BioOne COMPLETE

No Substitute for Survival: Perturbation Analyses Using a Golden Eagle Population Model Reveal Limits to Managing for Take

Authors: Tack, Jason D., and Noon, Barry R.

Source: Journal of Raptor Research, 51(3) : 258-272

Published By: Raptor Research Foundation

URL: https://doi.org/10.3356/JRR-16-32.1

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://complete.bioone.org/journals/Journal-of-Raptor-Research on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

J. Raptor Res. 51(3):258–272
© 2017 The Raptor Research Foundation, Inc.

NO SUBSTITUTE FOR SURVIVAL: PERTURBATION ANALYSES USING A GOLDEN EAGLE POPULATION MODEL REVEAL LIMITS TO MANAGING FOR TAKE

JASON D. TACK[1] AND BARRY R. NOON
Colorado State University, Department of Fish, Wildlife and Conservation Biology, Fort Collins, CO 80523 U.S.A.

ZACHARY H. BOWEN
U.S. Geological Survey, Fort Collins Science Center, Fort Collins, CO 80526 U.S.A.

LAUREN STRYBOS AND BRADLEY C. FEDY
University of Waterloo, Environment and Resource Studies, Waterloo, ON, N2L 3G1 Canada

ABSTRACT.—Conserving populations of long-lived birds of prey, characterized by a slow life-history (e.g., high survival and low reproductive output), requires a thorough understanding of how variation in their vital rates differentially affects population growth. Stochastic population modeling provides a framework for exploring variation in complex life histories to better understand how environmental and demographic variation within individual vital rates affects population dynamics. Specifically, we used life-stage simulation analysis (LSA) to identify those life-history characteristics that most affect population growth and are amenable to management actions. The Golden Eagle (*Aquila chrysaetos*) is a wide-ranging raptor of conservation concern, which has been adopted as a focal species for conservation planning. Golden Eagle population trends in western North America currently appear stable. Yet an expanding human footprint that may increase mortality stimulated our investigation into the ability of populations to sustain reduced survival. We fit mixed-effects models to published estimates of vital rates to estimate the mean and process variation of productivity (young fledged per pair) and survival for use in a LSA framework. As expected, breeding adult survival had the greatest relative effect on population growth, though productivity explained the most variation in growth. Based on perturbation analyses, we demonstrate that even minor reductions in breeding adult survival (<4.5%) caused otherwise stable populations to decline. Despite its importance, precise estimates of spatial and temporal variation in breeding adult survival are poorly documented. Importantly, we found that the ability for increases in reproductive output to compensate for decreased survival was very limited. To maintain stable populations, declines in survival >4% required increases in productivity that generally exceed the evolutionary potential for Golden Eagles. Our findings support the current U.S. Fish and Wildlife conservation strategy which mitigates eagle "take" via efforts to reduce mortality elsewhere.

KEY WORDS: *Golden Eagle*; Aquila chrysaetos; *life-stage simulation analysis (LSA)*; *population model*; *survival*; *take*.

SIN SUSTITUTO PARA LA SUPERVIVENCIA: ANÁLISIS DE PERTURBACIÓN UTILIZANDO UN MODELO POBLACIONAL DE *AQUILA CHRYSAETOS* REVELAN LOS LÍMITES AL MANEJO DE LAS REMOCIONES

RESUMEN.—La conservación de poblaciones de aves de presa longevas, caracterizadas por una historia de vida lenta (e.g., supervivencia elevada y bajo rendimiento reproductivo), requiere de un entendimiento profundo de cómo la variación en las tasas vitales afecta diferencialmente el crecimiento poblacional. El modelado de poblaciones estocásticas proporciona un marco de trabajo para explorar la variación en historias de vida complejas para comprender mejor cómo la variación ambiental y demográfica en las tasas vitales individuales afectan las dinámicas poblacionales. Específicamente, utilizamos un análisis de simulación de clases de edad (ASCE) para identificar las características de la historia de vida que más afectan el crecimiento poblacional y que son corregibles a través de acciones de gestión. *A. chrysaetos* es una

[1] Current address: U.S. Fish and Wildlife Service, Habitat and Population Evaluation Team, Missoula, MT 59812 U.S.A.; email address: jason_tack@fws.gov

Downloaded From: https://complete.bioone.org/journals/Journal-of-Raptor-Research on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

rapaz de distribución amplia de interés para la conservación, que ha sido adoptada como una especie focal para la planificación de la conservación. Actualmente, las tendencias poblacionales de *A. chrysaetos* en el oeste de América del Norte parecen estables. La huella humana en crecimiento y que puede incrementar la mortalidad de esta especie impulsó nuestra investigación sobre la capacidad de las poblaciones para soportar una supervivencia reducida. Adaptamos modelos de efectos mixtos a las estimaciones publicadas de tasas vitales para estimar la media y procesar la variación en la productividad (volantones por pareja) y supervivencia para su uso en un marco de trabajo ASCE. Como se esperaba, la supervivencia de adultos reproductores tuvo el mayor efecto relativo sobre el crecimiento poblacional, aunque la productividad explicó la mayor parte de la variación en el crecimiento. En base a los análisis de perturbación, demostramos que incluso disminuciones pequeñas en la supervivencia de adultos reproductores (<4.5%) causa la disminución de poblaciones que de otra manera serían estables. A pesar de su importancia, las estimaciones precisas de las variaciones temporales y espaciales en la supervivencia de adultos reproductores están pobremente documentadas. Principalmente, encontramos que la capacidad de incrementar el rendimiento reproductivo para compensar la disminución en la supervivencia fue muy limitada. Para mantener poblaciones estables, las disminuciones en la supervivencia >4% requieren incrementos en la productividad que generalmente exceden el potencial evolutivo de *A. chrysaetos*. Nuestros hallazgos apoyan la actual estrategia de conservación del Servicio de Pesca y Vida Silvestre de los Estados Unidos que mitiga las "remociones" de águilas a través de esfuerzos para reducir la mortalidad en cualquier otro lado.

[Traducción del equipo editorial]

As human transformation of the earth's ecosystems continues at unprecedented rates (e.g., Corlett 2015), it becomes increasingly difficult to sustain viable populations of species characterized by large area requirements. Long-lived vertebrates with high survival but low reproductive potential—deemed slow life-history species—are most at risk to stressors that exceed their evolutionary constraints and adaptive potential (Congdon et al. 1994). In particular, slow life-history species exposed to chronic stressors that lower survival rates are most vulnerable to population declines (Webb et al. 2002). Given the accelerating increase in extinction risks resulting from habitat loss and fragmentation (Purvis et al. 2000), spread of invasive species (Gurevitch and Padilla 2004), and global climate change (Thomas et al. 2004), threats experienced by slow life-history species are expected to increase. Ripple et al. (2014) have recently documented that these factors have disproportionately elevated the extinction risk for large, wide-ranging predators, which play critical roles in sustaining ecosystem functions. Management actions that increase the most influential vital rates of species with slow life histories may be key to their conservation.

Stage-based population models are widely used in ecology to gain insight into management practices most likely to achieve conservation objectives (Caswell 2001, Mills 2012). From population projections matrices, one can derive long-term (asymptotic) population growth rate, contribution of individual vital rates (e.g., reproduction, survival) to population growth, and a population's expected future st(age) distribution, assuming populations are at a stable stage distribution. Because demographic rates are often highly variable, driven by demographic and environmental stochasticity and individual heterogeneity, stochastic population models can reliably inform management and conservation decisions (Morris and Doak 2002, Lande et al. 2003). Incorporating vital rate uncertainty into population projection models is essential to reduce the likelihood of faulty inference that can arise when these rates are assumed to be static (White 2000). Life-stage simulation analysis (LSA; Wisdom et al. 2000) not only identifies a species' most influential vital rates, but also provides a framework for assessing how variability in these rates affects variation in population growth. These analyses, based on the analytical sensitivity and elasticity of individual vital rates, explore changes in growth rate over the realized range of demographic conditions experienced by actual populations. Furthermore, characterizing vital rates by probability distributions that reflect process variance (i.e., temporal and spatial heterogeneity arising from demographic and environmental processes; Mills 2012) lends insight into the ability of management to exploit the plasticity observed in life-history traits to increase population-level fitness.

Golden Eagles (*Aquila chrysaetos*) are wide-ranging raptors of considerable conservation interest that embody the attributes of a slow life-history species. Adult eagles can live >30 yr, and mature pairs (≥4 yr

Downloaded From: https://complete.bioone.org/journals/Journal-of-Raptor-Research on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

of age) often average fewer than one young fledged per year (Kochert et al. 2002). Golden Eagles span diverse habitats across all continents in the Northern Hemisphere, yet local populations among this widely distributed species often share common threats (Kochert et al. 2002). For example, starvation and poor productivity are natural outcomes that arise following adverse environmental conditions that affect prey abundance at broad spatial scales. Currently, however, human-induced sources of mortality dominate threats to Golden Eagle populations (Watson 2010). For example, retaliatory persecution as a response to livestock depredation persists among eagles despite protections provided by federal governments (Beecham and Kochert 1975, Whitfield et al. 2004). Yet it is inadvertent human actions that make up the majority of anthropogenic threats to Golden Eagles (Watson 2010), which include collisions with vehicles (Loss et al. 2014), poisoning following lead ingestion (reviewed in Craig et al. 1990), and electrocution resulting from perching on power distribution lines (Lehman et al. 2007). Threats arising from rapid energy development adversely affect the populations of many raptor species, including the endangered Bonelli's Eagle (*Aquila fasciata*; Chevallier et al. 2015). Perhaps the fastest growing threat to Golden Eagle conservation in North America is posed by the infrastructure used to generate renewable wind energy (Madders and Whitfield 2006, Kuvlesky et al. 2007, Smallwood and Thelander 2008, Garvin et al. 2011).

In the western U.S., a recent analysis of population trends supports the inference that populations of Golden Eagles are stable, though younger age classes may be in decline (Millsap et al. 2013, Nielson et al. 2014). However, increasing development of wind power is rapidly expanding the human footprint across the North American West (Leu et al. 2008). The growth of wind power development is likely to outpace that of all other energy sources as the U.S. aims to achieve an energy portfolio composed of 20% renewable sources by 2030 (Kiesecker et al. 2011). This response to increasing energy demands will increase the number of wind turbines and associated infrastructure including roads and power distribution lines (Jones and Pejchar 2013). The focus of our research is to better understand the population-level consequences of increasing mortality rates arising from growing development in the American West. Constructing stochastic population models with available demographic data provides a framework for investigating potential effects on populations and insight for effective management strategies. We employed perturbation simulations to explore life-history sensitivities of Golden Eagles to identify conservation strategies for these slow life-history populations.

The objectives of our research were to: (1) build a stochastic stage-based population model representative of Golden Eagles across western North America, (2) estimate probability distributions reflecting the central tendency and process variance inherent in vital rates for Golden Eagles derived from the published literature, (3) calculate the analytical sensitivity and elasticity of individual vital rates, and (4) use perturbation analyses to examine the ability of increased rates of reproduction to buffer the negative effects of increasing mortality rates. Viewed in total, our models evaluate the potential demographic consequences of a rapidly increasing human footprint.

METHODS

Literature Review. We conducted a literature review to identify and compile estimates of Golden Eagle demographic rates. Our goal was to develop a population model representative of Golden Eagle population dynamics in western North America. To search for published Golden Eagle vital rates in the peer-reviewed literature, we initiated our search in Google Scholar using search terms "*Aquila chrysaetos*" and "golden eagle," followed by the terms "survival," "nest," "productivity," and "reproduction." Because we found few estimates of stage-specific survival for Golden Eagles, we also searched for survival estimates for Golden Eagle and related "booted" eagle species globally. We also expanded our search to include government publications, theses and dissertations, and nongovernmental organization reports that contained estimated vital rates from Golden Eagle populations. Only data collected following the ban on dichlorodiphenyltrichloroethane (DDT; 1972 in the U.S. and 1986 in Europe) were considered, and all estimates of vital rates from countries where DDT use persists were omitted. This was done to eliminate potential negative biases in reproductive estimates.

Construction of a Life-Stage Model. We developed a stage-structured population model for a hypothetical, nonmigratory population of mid-continent Golden Eagles in western North America. Golden Eagles exhibit a life-stage progression similar to that of many long-lived raptors: nestlings to juveniles to

Downloaded From: https://complete.bioone.org/journals/Journal-of-Raptor-Research on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

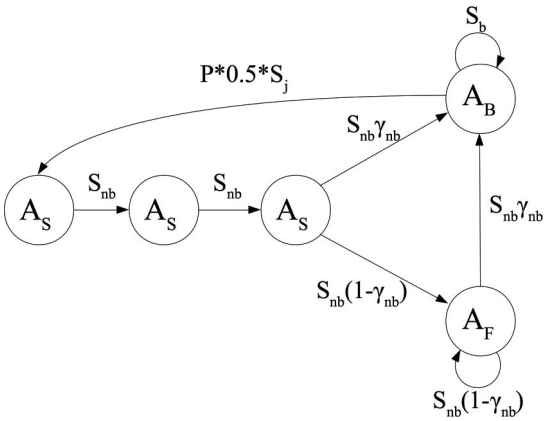


Figure 1. Female-based life-stage diagram for a hypothetical population of Golden Eagles in western North America (nonmigratory). Juveniles can survive and transition through three (*i*) subadult phases (A_{Si}). Upon surviving to adulthood, eagles may transition (γ) between the states of being breeders (A_B) or nonbreeding "floaters" (A_F).

subadults (1–3 yr old) to adults. Stage classes can be identified by plumage and molt patterns and individuals become reproductively competent at age 4 yr (Kochert et al. 2002; Fig. 1). Breeding adults typically form pairs and begin nest construction or repair during the late winter and early spring, producing one to two eggs, followed by approximately 42 d of incubation, with young hatching late March through early June (Kochert et al. 2002). Nestlings remain in the nests for approximately 2 mo (45–84 d), and usually fledge during the summer and enter the juvenile age class. Surviving first-year juveniles become subadults and remain in this life-stage for 3 yr, moving through three distinct molts during their second through fourth summers (Bloom and Clark 2001). In their fifth summer, Golden Eagles will typically obtain definite adult plumage.

Only adults breed in most populations, with age of first reproduction occurring at 4–7 yr old (Watson 2010). Subadults occasionally breed, but it is uncommon (<2% of nesting pairs), and may indicate a population with high rates of turnover in adult nesting pairs (Kochert et al. 2002) or a declining population (Ferrer et al. 2003). Not all adult Golden Eagles form pairs and initiate breeding territories; individuals that do not are colloquially termed "floaters" (nonbreeders). The number of floaters is believed to be density-dependent, reflecting the saturation of available nesting territories.

Based on identifiable stage classes, we constructed a five-stage, female-based life-cycle graph to describe transitions between juveniles (J), subadults (A_S), and adult breeding (A_B) or nonbreeding (A_F) Golden Eagles. Transitions between stages are a function of stage-specific survival probabilities (Fig. 1). We assume that adults probabilistically transition into breeding states (γ_{nb}), and remain in nonbreeding states with a complementary probability ($1-\gamma_{nb}$). In addition, we assume a pre-birth pulse "census" of the population in which fecundity (F) is the product of female productivity (P; the product of nest initiation probability, clutch size, and nest survival) and first year juvenile survival (S_j) multiplied by 0.5, assuming equal sex ratios of nestlings at hatch (Rudnick et al. 2005). We equated estimates of nonbreeding adults (or floaters) and subadults survival because these rates (S_{nb}) have been found to be very similar among available estimates in western North America (Hunt and Hunt 2006).

We characterized heterogeneity of Golden Eagle vital rates using probability distributions shaped by their estimated central tendencies and process variation. We assumed a gamma distribution for productivity (P) and estimated the shape of this distribution by fitting a Bayesian gamma regression model to literature-based productivity measures assigning random effects to the study area and year (i.e., Livingston, MT U.S.A., 2010; complete model details in Appendix 1). Accurate stage-specific estimates of survival estimated for multiple years are uncommon for many long-lived raptors (Sergio et al. 2011) including Golden Eagles. Thus, limited time series estimates of eagle survival precluded us from fitting a model with random effects to estimate process variation in survival. Rather, we fit a generalized linear model (GLM) with a normal error distribution to logit-transformed survival estimates using a factor covariate to describe variation among stage classes. We used coefficient estimates to obtain means of survival across stages. We back-transformed randomly sampled values from the multivariate normal distribution to obtain estimates on the scale of survival rates (0–1). Although demographic rates likely covary, available data were insufficient to reliably estimate covariance (J. Tack unpubl. data), and we generated vital rate values in our simulations by independently sampling from vital rate probability distributions.

The probability of transitioning among reproductive states (nonbreeding and breeding) are largely unknown for Golden Eagles (Kochert et al. 2002), so

Downloaded From: https://complete.bioone.org/journals/Journal-of-Raptor-Research on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

we derived a transition probability from nonbreeder to breeding adults (γ_{nb}) so population growth was stable ($\lambda = 1$) when other vital rate estimates were held at their mean value. We reasoned that because Golden Eagle populations in western North America are generally stable (Millsap et al. 2013, Nielson et al. 2014), deriving transition probabilities to reproduce the observed trends was the most defensible approach for estimating an unknown parameter. Furthermore, we assumed that breeding adults would not transition into a nonbreeding state (i.e., $\gamma_{nb} = 0$) as assumed elsewhere (Whitfield et al. 2004). Although antagonistic behavior may drive breeders into the floating population, we suspect that this would be a negligible occurrence in an otherwise stable population.

Life-Stage Simulation Analysis. We conducted a LSA by generating $k = 10{,}000$ population matrices following random draws from the probability distributions characterizing each vital rate. From each population matrix M_k, we calculated population growth rate as the dominant eigenvalue (λ_k) of the matrix and analytical sensitivity ($\left(\frac{\partial \lambda_i}{\partial a_{i,j,k}}\right)$ and elasticity $\left(\frac{\partial \lambda_i}{\partial a_{i,j,k}} * \frac{a_{i,j,k}}{\lambda_i}\right)$ for each vital rate (α). Across all simulations we: (1) calculated the distribution of sensitivities and elasticities across all simulations; (2) for each of the k matrices, ranked each vital rate by the relative magnitude of its sensitivity and elasticity metrics; and (3) regressed estimated λ against each vital rate to calculate a coefficient of determination (r^2), which provides measure for variation explained in population growth by variation within a vital rate.

The expanding wind power energy infrastructure in western North America, which includes transmission lines, roads, and wind turbines, is a source of anthropogenic mortality for Golden Eagles (Pagel et al. 2013), though it remains unclear which sex or age class is most at risk. One goal of our research was to investigate the possible demographic consequences of additive mortality arising from expanding development in the western U.S. We simulated a mean decrease in stage-specific survival rates by proportionally decreasing each survival rate up to 10%, while also including a simulation where survival was reduced equally across all stage classes. For each simulation, we calculated asymptotic population growth rate (λ) and the proportion of simulations for which population growth was <1.0.

Because we wanted to investigate the ability of increased productivity to offset decreases in stage-specific survival rates, we treated reproduction as an unknown parameter across simulations, and derived the productivity value necessary to achieve stable population growth. We compared simulated values of productivity necessary to achieve a stable population to the observed distribution of productivity based on field studies by calculating the proportion of simulations that fell within the 95% credible interval of the distribution of productivity estimates. This proportion provides insights into the eagle's reproductive potential to offset increased mortality. All demographic analyses were conducted using the Popbio package in program R (Stubben and Milligan 2007).

RESULTS

From our literature review, we compiled >500 records on various aspects of eagle demography. Ninety-eight published records of productivity and survival met our criteria for inclusion in estimating the distribution of demographic rates (Appendix 2). The number of productivity estimates was sufficiently large, allowing us to restrict data to those from western North American Golden Eagle populations ($n = 66$). Stage-specific survival estimates were rare, so we also used estimates from congeneric Bonelli's Eagle and Eastern Imperial Eagle (*A. heliaca*) populations. The estimated shape parameters from the gamma distribution describing productivity estimates were $\alpha = 4.80$, $\beta = 6.98$, yielding an expected (mean) productivity of 0.69 young fledged per pair, with 95% of the support falling between 0.21 and 1.41 young per pair. Survival estimates of juvenile, nonbreeding (subadults and adults), and breeding adults were 0.77, 0.80, and 0.92, respectively. A transition probability from nonbreeder to breeding adult of 0.23 produced stable population growth ($\lambda = 1$) when all other parameters were held at their mean values. Visual inspection of empirical data demonstrated that estimated distributions tracked the range of vital rates sampled in stochastic population models (Fig. 2).

Analytical sensitivity and elasticity from life-stage simulation analysis were highest for breeding adult survival, followed by nonbreeding adult and subadult survival rates (Table 1), and across simulations, breeding adult survival always ranked first with the largest values. However, productivity explained the greatest amount of variation in λ ($r^2 = 0.52$), followed by nonbreeding ($r^2 = 0.23$), adult ($r^2 = 0.22$), and juvenile survival ($r^2 = 0.01$; Table 1). Perturbation analyses revealed that reducing survival across stage classes independently from 0 to 10% resulted in disproportionate effects on asymptotic

Downloaded From: https://complete.bioone.org/journals/Journal-of-Raptor-Research on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

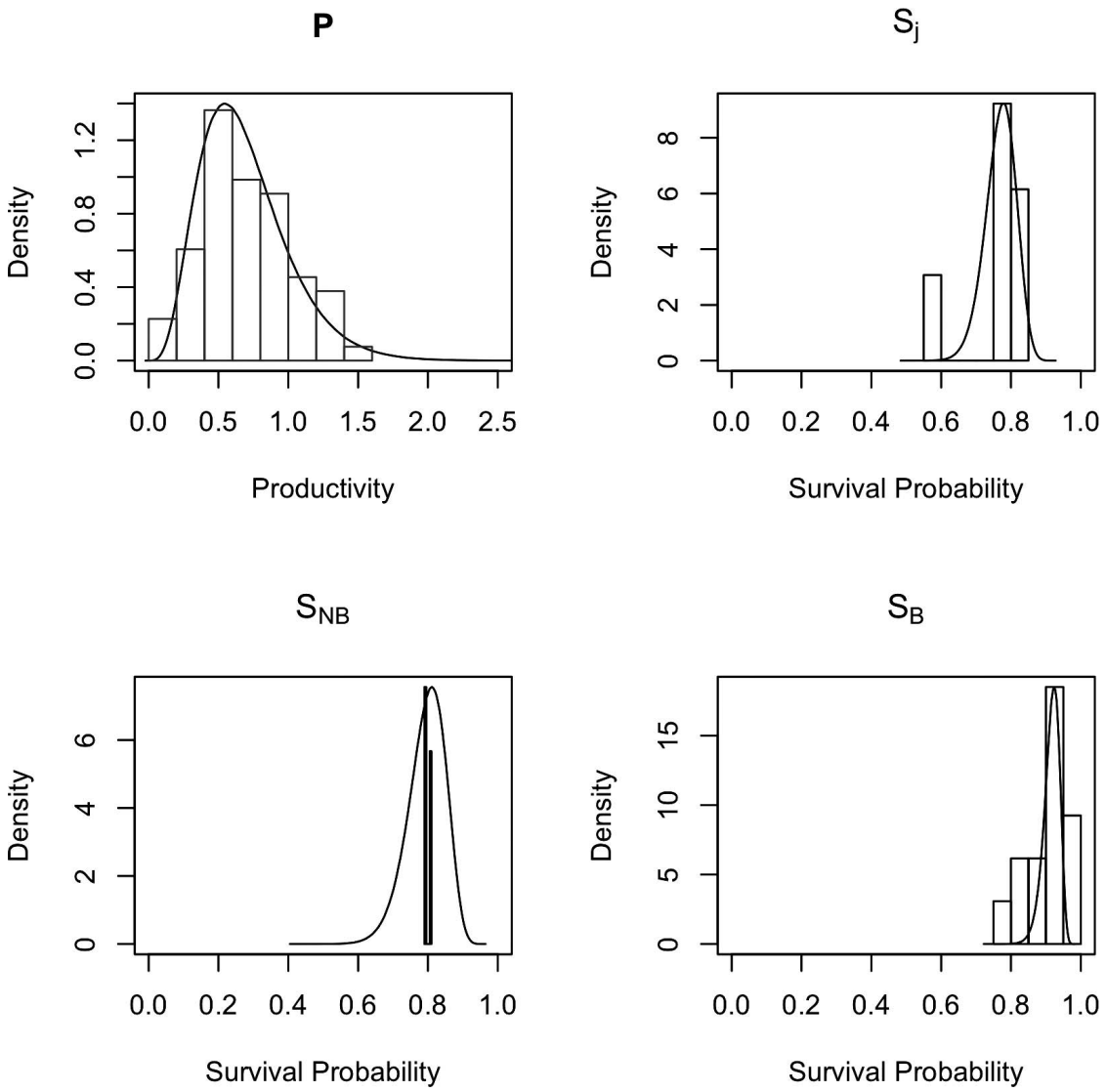


Figure 2. Estimated distributions of Golden Eagle vital rates for (a) productivity (P); (b) juvenile survival (S_j); (c) nonbreeding survival (S_{nb}); and (d) breeding adult survival (S_b), based on published estimates of these parameters. Histograms show data compiled to fit the respective distributions.

population growth. Decreasing juvenile survival up to 10% had only a minor effect on growth rates (Fig. 3). The proportion of simulations with negative population growth rose from 0.58 to 0.63 (Fig. 4). In contrast, decreasing breeding adult survival by 10% reduced mean λ values from 0.99 to 0.93 (Fig. 3). Simultaneously reducing survival rates across all stage classes by 3.8% resulted in >90% of simulations displaying asymptotic growth rates <1, whereas <1% of simulations resulted in positive growth rates following a 7.5% reduction in all survival rates (Fig. 3).

With no simulated reduction in survival, 91.5% of simulations had stable or increasing population growth ($\lambda \geq 1$) with a productivity value included within the 95% credible interval of the estimated distribution from empirical data. When survival rates were reduced by 10% across stage classes, fewer than

Downloaded From: https://complete.bioone.org/journals/Journal-of-Raptor-Research on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Table 1. Vital rate analytical sensitivity and elasticity estimates with 95% quantiles for productivity (P), transition probability from nonbreeders to breeding adults (γ_{nb}), and survival among juveniles (S_j), nonbreeders (S_{nb}), and breeding adults (S_b). Coefficient of determination (r^2) values describe variation explained in λ by vital rates, which was not calculated for γ_{nb} because it was held constant across simulations.

VITAL RATE	SENSITIVITY	ELASTICITY	r^2
P	0.08 (0.05–0.15)	0.05 (0.02–0.09)	0.52
γ_{nb}	0.12 (0.05–0.21)	0.03 (0.01–0.05)	—
S_j	0.07 (0.03–0.12)	0.06 (0.02–0.09)	0.01
S_{nb}	0.33 (0.14–0.50)	0.26 (0.11–0.40)	0.23
S_b	0.73 (0.60–0.89)	0.68 (0.51–0.87)	0.22

0.5% of simulations fell within the 95% credible interval of observed productivity estimates. All simulations with survival decreased by >4.5% yielded an average value of productivity higher than the maximum estimate from empirical data (1.5 fledglings per pair to obtain stable population growth; Appendix 2, Fig. 5).

DISCUSSION

As predicted by demographic theory for vertebrate species with slow life histories (reviewed in Mills 2012), population growth rate (λ) was most sensitive to changes in breeding adult survival rate, which contained the highest elasticity values across all LSA simulations. However, LSA analyses revealed that productivity (defined as the number of fledged young per pair) explained over half of the variation among population growth, whereas nonbreeder survival also eclipsed that of breeding adult survival for explaining variation in λ. The disparity in findings between elasticity and coefficient of determination values is attributed to the disparate variation among vital rates. As the most sensitive vital rate, breeding adult survival is likely canalized against demographic perturbations for Golden Eagle populations, leading to extremely low variation in this typically high demographic rate (Gaillard and Yoccoz 2003). However, productivity, providing limited incremental changes in population growth, is highly variable, offering management the plasticity necessary to target a vital rate with capacity for improvement. Importantly, productivity as represented in our population projection models is the combined product of nest initiation probability, clutch size, and nest survival. Because we did not have data on these estimates independently, it is unclear which components of productivity are most limiting among populations. Thus, when survival is high, efforts to improve Golden Eagle productivity (e.g., via prey management) may provide the best opportunity for attempts to bolster population growth. However, perturbation analyses revealed limits to improving productivity as an effective management tool.

The ability of reproductive output to compensate for reduced survival rates diminished quickly. To achieve population stability ($\lambda = 1$), over half of simulations with a ≥4% decrease in survival across stage classes required productivity to be greater than the maximum observed value from our literature review. Although we did not evaluate the ability of productivity to buffer against stage-specific reductions in loss, we can intuit that loss of breeding adult and nonbreeders are most influential. Furthermore, simulated declines of 4.5% in survival across life-stages reduced the ability of populations to exhibit at least stable population growth by 35%. This finding was similar to that of Whitfield et al. (2004), who reported that even modest (3–5%) increases in adult survival rates were sufficient to achieve stability in a declining, human-persecuted Golden Eagle population in Scotland. Findings from survival perturbation analyses underscore the importance of understanding how emerging development adversely affects adult survival. In particular, it is critical to understand the degree to which Golden Eagle populations demographically compensate for these novel sources of anthropogenic mortality.

Understanding whether cause-specific mortality is compensatory or additive requires information on the covariance among survival and its complementary components of natural and anthropogenic mortality. These parameter estimates will require long-term (or spatially replicated) demographic studies employing mark-recapture or known fate (e.g., radio-tracking) techniques. Although this information is an ongoing pursuit of ecologists, previous research has found that slow life-history species like the Golden Eagle have limited ability to compensate for increased anthropogenic mortality (Péron 2013). In particular, species with long generation times, living at densities near or below carrying capacity, are the most susceptible to cause-specific mortality resulting in additive effects to populations. Thus, emerging sources of anthropogenic mortality, particularly among breeding adults, are important concerns for the conservation of Golden Eagles.

Downloaded From: https://complete.bioone.org/journals/Journal-of-Raptor-Research on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

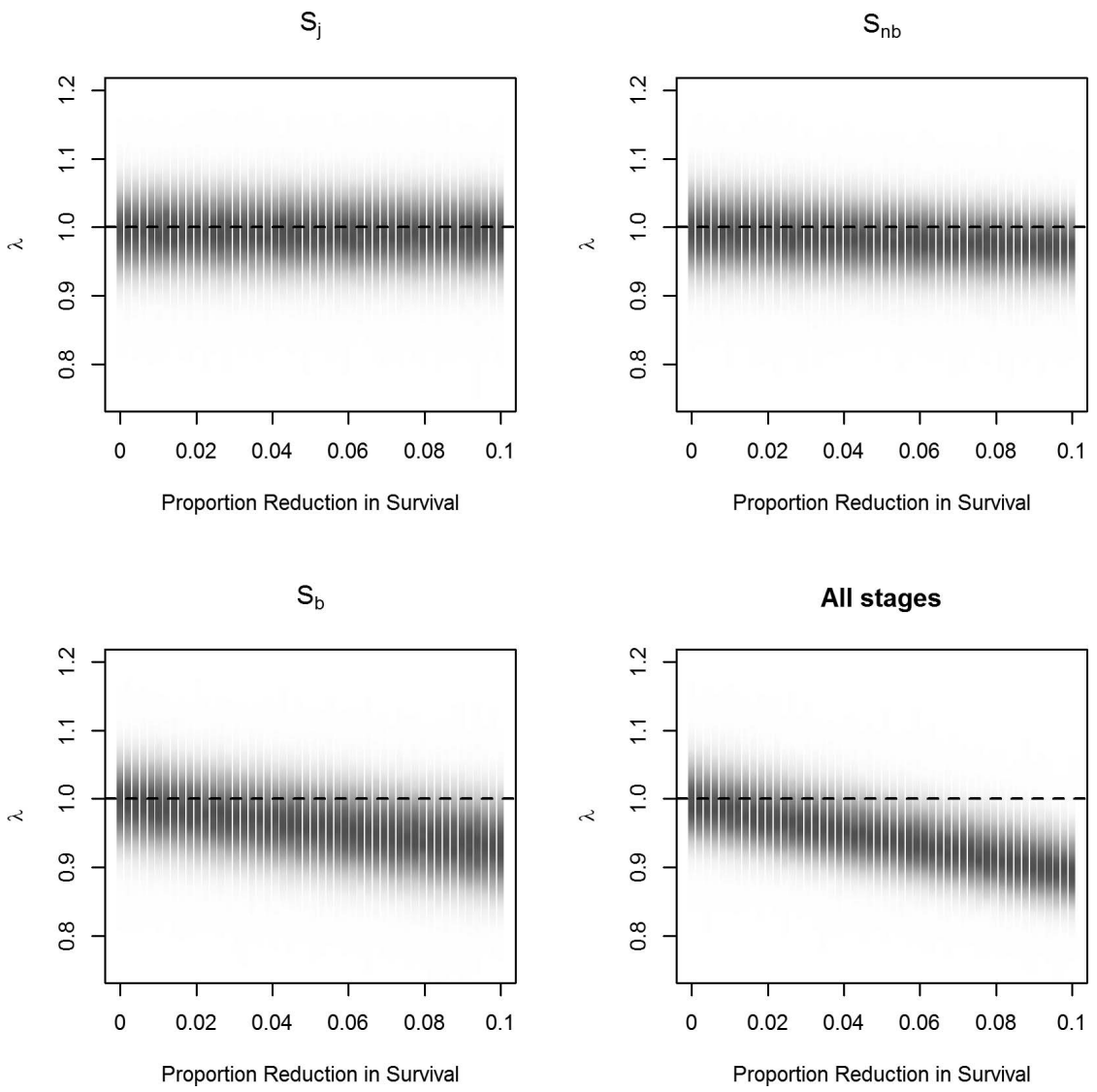


Figure 3. Plots of the dominant eigenvalue of simulated projection matrices (population growth rate, λ) on proportional reductions (0 to 10%) in the values of the vital rates considered individually [(a) juvenile (S_j), (b) nonbreeding (S_{nb}), and (c) breeding adult (S_b) survival], and (d) across all stages of survival.

Younger eagles, naive to threatening infrastructure, may be more at risk from stressors such as development and collisions with wind towers. However, if wind power development takes place in existing breeding territories, adult Golden Eagles may also be at risk because they are highly philopatric to these sites. For example, Chevallier et al. (2015) found that electrocution acted to increase mortality across all life stages of Bonelli's Eagles, although younger birds (juveniles and first-year individuals) experienced greater mortality. For Golden Eagles in the western U.S., subadults and nonbreeding adults made up all the mortalities at the Altamont Pass Wind Resource Area (Hunt and Hunt 2006). In contrast, a recent synthesis of eagle mortalities across wind farms in the U.S. revealed mortality across all stage classes (Pagel et al. 2013).

Downloaded From: https://complete.bioone.org/journals/Journal-of-Raptor-Research on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

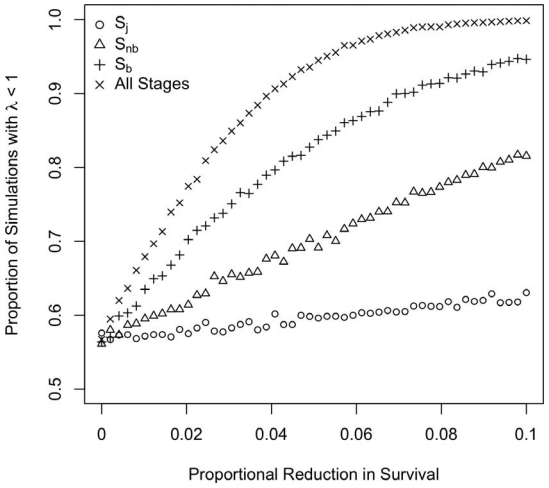


Figure 4. The proportion of simulations that resulted in declining asymptotic population growth rates ($\lambda < 1$) following incremental decreases in survival for each stage class including juvenile (S_j), nonbreeding (S_{nb}), and breeding adult eagles (S_b), and across all stages of survival.

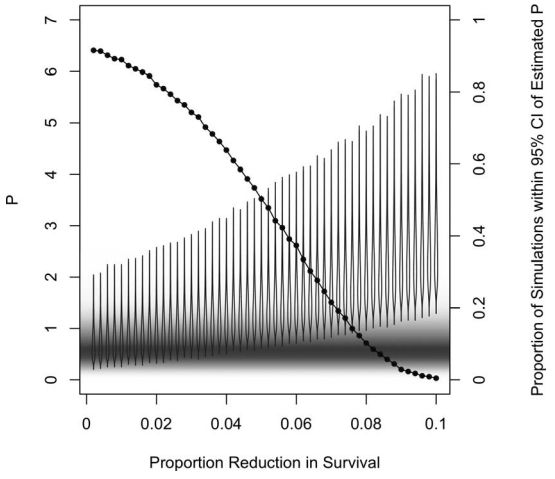


Figure 5. Distribution of simulated values of productivity (P; violin plots, y-axis, left) necessary to achieve stable asymptotic population growth ($\lambda = 1$) while simultaneously decreasing survival across all stage-classes up to 10% (x-axis) are displayed. Shaded density strip represents gamma distribution fit to empirical productivity data. Dotted curve is the proportion of derived values of P that fall within the 95% credible interval of the empirical productivity distribution (y-axis, right).

Our study likely did not identify all demographic data for Golden Eagles and similar species, as many estimates may exist among unpublished sources. Yet we were able to collect many productivity estimates across time and space, as there were several long–term study sites in western North America devoted to monitoring and publishing reproductive success in Golden Eagle territories (Phillips and Beske 1990, Steenhof et al. 1997, Hunt and Hunt 2006, McIntyre and Schmidt 2012). In fact, we omitted data from many demographic studies conducted at nesting sites because productivity estimates were conditional on nest initiation (i.e., egg-laying). However, few stage-specific survival estimates were available. We found only two estimates of breeding adult survival for Golden Eagles in western North America, and six range-wide. Tracking technology (Watson et al. 2014, Braham et al. 2015), genetic analyses (Rudnick et al. 2005, Doyle et al. 2014), and use of camera-traps (Katzner et al. 2012) are all promising technologies that can provide improved estimates of these key vital rates, provided methods do not affect demographic rates (e.g., transmitter-induced reduction in survival; Steenhof et al. 2006).

Perhaps the greatest demographic knowledge gap among Golden Eagle populations is identifying the role nonbreeding adults ("floaters") play in population dynamics. This cryptic component of raptor populations has proved elusive to document, such that the transition among breeding and nonbreeding states has been derived rather than directly estimated (Hunt 1998). We used the best available information on Golden Eagle population growth rates (Millsap et al. 2013) coupled with the assumption that breeding adults remain reproductive to derive a probability for nonbreeders transitioning into breeding adults. Following consultations with experts in Golden Eagle ecology, we reran elasticity analyses allowing for breeding adults to transition into nonbreeding states (up to 2.5%, with resulting decreases in γ_{nb} to achieve stable population growth), and found little effect on the inference from elasticity values (elasticity estimates within 3% of original model; J. Tack unpubl. data). Overall, improved estimates of life-history attributes for survival and transition among breeding states are needed to reduce the uncertainty in population models used for conservation and management.

Furthermore, the lack of long-term studies that simultaneously track survival and productivity precluded us from estimating covariance among vital rates. Among natural populations, life-history covariance is complex. For example, broad-scale weather patterns experienced across raptor (st)age classes

Downloaded From: https://complete.bioone.org/journals/Journal-of-Raptor-Research on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

may result in positively covarying survival rates. Similarly, a "cost" of reproduction can lead to negative covariance between survival and productivity within (Stearns 1989), and across seasons (Stoelting et al. 2015), though a "quality" of individual hypothesis suggests these rates may positively covary, as superior individuals enjoy higher survival and reproductive output (Blums et al. 2005). For slow life-history species, the influence of covariance among life-history traits on population growth has the ability to buffer or amplify negative population effects of persistent threats (e.g., climate change; Herfindal et al. 2015). Incorporating life-history covariance into our models would yield a more faithful representation of a Golden Eagle population, yet given the overwhelming influence of breeding adult survival on simulations throughout our analyses we suspect it would not substantially change our findings. Long-term demographic datasets would eliminate this critical knowledge gap.

Management actions focused on increasing a species' persistence likelihood can target a specific vital rate that significantly affects population growth. Increases in the vital rate's mean, decreases in its variance, or both simultaneously, are ways to achieve this objective. In our simulations, we have explicitly evaluated the ability of increases in Golden Eagle productivity to compensate for declines in survival. As a consequence of demographic constraints, we found that the potential for increases in reproductive output to compensate for declines in survival are very limited. Increases in productivity cannot be ignored as part of the conservation portfolio for Golden Eagles, particularly when breeding adult survival is known to be high. However, management that reduces threats to eagle survival should be a top priority, particularly among populations known to suffer from anthropogenic sources of mortality.

Our results support the U.S. Fish and Wildlife Services (U.S.F.W.S.) mitigation strategy of "no-net loss" before granting programmatic take permits for proposed wind energy facilities (U.S.F.W.S. 2013). As found for other long-lived vertebrates, variation in adult survival rate is the key demographic parameter affecting eagle population dynamics. Coupling this insight with the fact that >70% of eagle mortalities are linked to human development and influences (e.g., vehicle collisions, electrocution along power lines, and poisoning following lead ingestion; Craighead Beringia South unpubl. data), reducing anthropogenic sources of mortality should be a top management objective. For example, electrocution has been a known source of mortality for decades, and exposed lines remain a pervasive source of eagle mortality (Lehman et al. 2007). Insulating conductors or burying distribution lines are mitigation strategies that managers are already implementing to lower overall rates of eagle mortality. Importantly, modifications to existing lines ("retrofitting") in areas with high seasonal eagle density, not just those created for new energy development, are also needed to lower mortality rates (Chevallier et al. 2015). Additionally, ungulate viscera discarded by hunters may expose scavengers such as eagles to toxic lead during hunting seasons across North America. For example, Bedrosian et al. (2012) documented elevated levels of lead in Bald Eagles (*Haliaeetus leucocephalus*) during hunting seasons in Wyoming and the authors found that offering lead-free ammunition to hunters reduced blood lead levels in eagles. Subsidizing the increased cost of lead-free ammunition and removing discarded hunter-harvested viscera, especially in hunting districts with high density of eagles during the hunting season, may be an effective conservation tool to offset additional eagle mortality rates arising from energy development (Cochrane et al. 2015). Ultimately, bolstering survival for wide-ranging species of conservation concern like the Golden Eagle will rely on efforts that prioritize, apply, and test mitigation strategies across large-spatial scales within a conservation-planning framework.

Acknowledgments

We thank Brian Gerber, Dana Winkleman, and Adam Schwindt for help in developing the analyses we used in this research, and Brian Woodbridge, Brian Millsap, and Emily Bjerre for providing invaluable comments on a previous version. Comments from Associate Editor Chris Briggs, and two anonymous reviewers greatly improved this report. This paper is based on a presentation given at the Golden Eagles in a Changing World Symposium held at the 2015 Raptor Research Foundation Annual Meeting in Sacramento, CA. We thank the Academy for the Environment, University of Nevada, Reno, for providing financial support for publication costs. We also want to thank the U.S. Fish and Wildlife Service, especially the Western Golden Eagle Team, for their financial and logistical support of this work. Lastly, we are very appreciative of the work by Michael Collopy in collating and supporting this special issue.

Literature Cited

Bedrosian, B., D. Craighead, and R. Crandall. 2012. Lead exposure in bald eagles from big game hunting, the

Downloaded From: https://complete.bioone.org/journals/Journal-of-Raptor-Research on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

continental implications and successful mitigation efforts. *PLoS One* 7:e51978.

BEECHAM, J.J. AND M.N. KOCHERT. 1975. Breeding biology of the Golden Eagle in southwestern Idaho. *Wilson Bulletin* 87:506–513.

BLOOM, P.H. AND W.S. CLARK. 2001. Molt and sequence of plumages of Golden Eagles and a technique for inhand ageing. *North American Bird Bander* 26:97–116.

BLUMS, P., J.D. NICHOLS, J.E. HINES, M.S. LINDBERG, AND A. MEDNIS. 2005. Individual quality, survival variation and patterns of phenotypic selection on body condition and timing of nesting in birds. *Oecologia* 143:365–376.

BRAHAM, M., T. MILLER, A.E. DUERR, M. LANZONE, A. FESNOCK, L. LAPRE, D. DRISCOLL, AND T. KATZNER. 2015. Home in the heat: dramatic seasonal variation in home range of desert Golden Eagles informs management for renewable energy development. *Biological Conservation* 186:225–232.

CARRETE, M., J.A. SÁNCHEZ-ZAPATA, J.F. CALVO, AND R. LANDE. 2005. Demography and habitat availability in territorial occupancy of two competing species. *Oikos* 108:125–136.

CASWELL, H. 2001. Matrix population models. Second Ed. Sinauer Associates, Sunderland, MA U.S.A.

CHEVALLIER, C., A. HERNÁNDEZ-MATÍAS, J. REAL, N. VINCENT-MARTIN, A. RAVAYROL, AND A. BESNARD. 2015. Retrofitting of power lines effectively reduces mortality by electrocution in large birds: an example with the endangered Bonelli's Eagle. *Journal of Applied Ecology* 52:1465–1473.

COCHRANE, J.F., E. LONSDORF, T.D. ALLISON, AND C.A. SANDERS-REED. 2015. Modeling with uncertain science: estimating mitigation credits from abating lead poisoning in Golden Eagles. *Ecological Applications* 25:1518–1533.

CONGDON, J.D., A.E. DUNHAM, AND R.V.L. SELS. 1994. Demographics of common snapping turtles (*Chelydra serpentina*): implications for conservation and management of long-lived organisms. *American Zoologist* 34:397–408.

CORLETT, R.T. 2015. The Anthropocene concept in ecology and conservation. *Trends in Ecology and Evolution* 30:36–41.

CRAIG, T.H., J.W. CONNELLY, E.H. CRAIG, AND T.L. PARKER. 1990. Lead concentrations in Golden and Bald eagles. *Wilson Bulletin* 102:130–133.

CRAIGHEAD BERINGIA SOUTH. 2014. Golden Eagle breeding ecology in south central Montana, 2014 Summary. Craighead Beringia South, Kelly, WY U.S.A.

DOYLE, J.M., T.E. KATZNER, P.H. BLOOM, Y. JI, B.K. WIJAYAWARDENA, AND J.A. DEWOODY. 2014. The genome sequence of a widespread apex predator, the Golden Eagle (*Aquila chrysaetos*). *PLoS One* 9:e95599.

FERRER, M., V. PENTERIANI, J. BALBONTÍN, AND M. PANDOLFI. 2003. The proportion of immature breeders as a reliable early warning signal of population decline: evidence from the Spanish Imperial Eagle in Doñana. *Biological Conservation* 114:463–466.

GAILLARD, J.M. AND N.G. YOCCOZ. 2003. Temporal variation in survival of mammals: a case of environmental canalization? *Ecology* 84:3294–3306.

GARVIN, J.C., C.S. JENNELLE, D. DRAKE, AND S.M. GRODSKY. 2011. Response of raptors to a windfarm. *Journal of Applied Ecology* 48:199–209.

GUREVITCH, J. AND D.K. PADILLA. 2004. Are invasive species a major cause of extinctions? *Trends in Ecology and Evolution* 19:470–474.

HERFINDAL, I., M.V.D. POL, J.T. NIELSEN, B.E. SÆTHER, AND A.P. MØLLER. 2015. Climatic conditions cause complex patterns of covariation between demographic traits in a long-lived raptor. *Journal of Animal Ecology* 84:702–711.

HUNT, W.G. 1998. Raptor floaters at Moffat's equilibrium. *Oikos* 82:191–197.

———. 2002. Golden Eagles in a perilous landscape: predicting the effects of mitigation for wind turbine bladestrike mortality. California Energy Commission (CEC) Consultant Report P500-02-043F, Sacramento, CA, U.S.A.

——— AND T. HUNT. 2006. The trend of Golden Eagle territory occupancy in the vicinity of the Altamont Pass Wind Resource Area: 2005 survey. Unpubl. rep. of the California Energy Commission, PIER Energy-Related Environmental Research, CeC-500-2006-056, Sacramento, CA U.S.A.

JONES, N.F. AND L. PEJCHAR. 2013. Comparing the ecological impacts of wind and oil and gas development: a landscape scale assessment. *PLoS One* 8:e81391.

KATZNER, T.E., B.W. SMITH, T.A. MILLER, D. BRANDES, J. COOPER, M. LANZONE, D. BRAUNING, C. FARMER, S. HARDING, D.E. KRAMAR, C. KOPPIE, C. MAISONNEUVE, M. MARTELL, E.K. MOJICA, C. TODD, J.A. TREMBLAY, M. WHEELER, D.F. BRINKER, T.E. CHUBBS, R. GUBLER, K. O'MALLEY, S. MEHUS, B. PORTER, R.P. BROOKS, B.D. WATTS, AND K.L. BILDSTEIN. 2012. Status, biology, and conservation priorities for North America's eastern Golden Eagle (*Aquila chrysaetos*) population. *Auk* 129:168–176.

KIESECKER, J.M., J.S. EVANS, J. FARGIONE, K. DOHERTY, K.R. FORESMAN, T.H. KUNZ, D. NAUGLE, N.P. NIBBELINK, AND N.D. NIEMUTH. 2011. Win-win for wind and wildlife: a vision to facilitate sustainable development. *PLoS One* 6:e17566.

KOCHERT, M.N., K. STEENHOF, C.L. MCINTYRE, AND E.H. CRAIG. 2002. Golden Eagle (*Aquila chrysaetos*). *In* P.G. Rodewald [ED.], The birds of North America. Cornell Lab of Ornithology, Ithaca, NY U.S.A. https://birdsna.org/Species-Account/bna/species/goleag (last accessed 13 March 2017).

KUVLESKY, W.P., JR., L.A. BRENNAN, M.L. MORRISON, K.K. BOYDSTON, B.M. BALLARD, AND F.C. BRYANT. 2007. Wind energy development and wildlife conservation: challenges and opportunities. *Journal of Wildlife Management* 71:2487–2498.

LANDE, R., S. ENGEN, AND B.E. SAETHER. 2003. Stochastic population dynamics in ecology and conservation. Oxford University Press, Oxford, U.K.

Downloaded From: https://complete.bioone.org/journals/Journal-of-Raptor-Research on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

LEHMAN, R.N., P.L. KENNEDY, AND J.A. SAVIDGE. 2007. The state of the art in raptor electrocution research: a global review. *Biological Conservation* 136:159–174.

LEU, M., S.E. HANSER, AND S.T. KNICK. 2008. The human footprint in the west: a large-scale analysis of anthropogenic impacts. *Ecological Applications* 18:1119–1139.

LOSS, S.R., T. WILL, AND P.P. MARRA. 2014. Estimation of bird-vehicle collision mortality on US roads. *Journal of Wildlife Management* 78:763–771.

MADDERS, M. AND D.P. WHITFIELD. 2006. Upland raptors and the assessment of wind farm impacts. *Ibis* 148:43–56.

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.

——— AND J.H. SCHMIDT. 2012. Ecological and environmental correlates of territory occupancy and breeding performance of migratory Golden Eagles *Aquila chrysaetos* in interior Alaska. *Ibis* 154:124–135.

MILLS, L.S. 2012. Conservation of wildlife populations: demography, genetics, and management. Second Ed. Blackwell, Malden, MA U.S.A.

MILLSAP, B.A., G.S. ZIMMERMAN, J.R. SAUER, R.M. NIELSON, M. OTTO, E. BJERRE, AND R. MURPHY. 2013. Golden Eagle population trends in the western United States: 1968–2010. *Journal of Wildlife Management* 77:1436–1448.

MORRIS, W.F. AND D.F. DOAK. 2002. Quantitative conservation biology: theory and practice of population viability analysis. Sinauer Associates, Sunderland, MA U.S.A.

NIELSON, R.M., L. MCMANUS, T. RINTZ, L.L. MCDONALD, R.K. MURPHY, W.H. HOWE, AND R.E. GOOD. 2014. Monitoring abundance of Golden Eagles in the western United States. *Journal of Wildlife Management* 78:721–730.

ORTEGA, E., S. MAÑOSA, A. MARGALIDA, R. SÁNCHEZ, J. ORIA, AND L.M. GONZALEZ. 2009. A demographic description of the recovery of the Vulnerable Spanish Imperial Eagle *Aquila adalberti*. *Oryx* 43:113–121.

PAGEL, J.E., K.J. KRITZ, B.A. MILLSAP, R.K. MURPHY, E.L. KERSHNER, AND S. COVINGTON. 2013. Bald Eagle and Golden Eagle mortalities at wind energy facilities in the contiguous United States. *Journal of Raptor Research* 47:311–315.

PÉRON, G. 2013. Compensation and additivity of anthropogenic mortality: life-history effects and review of methods. *Journal of Animal Ecology* 82:408–417.

PHILLIPS, R.L. AND A.E. BESKE. 1990. Nesting ecology of Golden Eagles and other raptors in southeastern Montana and northern Wyoming. U.S.D.I. Fish and Wildlife Service Tech. Rep. 26. Washington, DC U.S.A.

PLUMMER, M. 2012. JAGS: just another Gibbs sampler. Version 3.3.0. http://mcmc-jags.sourceforge.net (last accessed 27 March 2017).

PURVIS, A., J.L. GITTLEMAN, G. COWLISHAW, AND G.M. MACE. 2000. Predicting extinction risk in declining species. *Proceedings of the Royal Society of London B: Biological Sciences* 267:1947–1952.

REAL, J. AND S. MAÑOSA. 1997. Demography and conservation of western European Bonelli's Eagle (*Hieraaetus fasciatus*) populations. *Biological Conservation* 79:59–66.

RIPPLE, W.J., J.A. ESTES, R.L. BESCHTA, C.C. WILMERS, E.G. RITCHIE, M. HEBBLEWHITE, J. BERGER, B. ELMHAGEN, M. LETNIC, M.P. NELSON, O.J. SCHMITZ, D.W. SMITH, A.D. WALLACH, AND A.J. WIRSING. 2014. Status and ecological effects of the world's largest carnivores. *Science* 343:1241484.

RUDNICK, J.A., T.E. KATZNER, E.A. BRAGIN, O.E. RHODES, AND J.A. DEWOODY. 2005. Using naturally shed feathers for individual identification, genetic parentage analyses, and population monitoring in an endangered Eastern Imperial Eagle (*Aquila heliaca*) population from Kazakhstan. *Molecular Ecology* 14:2959–2967.

SERGIO, F., G. TAVECCHIA, J. BLAS, L. LÓPEZ, A. TANFERNA, AND F. HIRALDO. 2011. Variation in age-structured vital rates of a long-lived raptor: implications for population growth. *Basic and Applied Ecology* 12:107–115.

SINCLAIR, K. 1999. Status of the US Department of Energy/National Renewable Energy Laboratory Avian Research Program. National Renewable Energy Laboratory, Golden, CO U.S.A.

SMALLWOOD, K.S. AND C. THELANDER. 2008. Bird mortality in the Altamont Pass wind resource area, California. *Journal of Wildlife Management* 72:215–223.

STEARNS, S.C. 1989. Trade-offs in life-history evolution. *Functional Ecology* 3:259–268.

STEENHOF, K., M.N. KOCHERT, AND T.L. MCDONALD. 1997. Interactive effects of prey and weather on Golden Eagle reproduction. *Journal of Animal Ecology* 66:350–362.

———, K.K. BATES, M.R. FULLER, M.N. KOCHERT, J.O. MCKINLEY, AND P.M LUKACS. 2006. Effects of radiomarking on Prairie Falcons: attachment failures provide insights about survival. *Wildlife Society Bulletin* 34:116–126.

STOELTING, R.E., R.J. GUTIÉRREZ, W.L. KENDALL, AND M.Z. PEERY. 2015. Life-history tradeoffs and reproductive cycles in Spotted Owls. *Auk* 132:46–64.

STUBBEN, C. AND B. MILLIGAN. 2007. Estimating and analyzing demographic models using the popbio package in R. *Journal of Statistical Software* 22:1–23.

THOMAS, C.D., A. CAMERON, R.E. GREEN, M. BAKKENES, L.J. BEAUMONT, Y.C. COLLINGHAM, B.F. ERASMUS, M.F. DE SIQUEIRA, A. GRAINGER, L. HANNAH, L. HUGHES, B. HUNTLEY, A.S. VAN JAARSVELD, G.F. MIDGLEY, L. MILES, M.A. ORTEGA-HERTA, A.T. PETERSON, O.L. PHILLIPS, AND S.E. WILLIAMS. 2004. Extinction risk from climate change. *Nature* 427:145–148.

UNITED STATES FISH AND WILDLIFE SERVICE (U.S.F.W.S). 2013. Eagle conservation plan guidance: Module 1—land-based wind energy. Version 2. U.S.D.I. Fish and Wildlife Service, Division of Migratory Bird Management, Washington DC U.S.A. https://www.fws.gov/migratorybirds/pdf/management/eagleconservationplanguidance.pdf (last accessed 27 March 2017).

Downloaded From: https://complete.bioone.org/journals/Journal-of-Raptor-Research on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

WATSON, J.W. 2010. The Golden Eagle. Second Ed. T. and A.D. Poyser, London, U.K.

———, A.A. DUFF, AND R.W. DAVIES. 2014. Home range and resource selection by GPS-monitored adult Golden Eagles in the Columbia Plateau Ecoregion: implications for wind power development. *Journal of Wildlife Management* 78:1012–1021.

WEBB, J.K., B.W. BROOK, AND R. SHINE. 2002. What makes a species vulnerable to extinction? Comparative life-history traits of two sympatric snakes. *Ecological Research* 17:59–67.

WHITE, G.C. 2000. Population viability analysis: data requirements and essential analyses. Research techniques in animal ecology: controversies and consequences. Columbia University Press, New York, NY U.S.A.

WHITFIELD, D.P., A.H. FIELDING, D.R.A. MCLEOD, AND P.F. HAWORTH. 2004. Modelling the effects of persecution on the population dynamics of Golden Eagles in Scotland. *Biological Conservation* 119:319–333.

WISDOM, M.J., L.S. MILLS, AND D.F. DOAK. 2000. Life stage simulation analysis: estimating vital-rate effects on population growth for conservation. *Ecology* 81:628–641.

Received 22 March 2016; accepted 26 September 2016
Associate Editor: Christopher W. Briggs

APPENDIX 1. Model description of Bayesian gamma regression model with random effects used to estimate distribution for Golden Eagle productivity (average number of young fledged per pair).

Posterior distribution for gamma regression model by fitting random effects for site (β_0) and year (β_1) to estimates of productivity ($\mathbf{y}$) from published literature:

$$[\alpha, \beta_0, \beta_1, \mu_{site}, \tau_{site}, \mu_{year}, \tau_{year}|\mathbf{y}] \propto [\mathbf{y}|\alpha, \beta_0, \beta_1][\beta_0|\mu_{site}, \tau_{site}]$$

$$[\beta_1|year, \tau_{year}][\mu_{site}][\tau_{site}]$$

$$[\mu_{year}][\tau_{year}][\alpha]$$

Full model description with distributions placed on estimated and prior parameters:

$$\begin{aligned}
y_i &\sim Gamma(\alpha, \beta_i) \\
\alpha &\sim Uniform(0, 100) \\
\beta_i &= \frac{\alpha}{\exp(\pi_i)} \\
\pi_i &= \beta_0[site_i] + \beta_1[year_i] \\
\beta_0 &\sim Normal(\mu_{site}, \tau_{site}) \\
\beta_1 &\sim Normal(\mu_{year}, \tau_{year}) \\
\mu_{site} &\sim Normal(0, 1000) \\
\tau_{site} &\sim Gamma(0.001,\ 0.001) \\
\mu_{year} &\sim Normal(0, 1000) \\
\tau_{year} &\sim Gamma(0.001, 0.001)
\end{aligned}$$

We fit this gamma regression model to estimates of productivity using JAGS implemented in program R (Plummer 2012), using three chains each with 10,000 iterations following 2000 samples as burn-in. We visually inspected chains to assess convergence and that an adequate number of samples were run to estimate posterior distributions. We used shape parameters for a gamma distribution describing productivity from the mean of posterior distribution estimates for shape parameters α and β.

APPENDIX 2. Sources of demographic vital rate estimates collated from published accounts for Golden Eagles and related species. Probability distributions fit to these data were subsequently used for the stochastic population models. We reduced components of Golden Eagle life history into productivity (P), 1st year survival juvenile survival (S_j), nonbreeding subadult and adult survival (S_{nb}), and breeding adult survival (S_b). When possible, we exclusively used estimates from western North American Golden Eagle (*Aquila chrysaetos*; GOEA) populations; however, when data were sparse, we supplemented these estimates using data from Bonelli's Eagles (*Aquila fasciata*; BOEA) and Eastern Imperial Eagles (*Aquila heliaca*; IMEA). Sample size (*n*) is reported if available in reports and publications.

VITAL RATE	SPECIES	ESTIMATE	*n*	YEAR(S)	REGION	CITATION
P	GOEA	0.400	NA	1973	SRBPNCA[a]	Steenhof et al. 1997
P	GOEA	0.530	NA	1974	SRBPNCA	Steenhof et al. 1997
P	GOEA	0.610	NA	1975	SRBPNCA	Steenhof et al. 1997
P	GOEA	0.540	NA	1976	SRBPNCA	Steenhof et al. 1997
P	GOEA	0.730	NA	1977	SRBPNCA	Steenhof et al. 1997
P	GOEA	0.980	NA	1978	SRBPNCA	Steenhof et al. 1997
P	GOEA	0.860	NA	1979	SRBPNCA	Steenhof et al. 1997
P	GOEA	1.180	NA	1980	SRBPNCA	Steenhof et al. 1997
P	GOEA	1.270	NA	1981	SRBPNCA	Steenhof et al. 1997

Downloaded From: https://complete.bioone.org/journals/Journal-of-Raptor-Research on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Appendix 2. Continued.

Vital Rate	Species	Estimate	*n*	Year(s)	Region	Citation
P	GOEA	1.380	NA	1982	SRBPNCA	Steenhof et al. 1997
P	GOEA	1.010	NA	1983	SRBPNCA	Steenhof et al. 1997
P	GOEA	0.640	NA	1984	SRBPNCA	Steenhof et al. 1997
P	GOEA	0.160	NA	1985	SRBPNCA	Steenhof et al. 1997
P	GOEA	0.260	NA	1986	SRBPNCA	Steenhof et al. 1997
P	GOEA	0.340	NA	1987	SRBPNCA	Steenhof et al. 1997
P	GOEA	0.590	NA	1988	SRBPNCA	Steenhof et al. 1997
P	GOEA	0.690	NA	1989	SRBPNCA	Steenhof et al. 1997
P	GOEA	1.150	NA	1990	SRBPNCA	Steenhof et al. 1997
P	GOEA	1.060	NA	1991	SRBPNCA	Steenhof et al. 1997
P	GOEA	0.830	NA	1992	SRBPNCA	Steenhof et al. 1997
P	GOEA	1.230	NA	1993	SRBPNCA	Steenhof et al. 1997
P	GOEA	0.540	NA	1994	SRBPNCA	Steenhof et al. 1997
P	GOEA	0.680	30	2010	Livingston, Montana	Craighead Beringia South, 2014
P	GOEA	0.550	29	2011	Livingston, Montana	Craighead Beringia South, 2014
P	GOEA	0.510	27	2012	Livingston, Montana	Craighead Beringia South, 2014
P	GOEA	0.630	29	2013	Livingston, Montana	Craighead Beringia South, 2014
P	GOEA	0.630	29	2014	Livingston, Montana	Craighead Beringia South, 2014
P	GOEA	0.820	60	1988	Denali National Park	McIntyre and Schmidt 2012
P	GOEA	1.210	58	1989	Denali National Park	McIntyre and Schmidt 2012
P	GOEA	0.910	58	1990	Denali National Park	McIntyre and Schmidt 2012
P	GOEA	0.890	62	1991	Denali National Park	McIntyre and Schmidt 2012
P	GOEA	0.360	69	1992	Denali National Park	McIntyre and Schmidt 2012
P	GOEA	0.390	72	1993	Denali National Park	McIntyre and Schmidt 2012
P	GOEA	0.200	56	1994	Denali National Park	McIntyre and Schmidt 2012
P	GOEA	0.430	56	1995	Denali National Park	McIntyre and Schmidt 2012
P	GOEA	0.460	61	1996	Denali National Park	McIntyre and Schmidt 2012
P	GOEA	0.840	69	1997	Denali National Park	McIntyre and Schmidt 2012
P	GOEA	0.500	66	1998	Denali National Park	McIntyre and Schmidt 2012
P	GOEA	0.960	72	1999	Denali National Park	McIntyre and Schmidt 2012
P	GOEA	0.730	70	2000	Denali National Park	McIntyre and Schmidt 2012
P	GOEA	0.460	68	2001	Denali National Park	McIntyre and Schmidt 2012
P	GOEA	0.050	73	2002	Denali National Park	McIntyre and Schmidt 2012
P	GOEA	0.270	71	2003	Denali National Park	McIntyre and Schmidt 2012
P	GOEA	0.270	73	2004	Denali National Park	McIntyre and Schmidt 2012
P	GOEA	0.500	76	2005	Denali National Park	McIntyre and Schmidt 2012
P	GOEA	0.950	80	2006	Denali National Park	McIntyre and Schmidt 2012
P	GOEA	0.900	81	2007	Denali National Park	McIntyre and Schmidt 2012
P	GOEA	0.690	75	2008	Denali National Park	McIntyre and Schmidt 2012
P	GOEA	0.910	74	2009	Denali National Park	McIntyre and Schmidt 2012
P	GOEA	0.650	75	2010	Denali National Park	McIntyre and Schmidt 2012
P	GOEA	1.500	NA	1975	Wyoming	Phillips and Beske 1990
P	GOEA	0.571	NA	1976	Wyoming	Phillips and Beske 1990
P	GOEA	0.700	NA	1977	Wyoming	Phillips and Beske 1990
P	GOEA	0.550	NA	1978	Wyoming	Phillips and Beske 1990
P	GOEA	0.750	NA	1979	Wyoming	Phillips and Beske 1990
P	GOEA	0.476	NA	1980	Wyoming	Phillips and Beske 1990
P	GOEA	1.083	NA	1981	Wyoming	Phillips and Beske 1990
P	GOEA	1.038	NA	1982	Wyoming	Phillips and Beske 1990
P	GOEA	1.250	NA	1983	Wyoming	Phillips and Beske 1990
P	GOEA	0.552	NA	1984	Wyoming	Phillips and Beske 1990
P	GOEA	0.367	NA	1985	Wyoming	Phillips and Beske 1990
P	GOEA	0.680	57	1996	Altamont Pass	Sinclair 1999

Downloaded From: https://complete.bioone.org/journals/Journal-of-Raptor-Research on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

APPENDIX 2. Continued.

VITAL RATE	SPECIES	ESTIMATE	*n*	YEAR(S)	REGION	CITATION
P	GOEA	0.590	59	1997	Altamont Pass	Sinclair 1999
P	GOEA	0.580	64	1998	Altamont Pass	Hunt 2002
P	GOEA	0.900	69	1999	Altamont Pass	Hunt 2002
P	GOEA	0.460	67	2000	Altamont Pass	Hunt 2002
S_0	GOEA	0.340[b]	22	1997–1997	Denali National Park	McIntyre et al. 2006
S_j	GOEA	0.190[b]	21	1999–1999	Denali National Park	McIntyre et al. 2006
S_j	GOEA	0.787	NA	1997–1997	Altamont Pass	Hunt and Hunt 2006
S_j	GOEA	0.840	NA	1997–2000	Altamont Pass	Hunt and Hunt 2006
S_j	GOEA	0.791	NA	1992–1992	Scotland	Whitfield et al. 2004
S_j	BOEA	0.780	NA	1990–1998	Spain	Carrete et al. 2005
S_j	IMEA	0.579	NA	1990–2001	Spain	Ortega et al. 2009
S_b	GOEA	0.909	NA	1997–2000	Altamont Pass	Hunt and Hunt 2006
S_b	BOEA	0.933	21	1980–1994	Burgos, Spain	Real and Mañosa 1997
S_b	BOEA	0.924	5	1984–1994	Navarra, Spain	Real and Mañosa 1997
S_b	BOEA	0.912	14	1980–1994	Valles, Spain	Real and Mañosa 1997
S_b	BOEA	0.871	46	1982–1994	Castello, Spain	Real and Mañosa 1997
S_b	BOEA	0.839	37	1983–1994	Murcia, Spain	Real and Mañosa 1997
S_b	BOEA	0.961	16	1982–1994	Provence, Spain	Real and Mañosa 1997
S_b	GOEA	0.959	NA	1992–1992	Scotland	Whitfield et al. 2004
S_b	GOEA	0.760	NA	1997–2001	Spain	Carrete et al. 2005
S_b	BOEA	0.890	NA	1990–1998	Spain	Carrete et al. 2005
S_b	IMEA	0.986	NA	1989–1993	Spain	Ortega et al. 2009
S_b	IMEA	0.918	NA	1994–1999	Spain	Ortega et al. 2009
S_b	IMEA	0.933	NA	2000–2004	Spain	Ortega et al. 2009
S_b	IMEA	0.840	NA	1998–2003	Kazakhstan	Rudnick et al. 2005
S_j	GOEA	0.787	NA	1997–1997	Altamont Pass	Hunt and Hunt 2006
S_j	GOEA	0.840	NA	1997–2000	Altamont Pass	Hunt and Hunt 2006
S_j	GOEA	0.791	NA	1992–1992	Scotland	Whitfield et al. 2004
S_j	GOEA	0.810	NA	1997–2001	Spain	Carrete et al. 2005
S_{nb}	GOEA	0.794	NA	1997–2000	Altamont Pass	Hunt and Hunt 2006
S_{nb}	GOEA	0.810	NA	1997–2001	Spain	Carrete et al. 2005
S_{nb}	GOEA	0.794	NA	1997–2000	Altamont Pass	Hunt and Hunt 2006
S_{nb}	GOEA	0.791	NA	1992–1992	Scotland	Whitfield et al. 2004
S_{nb}	GOEA	0.810	NA	1997–2001	Spain	Carrete et al. 2005
S_{nb}	GOEA	0.791	NA	1982–1982	Scotland	Whitfield et al. 2004
S_{nb}	GOEA	0.810	NA	1997–2001	Spain	Carrete et al. 2005

[a] Snake River Birds of Prey National Conservation Area (SRBPNCA).

[b] Survival estimates from migratory populations were omitted in our efforts to recreate a nonmigratory female-based population model. We assume that reproduction is similar between nonmigratory and migratory individuals.

Downloaded From: https://complete.bioone.org/journals/Journal-of-Raptor-Research on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use