18 November 2025

Estimating Survival and Population Trajectories of Golden Eagles in Nevada

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J. of Raptor Research, 59(4):1-15 (2025). https://doi.org/10.3356/jrr2521

Abstract

Golden Eagle (*Aquila chrysaetos*) populations in western North America have recently been reported as stable. Vital rates, however, can vary geographically and across life stages to the extent that local population sources and sinks may form. The little-studied population in Nevada is of particular interest in this regard based on its large contribution to the species' breeding population in the western USA. Our investigation in Nevada focused on additive and synergistic factors that may set local populations on a different course than regional or range-wide estimates. However, little is known about Golden Eagle populations in the state. We investigated the survival of Golden Eagles in Nevada, including a breeding population near a proposed solar energy development area in southern Nevada. We used a multistate model to estimate survival by age class, and parameterized population projection matrix models to predict intrinsic rates of population change. We found strong evidence that the Golden Eagle population in Nevada is declining, which is likely related to low survival estimates across age classes. Investigations at the time of transmitter recovery indicated a minimum of 6 of 18 attributable mortalities likely resulted from anthropogenic causes. Additive mortality related to drought, reduced prey base, and habitat loss experienced by Golden Eagles in Nevada suggests the potential for the existence of a population sink within the state, and we highlight the need for closer management of Golden Eagle populations in this rapidly changing landscape.

Las poblaciones de *Aquila chrysaetos* en el oeste de Norteamérica han sido reportadas recientemente como estables. Sin embargo, las tasas vitales pueden variar geográficamente y entre las diferentes etapas de vida, al punto de que pueden formarse fuentes y sumideros poblacionales locales, mientras que otras poblaciones pueden colapsar. La población de *A. chrysaetos* de Nevada esta muy poco estudiada, lo que la hace de gran interés dado su gran aporte a la población reproductiva de la especie en el oeste de EE. UU. Nuestra investigación en Nevada se centró en factores aditivos y sinérgicos que pueden poner a las poblaciones locales en una tendencia poblacional diferente al de las estimaciones regionales o de todo su área de distribución. Sin embargo, se sabe poco acerca de las poblaciones de *A. chrysaetos* en este estado. Investigamos la supervivencia de esta especie en Nevada, incluyendo una población reproductiva cerca de un área propuesta para el desarrollo de energía solar en el sur de este estado. Utilizamos un modelo multiestado para estimar la supervivencia por clases de edad y parametrizamos modelos de matriz de proyección poblacional para predecir las tasas intrínsecas de cambio poblacional. Encontramos fuerte evidencia de que la población de *A. chrysaetos* en Nevada está en declive, lo cual probablemente se relacione con bajas estimaciones de supervivencia en todas las clases de edad. Investigaciones realizadas tras la recuperación de transmisores indicaron que un mínimo de 6 de un total de18 muertes probablemente resultaron de causas antropogénicas. La mortalidad aditiva relacionada con la sequía, la reducción en el número de presas y la pérdida de hábitat que experimenta *A. chrysaetos* en Nevada sugiere la posible existencia de un sumidero poblacional dentro del estado. Destacamos la necesidad de un manejo más cercano de las poblaciones de esta especie en este paisaje en rápida transformación.

[Traducción del equipo editorial]

INTRODUCTION

Golden Eagles (*Aquila chrysaetos*) are long-lived, apex predators whose range includes most of the northern hemisphere (Watson 2010, Katzner et al. 2020). Golden Eagles occupy diverse habitat types and rely on a variety of prey (Watson 2010, Bedrosian et al. 2017, Craig et al. 2018). Concerns over the status of eagle populations in the United States, driven largely by habitat loss and human persecution, led to the Bald and Golden Eagle Protection Act (hereafter Eagle Act; Title 16 United States Code §§ 668–668d) in 1940 and five subsequent amendments from 1959 through 2024 (Millsap et al. 2007, 2022, Watson 2010). Despite the protections provided by the Eagle Act, Golden Eagle populations in North America appeared to decline throughout the latter half of the 20th century (Hoffman and Smith 2003, Millsap et al. 2013, 2022, Katzner et al. 2017). In the 21st century, Golden Eagle populations in western North America were reported as either stable or vulnerable and experiencing slight declines (Hoffman and Smith 2003, Millsap et al. 2013, 2022, Katzner et al. 2017).

Survival, immigration, emigration, breeding success, sources of mortality, and other important processes in Golden Eagle populations vary by region and migration

strategy (McIntyre et al. 2006, Bedrosian et al. 2017, Katzner et al. 2017, Watson et al. 2020, Murphy et al. 2023). Survival rates and cause of death often differ geographically and by age class in Golden Eagles, leading to altered population trajectories (Russell and Franson 2014, Katzner et al. 2017, Crandall et al. 2019, Millsap et al. 2022). In this species, natural mortality factors that can disproportionately affect age classes include disease (Russell and Franson 2014) and starvation (Russell and Franson 2014, US Fish and Wildlife Service [USFWS] 2016a). In contrast, primary anthropogenic causes of death are electrocution, lead poisoning, trauma, and gunshot (Russell and Franson 2014, USFWS 2016a, Crandall et al. 2019). Millsap et al. (2022) found that starvation accounted for most hatch-year mortality while anthropogenic factors accounted for most post-hatch-year mortality. Although survival across age classes plays a role in population dynamics, adult survival is often the most important factor regulating the population trajectory of long-lived species (Tack et al. 2017, Millsap et al. 2022). Regulations enacted under the Eagle Act permit the allowable take of Golden Eagles from anthropogenic sources if fully mitigated and consistent with maintaining stable or increasing regional populations, while avoiding local breeding population sinks (Millsap et al. 2013, USFWS 2016a). Due to its importance in influencing population trajectories and disproportionate association with anthropogenic sources of mortality, adult survival has become a focal point for range-wide management (Millsap et al. 2013, 2022, Katzner et al. 2017). However, the relationship between population trends and their causes can be complex.

Contributing to the complex relationship between population trends and their causes is spatial variation in the intensity of direct disturbance and anthropogenic factors such as habitat loss, fragmentation, and reductions in prey availability, which can disproportionately affect survival on a regional scale (Katzner et al. 2017). Variation in these disturbances and their intensity across regions can modify habitat quality or produce population sinks associated with high mortality and low recruitment. Identification of sinks is important for many reasons, and sink populations are often sustained through influxes of dispersing individuals or of nonbreeding adult floaters (Pulliam 1988, Dias 1996, Hunt 1998). Therefore, despite additive mortality, population sinks may appear stable when investigated through the lens of annual territory occupancy, particularly when the presence of a floater population is of unknown size but sufficient to replace territory holders (Katzner et al. 2017). Secondly, individuals entering sink populations may make minimal contributions to the broader population due to demographic constraints (Katzner et al. 2017). Sink populations, particularly those driven by additive anthropogenic sources of mortality and disturbance, have the potential to affect broader population segments. These segments (e.g., breeders, floaters, migrants) are not tracked and maintained under the USFWS permitting mechanism, which is driven by pooled regional population estimates (USFWS 2016a). Management strategies could be strengthened by incorporating insights into nonbreeding individuals, which remains a key gap in demographic understanding (Hunt et al. 2017).

Thus, more localized (e.g., statewide) studies are crucial for understanding region-specific threats and their broader implications on the range-wide population status (Millsap et al. 2013, 2022, Watson et al. 2020). One such area requiring closer examination is the Basin and Range Province of North America, which encompasses a substantial portion of the Golden Eagle's western USA range from portions of Oregon and Idaho in the north, southward through Nevada and Arizona, and well into Mexico to the south. This province also includes much of the sagebrush steppe, which is among the most threatened ecosystems in North America (Noss and Scott 1995, Knick et al. 2003, Meinke et al. 2009, Davies et al. 2011, 2021). Within this threatened ecosystem is the Great Basin Desert, a highly altered region within the sagebrush biome (Wisdom et al. 2005, Rowland et al. 2006). Threats to this region include biotic and abiotic factors such as altered fire regimes, climate-change-induced drought, the spread of invasive annual grasses, and an increasing number of large-scale solar energy and mining development projects (Knapp 1996, Kochert and Steenhof 2012, Hixson et al. 2022, Smith et al. 2023b). Just to the south, the Mojave Desert also faces extensive habitat alteration due to large-scale renewable energy development and changing climate (Smith et al. 2023a). Despite large-scale alterations across these two systems, the impacts of habitat loss on Golden Eagle populations are relatively unknown.

Within the Basin and Range Province, Nevada consists almost entirely of the Great Basin and Mojave Deserts, and there is a great paucity of information surrounding Golden Eagle populations and demographic rates within the state. Nevada is among the top five states in potential solar and geothermal energy generation, and has undergone rapid renewable energy development in recent years (Milbrandt et al. 2014, Brand et al. 2016). This large-scale industrial development creates potential impacts for many species, including Golden Eagles (Brand et al. 2016). Disturbance and alterations within the Great Basin and Mojave Deserts have likely led to reduced habitat quality, and limited availability of Golden Eagle prey within the state (Knapp 1996, Kochert and Steenhof 2012, Hixson et al. 2022, Smith et al. 2023b). Golden Eagles in Nevada rely heavily on lagomorphs during the breeding season (72% breeding season diet by frequency; J. Barnes unpubl. data), and exhibit low dietary breadth and lower levels of dietary shift, potentially due to lower diversity of potential prey items (Beatley 1975, Bloom and Hawks 1982, Bedrosian et al. 2017). In 2020, the first cases of rabbit hemorrhagic disease virus 2 (Lagovirus GI.2; hereafter RHDV2), a highly virulent pathogen affecting various lagomorph species, were identified in multiple wild lagomorph populations across Nevada, posing a significant threat to Golden Eagles due to potential dramatic reductions in prey availability (Crowell et al. 2023). Potential effects from steep declines in their primary prey species include reduced fecundity and/or lower survival across age classes. Along with reductions in availability of primary prey species, habitat loss and disturbance may negatively impact the quality of breeding territories across Nevada, leading to further reductions in survival and breeding success, even if annual territory occupancy remains stable.

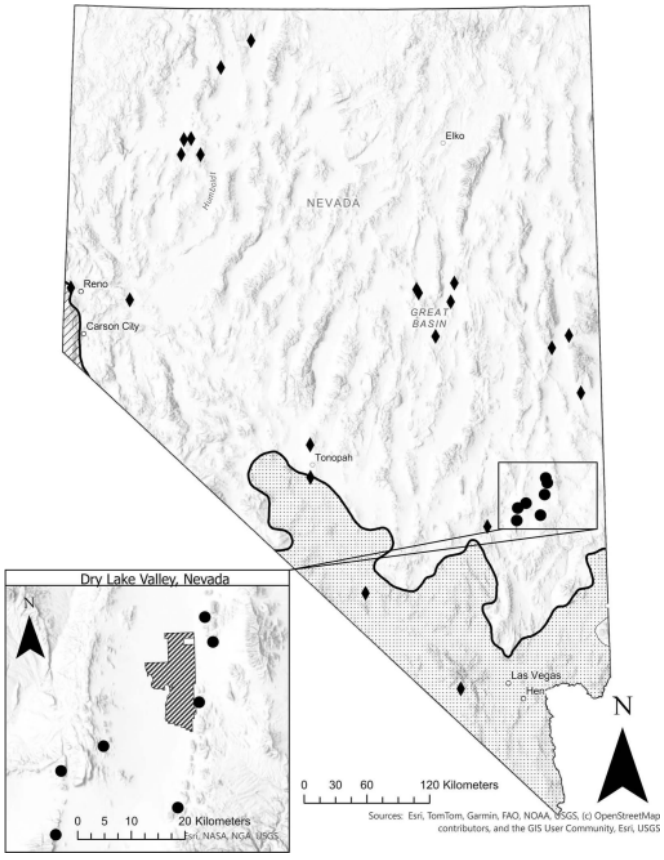
Our objective was to investigate the population dynamics of Golden Eagles within Nevada at two different scales. First, we investigated and described the survival of Golden Eagles captured across Nevada. We repeated this process at a finer scale for Golden Eagles originating from a breeding population located near the Dry Lake Valley North Solar Energy Zone (SEZ) in south-eastern Nevada (Bureau of Land Management 2012). Then, we investigated population trajectories at each scale using population projection matrix analyses and identified the most important parameter for the growth of each population using sensitivity and elasticity analyses. Based on extensive habitat loss and reduced availability of primary prey base in Nevada, we hypothesized that Golden Eagle populations at both scales would exhibit reduced survival and decline in the absence of immigration.

METHODS

Study Area and Data Collection. Our study occurred within the Nevada portions of the Great Basin Bird Conservation Region (BCR 9), Sonoran and Mojave BCR (BCR 33), and a small western portion included in BCR 15 (Sierra Nevada; Fig. 1; North American Bird Conservation Initiative 2000, Nielson et al. 2014). Nevada exists primarily within the Basin and Range Province, an arid physio-graphic region with isolated mountain ranges separated by broad endorheic drainage basins (i.e., terminal lakes; Eaton 1982). Included in our study was a breeding population of Golden Eagles located around the proposed Dry Lake Valley (DLV) North SEZ (Fig. 1). The site of this proposed solar project was within BCR 9, but in the vegetation transition zone between the Great Basin and Mojave Deserts (Fig. 1). The DLV, our primary study area (37.809° N, 114.770°W), consisted of mountainous areas surrounding an ephemeral lake (1396–2138 masl) with predominant vegetation consisting of sagebrush (*Artemisia* spp.), saltbush (*Atriplex* spp.), Joshua tree yucca (*Yucca brevifolia*), and pinyon-juniper woodlands (*Pinus monophylla* and *Juniperus* spp.).

Figure 1.

Map depicting capture locations of individual Golden Eagles tracked with satellite and cellular telemetry from 2014 to 2024 in Nevada. Black diamonds indicate capture locations outside of the Dry Lake Valley study area (DLV), while black dots indicate capture locations within the DLV. The stippled polygon in southern Nevada shows Bird Conservation Region (BCR) 33 (Sonora and Mojave), diagonal hashing in western Nevada indicates BCR 15 (Sierra Nevada), while BCR 9 (Great Basin) is unshaded. The inset map shows the DLV study area capture locations and Solar Energy Zone in the diagonal polygon.



We collected telemetry, banding, and annual survey data at DLV, our primary study area, from 2014–2024 as part of a comprehensive long-term population monitoring project of all known territories (n = 18 nesting territories). We selected individuals for tracking with territory-holding adults identified during the courtship stage and at those territories with sufficiently-aged nestlings in accessible nests. We selected eagles from territories in secondary study areas across Nevada (n = 28 territories considered) based on logistical constraints, and with less rigorous and consistent monitoring of annual territory occupancy or breeding success. We targeted birds outside the DLV opportunistically only when all available tags could not be deployed within the DLV each year.

We identified occupied Golden Eagle territories across Nevada and within the DLV. We then either attempted to capture the associated adult territory holders or captured nestlings near fledging age approximately 6.5–9.5 wk old. We used remotely activated bow nets and net launchers to capture adult and subadult Golden Eagles in nesting areas, and hand-captured nestlings in nests. We used photographic aging guides to age nestlings (Driscoll 2010, A. Schindler unpubl. data). We fitted eagles with 45- or 70-g backpack-mounted GPS-platform transmitter terminal (GPS-PTT) transmitters (Microwave Telemetry, Inc., Columbia, Maryland, USA) or 70 g Global System for Mobile Communications - Cellular Tracking Technology (GSM-CTT) transmitters (Cellular Tracking Technologies, LLC, Rio Grande, New Jersey, USA). We attached transmitters with a cross-chest Teflon ribbon harness with a breakaway point at the sternum composed of beeswax-coated cotton embroidery thread (Garcelon 1985, Hunt et al. 1992, García et al. 2021) intended to give way toward the end of transmitters' functional life. We captured more individuals than we

had transmitters available. Consequently, some eagles were banded only, not fitted with transmitters.

We programmed PTTs to collect 12 daylight hourly locations during spring, summer, and fall seasons and 6 daylight hourly locations in the winter, while CTTs collected locations every 15 min throughout the year. We retrieved transmitters as soon as possible when it became evident they were not moving, indicating possible mortality or a dropped unit. We monitored transmitter diagnostics (e.g., between-point movement distance, hourly charge, temperature) to understand probable unit failure, mortality, or dropped transmitter. We recorded individuals with failed or dropped transmitters as alive for their last known status. If transmitters were unrecoverable and transmitter failure could not be determined, we recorded the last status as unknown. We then used telemetry data with associated known and unknown fates to develop capture histories for each individual. Postmortem testing was outside the scope of our study, but we assessed all carcasses for signs indicating potential cause of death at the time of transmitter retrieval (e.g., signs of emaciation, electrocution, fractures or blunt force trauma, predation in the nest or on recently fledged individuals, nearby poison bait station).

To estimate annual survival for each age class, we formatted each individual's capture history into annual time steps. Although hatch-year (i.e., juvenile) individuals were typically captured around the same time each year (May–June), subadults and adults were captured during the courtship stage (January–February), or with nestlings at least 3 wk old. We used annual time intervals starting on 9 April, the average hatch date from 2014 to 2023 for Nevada (J. Barnes unpubl. data). Therefore, the first annual time interval started on 9 April 2014 and ended on 8 April 2015. We categorized individuals into four age classes: hatch-year birds (HY), year-one subadult birds (SA1), year-two subadult birds (SA2), and after year-three birds (hereafter adults [AY3]; Millsap et al. 2022). Hatch-year survival is commonly estimated using the period after fledging (varies between May and July; McIntyre et al. 2006, Murphy et al. 2017, Crandall et al. 2019, Millsap et al. 2022). However, survival can be low in periods leading up to fledging, which may result in the overestimation of hatch-year survival (Murphy et al. 2023). To account for potentially lower prefledging survival compared to post-fledging survival, we included individuals who died prior to estimated fledgling dates within the analysis. We included brood mortalities before tagging (at approximately 80% of fledging age) in our fecundity parameter (see Population Viability Analysis below), and included late-stage nestling mortality in our survival model.

Survival Analysis. We used a multistate capture-recapture model that accounted for transmitter loss or failure to estimate age class survival of Golden Eagles (Kéry and Schaub 2011). Our dataset included individual capture histories spanning 2014–2024, with each eagle categorized into one of several observable states based on age class, transmitter status, and recovery status. Specifically, eagles were classified into four age categories and were further distinguished by whether they carried an active transmitter or were identifiable by leg bands. Additionally, we incorporated observations of recently deceased transmitter-equipped or band-only individuals, and an unobservable category for undetected or long-deceased eagles (Millsap et al. 2019).

We used two multistate models to obtain survival estimates for Nevada, then used the second model to obtain survival estimates for just the DLV individuals. We modeled survival as a function of age class in both models, then separated estimates for each site (DLV and Nevada) in the second model using a linear predictor including fixed site effects for age-class survival. The null model allowed us to use all information available to obtain survival estimates for the entirety of Nevada, while the second model allowed us to estimate DLV survival with reduced variation by modeling differences in survival between the two regions. We assumed no difference in true survival rates between transmitter-equipped and band-only individuals, given a lack of evidence for transmitters increasing mortality (Crandall et al. 2019, García et al. 2021, Millsap et al. 2022). Detection probabilities were assumed to be 1 for transmitter-equipped individuals (r_{GPS}) due to daily recording intervals and 0 for band-only eagles (r_{BAND}) due to rarity in band resights (Millsap et al. 2022). The probability of recapture varied depending on whether an eagle had a functioning transmitter, which provided daily location data, or was identified solely by a band, which was subject to infrequent recaptures. We used a transition probability to account for transmitter failure and an individual's subsequent transition to a band-only state. We incorporated recovery probabilities for deceased individuals into the state-transition process to account for recovery differences between GPS and band-only eagles.

To estimate these parameters, we implemented a Bayesian modeling framework in JAGS (Plummer 2024) using Markov chain Monte Carlo (MCMC) methods. We fit each model using three independent chains, each running for 100,000 iterations, with a burn-in period of 25,000 iterations and thinning of 10. We used trace plots and Gelman-Rubin diagnostics to assess convergence, with values below 1.1 indicating convergence (Gelman and Hill 2006). We provide full details on the model structure, including transition matrices and probability distributions in Supplemental Material (JRR2521_Supplemental_Material_final.pdf).

Population Viability Analysis. To assess the long-term viability of Golden Eagles in Nevada and the DLV, we constructed population projection models incorporating site-specific age class survival estimates. These models followed a four-stage post-breeding structure, with survival probabilities drawn from the posterior distributions estimated in our survival analysis.

We estimated fecundity separately for the DLV and Nevada populations. For the DLV, we derived fecundity estimates from breeding surveys conducted between 2015 and 2023, adjusted to reflect female offspring production (Millsap et al. 2022, J. Barnes unpubl. data). We used the mean and variance from these surveys to parameterize a truncated normal distribution with a right truncation of 2, ensuring realistic constraints on the number of offspring per female (Katzner et al. 2020, J. Barnes unpubl. data) and a left truncation of 0 to preclude negative brood sizes. For the Nevada population, we used published estimates of Golden Eagle fecundity for the western US ($x = 0.27$, $\square = 0.001$; USFWS 2016a, Millsap et al. 2022).

We also incorporated site-specific estimates for the proportion of adults attempting to breed. The DLV population provided a unique opportunity for making inferences on mismatches between territory occupancy and population trajectory. We used breeding survey data collected within the DLV region from 2015 to 2024 to estimate the average percentage of breeding adults based on number of breeding attempts per occupied territory (J. Barnes unpubl. data). We only calculated breeding

effort from territories in years when survey effort was sufficient to verify an occupied territory and either a breeding attempt or not. Nonbreeding was determined for pairs occupying territories in which we had certainty about all nest locations, and when individuals were observed and confirmed not tending nests during visits during the laying/incubation period and after the latest known initiation date for breeding (6 April; J. Barnes unpubl. data). This provided an average percentage of adult individuals who held territories and attempted to breed for the DLV breeding population. We drew random samples from a beta distribution, with shape parameters moment-matched to the mean and standard deviation of breeding attempt estimates via the yearly DLV survey efforts (x = 0.76, ☐ = 0.23; J. Barnes unpubl. data). We did not have statewide breeding survey data collected similarly as for DLV. Therefore, we used mean and variance values from published sources from the western US (x = 0.85, ☐ = 0.001; USFWS 2016a, Millsap et al. 2022).

We estimated population growth rates (☐) by deriving the dominant eigenvalue of the site-specific projection matrices across 22,500 posterior samples (Caswell 2001, Millsap et al. 2022). We conducted lower-level sensitivity and elasticity analyses to capture the total influence of each parameter on ☐ and identify which of these demographic parameters had the greatest influence on population growth (Caswell 2001). We tested management scenarios by simulating a 10% increase in survival, breeding probability, and fecundity, potentially influenced by conservation interventions such as habitat restoration, reduced anthropogenic mortality, and increased prey availability. We estimated parameter sensitivities by dividing the change in ☐ over the change in each associated vital rate. We estimated parameter elasticities as the proportional change in ☐ divided by the proportional change in the associated parameter. Complete details on the structure of the population models, parameter distributions, and simulation framework are provided in Supplemental Material (JRR2521_Supplemental_Material_final.pdf).

RESULTS

Data Collection. We deployed transmitters on 43 Golden Eagles and banded an additional 4 individuals without transmitters in Nevada from 2014 to 2024. We tracked individuals (post-fledging for eagles tagged as nestlings) between 15 and 2041 d (mean = 629 d), with three individuals still carrying transmitters through 31 July 2024 when this project concluded. Thirty-three were HY, none were SA1, two were SA2, and seven were AY3. Eighteen of 47 were captured within the DLV study region (HY = 13, SA2 = 1, AY3 = 4) and 29 were captured in other parts of Nevada. Individuals could transition across age classes as they aged, except for AY3 (see Supplemental Material (JRR2521_Supplemental_Material_final.pdf)). In total, four transmitters appeared to malfunction prematurely (i.e., before 3 yr of deployment), three transmitters/harnesses were shed, one battery died after 5.5 yr of deployment, one transmitter ceased functioning for unknown reasons with suspected human influence, and five stopped sending data for unknown reasons. At least 30 tracked eagles died during our study (HY = 16, SA1 = 5, SA2 = 4, AY3 = 5). We could not verify cause of death with necropsy or postmortem laboratory testing in most cases; however, investigations at the time of transmitter retrieval indicated likely cause of death for 18 eagles resulting from starvation (HY = 8; i.e., emaciated with minimal muscle mass), electrocution (HY = 2; SA1 = 1), collision on road (SA1 = 1; SA2 = 1), predation (HY = 2), poisoning (SA1 = 1), disease (AY3 = 1), and collision with unknown structure (HY = 1). Without testing, it is often impossible to differentiate the proximate factors (e.g., starvation resulting from food scarcity or inability to acquire prey vs. inability to process food from lead poisoning) leading to emaciated individuals; however, our results suggest food scarcity as the most likely cause of death of these individuals because all of the mortalities we attributed to starvation occurred either prior to fledging (n = 1; supported by nest camera data), prior to dispersal from the natal area (n = 5), or shortly after departure from the natal area (n = 2).

Survival Analysis. Results of the multistate model indicated similar parameter estimates between Nevada and the DLV for Golden Eagle survival. However, results for the DLV population exhibited larger variation around mean estimates (Fig. 2, Table 1). Results of the multistate models indicated that mean annual HY survival was the lowest of all age classes for both the DLV region (ϕ_{HY} = 0.46, Fig. 2, Table 1) and Nevada (ϕ_{HY} = 0.52, Fig. 2, Table 1). Annual survival of SA1 was 0.62 for the DLV and 0.67 for Nevada (Fig. 2, Table 1). Annual survival for SA2 from the DLV region was 0.59 and 0.64 for all individuals captured in Nevada (Fig. 2, Table 1). The highest mean annual survival estimates were for the AY3 age class (ϕ_{AY3} = 0.82, ϕ_{AY3} = 0.85; DLV and Nevada estimates, respectively, Fig. 2, Table 1). We report recovery rate estimates for band-only and transmitter-equipped individuals, and probability of transmitter failure, using the full sample model as estimates from both models differed by less than an order of magnitude. Recovery rates for transmitters were relatively high (r_{GPS} = 0.96, Table 1), while the probability of transmitter failure was relatively low (☐$_{failure}$ = 0.18, Table 1). Lastly, recovery rates of bands following mortality were low (r_{BAND} = 0.09, Table 1).

Figure 2.

Violin plots depicting the posterior distribution of Golden Eagle age class survival estimates produced via the multistate survival model. Black dots represent the mean true survival estimate for each age class, while the bars represent 90% credible intervals for each estimate. (A) depicts the true survival estimates for the Dry Lake Valley region in southern Nevada, while (B) depicts true survival estimates and their 90% credible intervals for all of Nevada (all data).

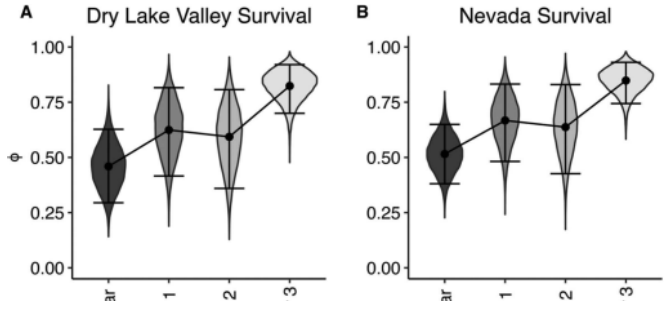


Table 1.

Parameter estimates with associated 90% Bayesian credible intervals (BCI) resulting from the multistate model analyses of Golden Eagles tracked from 2014 to 2024 in our Dry Lake Valley study area and elsewhere across Nevada. Age classes include hatch-year (HY), year-one subadult (SA1), year-two subadult (SA2), and after-third-year individuals (AY3). The table shows the mean true survival estimates (ϕ) for each age class with associated uncertainty from each multistate model (Nevada and fixed effect model for DLV). Estimates for r_{GPS}, r_{BAND} and $\square_{FAIL}$ are from the full sample model (Nevada). r_{GPS} represents the recovery probability for transmitters, while r_{BAND} represents the recovery probability for bands (following death). Lastly, $\square_{FAIL}$ represents the probability of transmitter failure (i.e., battery loss, removal by the individual, etc.).

Location	Parameters	Mean	SD	Lower 90% BCI	Upper 90% BCI
Dry Lake Valley study area	ϕ_{HY}	0.46	0.10	0.29	0.63
	ϕ_{SA1}	0.62	0.12	0.42	0.82
	ϕ_{SA2}	0.59	0.14	0.36	0.81
	ϕ_{AY3}	0.82	0.07	0.70	0.92
Remainder of Nevada	ϕ_{HY}	0.52	0.08	0.38	0.65
	ϕ_{SA1}	0.67	0.11	0.48	0.83
	ϕ_{SA2}	0.64	0.12	0.43	0.83
	ϕ_{AY3}	0.85	0.06	0.74	0.93
Shared parameters	r_{GPS}	0.96	0.03	0.90	1.00
	r_{BAND}	0.09	0.01	0.08	0.10
	ψ_{FAIL}	0.18	0.05	0.11	0.26

Population Viability Analysis. Our four-stage, post-breeding projection matrix models indicated that populations were likely declining in the DLV region ($\square_{DLV}$ = 0.88; 90% BCI: 0.75, 1) and across Nevada ($\square_{NV}$ = 0.91; 90% BCI: 0.81, 0.98). The matrix analysis estimates of $\square$ provide strong evidence our study population was declining in DLV (P ($\square$ < 1) = 0.94), corresponding to a 94% probability that the DLV population was declining. Similarly, results for the Nevada population indicate a 98% probability that the Nevada population was declining (P ($\square$ < 1) = 0.98). Elasticity analyses for the DLV and Nevada populations indicated that population change was most sensitive to small proportional changes in adult survival (elasticity ϕ_{AY3} = 0.90, all other parameters = 0.05; Table 2). Average $\square$ estimates following a 10% increase in adult survival were 0.96 (90% BCI = 0.82, 1.09) and 0.99 (90% BCI = 0.88, 1.07) for the DLV and Nevada populations, respectively.

Table 2.

Elasticity and sensitivity results for the Dry Lake Valley (DLV) and Nevada population matrix models. Survival estimates were generated from various age classes of Golden Eagles tracked with telemetry from our DLV study area and elsewhere across Nevada from 2014 to 2024, while estimates of fecundity and breeding estimates were obtained from territory monitoring at DLV during the 2015–2024 breeding seasons (J. Barnes unpubl. data). Fecundity and breeding estimates for the Nevada population matrix models were parameterized using published estimates from Millsap et al. (2022). All estimates provided in the table are mean estimates. Elasticities and sensitivities were calculated by increasing each parameter by 10%.

Location	Parameter	Eigen Value	Sensitivity Score	Elasticity
Dry Lake Valley study area	Adult survival	0.96	0.96	0.90
	Fecundity	0.89	0.12	0.05
	Hatch year survival	0.89	0.10	0.05
	Subadult (year 2) survival	0.89	0.08	0.05
	Subadult (year 1) survival	0.89	0.08	0.05
	Breeding territories	0.89	0.06	0.05
Remainder of Nevada	Adult survival	0.99	0.96	0.90
	Fecundity	0.91	0.17	0.05
	Hatch year survival	0.91	0.09	0.05
	Subadult (year 2) survival	0.91	0.07	0.05
	Subadult (year 1) survival	0.91	0.07	0.05
	Breeding territories	0.91	0.06	0.05

DISCUSSION

We found strong evidence that Golden Eagle populations in our DLV study area, and across Nevada, are declining. These declines are likely related to lower survival estimates in each age class compared to those previously reported from range-wide analyses (Millsap et al. 2022). Recent West-wide population assessments have indicated stable or slightly declining populations (Nielson et al. 2014, Millsap et al. 2022), yet focused monitoring of nesting territories in the DLV have shown very high territory occupancy rates during our study period (J. Barnes unpubl. data), so immigrant and floater populations are likely augmenting the populations we studied, suggesting that our DLV and statewide populations are sinks maintained by immigration. These findings suggest current management is not sustaining a stable Golden Eagle population in Nevada, and that if allowable take reduces adult survival through direct mortality or habitat loss, it could worsen declines both in Nevada and range-wide. Notably, allowable take may result in disproportionate mortality of breeding adults compared to nonbreeders, because take permits are nest territory-oriented, resulting in population instability. Distinguishing between allowable take of breeders and nonbreeders, however, is challenging and requires detailed demographic data, highlighting the need for improved monitoring to understand if management actions inadvertently target breeding adults.

Survival. We report survival estimates for a more recent period than previous studies. Notably, western US range-wide estimates reflect survival from 1997 to 2016 (Millsap et al. 2022), while our estimates reflect Golden Eagle survival from 2014 to 2024. Therefore, a confluence of increased periods of local drought, large-scale habitat loss from industrial mining and renewable energy project development, and the introduction of RHDV2 may have limited prey availability and led to lower survival during our study period in Nevada than what was reported in the western US study. We also provide the first survival estimates for Golden Eagles following the

introduction of RHDV2 to North America. Our study period overlapped the latter portion of Millsap et al. (2022), and it is likely that local, statewide, or regional differences may exist within their analysis.

We found low HY survival estimates (0.46 and 0.52; DLV and Nevada, respectively) compared to most previously reported estimates. A western range-wide analysis, conducted by Millsap et al. (2022), found mean HY survival to be 0.73, which is significantly higher than our Nevada estimate. Our reported annual survival for HY individuals is also markedly lower than those reported for west-central California (0.84; Hunt et al. 2017) and the southern Colorado Plateau (0.79; Murphy et al. 2017). These studies reported HY survival estimates beginning after fledging. Our analysis of HY survival accounts for all mortalities from the moment the young were captured (i.e., prior to fledging), as has been supported by Murphy et al. (2023). Murphy et al. (2023) also calculated very low HY survival in the southern Great Plains in a study area impacted by high levels of anthropogenic mortality.

The inclusion of deaths before fledging likely improves population monitoring precision and lowers our survival estimates for the HY age class, but only two of 33 nestlings died prior to fledging in our study. When we removed those two individuals and refit the models, mean HY survival for the DLV and Nevada populations increased by 0.06 ($\phi_{HY} = 0.51$) and 0.03 ($\phi_{HY} = 0.55$), respectively. Murphy et al. (2023) found that HY survival in the southern Great Plains was 0.24 when including the 2-wk period before fledging, but 0.45 when beginning estimation at the start of fledging. We assert that inclusion of pre-fledged deaths is important for understanding Golden Eagle populations, as late-stage nestling mortality may reflect insufficient prey availability during a period of high calorie demand or reduced adult nest attendance resulting from increased foraging time. Factors leading to mortalities can differ across age classes of Golden Eagles, and low juvenile survival can be indicative of more natural forms of mortality, such as starvation due to low prey availability or parasites (Hunt et al. 2017, Crandall et al. 2019, Millsap et al. 2022, Murphy et al. 2023). Murphy et al. (2023) found 31% of young HY deaths in the southern Great Plains were attributable to Mexican chicken bugs (*Haematosiphon inodorus*), an issue not yet identified as pervasive in Nevada (Dudek et al. 2018; J. Barnes unpubl. data). Low juvenile survival may also be indicative of differing movement strategies among populations. McIntyre et al. (2006) reported survival for an 11-mo post-fledging period over 2 yr as 0.19 and 0.34 for a migratory population of Golden Eagles in Alaska, USA. Unlike the nonmigratory population we studied, the migratory Alaska population displayed long-distance movement strategies that likely contributed to their low survival (McIntyre et al. 2006).

Our relatively low survival estimates for SA1, SA2, and AY3 individuals also warrant discussion. Millsap et al. (2022) reported mean annual SA1 survival, SA2, and AY3 survival to be 0.83, 0.87, and 0.9 respectively. These estimates exceed mean estimates we report for the Nevada populations (i.e., Nevada survival = 0.67, 0.64, and 0.85, respectively), despite their use of a small subset of data from this study collected in 2014 and 2015. Overall, post-hatch-year survival varies from region to region (McIntyre et al. 2006, Crandall et al. 2019, Millsap et al. 2022). Harmata et al. (2018) reported similar annual adult survival to our study for a population of Golden Eagles in southwestern Montana (0.86), while another study in southwestern Montana reported adult survival as 0.93 (Crandall et al. 2019). Murphy et al. (2023) reported annual preadult survival (<3 yr old) as 0.51 in the central Great Plains and 0.11 in the southern Great Plains. Large variation accompanied these estimates, however, and they included HY survival, which likely negatively biased the estimates. At least 80% of the mortalities that could be assigned to post-hatch-year eagles in their study were attributed to anthropogenic causes (Murphy et al. 2023). Despite starvation not being attributed to known post-hatch-year mortality, increased drought, fire, and other environmental factors may likely lead to riskier foraging behaviors among subadults and adults. Highly mobile or non-territory-holding subadults and adults may also use suboptimal foraging habitats and behavior to avoid competition with territory holders, exposing them to increased mortality risks from anthropogenic sources.

Starvation accounted for 62% of recovered HY birds in our sample where cause of death could be assigned, which is higher than most studies (USFWS 2016a, Millsap et al. 2022). Millsap et al. (2022) found starvation was the primary cause of death (50%) for HY individuals in their sample spanning a time frame of 1997–2016, while USFWS (2016a) reported 56.5% ($n = 62$) of satellite-tagged HY Golden Eagles in their study died from starvation or disease. McIntyre et al. (2006) reported similar starvation estimates to ours, with 9 out of 13 Golden Eagles (69.2%) in their sample from Alaska assigned starvation as a cause of death. Their documented instances of starvation, however, were attributed to a lack of hunting experience coupled with large migratory movements (McIntyre et al. 2006). We suspect the relatively high prevalence of starvation found in our study likely reflects declines in lagomorph populations due to long-term drought conditions during much of our study period, and RHDV2 following its introduction in 2020. Changes in resource use and foraging patterns have been found in breeding Bonelli's Eagle (*A. fasciata*) populations following outbreaks of rabbit hemorrhagic disease 1 (RHDV1) in Europe (Moleón et al. 2012). In the wake of RHDV2 and its spread across the western US since 2020, reduced prey abundance and starvation may become an even more important driver of population changes for many western populations of Golden Eagles that rely on lagomorphs as a main dietary resource (Asin et al. 2021, Crowell et al. 2023, US Department of Agriculture Animal and Plant Health Inspection Service 2024).

Population Viability Analysis. Overall, our results indicate that the DLV and Nevada populations of Golden Eagles are probably declining, or at best are stabilized by dispersing adults or the floating population segment. We agree with the conclusions drawn by Millsap et al. (2022) that slight increases in anthropogenic mortality could shift these populations to a declining growth rate. In line with this conclusion, our elasticity and sensitivity results indicate slight increases (~10%) in adult Golden Eagle survival by minimizing factors such as anthropogenic mortality could result in stable or increasing Golden Eagle populations for the DLV and Nevada populations. As habitat loss from solar energy development, mining, and other types of industrial development increases in Nevada, it is possible that carrying capacity in local areas may be reduced when large areas of formerly suitable foraging habitat are rendered unsuitable after conversion. Furthermore, additive increases in anthropogenic mortality may be expected to occur in association with the proliferation of roads, powerlines, and other supporting infrastructure needed to support industrialized development. The current Golden Eagle management approach in Nevada focuses on offsetting anthropogenic take resulting from landscape development through application of seasonal 1.6-km direct disturbance buffers at nests to promote productivity through reduced disturbance. However, these buffers do not adequately address large-scale and widespread habitat loss at a scale currently realized in Nevada. Cumulative, large-scale habitat loss from landscape

development, climate change and long-term drought, increased frequency and intensity of the wildland fire regime, conversion of native habitat to invasive grasslands, and novel disease impacts to lagomorphs exacerbate low annual survival of pre-adults and suitability of habitats for adult recruitment. Even with full compensatory mitigation of direct suspected take, this indirect loss of birds would potentially lead to net population loss of Golden Eagles, which is contrary to the no-net-loss preservation standard sought by the USFWS under the Eagle Act (USFWS 2016a, 2016b, Millsap et al. 2022).

The downward growth rates we detected at two spatial scales, coupled with low survival across age classes, suggest mortality within the current population is additive. Low fecundity and subadult survival compound the problem, as fewer individuals survive and are recruited into the breeding population. We used locally derived fecundity estimates for DLV (2015–2023; J. Barnes unpubl. data) while relying on earlier western US fecundity estimates for Nevada (USFWS 2016a, Millsap et al. 2022). Without supporting data, fecundity estimates from the DLV may more closely reflect fecundity across Nevada during our study. However, our sensitivity results indicated DLV population growth to be most sensitive to adult survival, despite low fecundity, which strengthens our confidence in the sensitivity analysis results for Nevada and justifies a more expansive consideration of fecundity. Additive mortality potentially creates a population sink for the greater regional population of Golden Eagles. Katzner et al. (2017) found evidence that high Golden Eagle mortality associated with wind development at the Altamont Pass Wind Resource Area in California was additive, and approximately 25% of the general population within that area was made up of immigrants. Those results suggest that the apparent population stability in the region was underpinned by the influx of dispersers or floaters, with the area serving as a sink habitat for the greater range-wide population due to sustained high mortality (Katzner et al. 2017).

High annual territory occupancy rates in an area experiencing relatively low annual survival of adults and a declining overall population suggests the existence of floater and/or dispersing population segments to sustain a steady breeding population over time. Annual territory occupancy within the DLV study area from 2015 to 2024 averaged 0.98 with 142 of 145 assessed territories occupied (9–17 territories monitored/yr; J. Barnes unpubl. data). Our monitoring efforts at secondary study areas across Nevada were not as robust or consistent annually as at DLV (i.e., 28 nesting territories considered for banding and transmitter deployment), but territories were confirmed occupied each year they were checked. Maintaining consistently high rates of annual territory occupancy across Nevada with relatively elevated mortality rates suggests an increase in habitat degradation within the state could exacerbate similar sink-effects for the greater region-wide population as observed in Katzner et al. (2017).

While our population matrices account for fecundity and breeding probability, we lack information for restricting these populations via territory availability and quality. The scarcity of information on Golden Eagle abundance and territory availability in Nevada limits our ability to fully understand the causes of their population declines (Monzón and Friedenberg 2018). Factors such as reduced prey availability, increased wildland fire frequency, habitat fragmentation, agricultural conversion, and invasive species encroachment likely reduce the number of successful territory holders (Knapp 1996, Penteriani et al. 2011, Kochert and Steenhof 2012, Monzón and Friedenberg 2018). Our sensitivity and elasticity analyses confirmed that adult survival is the most critical factor regulating Golden Eagle populations. This is consistent with demographic theory for long-lived species (Mills 2012, Tack et al. 2017). However, without data on territory availability and quality, our population model assumes a relatively stable breeding probability derived from range-wide estimates contributing to fecundity, which may not reflect reality if high-quality habitats are limited and declining within Nevada (Millsap et al. 2022). This limitation could impact the population growth estimates and change the most important parameter for population management.

Conclusions. Our results suggest a declining Golden Eagle population in Nevada and low survival across age classes compared to recent western range-wide estimates (Millsap et al. 2022). Nevada and the Great Basin are facing a changing climate, increased fire regimes, increased distributions of invasive species, the spread of new pathogens, and increased energy and industrial development pressure (Knapp 1996, Kochert and Steenhof 2012, Milbrandt et al. 2014, Brand et al. 2016, Hixson et al. 2022, Crowell et al. 2023, Murphy et al. 2023, Smith et al. 2023a, 2023b). Thus, it appears that Golden Eagle populations in Nevada may be increasingly sensitive to further impacts across the landscape, including current renewable energy development pressure. Our study was limited to Nevada; researchers in other parts of the West should examine productivity and survival elsewhere to assess whether our results are unique or are harbingers of changing patterns in the western US. Managers and wildlife practitioners should carefully consider management actions that may lead to increased direct or indirect anthropogenic impacts. While adult survival is important for maintaining a stable population, decreased primary prey abundance may lead to reduced recruitment and lower numbers of individuals attempting to breed. High mortality rates due to starvation and low survival of hatch-year and subadult individuals in this study may reflect long-term drought and/or RHDV2 and their effects on prey populations. Therefore, further investigation as to how the introduction of RHDV2 has affected predator populations, including raptors is warranted.

SUPPLEMENTAL MATERIAL (available online): Appendix: Statistical description of methods for estimating Golden Eagle survival and population trajectory.

ACKNOWLEDGMENTS

J. Newmark and the Nevada Department of Wildlife supported the project, with substantial support from the USFWS Wildlife and Sport Fish Restoration Program. We are grateful for funding support from the Bureau of Land Management Caliente Field Office and the Nevada State Office, which was aided greatly by A. Styles, T. Trapp, and S. Brewer. J. Brown with the USFWS Western Golden Eagle Team provided initial encouragement to begin our study. Hycroft Mining and the Spring Valley Wind Technical Advisory Committee supported portions of our work. We received critical field support from J. Johnson, E. Barnes, M. Kolada, B. Wolff, and S. Fox. We thank D. Driscoll, G. Doney, D. Haines, N. Todd, and others with the American Eagle Research Institute for trapping adults. Our manuscript benefited from input and suggested edits from G. Hunt, J. Kolowski, and two anonymous reviewers. Trapping and handling were permitted under USGS banding permits 24006 and 23723 and Nevada Scientific Collection Permit 41340, and all animal handling elements of our study were reviewed and approved by the Nevada Department of Wildlife State

Veterinarian without a formal permitting mechanism available. The findings and conclusions in this article are those of the authors and do not necessarily represent the views of the USFWS.

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Citation Download Citation

James E. Golden, Joseph G. Barnes, and Perry J. Williams "Estimating Survival and Population Trajectories of Golden Eagles in Nevada," *Journal of Raptor Research* 59(4), 1-15, (18 November 2025). https://doi.org/10.3356/jrr2521

Received: 11 February 2025; Accepted: 30 July 2025; Published: 18 November 2025