

SURVIVAL ESTIMATES AND CAUSES OF MORTALITY OF GOLDEN EAGLES IN SOUTH-CENTRAL MONTANA

ROSS H. CRANDALL,¹ DEREK J. CRAIGHEAD, BRYAN BEDROSIAN,² AND VINCENT A. SLABE³
Craighead Beringia South, P.O. Box 147, Kelly, WY 83011 USA

ABSTRACT.—Golden Eagles are a long-lived, wide-ranging bird of conservation concern in North America. To create a comprehensive conservation strategy, managers and researchers need to know the primary causes of mortality and must have reliable survival estimates. We monitored nesting Golden Eagles in a 2700 km² area of south-central Montana from 2010–2017. As part of our effort, we fitted 16 adult and 13 nestlings with platform terminal transmitters for satellite telemetry. We determined causes of mortality from recovered Golden Eagles and, using multi-state models in program MARK, we estimated monthly and annual survival probabilities. We confirmed five total mortalities, including two cases of lead toxicity, one occurrence of intraspecific aggression, and two mortalities with unknown cause. The monthly survival estimate of adult Golden Eagles in our study area was 0.994 and the annual adult survival probability was 0.930. The monthly survival probability estimate from birds transmittered as nestlings was 0.991 and the annual survival estimate was 0.897. Lead toxicity and intraspecific aggression are known causes of Golden Eagle mortality, but the birds we tracked died from lead toxicity at a higher rate than would be expected based on results from other studies. The survival probability estimates from the Golden Eagles we monitored were higher than reported estimates from other locations. Further, the information we provide can assist with the development of population matrices and increase our knowledge on causes of Golden Eagle mortality.

KEY WORDS: *Aquila chrysaetos*; *Golden Eagle*; *lead*; *Montana*; *mortality*; *satellite telemetry*; *survival probability*.

ESTIMACIONES DE SUPERVIVENCIA Y CAUSAS DE MORTALIDAD DE *AQUILA CHRYSAETOS* EN EL CENTRO SUR DE MONTANA

RESUMEN.—*Aquila chrysaetos* es una especie longeva y con una amplia área de distribución cuyo estado de conservación en América del Norte es preocupante. Para crear una estrategia de conservación integral, los gestores y los investigadores necesitan conocer las principales causas de mortalidad y deben contar con estimaciones fiables de supervivencia. Hicimos el seguimiento de individuos de *A. chrysaetos* nidificantes en un área de 2700 km² en el centro sur de Montana entre los años 2010 y 2017. Como parte de nuestro esfuerzo, colocamos transmisores satelitales en 16 adultos y 13 polluelos. Determinamos las causas de mortalidad a partir de águilas recuperadas y, usando modelos de estados múltiples en el programa MARK, estimamos las probabilidades de supervivencia mensual y anual. Confirmamos un total de cinco muertes, incluyendo dos casos de intoxicación por plomo, un evento de agresión intraespecífica y dos muertes sin causa conocida. La estimación de la supervivencia mensual de adultos de *A. chrysaetos* en nuestro área de estudio fue 0.994 y la probabilidad de supervivencia anual de adultos fue 0.930. La estimación de la probabilidad de supervivencia mensual de las aves con transmisores colocados desde polluelos fue 0.991 con una estimación de supervivencia anual de 0.897. La intoxicación por plomo y la agresión intraespecífica son causas conocidas de mortalidad en *A. chrysaetos*, pero las aves que nosotros seguimos murieron por intoxicación por plomo a una tasa mayor de lo esperado en base a los resultados de otros estudios. Las estimaciones de la probabilidad de supervivencia de los individuos de *A. chrysaetos* que seguimos fueron mayores que las estimaciones presentadas para otras localidades. La información que mostramos puede ayudar al desarrollo de matrices poblacionales y a aumentar nuestro conocimiento de las causas de mortalidad en esta especie.

[Traducción del equipo editorial]

¹ Email address: ross@beringiasouth.org

² Present address: Teton Raptor Center, P.O. Box 1805, Wilson, WY, 83014 USA.

³ Present address: West Virginia University, School of Natural Resources, Morgantown, WV, 26506 USA.

Golden Eagles (*Aquila chrysaetos*) are a long-lived and slow-reproducing species of conservation concern in North America (Kochert et al. 2002, US Fish and Wildlife Service [USFWS] 2016). Two important aspects of Golden Eagle ecology with conservation applications are the identification of the primary causes of death, and estimating survival probability. Identifying patterns of Golden Eagle mortality is important for understanding limitations to Golden Eagle abundance and can provide options for mitigation efforts. Golden Eagles in North America are known to die from diseases such as aspergillosis and avian pox (Russell and Franson 2014), electrocution from power lines (Mojica et al. 2018), gunshot, poison such as lead or pesticides, starvation, trauma such as vehicle collisions (Russell and Franson 2014, USFWS 2016), and wind turbine strikes (Hunt et al. 2017). Until recently, many of the documented causes of Golden Eagle mortality have been determined from birds found opportunistically, which are biased by low recovery rates of banded birds (Harmata 2002) and toward easily found carcasses (Russell and Franson 2014). Golden Eagle mortalities identified from opportunistically recovered carcasses can misrepresent the most common causes of death because easily recovered birds, such as those closer to roads, or those at the bases of power poles may not represent causes of mortality of all Golden Eagles. For example, Golden Eagles recovered and sent to the National Wildlife Health Center primarily died as a result of electrocution ($n = 381$, 26.7%) and trauma ($n = 384$, 26.9%) followed by gunshot ($n = 196$, 13.7%) and undetermined ($n = 131$, 9.2%; Russell and Franson 2014). In contrast, Golden Eagles fitted with satellite transmitters as nestlings in Alaska primarily died of starvation ($n = 9$, 64.3%) followed by unknown ($n = 3$, 21.5%), poached ($n = 1$, 7.1%) and electrocution (7.1%; McIntyre 2012). McIntyre (2012) also noted that all birds were recovered greater than 5 km from any road. In a more comprehensive effort, Golden Eagles fitted with satellite transmitters across North America primarily died from starvation and disease ($n = 39$, 40.2%) followed by electrocution ($n = 11$, 11.3%) and gunshot ($n = 11$, 11.3% each; USFWS 2016). These examples suggest the bias associated with opportunistic carcass recoveries can lead researchers to misidentify the most common causes of death. The USFWS (2016) effort spanned across the North American range

but did not include a spatially explicit component. Given the wide distribution of the species, causes of mortality may vary locally or regionally. Consequently, we need unbiased information on causes of Golden Eagle mortality over a wide geographic extent as well as local information on causes of mortality to help direct management activities.

Golden Eagle survival estimates can inform stage-structured population models to determine sustainable survival rates for the species. In addition, having estimates of survival from broad geographic areas can help prioritize locations for protection or mitigation efforts. Current published examples of annual survival probability of Golden Eagles range from 0.190 (SE = 0.070; McIntyre et al. 2006) to 0.905 (SE = 0.022; Hunt et al. 2017). McIntyre et al. (2006) only estimated annual survival probabilities of first-year eagles, whereas the high annual survival rate provided by Hunt et al. (2017) was for adults. Golden Eagles do not typically breed until their fifth year of life and survival rates vary among adults, juveniles (hatch-year), and subadults (2–4 yr old; Harmata 2002, McIntyre et al. 2006, USFWS 2016, Hunt et al. 2017). Although some estimates of survival probability do exist, determining the extent of the variation of survival among age classes is hampered due to difficulties of gathering estimates from multiple age classes throughout North America. Golden Eagle behavior (e.g., migratory or nonmigratory) exacerbates these difficulties because behavior likely has a large influence on the probability of survival (McIntyre et al. 2006). Given the local and behavioral influences on survival, variation of survival among age classes, and the potential benefit of assessing survival probabilities at multiple spatial scales, more information is warranted.

From 2010–2017, we monitored breeding Golden Eagles near Livingston, Montana. As part of our nest monitoring effort, we deployed platform transmitter terminal (PTT) satellite transmitters on breeding Golden Eagles and their offspring. Our goals were to understand current threats to the Golden Eagles in our study area, to compare Golden Eagle survival in our study area to survival in other areas, and to provide information for the species in western North America. To accomplish our goal, our objectives were to (1) determine causes of mortality of Golden Eagles in south central Montana, and (2) estimate monthly and annual survival probabilities of Golden Eagles.

METHODS

We deployed transmitters in a 2700 km² study area in south-central Montana (approximately 45°45.00'N, 110°34.00'W, Fig. 1), which included portions of Park and Sweet Grass Counties. Our study area was primarily a mix of gently rolling plains and steep, mountainous terrain with subalpine forests in the higher elevations and intermixed sagebrush-steppe and grasslands, and riparian areas dominated by cottonwood (*Populus* spp.) in the lower elevations. All monitored Golden Eagle nesting territories were composed almost entirely of private land; cattle ranching was the primary land use in and around eagle territories. We trapped and deployed transmitters on adult Golden Eagles in known nesting territories from February through April, 2011–2013. We used net launchers (Trapping Innovations, Kelly, WY, USA) placed near road-killed ungulates for bait. We captured nestling Golden Eagles when they were at least 51 d old, which is near the age of fledging (Crandall et al. 2016). We aged all nestlings using a photographic guide (Driscoll 2010). All individuals captured as nestlings will hereafter be referred to as preadults since they were not of breeding age for the duration of our study. We deployed 30-g or 45-g GPS/Argos PTT satellite transmitters (Microwave Telemetry, Columbia, MD, USA) on all adult Golden Eagles and a mix of the smaller GPS/PTT units or 70-g Argos PTTs (Wildlife Computers, Redmond, WA, USA) on preadults. To attach transmitters, we used 1.4-cm Teflon ribbon with a cross-chest breakaway harness (Crandall et al. 2015). Our harness was made of four pieces of Teflon ribbon sewed together on a leather breast patch with one or two stitches of silk thread for adults and four to five stitches for nestlings. We applied super glue to the thread ends on the ventral side of the breast patch to prolong the attachment duration on the eagle.

Distinguishing Mortalities from Dropped Transmitters. To assess causes of mortality, we monitored movement data from each bird every 3 d to identify when a transmitter stopped moving, indicative of either a mortality or a dropped transmitter. We attempted to recover any dead Golden Eagles or dropped transmitters as soon as possible. Nearly all adult Golden Eagles in our study area were nonmigratory (Crandall et al. 2015), which assisted our ability to investigate most stationary transmitters. Upon finding a dead Golden Eagle, we recorded any pertinent information immediately obvious that might provide insight into cause of death. For

example, we collected information on the bird's position on the ground (e.g., wings splayed, legs extended with talons clenched), presence or absence of green mutes, presence or absence of obvious puncture wounds, and general state of the bird. Emaciation, dehydration, loss of motor skills resulting in restricted movement, and green mutes are all signs of poisoning in raptors and potentially obvious when recovering a dead bird (Kramer and Redig 1997, Pain et al. 2009). We then submitted the carcass for formal necropsy. Board-certified pathologists performed necropsies at diagnostic laboratories accredited by the American Association of Veterinary Laboratory Diagnosticians. We considered a wet-weight liver lead concentration of 10.0 ppm as the quantitative threshold for severe clinical lead poisoning leading to mortality (Franson and Pain 2011).

In addition to monitoring general movements, we also monitored tag diagnostics, specifically voltage and temperature, and movements directly prior to losing contact with transmitters. By monitoring voltage and temperature, we were able to assess probable tag failure vs. potential dropped transmitters or mortality. If voltage decreased steadily, temperature remained constant, and the bird was moving but we lost contact with a transmitter, we assumed tag failure vs. dropped transmitter or mortality.

Survival Analysis. To estimate survival probabilities, we used multistate mark-recapture models in program MARK (White et al. 2006, Devineau et al. 2014). We used the multistate framework to account for unrecovered transmitters. The benefit of the multistate framework vs. the known-fate framework is that we did not have to censor individuals with tag failure or unrecovered mortalities, allowing us to use all available data (Devineau et al. 2014). Our multistate model was simple, with three states: alive (A), dead (D), and unknown (U). We only assigned fate to birds with recovered transmitters or mortalities; all birds with transmitters that we believed failed based on tag diagnostics were classified as U. We were specifically interested in estimating the transition probability from A to D (Devineau et al. 2014). To estimate monthly and annual survival probabilities, we reduced each individual's tracking history to one state per month, based on the status of the individual on the first transmission period. We explored a simple model set including a null model and a model that allowed for differences in survival probabilities between age classes (preadult vs.

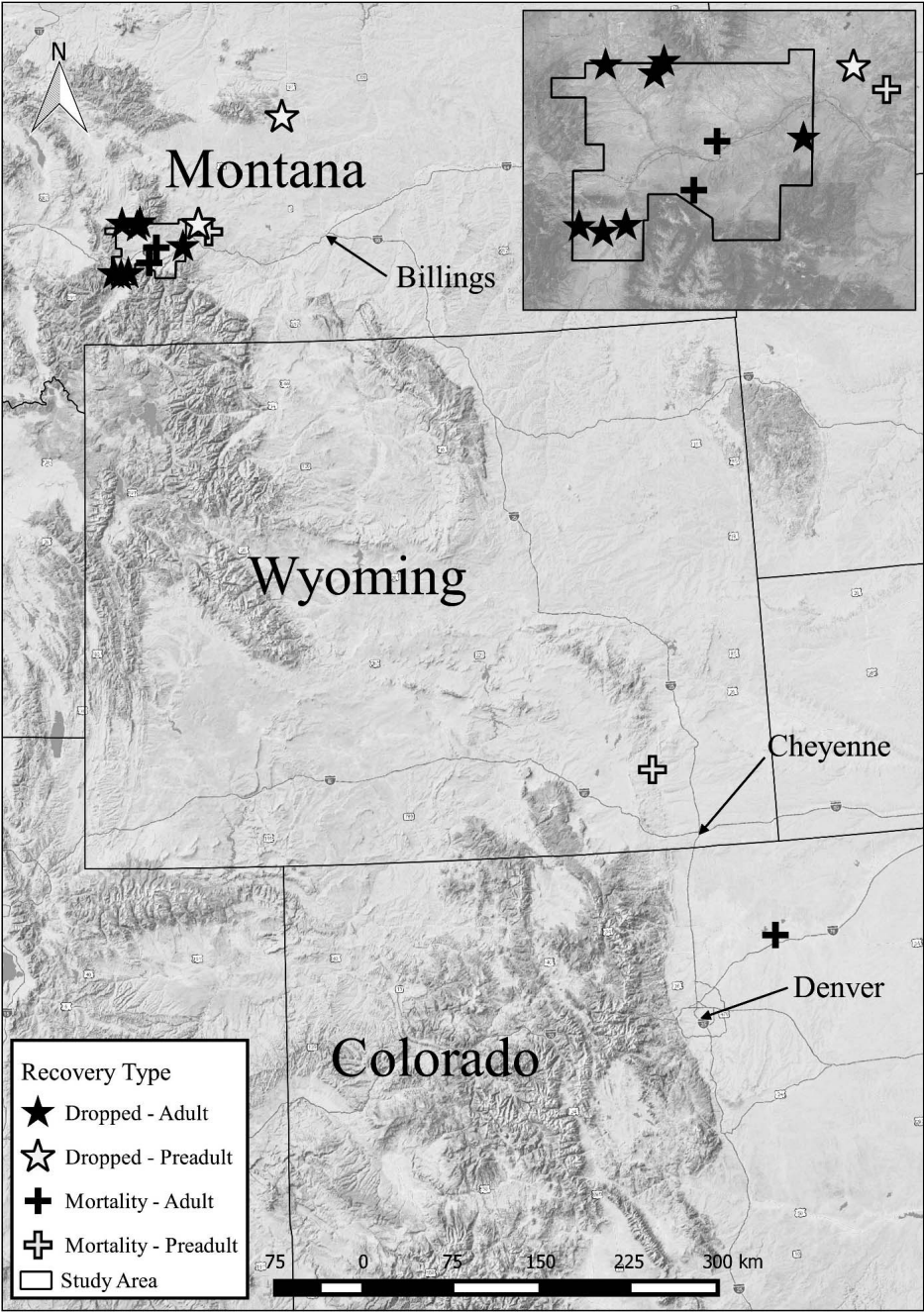


Figure 1. Location of study area and all recovered transmitters and mortalities for adult and preadult Golden Eagles where “Dropped” represents a dropped transmitter and “Mortality” represents the recovery of a dead Golden Eagle that was outfitted with a transmitter. Inset is close-up of study area.

Table 1. Detailed information for each adult and preadult Golden Eagle captured and tracked for our study, not including transmitters still functioning as of 31 October 2017. End date is date and month transmitter stopped collecting locations on a Golden Eagle; Duration is total number of days transmitter collected locations; Status is the state of the eagle or transmitter when found; Recovery Location is the county and state where eagle or transmitter was found; and Cause indicates cause of mortality (if known) or transmitter failure.

BIRD ID	AGE	END DATE	DURATION (d)	STATUS	RECOVERY LOCATION	CAUSE
Mission male	Adult	Nov 2011	233	Mortality	Park, MT	Lead toxicity
Bonhomme male	Adult	Jan 2012	282	Assumed mortality	Weld, CO	Believe human-caused mortality
CMR male	Adult	March 2017	1865	Dropped	Park, MT	N/A
CP female	Adult	Aug 2014	918	Dropped	Park, MT	N/A
Criswell female	Adult	Dec 2015	1390	Dropped	Park, MT	N/A
Woodhouse female	Adult	July 2012	132	Unknown	N/A	N/A
Suce male	Adult	Apr 2014	428	Dropped	Park, MT	N/A
Trail male	Adult	Nov 2015	1003	Dropped	Park, MT	N/A
Woodhouse male	Adult	Sept 2013	210	Dropped	Sweet Grass, MT	N/A
Divide female	Adult	Oct 2013	235	Dropped	Park, MT	N/A
Springdale male	Adult	Oct 2013	234	Mortality	Park, MT	Intraspecific interaction
WT female	Preadult	June 2013	368	Dropped	Musselshell, MT	N/A
FC female	Preadult	May 2013	338	Unknown	N/A	Transmitter failure
PN male	Preadult	Jan 2013	187	Unknown	N/A	Transmitter failure
PN female	Preadult	March 2013	274	Unknown	N/A	Transmitter failure
WT male	Preadult	Aug 2013	57	Unknown	N/A	Transmitter failure
E1 female	Preadult	March 2015	628	Mortality	Laramie, WY	Lead toxicity
CPN female	Preadult	March 2017	1368	Unknown	N/A	Transmitter failure
MC female	Preadult	Aug 2013	60	Unknown	N/A	Transmitter failure
HH male	Preadult	Sept 2013	72	Unknown	N/A	Transmitter failure
CPN2 female	Preadult	Oct 2015	480	Dropped	Sweet Grass, MT	N/A
E2 female	Preadult	Aug 2016	777	Mortality	Sweet Grass, MT	Unknown cause
E3 male	Preadult	Aug 2016	763	Unknown	N/A	Transmitter failure

adult). We did not consider any covariates or time-varying models for our survival analysis based on the sample-size limitations of our data, and based on the pattern of mortalities (i.e., male vs. female mortalities and age-class limitations). We used Akaike information criteria adjusted for small sample size (AIC_c) to choose a best model and considered each model competitive if they were within 2 AIC_c values. We also compared support for our best model using evidence ratios (Burnham et al. 2011).

RESULTS

We telemetered 16 adult and 13 nestling Golden Eagles during our study period. We recovered two dead adults and two dead preadults; we recovered seven dropped transmitters from adults and two dropped from preadults (Table 1). We recovered one transmitter from an adult that appeared to have been purposefully removed by a person and we had one adult with an unknown outcome (transmitter failure or mortality). We had eight transmitters on preadults fail. Four transmitters on adults and one

on a preadult lasted through the conclusion of the study in October of 2017. We recovered most, but not all, transmitters and dead birds within the study area (Fig. 1).

Of the two confirmed adult mortalities, one bird died as a result of an intraspecific interaction and one died from lead toxicity. The bird that died from an intraspecific interaction had gross lesions caused by trauma, multiple puncture wounds in the skull and coelom, and subdural hematoma. The adult that died as a result of lead poisoning had a liver lead concentration of 25.2 ppm wet weight. In addition, the adult also showed signs of emaciation and dehydration and was found in close proximity to multiple spots of green watery excreta. Lastly, we believe the adult with the removed transmitter likely died from anthropogenic causes because we found the transmitter below a bridge, near moving water, and all four Teflon ribbons had been cut between attachment points on the transmitter and the leather breast patch, which was indicative of the transmitter having been removed by a person.

Nevertheless, the cause of death of that bird is unknown because only the transmitter was recovered.

The preadult that died of lead toxicity had a liver lead concentration of 52.6 ppm wet weight and also showed signs of emaciation and dehydration. Cause of death for the other confirmed preadult mortality could not be determined through necropsy due to the state of the recovered carcass.

Our age-class model, which allowed for differences between adult and predadult survival was the only competitive model, supported by nearly all of the model weight (Table 2). In addition, the evidence for the age-class model was 53 times stronger than the null model. Using our best model, the monthly adult survival estimate from Golden Eagles nesting in our study area was 0.994 (95% CI = 0.983–0.998). The annual adult Golden Eagle survival estimate was 0.930 (95% CI = 0.814–0.976). The monthly survival estimate for preadults was 0.991 (95% CI = 0.966–0.998), and the annual preadult survival estimate was 0.897 (95% CI = 0.660–0.976).

DISCUSSION

Causes of Mortality. Golden Eagles in our study were most likely to die from lead toxicosis. Lead poisoning is a known source of mortality for Golden Eagles, yet when compared to other anthropogenic causes, best available data suggest relatively few Golden Eagles die from lead toxicity. For example, the two most comprehensive studies on causes of Golden Eagle mortality cite lead toxicosis in 4.8% of 1427 Golden Eagles (Russell and Franson 2014) and 2.1% of 97 Golden Eagles (USFWS 2016). The USFWS (2016) report, which is the most comprehensive document outlining causes of Golden Eagle mortality in North America based on PTT-tracked birds, summarized all available mortality information from 97 Golden Eagles of all ages. One of our two eagles that died of lead toxicity was included in the USFWS (2016) report, thus comprising 50% of the identified cases of lead toxicity. By comparison, 26.7% and 11.3% of Golden Eagles died from electrocution in each respective study. Intraspecific interactions, or fighting, on the other hand is a relatively common source of mortality for Golden Eagles. The USFWS (2016) found 17.4% of 23 adult Golden Eagles died as a result of intraspecific aggression, which included the bird from our study. In the Altamont Pass area of California, intraspecific aggression was the most common source of natural deaths of Golden Eagles (Hunt et al. 2017). The

Table 2. Model selection results from our multi-state, discrete-time survival analysis for adult and preadult Golden Eagles, where $S(\text{age-class})$ represents the model allowing for differences between adult and preadult survival and $S(\text{null})$ indicates the null model. K is the number of model parameters, ΔAIC_c is the difference in Akaike Information Criteria (AIC) value adjusted for small sample size, and w_i is the model weight of both competing models.

MODEL	K	ΔAIC_c	w_i
$S(\text{age-class})$	4	0	0.98
$S(\text{null})$	2	7.93	0.02

obvious limitation in our study was the low number of total mortalities we recorded, thus we do not know whether our documented patterns of mortality are representative of the true proportion of causes of mortality from birds nesting and hatched in our study area. And although we documented two lead-toxicosis mortalities, one occurred in Montana and the other in Wyoming, so we cannot suggest spatial patterns to lead exposure either. Nevertheless, two cases of lead toxicosis, a human-caused source of mortality, support the need for continued efforts to reduce the amount of available lead in the environment. Intraspecific aggression is a natural cause of mortality and will persist given the territorial nature of Golden Eagles.

In addition to the causes of death we documented, we note that we did not find several common or predictable causes of death. Electrocution, shooting, starvation, and trauma specifically were not identified as sources of mortality among the birds we tracked, but are common causes of death for adult and preadult Golden Eagles elsewhere (McIntyre et al. 2006, Russell and Franson 2014, USFWS 2016, Hunt et al. 2017, Mojica et al. 2018). It is likely that we did not detect any of these common sources of mortality because of the low number of total mortalities during our study period, but it is also possible we had mortalities that we did not detect. For example, electrocutions or trauma may destroy the transmitters, making it impossible to identify a mortality. If, for example, one or more preadults died of electrocution instead of transmitter failure, our survival estimate would be inflated. Yet, eight of our 13 preadults had transmitters that lasted longer than 1 yr. Starvation and electrocution, the most common sources of Golden Eagle mortality, appear to disproportionately kill preadult eagles (USFWS 2016, Mojica et al. 2018). Between our monitored

tag diagnostics, high first-year survival, and few issues with adult transmitters, we are confident that our survival estimates are reliable but acknowledge some level of uncertainty with unrecovered transmitters or tracked birds.

Survival Probability. We report relatively high annual survival probabilities for adult and preadult Golden Eagles. Annual adult Golden Eagle survival estimates in the United States vary from 0.860 (CI = 0.600–1.000; Harmata 2016) to 0.905 (SE = 0.022; Hunt et al. 2017). Preadult annual Golden Eagle survival, on the other hand, is more varied, ranging from 0.190 (SE = 0.070; McIntyre et al. 2006) to 0.842 (SE = 0.038; Hunt et al. 2017). For a long-lived and slow-reproducing species, adult survival is the most important factor regulating population trends (Tack et al. 2017) and therefore should be relatively high. However, preadult survival also influences population growth rates and variation in population growth rates, although not to the degree of adult survival (Tack et al. 2017). The difference in local abundance trends in areas with high annual adult and preadult survival, such as we documented in our study area, compared to lower estimated annual survival, is largely unknown. Although the US Fish and Wildlife Service must focus on the larger-sized eagle management units for directing management activities, we suggest identifying locations with high survival may be of interest when considering management activities focused on maintaining robust and productive breeding subpopulations of Golden Eagles in North America.

One issue we believe worthy of discussion is the potential influence of transmitters on the tracked individuals' survival through changes in maneuverability, and issues associated with transmitter harnesses (Obrecht et al. 1988, Putaala et al. 1997, Harmata 2016, Harmata et al. 2018). Prairie Falcons (*Falco mexicanus*), Spotted Owls (*Strix occidentalis*), and Northern Goshawks (*Accipiter gentilis*) can be negatively influenced by transmitters (Paton et al. 1991, Foster et al. 1992, Reynolds et al. 2004, Steenhof et al. 2006). Harmata (2016) suggests mounting transmitters to the tail of an eagle minimizes the potential influence of transmitters on survival. Harmata (2016) also documented much shorter transmitter retention periods. Based on the length of our transmitter deployments and the limited number of individuals with fates that may have been related to transmitter or transmitter harness, we believe the transmitters we used and

our transmitter attachment technique had little to no effect on the survival of the Golden Eagles we tracked. Furthermore, we suggest the longevity of transmitters attached using the backpack-style technique is beneficial when assessing Golden Eagle survival.

We sought to identify causes of mortality and determine survival probability of Golden Eagles nesting and fledged from our study area in Montana. We found that adult and preadult Golden Eagles nesting and hatched within our study area were more likely to die of anthropogenic sources versus natural causes. We also determined that adults had higher annual survival probabilities than preadults. Our results support other work on this topic, specifically that human-caused mortality is of concern (USFWS 2016) and preadult Golden Eagle survival is lower than adult survival (USFWS 2016, Hunt et al. 2017). To maintain population stability of Golden Eagles across North America, we must focus on reducing anthropogenic sources of Golden Eagle mortality including but not limited to lead toxicosis. In addition, more work should be done to expand our knowledge on the primary sources of Golden Eagle mortality by increasing the total number of satellite-tracked individuals with associated survival data. Lastly, we need to determine localized contributions to Golden Eagle populations to assess the benefits of targeted management actions.

ACKNOWLEDGMENTS

We thank T. Haynam, S. Wilson, A. Moon, K. Gura, A. Nolan, G. Leslie, M. Cuthill, G. Rogers, and T. Veto for assistance in the field. We thank J. Paugh, D. Haines, S. Tripp, L. Knox, R. Amundson, J. Bedrosian, T. Ferguson, and R. Washenfelder for assisting with transmitter recovery. We thank J. and K. Engwis, G. and V. Brittan, C. Aspivig, C. Guzman-Aspivig, E. Lamb, and numerous other landowners and ranch managers for allowing us access to retrieve transmitters and to capture Golden Eagles. We thank G. Williams and two anonymous reviewers for providing critical feedback of an early version of the manuscript. Our work was funded by the United States Fish and Wildlife Service, Bureau of Land Management, Altria Group Incorporated, the Charles Engelhard Foundation, Cinnabar Foundation, National Geographic Foundation, Western Bird Banding Association, and various private donors. All trapping and handling of Golden Eagles was approved and certified by University of Montana Institutional Animal Care and Use Committee #009-12EGDBS-020812. All research was conducted under USGS banding permit number 22637 and Montana Department of Fish, Wildlife and Parks Scientific Collector's Permits 2011-024, 2012-003, 2013-005, 2014-010, 2015-072, and 2016-064.

LITERATURE CITED

- Burnham, K. P., D. R. Anderson, and K. P. Huyvaert (2011). AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behavioral Ecology and Sociobiology* 65:23–35.
- Crandall, R. H., B. E. Bedrosian, and D. Craighead (2015). Habitat selection and factors influencing nest survival of Golden Eagles in south-central Montana. *Journal of Raptor Research* 49:413–428.
- Crandall, R. H., D. J. Craighead, and B. E. Bedrosian (2016). A comparison of nest survival between cliff-and tree-nesting Golden Eagles. *Journal of Raptor Research* 50:295–300.
- Devineau, O., W. L. Kendall, P. F. Doherty, T. M. Shenk, G. C. White, P. M. Lukacs, and K. P. Burnham (2014). Increased flexibility for modeling telemetry and nest-survival data using the multistate framework. *Journal of Wildlife Management* 78:224–230.
- Driscoll, D. (2010). Protocol for Golden Eagle occupancy, reproduction, and prey population assessment. American Eagle Research Institute, Apache Junction, AZ, USA.
- Foster, C. C., E. D. Forsman, E. C. Meslow, G. S. Miller, J. A. Reid, F. F. Wagner, A. B. Carey, and J. B. Lint (1992). Survival and reproduction of radio-marked adult Spotted Owls. *Journal of Wildlife Management* 56:91–95.
- Franson, J. C., and D. J. Pain (2011). Lead in birds. In *Environmental Contaminants in Biota: Interpreting Tissue Concentrations*, Second ed. (W. N. Beyer and J. P. Meador, Editors). CRC Press, Boca Raton, FL, USA. pp. 563–594.
- Harmata, A. R. (2002). Encounters of Golden Eagles banded in the Rocky Mountain West. *Journal of Field Ornithology* 73:23–32.
- Harmata, A. R. (2016). Retention, effect, and utility of tail-mounted satellite-tracked transmitters on Golden Eagles. *Journal of Raptor Research* 50:265–275.
- Harmata, A. R., J. M. Marzluff, and J. J. Rotella (2018). Survival of Montana Golden Eagles (*Aquila chrysaetos*). *Wilson Journal of Ornithology*. <https://doi.org/10.1676/16-123.1>.
- Hunt, W. G., J. D. Wiens, P. R. Law, M. R. Fuller, T. L. Hunt, D. E. Driscoll, and R. E. Jackman (2017). Quantifying the demographic cost of human-related mortality to a raptor population. *PLoS ONE* 12(2):e0172232. <https://doi.org/10.1371/journal.pone.0172232>.
- Kochert, M. N., K. Steenhof, C. L. McIntyre, and E. H. Craig (2002). Golden Eagle (*Aquila chrysaetos*). In *The Birds of North America* (A. F. Poole and F. B. Gill, Editors). Cornell Lab of Ornithology, Ithaca, NY, USA. <https://birdsna.org/Species-Account/bna/species/goleag>.
- Kramer, J. L., and P. T. Redig (1997). Sixteen years of lead poisoning in eagles, 1980–95: an epizootiologic view. *Journal of Raptor Research* 31:327–332.
- McIntyre, C. L. (2012). Quantifying sources of mortality and wintering ranges of Golden Eagles from interior Alaska using banding and satellite tracking. *Journal of Raptor Research* 46:129–134.
- McIntyre, C. L., M. W. Collopy, and M. S. Lindberg (2006). Survival probability and mortality of migratory juvenile Golden Eagles from interior Alaska. *Journal of Wildlife Management* 70:717–722.
- Mojica, E. K., J. F. Dwyer, R. E. Harness, G. E. Williams, and B. Woodbridge (2018). Review and synthesis of research investigating and mitigating Golden Eagle electrocutions. *Journal of Wildlife Management* 82:495–506.
- Obrecht, H. H., C. J. Pennycuik, and M. R. Fuller (1988). Wind tunnel experiments to assess the effect of back-mounted radio transmitters on bird body drag. *Journal of Experimental Biology* 135:265–273.
- Pain, D. J., I. J. Fisher, and V. G. Thomas (2009). A global update of lead poisoning in terrestrial birds from ammunition sources. In *Ingestion of Lead from Spent Ammunition: Implications for Wildlife and Humans*. (R. T. Watson, M. Fuller, M. Pokras, and W. G. Hunt, Editors). The Peregrine Fund, Boise, ID, USA.
- Paton, P. W., C. J. Zabel, D. L. Neal, G. N. Steger, N. G. Tilghman, and B. R. Noon (1991). Effects of radio tags on Spotted Owls. *Journal of Wildlife Management* 55:617–622.
- Putala, A., J. Oksa, H. Rintamäki, and R. Hissa (1997). Effects of hand-rearing and radiotransmitters on flight of Gray Partridge. *Journal of Wildlife Management* 61:1345–1351.
- Reynolds, R. T., G. C. White, S. M. Joy, and R. W. Mannan (2004). Effects of radiotransmitters on Northern Goshawks: do tailmounts lower survival of breeding males? *Journal of Wildlife Management* 68:25–32.
- Russell, R. E., and J. C. Franson (2014). Causes of mortality in eagles submitted to the National Wildlife Health Center 1975–2013. *Wildlife Society Bulletin* 38:697–704.
- Steenhof, K., K. K. Bates, M. R. Fuller, M. N. Kochert, J. O. McKinley, and P. M. Lukacs (2006). Effects of radio-marking on Prairie Falcons: attachment failures provide insights about survival. *Wildlife Society Bulletin* 34:116–126.
- Tack, J. D., B. R. Noon, Z. H. Bowen, L. Strybos, and B. C. Fedy (2017). No substitute for survival: perturbation analyses using a Golden Eagle population model reveal limits to managing for take. *Journal of Raptor Research* 51:258–272.
- US Fish and Wildlife Service (USFWS) (2016). Bald and Golden Eagles: Population Demographics and Estimation of Sustainable Take in the United States, 2016 Update. Division of Migratory Bird Management, US Fish and Wildlife Service, Washington, DC, USA.
- White, G. C., W. L. Kendall, and R. J. Barker (2006). Multistate survival models and their extensions in Program MARK. *Journal of Wildlife Management* 70:1521–1529.

Received 26 February 2018; accepted 9 July 2018
Associate Editor: James F. Dwyer