monitoreadas a partir de la etapa tardía de polluelo y 11 inmigraron desde regiones del oeste. Para hacer una comparación, monitoreamos 15 águilas preadultas de *A. chrysaetos* en nidos de las Grandes Llanuras Centrales (GLC), donde el desarrollo energético

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era menos extenso. Estimamos las tasas de supervivencia utilizando un modelo multi-estado en un marco de trabajo bayesiano que tuvo en cuenta las probabilidades de las causas de muerte. La supervivencia media anual en las GLS durante el periodo preadulto fue de 0.060, en comparación con 0.512 en las GLC y ∼0.7–0.9 en otras partes del oeste contiguo de EEUU. La chinche *Haematosiphon inodorus* estuvo implicada en la muerte de al menos siete águilas durante las últimas ∼2 semanas de la etapa tardía de polluelo y en dos muertes durante el inicio del postemplumamiento. La infraestructura energética, especialmente las electrocuciones, representaron 12 (57.1%) de las 21 muertes de preadultos después de emplumar. Siete de las 11 águilas inmigrantes murieron. En general, las probabilidades de muerte de un individuo de *A. chrysaetos* durante el período preadulto en las GLS debido a las chinches y a la electrocución fueron ambas de 0.345. Estimamos que la población de las GLS puede estar disminuyendo un 9% anual debido al bajo reclutamiento; la mitigación de los factores subyacentes debería ser una prioridad para la gestión de *A. chrysaetos* en el oeste de EEUU.

[Traducción del equipo editorial]

INTRODUCTION

The Southern Great Plains (SGP) Region of North America supports a substantial number of Golden Eagles (*Aquila chrysaetos*) including ≥123 breeding pairs (Stahlecker et al. 2022) and many local nonbreeding, dispersing, and overwintering or migrating individuals (e.g., up to 3.5 Golden Eagles/100 km^2 occur during winter; Boeker and Bolen 1972, Mitchell et al. 2020). Energy development, namely oil and gas extraction or wind energy, is widespread and growing in the region. The Great Plains supports the greatest concentration of wind energy resources in the USA in general (Ott et al. 2021) and Texas leads the nation in developed wind energy capacity (US Department of Energy 2022). The Permian Basin of southeastern New Mexico and west central Texas has long been considered the country's most important oil and gas field (Vertrees 2010). Cropland irrigated by pumped groundwater is prevalent in much of the region, adding to the high demand for electrical distribution that is created by oil and gas extraction (Dwyer et al. 2020a). Collision and electrocution risks to Golden Eagles posed by this steady growth of energy infrastructure in the SGP could threaten stability of the eagle's regional population, but impacts are unquantified and must be understood to help prioritize actions for conserving the species within and among western regions of the USA. Collisions and electrocutions are two of the four most important mortality factors among Golden Eagles elsewhere in the western USA, limiting population growth; increases in these likely will lead to population declines unless ameliorated (Millsap et al 2022).

Therefore, we collected satellite telemetry data from platform transmitter terminals (PTTs) to help address two critical gaps in knowledge of the Golden Eagle's status and management needs in the SGP: survival probability and the influence of chief mortality factors on survival. Our first objective was to estimate survival of Golden Eagles in the SGP during the juvenile age period (late nestling or fledgling age to 1 yr of age) and overall preadult period (late nestling or fledgling age to 3 yr of age) stages, including individuals from nesting territories in the SGP and individuals that originated from nesting territories in adjoining regions and subsequently immigrated into the SGP. As part of this objective, we estimated annual growth rate (λ) of the SGP population and compared survival rates to those of juvenile and preadult Golden Eagles that originated in or immigrated into a less developed area in the Central Great Plains (CGP). Our second objective was to document causes of mortality among preadult Golden Eagles in the SGP and estimate the proportion of deaths attributable to each mortality factor.

STUDY AREA

Our SGP study area covered ∼200,000 km^2 and approximated the US Great Plains Region south of the Arkansas River (study area center ∼35°N, 103°W; Fig. 1). Its boundary was that of the southern one-half of the Shortgrass Prairie Bird Conservation Region 19 (US North American Bird Conservation Initiative Monitoring Subcommittee 2007) except that it extended further southwest, into central New Mexico, aligning with that of the Great Plains Ecoregion (Ecoregion Level I; https://www.epa.gov/eco-research/ecoregions). Land use in the western half of the area was primarily rangeland for grazing by cattle (*Bos taurus*) and, to a lesser extent, sheep (*Ovis aries*), while crop production, wind energy, and oil and gas extraction dominated most of the eastern half. Land cover was characterized mainly by native shortgrass prairie, tame (nonnative) grasslands, and cropland characterized by pivot irrigation to produce corn (*Zea mays*), alfalfa (*Medicago sativa*), sorghum (*Sorghum bicolor*), and cotton (*Gossypium hirsutum*), or dryland cropping of winter wheat (*Triticum aestivum*). Physiography generally was level to rolling plains with widely dispersed canyons, mesas, and small mountains. Notably, the Llano Estacado mesa spanned the mid-region and its northern and eastern portions supported relatively high Golden Eagle nesting densities (Stahlecker et al. 2022).

Our CGP study area encompassed the northern half of the Shortgrass Prairie Bird Conservation Region (US North American Bird Conservation Initiative Monitoring Subcommittee 2007), extending north of the Arkansas River (study area center ~42°N, 104°W; Fig. 1). Land use was chiefly rangeland for grazing by cattle and crop production. Land cover was characterized by native shortgrass prairie but also included much sandsage (*Artemisia filifolia*) prairie, some ponderosa pine (*Pinus ponderosa*) woodland especially in northwestern Nebraska, and dryland cropland. Cropland with pivot irrigation, primarily for corn and alfalfa production, was limited mainly to the Platte River valley and south to within ~100 km of the Colorado-Nebraska state line. Physiography of our CGP study area generally was characterized by extensive level to rolling plains, buttes in northwestern Nebraska and east central Wyoming, and broad floodplains of the Platte River.

METHODS

Annually during late March and April in the SGP, 2014–2017, we used ground-based observation and fixed- or rotary-wing aircraft to search for nests being used by Golden Eagles in potential nesting habitat and to examine nests in use within nesting territories known to be occupied during previous years (Stahlecker et al. 2022). We similarly surveyed nests in the CGP during 2014–2016. If we observed an adult eagle in an incubating/brooding position on a given nest, we observed the nest again in May to determine whether nestlings were present and estimate their ages (Hoechlin 1976). We then subsequently returned to enter nests and fit nestlings with PTTs at about 52 d of age. At this age, nestlings were almost completely feathered, with their heads mostly covered by newly emerged contour feathers (Hoechlin 1976, Steenhof et al. 2017). We used this age range to approximate the 80% criterion of 51 d recommended by Steenhof et al. (2017) as a starting point for estimating survival rates of Golden Eagles. However, we also used a 65-d fledging age criterion as a starting point for estimating survival rate, projecting this from our estimates of age when we entered nests. The criterion was based on Palmer's (1988:208) assertion that Golden Eagles usually fledge at about 65 d of age, corroborating a 65-d median age at fledging for 61 broods in southwestern Idaho (Steenhof et al. 2017; US Geological Survey [USGS] unpubl. data in Katzner et al. 2020). We used this alternative approach mainly to verify that our counts of ~52-d old nestlings closely reflected numbers fledged (Steenhof et al. 2017). We defined the "late nestling stage" as the ~2-wk period from ~52 d old to fledging.

We monitored individual Golden Eagles by using PTTs equipped with Global Positioning System (GPS) units and solar-recharged batteries (model PTT-45, Microwave Telemetry, Inc., Columbia, MD, USA). GPS location accuracy was ±19 m. We attached PTTs via "Y-harnesses" (Buehler et al. 1995) made with 0.64-cm wide Teflon ribbon (Bally Ribbon Mills, Bally, PA, USA). With harnesses attached, PTTs weighed ~55 g, (<2.5% of a nestling's mass). PTTs were programmed to record GPS locations hourly from 0700 to 1900 H local time, plus midnight, each day. We accessed new PTT data every 3 d via the Argos satellite system (www.argos-system.org). If non-movement of a given eagle was evident based on stationary GPS locations and a constant numeric activity value in parsed data downloads, we or collaborators investigated the respective site within 4–24 hr although some mortality events were not investigated until 2–3 d after death occurred due to a time lag created by the 3-d duty cycle of PTTs. Most carcasses were collected, frozen, and submitted to the Southeastern Cooperative Wildlife Disease Studies laboratory at Athens, Georgia or to the US Fish and Wildlife Service (USFWS) Wildlife Forensics Laboratory at Ashland, Oregon, for comprehensive necropsy. We did not submit three eagle carcasses that were found at bases of power line (i.e., distribution) poles posing high electrocution risk (Avian Power Line Interaction Committee [APLIC] 2006) and presented singed feathers or, in one case, a plantar surface burn (Kagan 2016); we concluded these eagles were electrocuted. Carcasses of five other eagles were badly decomposed or scavenged when recovered so were not submitted for necropsy but were examined with aid from a local veterinarian for evidence of

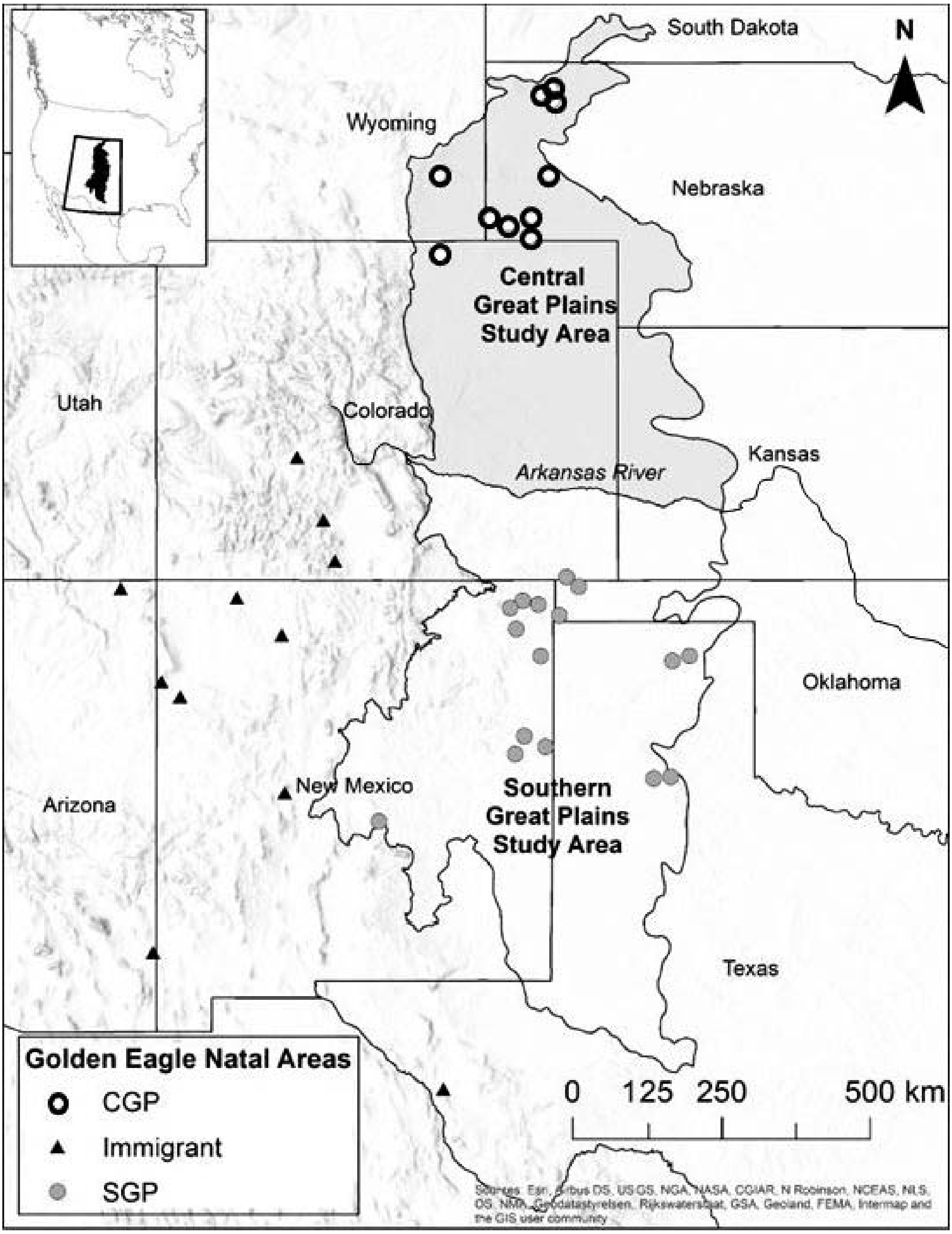

Figure 1. Locations of nesting territories from which preadult age Golden Eagles studied in the Central Great Plains (CGP) and Southern Great Plains (SGP) study area regions originated, including those of preadults that immigrated into the SGP.

general physical trauma e.g., skeletal fractures, fragments from firearm projectiles. In addition to Golden Eagles originating in our SGP study area, we included individuals that had moved to the SGP after being tagged with PTTs as nestlings in the Southern Rocky Mountains and Colorado Plateau regions west of our study area during 2011–2014 (Murphy et al. 2017) and from southwestern Texas and southeastern Arizona (Fig. 1). Millsap et al. (2022) included data from three of these eagles when estimating the species' survival across the western USA, and two of the three eagles accounted for the deaths due to aldicarb poisoning reported by Millsap et al. (2022). These data were included in our study.

When we entered some Golden Eagles' nests in the SGP, we found late nestlings that had died within ~3 d. We collected such birds for formal necropsy as described above unless their remains were badly decomposed due mainly to ambient temperatures exceeding 32°C. During 2017 we found that many late nestlings in the SGP were heavily parasitized by Mexican chicken bugs (*Haematosiphon inodorus*; MCBs), a haematophagous member of the Cimicidae (Hemiptera; Lee 1954, Dudek 2021). We attached PTTs to the affected nestlings if they did not appear weak and had normal mass ($\geq$2800 g and $\geq$3800 g for males and females, respectively; sex subsequently confirmed by DNA analysis [Animal Genetics, Tallahassee, FL, USA]). Before doing so, however, we used forceps to remove MCBs from the nestlings' heads and apteria, regions of the body where the insects seemed most concentrated. Next, we liberally applied pet-grade pyrethrin dust (Zodiac US, Schaumberg, IL, USA) to affected areas on nestlings. Then, after attaching PTTs, we moved the nestlings from their nests—which also were infested by MCBs—to nearby cliff ledges that appeared to lack MCBs and provided nestlings with adequate protection from sun and severe weather. In three cases where MCB parasitism of a late nestling was moderate to heavy (i.e., >50 individuals of second to third nymph stage or larger detected) and the nestling subsequently died within its natal area due to undetermined causes within 3 mo of being tagged, we considered MCB parasitism to be the ultimate cause of death.

To assess survival, we used a multi-state model to account for, upon death, the transition probability to different causes of mortality (Schaub and Pradel 2004; Supplemental Material A, B) as described in detail by Millsap et al. (2019, 2022). Unlike incidentally discovered band recoveries, birds equipped with telemetry devices can provide relatively unbiased information on causes of death, a critical factor when inferring the population significance of different mortality factors (Schaub and Pradel 2004, Millsap et al. 2022). We fitted the model in a Bayesian framework (Kery and Schaub 2012), using Markov chain Monte Carlo methods implemented via *rjags* in Program R (R Core Team 2015; Supplemental Material A, B). We implemented three chains of 100,000 iterations each, 50,000 of which were discarded as burn-in, and with a thinning rate of 3; inferences were made from 49,998 samples from the posterior distributions. This model allowed us to estimate probabilities that, during the ~2.8-yr preadult period, a given eagle in the SGP: (1) would die, regardless of cause; and (2) would die from each major cause of death documented during the study.

We ran the multi-state model with a capture history file that comprised data from all individual Golden Eagles from the SGP and CGP combined (Supplemental Material A, B). Time steps in the capture history were 90-d intervals, which allowed information from short ($\geq$45 d, i.e., at least one-half of a given 90-d period) pre-settling visits to the SGP by immigrant eagles to be included in estimates of their survival while residing in the region. We used a staggered entry design for our capture history, starting in May 2011 and ending in March 2020, for a total of 108 3-mo intervals (Supplemental Material A, B); our May start coincided with the start of the late nestling stage of Golden Eagles at most nesting territories in the SGP (Murphy and Stahlecker 2022). Although our interest was in estimating mean annual survival rates, we included random effects in our model for temporal interval and nest site to account for pseudoreplication in these aspects of our sample. The random effect standard deviations (SDs) provided no evidence of significant spatial or temporal variation within each population (Supplemental Material A, B), thus we felt comfortable using mean values for inference. We also estimated the period survival rate for juvenile Golden Eagles that we monitored during the ~2-wk late nestling stage in both the SGP and CGP. Because we knew fates of all nestlings in this analysis, we used a simple binomial model to compare late nestling survival rates between the two study areas (Supplemental Material A, B).

Bayesian analyses require use of prior probability distributions for the parameters to be estimated.

Priors can be informed, reflecting estimates from prior studies, or they can be uninformed if no relevant prior information is available (Kery and Schaub 2012). Here we used uninformed priors, in which case the data from our study provided all information for the parameter estimates from our model. We used the following five priors in our models (values in parentheses represent bounds of 95% credible intervals [CRIs] within which unobserved parameter values were believed to fall): (1) Normal (0, 0.01), truncated to the range of –10 to 10 to expedite convergence, for quarterly survival on the logit scale; (2) Normal (0, 10), for all random-effect SDs; (3) Normal (0, τ), truncated to the range –10 to 10, for the year and territory random effects, where $\tau = 1/\text{SD}^2$ (precision); (4) Uniform (0, 1), for probabilities of emigration, PTT failure, and whether cause of a mortality could be determined; and (5) Gamma (1, 1), for probabilities of the different causes of death. We estimated the probability that parameter distributions differed significantly by subtracting the posterior samples of the relevant parameters and reporting the proportion of the differences that were the same sign as the distribution with the larger mean value.

We also estimated the annual rate of growth (λ) for the SGP population of Golden Eagles by using a matrix model in Program R (R Core Team 2015), incorporating survival rate estimates from this study for first-, second-, and third-year stages, starting with the late nestling stage for individuals from nests in the region. For adults we used the survival rate estimate reported by the USFWS (2016a; Supplemental Material A, B). For fecundity, we sampled from the predictive distribution for Golden Eagles reported by the USFWS (2016a), with the assumption that fecundity in the SGP matched the average for the species across its western North America range; the parameters of that distribution, adjusted to reflect the expected number of females produced per breeding female per year, were normal (0.275, 0.087; see Supplemental Material A, B for more details). We used the population model structure described by Caswell (2001) and the *popbio* package in R software (Stubben and Milligan 2007) to extract λ (i.e., the dominant eigenvalue from the matrix) and the stable age distribution. We incorporated uncertainty into the estimates by sampling from the distributions of each model parameter (β for survival, lognormal for fecundity) over 500 simulations.

RESULTS

We monitored 29 preadult Golden Eagles in the SGP region beginning when the nestlings were tagged (at ~52 d of age) during the 2015–2017 breeding seasons; 69% of these were from nesting territories in northeastern New Mexico and immediately adjacent areas of Colorado and Oklahoma, an area encompassing a nearly equal proportion (76%) of the region's Golden Eagle nesting territories (fig. 1 in Stahlecker et al. 2022). Ten (34.5%) of the eagles died during the late nestling stage, two (6.9%) fledged and dispersed from the region <5 mo later, 14 (48.3%) fledged but died before reaching 3 yr of age, and three (10.3%) lived beyond 3 yr of age and the end of the study (Fig. 2, 3). We also monitored 11 preadult Golden Eagles that originated from nests in adjoining (west) regions (Fig. 1) during the 2011–2014 breeding seasons and subsequently immigrated into the SGP during their first ($n = 10$) or second ($n = 1$) year of life. Seven of these immigrants died while in the SGP and the other four left the region 3.1, 5.1, 5.2, and 10.0 mo after arriving there. In the CGP, we studied 15 preadult Golden Eagles beginning at the late nestling stage during 2014–2016 (Fig. 1); all fledged and eight (53.3%) lived through at least their third year of life (Fig. 3). In addition, one of the two tagged eagles that dispersed as juveniles from natal areas in the SGP settled in the CGP and remained there through the end of the study. Another eagle, which immigrated into the SGP, moved to the CGP for 2.2 mo then returned to the SGP.

All PTTs we deployed remained attached to the respective eagles and functioned properly. One PTT abruptly stopped transmitting when the eagle bearing it apparently was shot or poisoned (see below) and the PTT may have been taken with the eagle's carcass. We recovered all other carcasses; only three had been scavenged.

Survival Rate and Population Growth Rate. With period survival beginning at the late nestling stage, estimated annual survival rates for juvenile and overall preadult age classes of Golden Eagles in the SGP were 0.238 and 0.060, respectively (Table 1, Fig. 4). These were far less than estimates of 0.683 and 0.512 for corresponding age classes of Golden Eagles in the CGP ($P\,[\text{CGP} > \text{SGP}] = 0.99$ for juveniles and 1.0 for preadults), even though 95% CRIs encompassing means for CGP eagles were relatively wide due to small sample size (Fig. 4). The estimated survival rate of eagles during the ~2-wk late nestling stage was greater in the CGP (0.992) than in the SGP

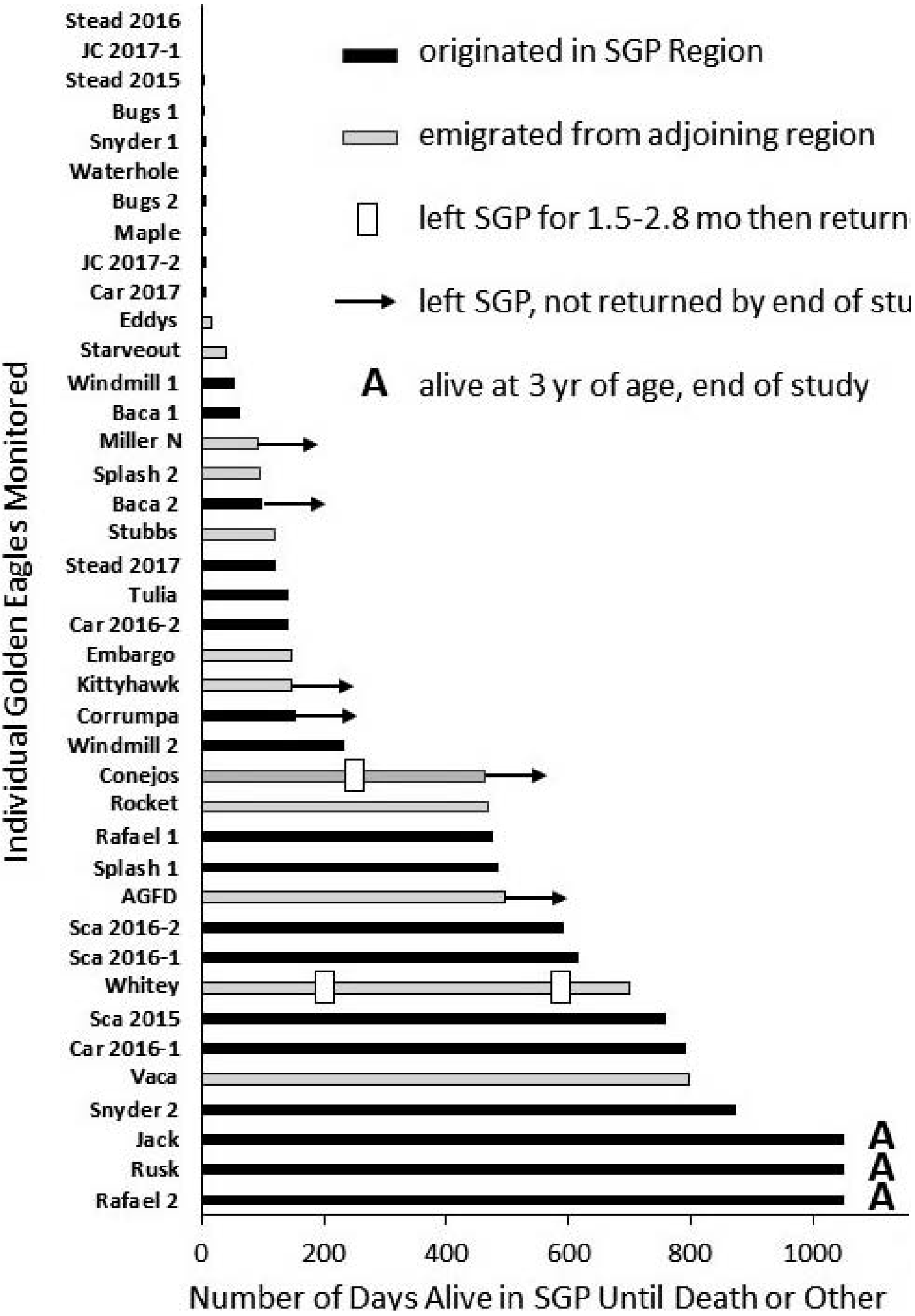

Figure 2. Total documented days alive in the US Southern Great Plains (SGP) for 40 Golden Eagles monitored between September 2011 and March 2020. Ends of bars without arrows or "A" indicate point of mortality while in the SGP. Length of residence time for the 29 eagles that originated in the SGP begins at the late nestling stage (~52 d of age). On the vertical axis, individuals with like names came from the same respective nesting territories; individuals with like names but accompanied by different years originated from the same nesting territories but in different breeding seasons, while individuals with like names followed by "1" and "2" were nestmates. All eagles initially occurred in the SGP sometime during their first year of life except for "Rocket," which immigrated into the region during its second year of life.

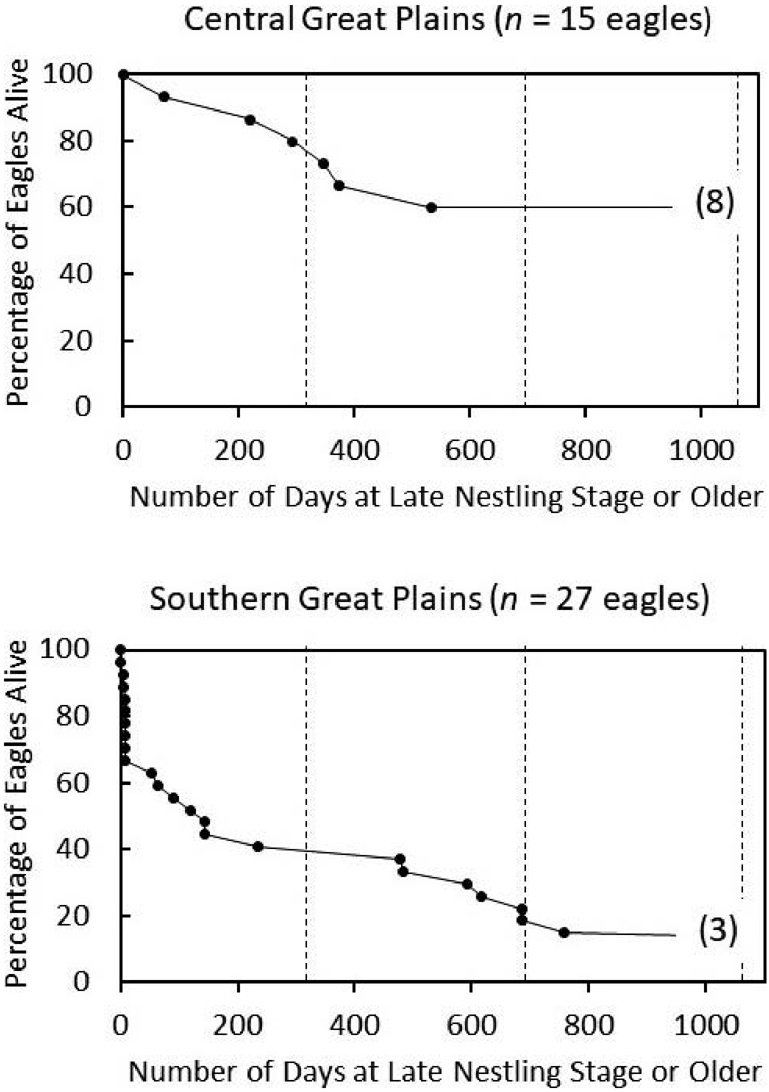

Figure 3. Temporal change in the percentage of Golden Eagles from nests in the US Central Great Plains and Southern Great Plains regions that remained alive from the late nestling stage (~52 d of age) through the third preadult year (~1095 d of age). Eagles that survived beyond the late nestling stage were monitored by satellite telemetry. Vertical dashed lines approximate (from left to right, respectively) the end of the first, second, and third years of life; parentheticals are numbers of individuals alive at end of the study. Two eagles that originated in the Southern Great Plains and dispersed to other regions at age ~6 mo are excluded. Not accounted for is the possible loss of some juveniles before the late nestling stage.

(0.656; *P* [CGP > SGP]) = 1.0). When we used fledging age as the starting point for period survival, estimated annual survival rates for juvenile and overall preadult age classes of Golden Eagles in the SGP were 0.450 and 0.113 (Table 1). These were less than estimates of 0.684 and 0.513 for corresponding age classes of Golden Eagles in the CGP (*P* [CGP > SGP] = 0.87 for juveniles and 1.0 for preadults). The estimated annual growth rate of the SGP population of Golden Eagles, with period survival beginning at the late nestling stage for individuals from nests in the region, was $\lambda = 0.912$ (± 0.011, interquantile range = 0.893–0.937).

Table 1. Estimated annual survival rates of juvenile (<1 yr of age) and overall preadult (<3 yr of age) Golden Eagles in the Southern Great Plains (SGP) during 2011–2020 ($n = 40^a$) and in the Central Great Plains (CGP; $n = 15^b$) during 2014–2019, with period survival beginning at either the start of the late nestling stage (~52 d of age) or at fledging age (~65 d of age) stages for individuals that originated from the SGP.

		Annual Survival Rate	
Location and Age	Starting Stage	Mean ± SD	95% CRI[c]
SGP juvenile	Late nestling start	0.238 ± 0.085	0.101–0.433
	Fledgling start	0.450 ± 0.119	0.232–0.691
SGP all preadults	Late nestling start	0.060 ± 0.032	0.016–0.139
	Fledgling start	0.113 ± 0.054	0.034–0.242
CGP juvenile	Late nestling start	0.683 ± 0.145	0.370–0.922
CGP all preadults	Late nestling start	0.512 ± 0.129	0.258–0.757

[a] Eleven individuals in the SGP emigrated from adjoining regions (10 in their first year of life and one in its second year of life).

[b] All individuals in the CGP originated in the region.

[c] Credible interval.

Causes of Mortality and their Probability. In all, 31 of 40 preadult Golden Eagles died while being monitored in the SGP; cause of death was determined for 24 (77.4%) of these. Observed causes of death were mostly anthropogenic (62.5% of total for which cause of death was determined) and included power line electrocution ($n = 10$) and collision ($n = 1$); wind turbine collision ($n = 1$); and poisoning or shooting ($n = 3$). Observed natural causes of death (37.5% of total) included MCB parasitism ($n = 8$) and starvation ($n = 1$). Cause of death could not be determined for three late nestlings, three recently fledged eagles, and one immigrant.

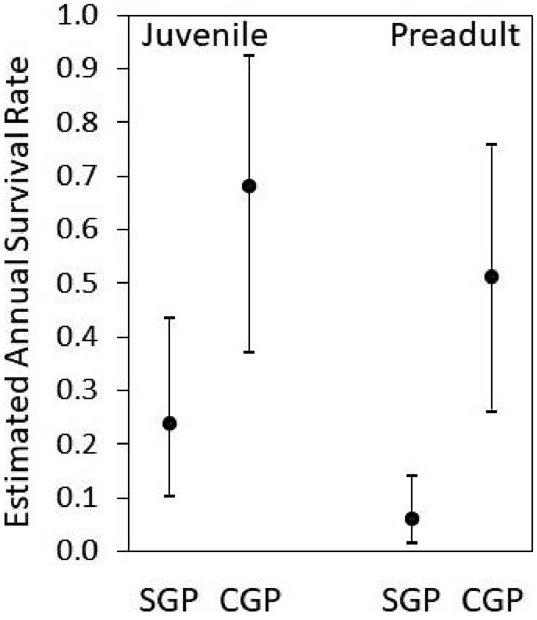

Figure 4. Estimated (± 95% credible interval) annual survival rates of juvenile (< 1 yr of age) and preadult (< 3 yr of age) Golden Eagles in the Southern Great Plains (SGP) and Central Great Plains (CGP) regions during 2011–2020, with period survival beginning at the late nestling (~52 d of age) stage.

We attribute deaths of seven of the ten Golden Eagles that died during the late nestling stage in the SGP to MCB parasitism; six of these deaths involved three nestmate pairs, each at a different nesting territory. At one nest, we treated a late nestling for heavy MCB parasitism then placed it on a nearby cliff ledge; it died 4 d later after gradually moving 2.8 km away likely by a combination of walking and hop-flying. When recovered, the eagle's carcass was too greatly scavenged for necropsy, but we believe the mortality ultimately was due to MCB parasitism; the eagle's nestmate presented a similarly heavy MCB load and was found dead below the cliff ledge to which we had moved both eagles 5 d earlier. At a nest in another nesting territory, we documented moderate MCB parasitism of a late nestling in 2017. The bird fledged after being treated. At the same nest, however, one late nestling was produced and died just before fledging in each of 2015 and 2016. We observed four to six complete carcasses plus partial remains of black-tailed prairie dogs (*Cynomys ludovicianus*) when we entered the nest each year, indicating that the nestlings had been adequately provisioned. We believe deaths of nestlings in 2015 and 2016 likely were due to MCBs because we documented MCBs at the nest site in 2017; we likely overlooked MCBs in 2015 and 2016 because the nestlings had been dead several days and most

MCBs likely would have withdrawn into the nest substrate and surrounding rock. Deaths of three other late nestlings were ascribed unequivocally to MCBs. Two of these were nestmates that were replete with MCBs when we reached their nest; one died ∼5 min later and the other had been dead <2 d. The third nestling was observed standing in its nest but when we entered the nest the following morning it had just died; we estimated that the carcass was covered by at least five MCBs/cm^2, mostly third instar to adult stage individuals. Cause of mortality of three other late nestlings could not be determined. However, we believe that at least two of the nestlings did not die from starvation because nests of each contained three or four recent (∼1- to 5-d old) carcasses of black-tailed prairie dogs plus older prairie dog remains when we visited.

Deaths of two Golden Eagles within their respective natal areas ∼3 mo after fledging likely were due to moderate parasitism by MCBs that we documented when the birds were late nestlings, despite our attempts to manually remove MCBs, kill remaining MCBs with pyrethrin dust, and move nestlings to nearby ledges that we believed to be free of the bugs. However, another eagle treated at the late nestling stage for moderate MCB parasitism fledged and remained alive through the end of the study. In all, we believe that at least nine (31.0%) of 29 Golden Eagles from nesting territories in the SGP died from MCB parasitism between the late nestling stage and 3 mo post-fledging. We detected MCBs at nests within six (37.5%) of the 16 Golden Eagle nesting territories that we studied in the region, including four in northern Texas and two in northeastern New Mexico. All nests at which MCBs were detected were on cliffs.

We monitored 30 post-fledged Golden Eagles while they resided in the SGP. Twenty-one (70.0%) of these died while in the region, six before dispersing from their natal areas. Most (71.4%) of the deaths were human-caused; energy infrastructure accounted for 57.1% of the deaths and electrocution on power lines was the single most important mortality factor. Seven of ten electrocutions occurred at power line poles with transformers, associated either with oil or gas wells (two electrocutions), or with pumps for cropland irrigation (three electrocutions) or livestock watering (two electrocutions). Five of ten electrocution events occurred <1 km from isolated colonies (8–45 ha) of black-tailed prairie dogs, which otherwise were sparsely distributed across the SGP study area. Two eagles that immigrated into the SGP were electrocuted only 6 d and 39 d after entering the area of southeastern New Mexico that overlaps the Permian Basin's landscape of intensive oil and gas development.

Poisoning or shooting accounted for two and likely three (14.3%) of the 21 mortalities of fledged Golden Eagles in the SGP. Two poisonings, 120 km apart in remote rangeland used for sheep grazing in central New Mexico, were caused by ingestion of aldicarb, a restricted-use, acutely toxic carbamate insecticide and nematicide; its presence in a non-agricultural landscape suggests it was being used to kill predators. The esophagus of each eagle contained aldicarb-contaminated muscle tissue from unidentified animal species. Data transmission from the PTT of a third eagle abruptly ended when the eagle perched atop the single-phase power line pole where one of the aforementioned eagles had succumbed to aldicarb poisoning 5 yr earlier, but a carcass could not be found when the site was investigated 2 d later. We believe this eagle either was similarly poisoned then collected by a person or scavenged, or it may have been shot; a paved road passed 62 m from the pole where the eagle's last GPS location was recorded.

One eagle was killed by collision with a 1.5-megawatt wind energy turbine sited 34 m from the edge of a 20-m high vertical cliff face. The eagle had fledged 6 wk earlier from a nest 1.1 km away. Assuming one hourly GPS record coarsely represents 1 hr of activity, it had spent roughly 17 hr flying or perching within 200 m of the 28-m rotor-swept zones of six turbines before being killed. Using the same coarse metric, the eagle's nestmate spent roughly 234 hr within 200 m of rotor-swept zones of 52 turbines along the edge of the same cliff before it dispersed from the area, 3.5 mo after fledging.

Based on our multi-state fate models, the probabilities that a preadult Golden Eagle in the SGP region would die from the two most important mortality factors, MCB parasitism and power line electrocution, were both 0.345 (Table 2) even though MCB parasitism only occurred early in the period and did not affect immigrants. When beginning the preadult period at the fledging age rather than late nestling stage for individuals from nests in the region, probability of death due to MCB parasitism was 0.136 (± 0.072, 0.030–0.304) and that due to electrocution was 0.455 (± 0.104, 0.257–0.661).

Table 2. Model-based estimated proportion of total deaths attributed to each of various mortality factors among preadult (<3 yr of age) Golden Eagles in the Southern Great Plains based on individuals that died while being monitored by satellite telemetry in the region during 2011–2020 and for which cause of death could be determined ($n = 31$[a]).

Cause of Mortality	Proportion of Total Deaths	
	Mean ± SD	95% CRI[b]
Mexican chicken bug parasitism	0.345 ± 0.086	0.187–0.522
Power line electrocution	0.345 ± 0.087	0.187–0.522
Power line collision	0.069 ± 0.046	0.009–0.183
Wind turbine collision	0.069 ± 0.046	0.009–0.183
Poisoning or shooting	0.103 ± 0.056	0.022–0.235
Winter exposure-starvation	0.069 ± 0.046	0.009–0.186

[a] Includes 24 individuals that were tagged with transmitters as large nestlings (∼51 d of age) in the SGP and seven individuals that were tagged as large nestlings in adjoining regions and subsequently immigrated into the SGP during either their first or second year of life.

[b] Credible interval.

DISCUSSION

Our study in the SGP indicates that survival rates of preadult Golden Eagles in at least one western region of the USA may be far less than those for the western USA as a whole reported in Millsap et al. (2022; summarized in Table 3), although banding and telemetry efforts supporting the latter were not uniformly distributed. Indeed, our mean survival rate estimate of 0.060 for preadult Golden Eagles in the SGP is only about 5–10% that of published estimates from elsewhere in the western USA; although these are few and vary in methods of derivation, all are in the 0.7–0.8 range (Table 3). An exception is the study by Crandall et al. (2019), who reported an even greater survival rate estimate for preadult Golden Eagles in south-central Montana. However, we are unsure whether theirs was an estimate for the entire preadult period, as was ours (i.e., $S^1 \times S^2 \times S^3$, where $S^a =$ the mean annual survival rate by preadult age-class year) or if it was a mean of the estimated annual survival rates for each preadult age-class year (i.e., $S^1 + S^2 + S^3/3$; the authors also included a fourth preadult year, S^4). Although analytical methods used by Crandall et al. (2019) more closely resembled ours than did those of other studies, their sample size was much smaller (Table 3) and did not include immigrants. Our CGP sample also was relatively small ($n = 15$) and did not include immigrants, but methods we used for estimating survival rates matched those we used for Golden Eagles in the SGP, and timeframes of the datasets closely overlapped; the estimated survival

Table 3. Survival rate estimates published for preadult Golden Eagles (note that periods of time supporting estimates are not necessarily consistent among all studies).

Location	Age (mo) at Period Start, End	*n*	Point Estimate	Data Source and Estimation Method	Source
Scotland	"fledging," 48	NA[a]	0.79	Indirectly from adult turnover rate estimates; Monte Carlo model	Whitfield et al. (2004)
South-central Montana	"nestling" ≥1.7, 48	13	0.897	Satellite telemetry; multi-state model in Program MARK	Crandall et al. (2019)
California: Altamont Pass	1.6–14, 14	101	0.842	VHF telemetry; known-fate model in Program MARK	Hunt et al. (2017)
	15, 50	155	0.801		
Southern Great Plains	1.7, 36	40	0.060	Satellite telemetry; multi-state model with transition probabilities	This study
Central Great Plains	1.7, 36	15	0.512	Satellite telemetry; multi-state model with transition probabilities	This study
Western USA[b]	1.6, 12	2948	0.70	Pooled telemetry and band recovery data; integrated population model	Millsap et al. (2022)
	13, 24	125	0.83		
	25, 36	31	0.88		

[a] Number and ages of eagles not reported.

[b] For each age period, the total number of eagles banded and total tagged with transmitters are (1) 1.7–12 mo, 2656 and 292; (2) 13–24 mo, 102 and 23; and (3) 25—mo, 27 and 4 (from Table 1 in Millsap et al. 2022).

Table 4. Survival rate estimates published for Golden Eagles during their first (juvenile) year of life (note that periods of time supporting estimates are not consistent among all studies).

Location	Age (mo) at Period Start, End	*n*	Point Estimate	Data Source and Estimation Method	Source
Norway[a]	1.6–2.7, 12	25	0.58	Satellite telemetry; Kaplan-Meier	Nygård et al. (2016)
Central Alaska[b]	∼2.3, 3.6–4.4[c]	22, 21[d]	0.340, 0.190	Satellite telemetry; known-fate model in Program MARK	McIntyre et al. (2006)
California: Altamont Pass	1.6–14, 14	101	0.842	VHF telemetry; known-fate model in Program MARK	Hunt et al. (2017)
Colorado Plateau	6–12[e]	63	0.788	Satellite telemetry; logit-link generalized linear model in Bayesian framework	Murphy et al. (2017)
Southern Great Plains	1.7–12	40	0.238	Satellite telemetry; multi-state model with transition probabilities	This study
Central Great Plains	1.7–12	15	0.683	Satellite telemetry; multi-state model with transition probabilities	This study
Western USA	1.6–11, 12	2656, 292 [f]	0.70	Pooled telemetry and band recovery data; integrated population model	Millsap et al. (2022)

[a] Mostly migratory population.

[b] Strongly migratory population.

[c] Based on indication of ≥56 d of age as 80% of estimated fledging age, and estimated survival during post-fledging dependence period of 39–63 d.

[d] Study divided into 2 yr.

[e] Period survival spans the median date of onset of dispersal from natal areas (22 October) through the median date of end of the first year of life (14 April).

[f] Total number banded, total number tagged with transmitters (from Table 1 in Millsap et al. 2022).

rate of preadults (0.512) was 8.5 times greater than that in the SGP.

We believe Golden Eagle survival rates differed between SGP and CGP regions largely because oil and gas production and pivot irrigation were more ubiquitous in the SGP, requiring a more extensive network of electrical distribution lines and thus increasing overall electrocution risk. Oil and gas wells were distributed across roughly two-thirds of the SGP versus roughly one-third of the CGP, based on overlap of our study area boundaries (Fig. 1) and oil and gas wells in Ott et al. (2021; figure 2). Pivot irrigation in the CGP was limited mainly to the Platte River valley and south to within ∼100 km of the Colorado-Nebraska state line, but in the SGP it characterized much of the landscape from east central New Mexico through most of northwestern Texas to southwestern Kansas. Contrast in survival rates between the two regions also was due largely to parasitism of young eagles by MCBs in the SGP, a mortality factor that has not, to our knowledge, been noted among Golden Eagles further north in the Great Plains.

Most Golden Eagle preadult mortality we documented in the SGP occurred among juveniles, regardless of origin. Our survival rate estimate for juveniles (0.238) was far less than what we documented in the CGP (0.683), which in turn was less than reported elsewhere (Table 4) except that survival of juvenile Golden Eagles from a migratory population in central Alaska (McIntyre et al. 2006; Table 4) approached the low estimate for SGP juveniles. In general, diurnal raptors are thought to incur little mortality between the time they reach 80% of fledging age and when they actually fledge (Millsap 1981, Steenhof 1987). For Golden Eagles, these two timepoints roughly correspond with ~51 d and ~65 d of age (Steenhof 1987, Palmer 1988, Steenhof et al. 2017). During the ~2-wk late nestling stage between these in our study, we found that the estimated survival rate of eagles from nests in the SGP was only 0.656, largely explaining why the juvenile survival rate beginning at the start of the late nestling stage was about one-half of that when beginning at fledging age (respective point estimates 0.238 versus 0.450, Table 1). This also was true for preadults overall (0.060 versus 0.113). In assessments of Golden Eagle reproductive success, such late nestling mortality could lead to inflated estimates of fledging rates and recruitment potential. Our findings in this regard support advice by Steenhof et al. (2017) that, for Golden Eagles, survival after 51 d of age be considered a component of post-fledging, juvenile survival.

High mortality among Golden Eagles during the ~2-wk late nestling stage was most if not all due to parasitism by MCBs, although we acknowledge that deaths of three nestmate pairs due to MCBs reduced independence among our samples. Nestling Golden Eagles probably have been parasitized by MCBs in the SGP for at least 50–70 yr. The first records of such were from Texas in 1954, including a nest near Silverton (R. Strandtmann *in litt.*, in Lee [1954]) in the eastern part of our SGP study area and possibly within the same nesting territory where we observed MCB parasitism of a late nestling in 2017. Perhaps an apparent 50% decline in nesting territories occupied by Golden Eagles in this part of our study area during 1980–2016 (the "Eastern Caprock Nest Search Area" in Stahlecker et al. [2022]) was due largely to MCB parasitism. Platt (1975) also documented MCBs at cliff nests of Golden Eagles and three other raptor species in northeastern New Mexico in 1974. We note, however, that juvenile eagles we studied were not selected randomly from nesting territories across the SGP, and thus we cannot report or speculate about distribution of MCB parasitism across the region. Parasitism of nestling Golden Eagles by MCBs has been documented across a relatively small part of the eagles' range elsewhere in North America: Chihuahua, Mexico (Morales-Yañez and Rodríguez-Estrella 2019), Arizona (K. Jacobsen, Arizona Game and Fish Department, unpubl data), and Idaho (McFadzen et al. 1996, Dudek 2021). The range of MCBs may be increasing, however, in response to increasing temperatures under a changing global climate regime (Dudek 2017). For example, documentation by McFadzen et al. (1996) of MCBs in raptor nests at the Morley Nelson Snake River Birds of Prey National Conservation Area in southwestern Idaho during 1992 and 1993 represented a significant northerly range shift. Now, MCBs frequently occur in Golden Eagle nests in the area especially at nests with southerly exposures and at nests of pairs that breed late in the season, indicating a link between incidence of MCB parasitism and warmer temperatures (Dudek 2017). Hematophagy by MCBs affects nestling Golden Eagles by reducing hematocrit levels and mass, and increasing corticosterone levels (Dudek 2021). Nestlings either fledge prematurely or die in the nest as we noted, although our observations imply they also may die after fledging. Our attempts to reduce mortality among late nestling Golden Eagles affected by MCBs by manually removing individual parasites, applying pyrethrin dust, and moving the nestlings to alternate ledges on cliff faces appeared to have had limited success. Three such eagles fledged; two of these survived an additional 3 mo, suggesting a possible latent effect of MCB parasitism, yet the other remained alive through the end of the study. To our knowledge, fates of post-fledged Golden Eagles parasitized by MCBs as nestlings have not been documented previously. If successful, control of MCB parasitism to boost fledging rates and post-fledging survival of juvenile Golden Eagles may be a relatively inexpensive way to offset anthropogenic mortality incurred by the eagle (Allison et al. 2017), but to our knowledge such measures have not been well explored.

Electrocution at power line poles was the single most important cause of mortality among fledged, preadult Golden Eagles in the SGP, accounting for about half of deaths recorded. Several major electrocution risk factors for Golden Eagles, presented by Mojica et al. (2018), were prevalent in our study in the SGP, especially young age class of eagles (more vulnerable) and concentrated prey (black-tailed prairie dog colonies) or prey habitat (tame grasslands, prairie) close to power line poles especially those with particularly hazardous equipment configurations (e.g., transformers with exposed jumper wires, potential contact points <152 cm apart; APLIC 2006). Dwyer et al. (2020b) found that preadult Golden Eagles tracked via PTTs in the

SGP region preferred to perch on power line equipment poles, specifically those with transformers rather than on the less hazardous non-equipment poles. Overall, power line poles accounted for 10.8% of 1050 randomly selected events of perching by the eagles. These findings indirectly corroborate ours that preadult Golden Eagles in the SGP are exposed to much electrocution risk. Ideally, systematic spatial prioritization of efforts to retrofit hazardous poles would be used to most effectively and economically mitigate such risk; maps of the distribution and general equipment configurations of poles across the SGP would support this work but are unavailable for much of the region. In lieu of such comprehensive spatial information, however, knowledge of pole density can be used to prioritize retrofitting efforts. Based on a sample of electric utilities, Dwyer et al. (2016) found pole density in parts of Colorado and Wyoming increased with the local extent of roads, oil and gas wells, pivot irrigation, and general development, and also was influenced by slope and land cover type. Dwyer et al. (2020a) used a model to predict pole density across the remaining areas of the two states; and they used this same model to predict pole density across the Southwestern Plains ecoregion (figure 9 in Dwyer et al. 2020a), which closely approximates our SGP study area. To identify areas of the SGP that pose high electrocution risk, the model could be used in conjunction with approximate locations of Golden Eagle nesting territories in the region (Stahlecker et al. 2022), relative abundance based on eBird data (Ruiz-Gutierrez et al. 2021), and a spatially explicit model of the intensity of the eagle's use of landscape features based on telemetry data from individuals tracked in our study; a survey of black-tailed prairie dog colonies may provide key support for such a model.

Golden Eagles seem unusually vulnerable to collision with blades of wind energy turbines (Smallwood and Thelander 2008, Pagel et al. 2013). During our study, >5000 1.5- to 3.3-megawatt turbines were operating in the New Mexico, Oklahoma, and Texas portions of the SGP (Stahlecker et al. 2022). Turbines operated within areas used by Golden Eagles that we monitored, especially in the Northern Caprock and Eastern Caprock areas delineated by Stahlecker et al. (2022). However, we ascribed only one death of a Golden Eagle to collision with a turbine, this by an individual that had fledged from a nest 1.1 km away about 6 wk earlier and had spent relatively few hours near turbines. Our note on the relatively low frequency of Golden Eagle mortality associated with wind turbines comes with an important caveat. The sample of Golden Eagles we monitored in the SGP did not include adult eagles, some of which nest on faces of cliffs that have turbines with blade tips that can extend beyond cliff edges (Stahlecker et al. 2022). We also note that only four nesting territories occupied by Golden Eagles in the SGP had turbines within 3.2 km of nests during years of our study (Stahlecker et al. 2022) and we only monitored survival of two juvenile eagles fledged from a nest at one of these.

Based on cause-of-death determinations for 126 Golden Eagles tracked by telemetry across the conterminous western USA, Millsap et al. (2022) estimated that shooting, collisions, power line electrocution, and poisoning were the most important mortality factors for all age classes combined. Deaths of juveniles were due mainly (74%) to natural factors especially starvation, most of which occurred before or shortly after the onset of dispersal from natal areas. Deaths of eagles in older age classes were mainly (73%) anthropogenic. Chief causes of mortality of preadult Golden Eagles we studied in the SGP differed in some important ways. First, MCB parasitism was not reported by Millsap et al. (2022) as a mortality factor. Second, we observed no evidence that starvation caused deaths of preadult Golden Eagles in the SGP except that a 7-mo old, dispersed juvenile died from starvation 1 wk after a severe, 3-d blizzard, and starvation could not be ruled out as the cause of death of one juvenile near fledging. Third, nearly half of the deaths of post-fledged eagles in our study were due to electrocution, versus only ~10% of deaths, for which cause was determined in Millsap et al. (2022). Fourth, in contrast with the significant finding by Millsap et al. (2022) that shooting was, overall, the most important cause of death among Golden Eagles across most of the western US, we recorded only one instance in which an eagle was killed by shooting, and that determination was based on circumstantial evidence. Last, we did not observe mortality due to intraspecific fighting. Young Golden Eagles such as those we studied may be less likely than older individuals to fight conspecifics. Millsap et al. (2022) reported intraspecific fighting as the cause of death of seven Golden Eagles tracked by telemetry in the western United States, noting that six of these were >3 yr of age. Moreover, differences in the importance of various causes of mortality among eagles in the SGP and those studied elsewhere could in part be confounded by the fact that few eagles we studied lived long enough to be exposed to some mortality factors.

Our multi-state model incorporated immigration of young Golden Eagles into the SGP and thus accounted for some potential for recruitment and rescue effect (Eriksson et al. 2014) by this cohort. If the low preadult survival we documented is typical for Golden Eagles in the SGP, the region likely is an ecological trap (Schlaepfer et al. 2002) for the species because preadults experienced high mortality whether they originated in or immigrated into the region. Based on our estimate of λ (0.912, beginning at the late nestling stage for individuals from nests in the region), the SGP Golden Eagle population could be declining at a rate of about 9% annually. We acknowledge, however, that our sample size for the region was only moderate and that the bulk of our study extended across only ~6 yr. As Millsap et al. (2022) point out, the 20-yr length of their dataset likely smoothed out possible influences of short-term anthropogenic risks, prey abundance changes, dispersal incidence, or precipitation cycles on survival. Regardless, results of surveys of the SGP breeding population tentatively suggest that nesting territory occupancy rates may be declining in parts of the region (Boal et al. 2008, Stahlecker et al. 2022). To achieve and maintain the USFWS preservation standard for Golden Eagles (USFWS 2016b), factors underlying local to regional population sinks will have to be reconciled. The SGP region may be a priority in this regard.

SUPPLEMENTAL MATERIAL (available online). A. Golden Eagle Survival in the Great Plains, Nestlings, with Territory and Time Random Effects. B. Golden Eagle Survival in the Great Plains, Fledglings, with Territory and Time Random Effects.

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