Spatial Demographic Models to Inform Conservation Planning of Golden Eagles in Renewable Energy Landscapes

Author(s): J. David Wiens, Nathan H. Schumaker, Rich D. Inman, Todd C. Esque, Kathleen M. Longshore and Kenneth E. Nussear

SPATIAL DEMOGRAPHIC MODELS TO INFORM CONSERVATION PLANNING OF GOLDEN EAGLES IN RENEWABLE ENERGY LANDSCAPES

J. David Wiens[1]

U.S. Geological Survey Forest and Rangeland Ecosystem Science Center, Corvallis, OR 97330 U.S.A.

Nathan H. Schumaker

U.S. Environmental Protection Agency, Corvallis, OR 97333 U.S.A.

Rich D. Inman, Todd C. Esque, and Kathleen M. Longshore

U.S. Geological Survey Western Ecological Research Center, Henderson, NV 89074 U.S.A.

Kenneth E. Nussear

Department of Geography, University of Nevada, Reno, NV 89557 U.S.A.

Abstract.—Spatial demographic models can help guide monitoring and management activities targeting at-risk species, even in cases where baseline data are lacking. Here, we provide an example of how site-specific changes in land use and anthropogenic stressors can be incorporated into a spatial demographic model to investigate effects on population dynamics of Golden Eagles (*Aquila chrysaetos*). Our study focused on a population of Golden Eagles exposed to risks associated with rapid increases in renewable energy development in southern California, U.S.A. We developed a spatially explicit, individual-based simulation model that integrated empirical data on demography of Golden Eagles with spatial data on the arrangement of nesting habitats, prey resources, and planned renewable energy development sites. Our model permitted simulated eagles of different stage-classes to disperse, establish home ranges, acquire prey resources, prospect for breeding sites, and reproduce. The distribution of nesting habitats, prey resources, and threats within each individual's home range influenced movement, reproduction, and survival. We used our model to explore potential effects of alternative disturbance scenarios, and proposed conservation strategies, on the future distribution and abundance of Golden Eagles in the study region. Results from our simulations suggest that probable increases in mortality associated with renewable energy infrastructure (e.g., collisions with wind turbines and vehicles, electrocution on power poles) could have negative consequences for population trajectories, but that site-specific conservation actions could reduce the magnitude of negative effects. Our study demonstrates the use of a flexible and expandable modeling framework to incorporate spatially dependent processes when determining relative effects of proposed management options to Golden Eagles and their habitats.

Key Words: *Golden Eagle*; Aquila chrysaetos; *HexSim*; *population model*; *renewable energy*; *source-sink dynamics*.

Resumen.—Los modelos de demografía espacial pueden ser útiles para las actividades de seguimiento y gestión de especies en riesgo, incluso en casos donde faltan los datos de base. Proporcionamos un ejemplo de cómo los cambios específicos en el uso del suelo y las molestias de origen antrópico pueden ser incorporados en un modelo de demografía espacial para investigar los efectos en la dinámica poblacional de *Aquila chrysaetos*. Nuestro estudio se centró en una población de esta especie expuesta a riesgos asociados con los cambios rápidos ocasionados por el desarrollo de energías renovables en el sur de California, EE.UU. Desarrollamos un modelo de simulación espacial basado en individuos que integró datos demográficos de *A. chrysaetos* con datos espaciales sobre la distribución de hábitats de nidificación, recursos tróficos y lugares donde se planifica el desarrollo de energías renovables. Nuestro modelo permitió que águilas simuladas de

[1] Email address: jwiens@usgs.gov

diferentes clases pudieran dispersarse, establecer áreas de campeo, adquirir recursos tróficos, explorar posibles sitios de nidificación y reproducirse. La distribución de los hábitats de nidificación, de los recursos tróficos y de las amenazas dentro del área de campeo individual influyó en el movimiento, la reproducción y la supervivencia. Utilizamos nuestro modelo para explorar los efectos potenciales de escenarios alternativos con presencia de molestias así como para proponer estrategias de conservación sobre la distribución futura y la abundancia de *A. chrysaetos* en la región de estudio. Los resultados de nuestras simulaciones sugieren que los incrementos probables en la mortalidad asociados con infraestructuras de energías renovables (e.g., colisiones con aerogeneradores y vehículos, electrocución en postes eléctricos) pueden tener consecuencias negativas para las trayectorias de las poblaciones, pero que acciones específicas en cada lugar pueden reducir la magnitud de los efectos negativos. Nuestro estudio demuestra el uso de un marco de trabajo flexible y extensible que integra procesos espacialmente dependientes a la hora de determinar los efectos relativos de las estrategias de gestión propuestas para *A. chrysaetos* y sus hábitats.

[Traducción del equipo editorial]

Development of renewable energy in the western United States has increased dramatically to meet legislative goals of providing greater retail electricity sales through renewable energy resources. In California, U.S.A., the Mojave and Sonoran deserts have been targeted for rapid development of renewable energy, in part because of the region's abundant wind and solar irradiation. To monitor and minimize potential effects of future renewable energy installations, state and federal government agencies initiated the Desert Renewable Energy Conservation Plan (DRECP; California Energy Commission [CEC] 2011, 2014). This conservation plan is intended to identify areas well suited for energy development relative to areas of high biodiversity that are better suited for conservation. The Golden Eagle (*Aquila chrysaetos*) is a species specifically targeted for conservation under the DRECP that may be especially sensitive to anticipated changes in land use associated with both wind and solar energy development. Development of wind-energy facilities in areas occupied by Golden Eagles poses a unique challenge to land managers because of this species' vulnerability to collisions with wind turbines, and sensitivity to changes in land use (Hunt 2002, Kochert and Steenhof 2002, Steenhof et al. 2014). The risk to Golden Eagles posed by solar developments may be primarily from indirect disturbance, occurring through loss of foraging habitat and changes to prey availability (Whitfield et al. 2007), although solar concentrating facilities do present a risk of direct mortality (Hernandez et al. 2014, Diehl et al. 2016, Walston et al. 2016). The infrastructure associated with both wind and solar energy projects, especially roads and power lines, can cause significant mortality in Golden Eagles through collisions with vehicles or energy-related infrastructure (Hunt 2002,

U.S.F.W.S. 2016), and because of electrocution risk from power poles (Lehman et al. 2007, Dwyer et al. 2014).

The life history of Golden Eagles is characterized by high survival of long-lived territorial adults (Kochert et al. 2002), but relatively low annual reproduction (Watson 2010), and a delayed age at first breeding (4–7 yr old; Steenhof et al. 1997, 2014). These life-history traits make it difficult for short-term field studies to quantify effects of threats associated with renewable energy development, because long time lags may separate disturbance events from their population-level consequences (Krauss et al. 2010, Hylander and Ehrlén 2013). In addition, emergent risks from wind energy development may interact with existing, more pervasive threats (e.g., lead or rodenticide contamination; Herring et al. 2017), making it especially difficult for traditional field studies to identify the relative importance of different anthropogenic threats. This problem of assessing effects of multiple interacting stressors is particularly challenging with long-lived, wide-ranging apex predators like the Golden Eagle.

For science to effectively inform conservation policy, it is necessary to understand a population's responses to a range of management actions across multiple spatial scales (Turner et al. 1995). Obtaining such insights, even from rigorous field experiments, is expensive and can be logistically prohibitive. With Golden Eagles, for example, forecasting population responses to an increasing array (or intensity) of anthropogenic stressors is complicated because individual contributions to population dynamics vary depending on age, social status, and the ability to acquire resources in spatially variable environments. Mechanistic population models provide a means to address this conundrum

because: (1) they provide a standardized framework for integrating empirical data with expert knowledge and biological intuition, and (2) they are well suited for developing, testing, and communicating hypotheses and predictions about the relative influence of multiple interacting stressors (Schumaker et al. 2014, Stenglein et al. 2015, Tuma et al. 2016). Additionally, the process of developing a mechanistic population model demands that authors make explicit assumptions about system dynamics, which ultimately enhances transparency within a management context (Grimm 1999, Munns 2006). This process allows researchers to synthesize and extend knowledge gained from empirical field studies while allowing managers to understand and utilize scientific information in the pursuit of effective conservation policy (Katzner et al. 2007, Schmolke et al. 2010, Albeke et al. 2015).

We developed a spatially explicit, individual-based model to explore interactions between existing threats, planned increases in renewable energy development, and population dynamics of Golden Eagles in the DRECP area of southern California, U.S.A. Our goal was to develop a flexible modeling tool that can aid in the spatial conservation prioritization of Golden Eagles exposed to increases in renewable energy development or other threats. Our baseline population model included stage-specific survival, reproduction, movement, and resource use of Golden Eagles that was informed by spatial data on nesting habitats and prey availability derived from local field studies. We evaluated model assumptions with empirical data, and assessed how uncertainty affected the model's predictions. We then used the model to explore potential effects of future renewable energy development on population dynamics of Golden Eagles. We emphasize that the purpose of our population model was not to predict actual changes in the size of the target population, but rather to identify possible population responses to anticipated changes in land use, and to assess possible conservation strategies by their relative effects on Golden Eagles. Our specific objectives were to: (1) develop and document a spatially explicit, individual-based simulation model for the local population of Golden Eagles in the DRECP area, (2) assess the performance of the model in capturing expected conditions of the population, (3) determine sensitivity of results to uncertain demographic parameters, and (4) use the model to explore possible demographic consequences of renewable energy development.

STUDY AREA

We modeled the local population of Golden Eagles within the DRECP (91,400 km^2) and surrounding areas within a 50-km radius of the planning area boundary (total area = 192,444 km^2; Fig 1). We established a 50-km radius around the plan area boundary to account for areas where resident eagles may encounter both risks and resources beyond those typically encountered within the DRECP area (Braham et al. 2015). This radius also approximated median natal dispersal distance of Golden Eagles (46.5 km; Millsap et al. 2014). Areas covered under the DRECP included a mixture of federal (75%), state (3%), tribal (0.6%), and county- or private-administrated lands (CEC 2014). The study area included the Mojave and Colorado Deserts (Schoenherr and Burk 2007), or the Lower Colorado subdivision of the Sonoran Desert (Turner and Brown 1994). Elevations ranged from 86 m below sea level (Death Valley National Park) to 4420 masl, and the landscape was characterized by broad valleys separated by rugged mountain ranges and plateaus. Minimum temperatures ranged from −11.3 to 4.8°C, and maximum temperatures ranged from 16.6 to 44.4°C. Regional precipitation ranged from 100 to 350 mm per year, with more rainfall occurring in the winter than in the summer and at higher elevations (Hereford et al. 2004). Vegetation communities vary widely from barren salt flats and playas at the lowest elevations, to bajadas (slopes with large boulders), shrublands, chaparral, woodlands, and coniferous forests on the highest mountain peaks (Sawyer et al. 2009). Woodlands were interspersed by large areas with sparse vegetation. Small, isolated patches of mixed conifer forests occupied north-facing slopes at higher elevations.

METHODS

Availability of food and nesting sites are strong determinants of distribution, nesting density, and other life-history traits of Golden Eagles (Kochert et al. 2002, Watson 2010). Accordingly, our assessment included three interacting models we developed for the study area: a nest habitat suitability model, a prey availability model, and a Golden Eagle population model. The nest habitat model estimated areas with suitable nesting conditions for Golden Eagles in the study area, and was developed from a species distribution model (SDM; Franklin 2010) that related known nesting locations with physiographic conditions associated with those sites. The prey availability model estimated the distribution of
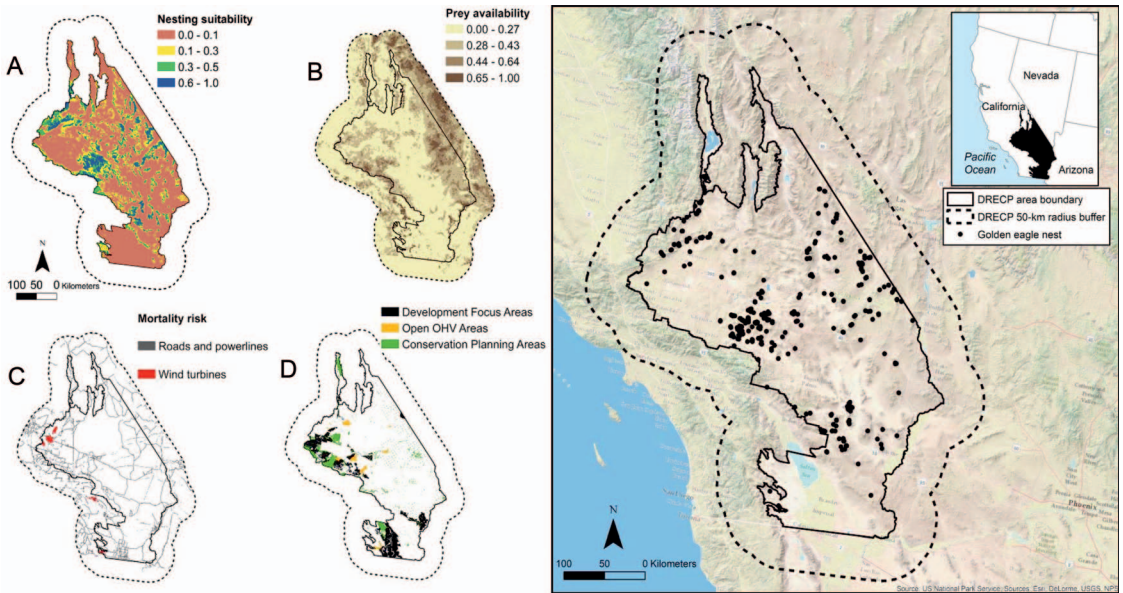
Figure 1. The Desert Renewable Energy Conservation Plan area of southern California, U.S.A., and encompassing 50-km radius buffer, where we modeled population response of Golden Eagles to renewable energy development and other anthropogenic stressors. We also show spatial data used to inform an individual-based, spatially explicit simulation model for Golden Eagles, including: (A) relative nesting habitat suitability, (B) estimated prey availability, (C) spatial mortality risk from wind turbines, high-risk roads, and powerlines, and (D) locations of planned renewable energy development (Development Focal Areas), off-highway vehicle (OHV) use areas, and sites identified for conservation actions (Conservation Planning Areas; CBI 2014).

primary prey species that occur in diets of Golden Eagles in the study area (Longshore et al. 2017), and was developed from line-transect density surveys of prey species conducted in 2014 and 2015. Spatial information from the nest habitat suitability and prey distribution models served as the landscapes for a spatially explicit, individual-based model of Golden Eagle population dynamics. The spatial distribution of nesting and food resources thus provided an environment within which movement, resource acquisition, reproduction, and survival could be simulated. We initially developed a baseline population model reflecting current conditions, and then used this model to evaluate potential consequences of future renewable energy development to the local population. Our model was also well suited to assess conservation actions proposed to offset probable effects of future renewable energy projects (CEC 2014).

Nesting Habitat Model. We created a map of the spatial distribution of nesting areas for Golden Eagles using a SDM approach informed by 644 known nest locations identified from 1972 to 2012

(Fig. 1). We compiled the sample of nest locations from multiple data sources, including the California Department of Fish and Wildlife Natural Diversity Database (CNDDB version; accessed July 2013), records provided by Southern California Edison (SCE Golden Eagle Surveys, 2015, unpubl. data), and nesting locations identified during helicopter surveys (Latta and Thelander 2013). All records of nest locations were checked for quality and accuracy, and duplications were removed. We included nest sites with observations of use by Golden Eagles in 1 or more years.

Historical nesting sites of Golden Eagles in the study area tended to occur primarily along rocky cliffs, and to a lesser extent in large trees or other vertical structures (e.g., power poles) capable of supporting the weight of the bird's large stick nests (Brown 2014). We calculated a set of environmental covariates to capture environmental conditions we hypothesized to be associated with the presence of nest locations using remote-sensing data and a digital elevation model (DEM). Terrain features derived from the 30-m resolution DEM included

slope, surface roughness, elevation drop range, topographic position index, and solar insolation, and variables derived from remote-sensing data included a quartz index, and albedo (see Inman et al. 2014 for details). We initially considered vegetation characteristics throughout the modeling region, but subsequently removed these variables to ensure that nesting-site potential was based predominantly on desert landscapes of the DRECP area. Rather, we included vegetation conditions in the development of the prey availability model (see below). All spatial layers were aggregated to a 150-m resolution for computation of model covariates.

Nesting suitability of Golden Eagles was estimated using a hierarchical Bayesian model conditional on latent processes of clustered sampling bias and spatial autocorrelation (Wikle 2003, Cressie et al. 2009). We modeled the observation process at a 1-km spatial resolution to capture nesting suitability following a binomial distribution, and included process models for survey bias and spatial autocorrelation (Besag et al. 1991). A benefit of this approach was its ability to directly quantify uncertainty in the modeling process due to spatially correlated, or clumped, point data (Cressie et al. 2009), which were common in our dataset because many of the nest locations were alternate nests grouped within a smaller number of more widely dispersed breeding territories.

To evaluate the predictive capability of the nest habitat model, we randomly withheld 30% of the nest observations using a geographically weighted sampling approach that approximated a uniform spatial distribution. We then used the randomly withheld subset of nests to evaluate the nest model using three complimentary measures: Area Under the receiver-operating Curve (AUC; Fielding and Bell 1997), Root Mean Square Error (RMSE), and Mean Cross Entropy (MXE). Despite the extensive use of AUC for evaluating SDMs (Franklin 2010), it may represent artifacts of species prevalence ratios, thereby providing an incomplete picture of model performance (Lobo et al. 2008). As a consequence, we also used MXE, a metric that has gained recognition in evaluating the performance of machine learning classification models and has shown good potential for use with SDM-type approaches (Georgiou and Lindquist 2003).

Prey Availability Model. The two most common prey items documented at Golden Eagle nests in the study area were black-tailed jackrabbits (*Lepus californicus*) and cottontail rabbits (*Sylvilagus* spp.;

Longshore et al. 2017). In a concurrent study, abundance data were collected for these two prey species and others during the breeding season (Jan–Jul) using nocturnal spotlight line-transect distance surveys conducted in 2014 and 2015 (Longshore et al. 2017). These survey data were used to estimate landscape density of rabbits in the study area. We analyzed detections of jackrabbits ($n = 622$) and cottontail rabbits ($n = 41$) from 182 survey occasions and evaluated the potential effects of environmental covariates on prey density using the Distance package in R (v 3.2.3, R Core Team 2015). Specifically, we calculated covariates for terrain aspect, elevation, slope, and topographic position using a 30-m DEM (Inman et al. 2014). We developed distance detection functions to compare null models with no covariates to models including different combinations of topographic and vegetation covariates (normalized difference vegetation index) hypothesized to influence detection of prey species (Longshore et al. 2017). We binned distance data at 25-m intervals (Buckland et al. 2005), and ranked distance models using an information-theoretic method (AIC; Burnham and Anderson 2002, Buckland et al. 2005), where the model with the best support from the data was used to create a predictive density surface at a 1-km^2 scale.

Population Simulation Model. We used HexSim (Heinrichs et al. 2010, Schumaker et al. 2014) to construct a population simulation model for Golden Eagles. HexSim is a spatially explicit, individual-based population modelling platform designed for simulating dynamic interactions between terrestrial wildlife and associated landscapes. The spatial grain and extent of the models can be set by users to any values appropriate for the study system, from local population level to a species' entire geographic range (Schumaker et al. 2014, Tuma et al. 2016). Our baseline HexSim model integrated life-history and demographic traits of Golden Eagles with spatial data layers characterizing the distribution of nesting habitats, prey resources, and potential threats. The region available to individual eagles simulated in HexSim (Fig. 1) consisted of 185,499 hexagonal cells, with each hexagon 1 km^2 in area and 1074 m in diameter. We selected this resolution to capture relevant details of landscape conditions at broad spatial scales while minimizing model run time. We used the nesting suitability and prey base maps, along with spatial data of mortality risks (see below), to determine movements, resource acquisition, and exposure to threats. This framework enabled us to
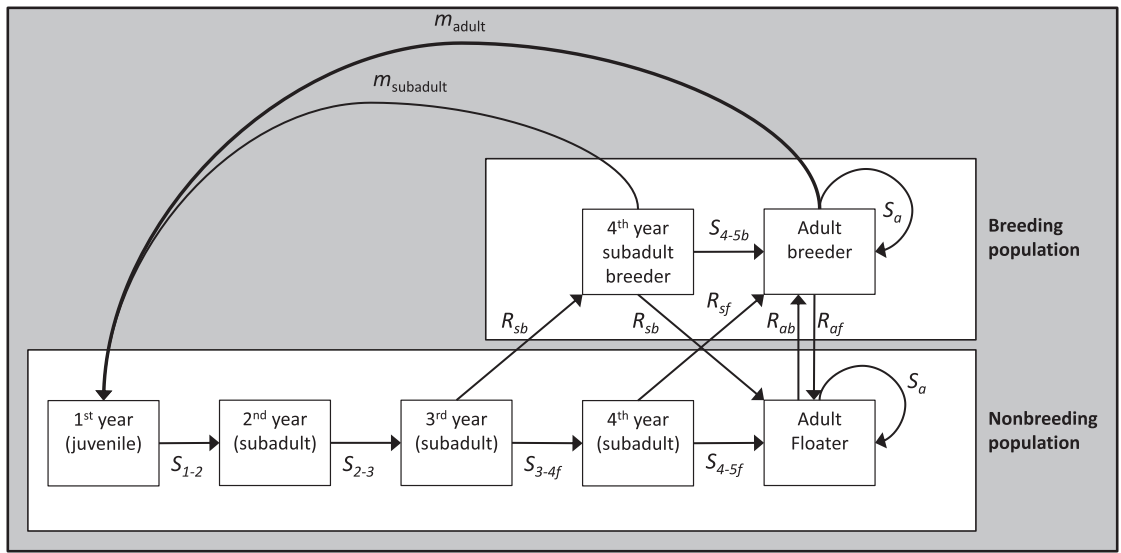
Figure 2. Life cycle of the modeled population of Golden Eagles in the Desert Renewable Energy Conservation Plan area, California, U.S.A. Boxes represent the different age- and stage-classes represented in an individual-based, spatially explicit simulation model, where S_i is the survival for age-class i, m_i is fecundity (mean number of female young fledged per territorial female) for age-class i, and R_i is recruitment for age-class i between breeding and nonbreeding segments of the population.

directly integrate empirical data on the spatial distribution and availability of nest sites and primary prey species into our demographic model, which ultimately determined fitness of simulated eagles as a consequence of each individual's ability to acquire these resources.

Our approach to model development was similar to that used for assessments of critical habitat configurations for the federally threatened Northern Spotted Owl (*Strix occidentalis caurina*; U.S.F.W.S. 2012, Schumaker et al. 2014). Our population model represented only the female component of the Golden Eagle population because we found little data on sexual variation in published estimates of demographic parameters. The population simulations used a stage-dependent demographic model that reflected different age-classes (1st-yr juveniles, 2–4-yr-old subadults, adults) and breeding states (breeders, nonbreeders; Fig. 2). The five age classes in our model allowed us to examine age-related mortality effects on population size by simulating processes affecting key annual life-history events of individuals, including territory prospecting and establishment, foraging and resource acquisition, reproduction, dispersal, and survival (Fig. 3). We provide parameter values used in the baseline

HexSim model for each life-history event in Appendix.

Starting population size and territory establishment. Simulations began with 500 individual female Golden Eagles introduced at random locations across the study area. A large starting population ensured that individuals were well-distributed throughout the entire modeling region. The ages of individuals in the initial population were randomly distributed. Once model initialization was complete, each individual eagle was subjected to the annual event cycle shown in Fig. 3. At the beginning of each annual time step, each surviving individual becomes a year older and advances to the next age class. Next, 3d- and 4th-yr subadults and adults prospect for a breeding territory, which was informed by the nesting habitat model. This process required individuals to build nonoverlapping breeding territories (i.e., defended areas) by exploring and occupying a sufficient number of adjacent hexagons in the underlying nesting suitability map. The quality of each hexagon ranged from 0.0–1.0 according to values of the nesting habitat map, and simulated eagles required a cumulative nesting habitat quality score of ≥10 before a territory could be established in an area for subsequent construc-
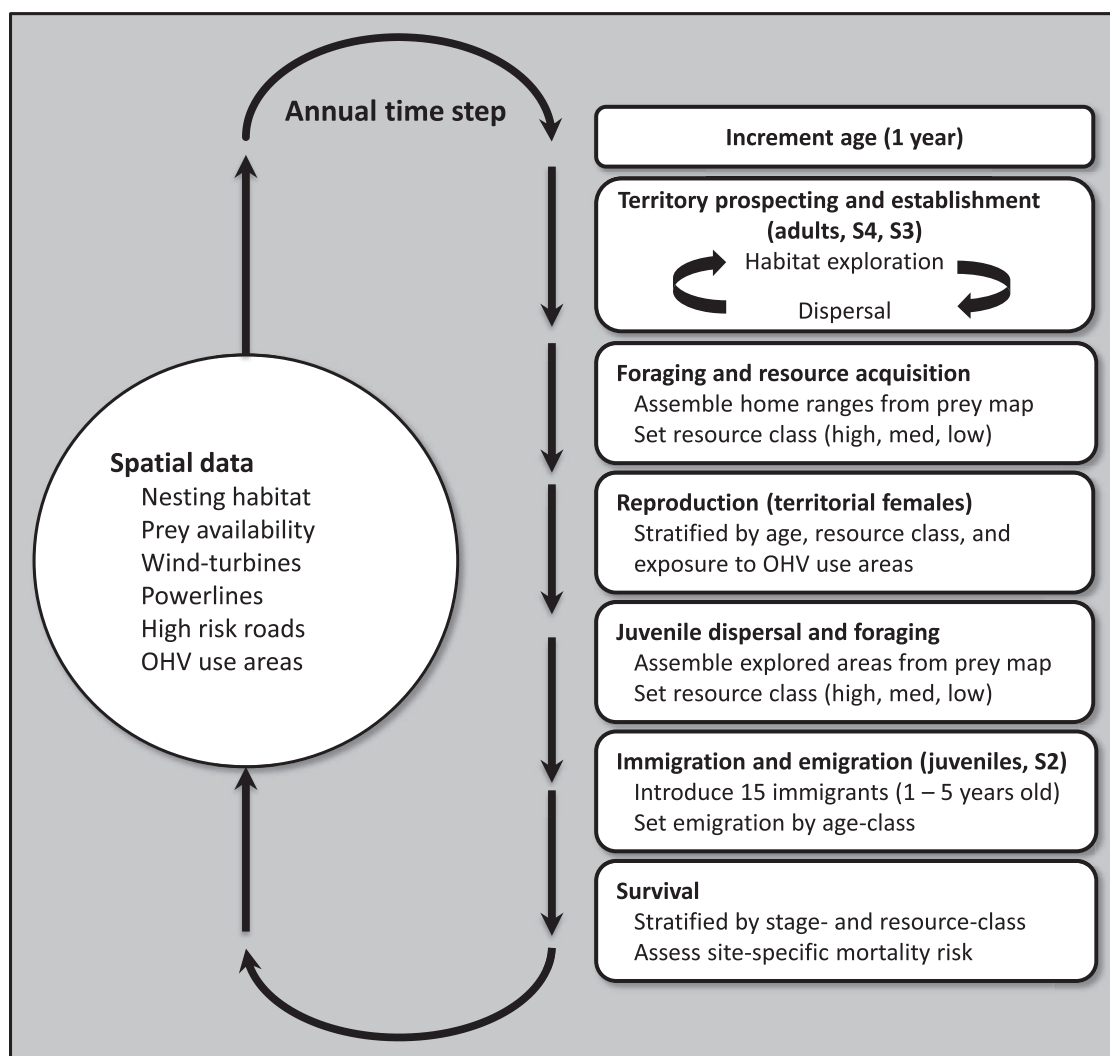
Figure 3.   Modeling sequence of an individual-based, spatially explicit simulation model for Golden Eagles in the Desert Renewable Energy Conservation Plan area, California, U.S.A.

tion (Appendix). We used a threshold value of 10 based on a visual assessment of hexagon scores surrounding actual nest locations used by Golden Eagles in the study area. The goal of territory construction was to acquire a cumulative target nesting habitat score of 40, which had the effect of increasing territory sizes, but only in the best quality areas. Prospecting eagles that were unable to achieve a nesting habitat score of 10 in one location were permitted to disperse between 50 and 100 km in an attempt to build a territory elsewhere. Adults that could not achieve their target nesting value within

five prospecting-dispersal cycles in a single time step transitioned to the non-territorial segment of the population as floaters (i.e., individuals capable of reproducing but that do not hold a breeding territory; Hunt 1998). Prospecting subadults remained non-territorial floaters if they could not establish a territory within three prospecting-dispersal cycles in a single time step (Fig. 2).

Once settled on a breeding territory, Golden Eagles exhibit strong site fidelity (Kochert et al. 2002, Watson 2010). Accordingly, our model assumed that once a simulated eagle acquired a

breeding territory at age ≥4 yr, it would remain on or return to that same breeding territory on each subsequent time step. Juveniles and 2nd-yr subadults do not prospect for territories in our model, but instead establish temporary home ranges in which to draw prey resources. This parameterization of territory prospecting and establishment resulted in density-dependent feedback on population growth by limiting availability of nesting sites and foraging areas (Brown and Watson 1964, Newton 1992).

Foraging and resource acquisition. In the next step of our model (Fig. 3), simulated eagles acquired food resources by establishing large, overlapping home ranges. Home ranges were constructed using the prey availability map, where individual eagles attempted to acquire hexagons with the highest prey value scores unitl they either reached their stage-specific resource target value, or maximum allowable home range size (Appendix). This resulted in large, irregularly shaped home ranges centered on smaller territories. Modeled home ranges approximated published estimates of space use by Golden Eagles in the study region (Braham et al. 2015, Poessel et al. 2016), and varied in size from 500 to 800 km^2, and among stage classes, such that territorial adults used the smallest ranges and 2nd- and 3rd-yr subadults used the largest (Appendix). Home ranges could overlap among modeled eagles, which meant that they experienced competition for prey resources from other eagles. Access to resources within overlapping home ranges was prioritized based on territorial status and age class in the following order (from highest to lowest priority): territorial adults and 4th-yr subadults, adult and 4th-yr subadult floaters, 3rd-yr subadults, 2nd-yr subadults, and juveniles.

All individual eagles were placed into one of three resource classes (low, medium, high) based on the total amount of prey resources within their assembled home range (Appendix). We then used resource classes to influence each individual's reproduction and survival. We approximated relationships between food availability and reproduction and survival based on empirical studies of Golden Eagles and similar species (Steenhof et al. 1997, McIntyre and Schmidt 2012, Resano-Mayor et al. 2016). Each simulated eagle also had a resource target, which we used to determine how many prey resources individuals needed to be placed into the best resource class. We approximated resource target values based on a visual assessment of prey values in hexagonal cells surrounding actual nest locations in the study area. Simulated eagles that acquired ≥90% of their prey resource target were placed into the high resource class, those that acquired <40% of their prey resource target were placed into the low resource class, and all others were placed into the medium resource class. We used this categorization of resource acquisition so that there were few individuals being placed into the high resource class with relatively higher reproduction and survival.

Reproduction. We modeled fecundity (i.e., number of young fledged per territorial female per year) to approximate published estimates from long-term field studies of Golden Eagles in California (0.345; Hunt 2002), southwestern Idaho (0.395; Steenhof et al. 1997, 2014), and southeastern Alaska (0.31; McIntyre and Schmidt 2012, also see Tack et al. 2017). We divided published estimates by two to obtain estimates of fecundity for these studies (assumes a 1:1 sex ratio). Annual reproduction for each territorial female was drawn from a Poisson distribution to determine clutch sizes of zero to three young, such that clutch sizes were not equally likely and nesting events with three young were uncommon (Kochert et al. 2002). The Poisson parameter value was subsequently multiplied by coefficients for an individual's age class (adults, 4th-yr subadults), resource acquisition class (low, medium, high), and amount (%) of territory overlap with off-highway vehicle (OHV) recreation sites (Appendix). For the age-class coefficient, we assumed that 4th-yr subadults would establish territories less frequently and have lower reproductive rates (i.e., forgo reproduction more frequently) than older adults (Steenhof et al. 1983, Sánchez-Zapata et al. 2000). Eagles younger than 4 yr old did not breed in our model (Steenhof et al. 1983, Ferrer et al. 2003, Katzner et al. 2006).

In Idaho, Steenhof et al. (2014) and Spaul and Heath (2016) observed increased rates of nesting failure and reduced reproductive output at breeding territories exposed to increasing levels of OHV use. Based on these findings, we assumed that modeled eagles whose breeding territories overlapped with designated OHV sites by ≥85% would fail to produce young. The OHV areas ranged in size from <0.01 to 231 km^2 (mean = 21.8 km^2), and were locations designated for open recreational use of OHVs (Fig. 1; Conservation Biology Institute [CBI] 2014). We chose a large (conservative) level of territory overlap to trigger OHV effects, but varied the overlap parameter systematically to determine its

influence (see Methods: Model Assessment). The size and shape of simulated breeding territories varied among time steps, so nesting eagles whose territories were spatially associated with OHV areas were not always disturbed at every time step. Reproductive output of Golden Eagles tends to be highly variable among years, perhaps due in part to annual fluctuations in weather and prey population (Steenhof et al. 1997, McIntyre and Schmidt 2012). We simulated this form of environmental (climatic) stochasticity in our model by multiplying values of expected reproduction by a single coefficient (range = 0 to 1) drawn randomly from a uniform distribution at each time step. As a result, our model assumed both demographic (i.e., individual) and environmental stochasticity in population growth.

Dispersal movements. After reproduction, juveniles initiated dispersal from their natal territories (Fig. 3). Dispersing juveniles moved in any direction from 90–175 km, and their movements were informed by the prey availability map (Appendix). Dispersers moved with high spatial autocorrelation (i.e., fairly linear paths), but increased their turning frequency as necessary to avoid areas with very low prey availability, and to move increasingly toward areas with relatively greater prey. Once simulated juveniles made initial dispersal movements, they established a temporary home range up to 800 km^2 in size in which to draw prey resources. As with other age classes, juveniles were assigned to a resource class based on the amount of prey resources calculated within their home range. Recent studies show that resident Golden Eagles in the study area have wide-ranging movements that extended to higher elevations beyond the DRECP boundary, especially in hot summer months (Braham et al. 2015). In addition, eagles from beyond the study area may migrate to the area in winter (George et al. 2014). To simulate movement of Golden Eagles into and out of the study area, we assigned an annual emigration probability of 0.12 and 0.10 for simulated juvenile and subadult eagles, respectively, and introduced 15 preadult immigrants of random age to the population each year (Appendix).

Survival. Annual survival of simulated eagles was based on empirical, age-specific estimates obtained from analyses of band-recovery data collected between 1968 and 2014 in the western U.S. (U.S.F.W.S. 2016). We allowed baseline survival rates of individuals to vary with age and resource class (Appendix). We imposed additional mortality (5–10%) on individuals that occupied home ranges in the low resource class (i.e., individuals with prey acquisition scores <40% of target values), and increased survival by 3–4% for individuals that occupied home ranges in the high resource class (scores ≥90% of target values). Survival of individuals was also influenced by sources of mortality within home ranges (i.e., collisions with wind turbines, electrocution, vehicle collisions). This parameterization resulted in stage-specific survival rates that varied spatially according to resource availability and site-specific sources of mortality. We also reduced the annual survival rate of senescent individuals (eagles >20 yr old) to 0.50, which still allowed a few simulated eagles (<0.05% of the total population) to attain ages of between 20 and approximately 35 yr old (Kochert et al. 2002).

Our population model was informed by several publically available spatial data layers developed for the DRECP, including the locations of current powerlines, wind turbines, and roads and highways (CEC 2014, CBI 2014). We used these data to develop a site-specific risk map of mortality (Fig. 1). The risk map of the current distribution of potential threats was included in the baseline population model described above, which increased mortality of simulated eagles by subtracting between 0.0001 (collisions with vehicles on high-risk roads) and 0.0026 (powerline electrocutions and collisions with wind turbines) from baseline survival rates (Appendix). Our spatial mortality risk map characterized the cumulative effects of select anthropogenic stressors, which reflected only a portion of annual mortality sources for Golden Eagles (Hunt 2002, U.S.F.W.S. 2016). As a result, baseline survival rates were scaled appropriately to better approximate published estimates, and to capture other sources of natural (e.g., disease) and anthropogenic (e.g., lead exposure) mortality not specifically included in our model.

Potential Effects of Renewable Energy Development. We simulated the potential influence of anticipated changes in land use on the local population of Golden Eagles by introducing Development Focal Areas (DFAs; Fig. 1). The DFAs ranged in size from 0.001 to 2882 km^2 (mean = 3.93 km^2), and were locations where planned renewable energy generation and transmission projects could be streamlined for approval and construction (CBI 2014, CEC 2014). These areas do not necessarily represent actual project sites, but were useful to estimate the land area where fatality rates and foraging habitats of Golden Eagles are

most likely to be affected by future renewable energy projects and associated infrastructure.

Development Focal Areas were added to the baseline mortality risk map by increasing the risk of mortality in these areas. We used estimated turbine blade-strike collision probabilities calculated for Golden Eagles (0.0037 ± 0.0015 [SD]) by New et al. (2015) to approximate increases in fatalities within DFAs. We also simulated the potential for degradation of foraging habitats in DFAs by subtracting 25% of baseline hexagon scores of the underlying prey availability map. This resulted in a new set of maps of mortality risk and prey availability, with the new DFAs in place. We developed four risk scenarios using the new disturbance and resource maps, each representing a different assumption about fatality rates, or habitat degradation, within future DFAs, including: (1) an increase in mortality risk by 0.0027 with no effect on prey availability (low effect), (2) an increase in mortality risk by 0.0047 with a 25% reduction in prey availability (moderate effect), (3) an increase in mortality risk by 0.0077 with a 25% reduction in prey availability (severe effect), and (4) mortality risk and habitat disturbance had moderate effects in DFAs as specified above, but coupled with a 99% reduction in the baseline risk of mortality from collisions and electrocution within Conservation Planning Areas (moderate effect with conservation). Conservation Planning Areas (Fig. 1D) were areas specified for conservation actions to offset the potential negative effects of development (CBI 2014, CEC 2014). All mapping was completed in ArcGIS 10.1.

Simulations and Model Assessment. Our primary results were calculated from 10 replicate simulations of 500 time steps each. Data other than population size used to assess our baseline population model were gathered from time steps 150–500, well after the population had reached a stable age-distribution. For disturbance scenarios, we introduced effects into the baseline model at time step 200, and observed population response for the subsequent 300 time steps. We emphasize that these simulation times were not used to project population dynamics of Golden Eagles into the distant future, but rather to allow the models adequate time to reach steady state pre- and post-disturbance (Schumaker et al. 2014, Tuma et al. 2016), and to evaluate the relative population responses among different development scenarios. We analyzed future risk scenarios by comparing mean population size over 50 time steps between pre- and post-distur-

bance. Here, we arbitrarily selected time steps 149–199 and 450–500 for the pre- and post-disturbance periods, respectively, which were periods well beyond the asymptote for the population growth curve prior to, and following, disturbance introductions. We used analysis of variance (ANOVA) to compare pre- and post-disturbance population sizes.

We parameterized our baseline population model using a limited amount of empirical data. As a consequence, there were considerable uncertainties about model parameters that required us to make assumptions about demographic rates, resource acquisition, and the influence of anthropogenic stressors. We determined how these assumptions could have influenced our results in two ways. First, we examined the general performance of the model by comparing estimates of population size and associated demographic parameters derived from simulated data to existing field data. Second, we used a sensitivity analysis approach (Marcot et al. 2015) to help identify the influence of uncertain model parameters or demographic rates that are difficult to measure in actual eagle populations. Specifically, we estimated how incremental changes in demographic parameters (adult survival, pre-adult survival, fecundity, emigration, immigration) affected population trajectories. We also examined sensitivity of the model to parameter values we used to inform territory size, stage-based resource acquisition rates, and effects of OHV disturbance. Input parameters were adjusted by ±10% by multiplying baseline values by 1.1 and 0.9, respectively. We calculated departure from the baseline model as the percent change in median population size, estimated from 10 replicates of each proportional change scenario. We also developed a model without emigration and immigration to determine how these parameters influenced population size.

Results

Nesting Habitat and Prey Availability. The best-performing model characterizing nesting habitat in the study area included variables for surface roughness and quartz index. Validation test scores were 0.981, 0.239, and 0.199 for the AUC, RMSE, and MXE validation indices, respectively, indicating relatively good performance of the model in correctly classifying nest locations. We rescaled modeled nesting suitability scores to a continuous measure ranging from 0 to 1, which represented the relative likelihood of finding nest locations in the DRECP landscape (Fig. 1A).

Model selection results indicated that density of lagomorphs was best characterized by topographic position, elevation, and surface roughness (also see Longshore et al. 2017). Areas with lower values (e.g., mountain tops, ridges, and local peaks) had a negative influence on prey abundance, and areas with higher values (e.g., valley bottoms) had a positive influence. Elevation had a generally positive relationship with detections of rabbits, where the lowest elevations showed a negative influence, moderate elevations (i.e., 1000–1500 masl) were effectively neutral, and higher elevations predicted increased abundance until elevations >2000 masl. Surface roughness was negatively associated with estimated density of rabbits, with a decrease in density with roughness values above 1.02, although fewer of these areas were sampled. We fitted the rabbit detection data to the best-supported distance model to create a density surface of prey availability for the study region (Fig. 1B; Longshore et al. 2017).

Simulation Model Output and Assessment. Replicates of the baseline simulation model produced a mean steady-state population size of approximately 145 female Golden Eagles (Fig. 4A). Modeled population size was somewhat greater than a recent estimate from aerial surveys of Golden Eagles in the DRECP area (George et al. 2014), but the range of variability we observed in population size over time was well within the margin of error reported by that study (Table 1). Mean number of occupied territories (i.e., territorial females) ranged from 33 to 94 ($\bar{x}$ = 62.2 territories; Table 1, Fig. 4A), which was similar to a field-based estimate ($n = 74$ used nests [i.e., nests with incubating adult or eggs], Latta and Thelander 2013). Simulated values of average fecundity and age-specific survival rates were all close to point estimates from studies conducted in the western U.S. (Table 1; Fig. 4B). Collisions with wind turbines at existing wind energy facilities, collisions with vehicles, and electrocutions on power poles accounted for 20% of total annual mortality of simulated eagles ($\bar{x} = 7.0$ deaths per year, SD = 2.8; Table 1, Fig. 4C), which approximated observed data on causes of death in a sample of 97 Golden Eagles tracked with satellite telemetry in the western U.S. (U.S.F.W.S. 2016). Territories constructed by simulated eagles ranged from 19 to 50 km^2 ($\bar{x} = 44.9$ km^2). The size of home ranges varied among stage-classes, such that territorial adults used the smallest ranges and preadults (i.e., juvenile and subadults) used the largest. The sizes of modeled territories and home ranges tended to be larger than mean estimates from observed data (Table 1), but were within the wide range of estimates reported for eagles in the region (Braham et al. 2015).

Results of the sensitivity analysis (Table 2) showed that incremental changes in adult survival resulted in the greatest proportional change to total population size (i.e., a 10% decrease in baseline values of survival led to a 43% decrease in median total population size, whereas a 10% increase led to a 110% increase in median total population size). Our analyses also showed that proportional changes in values of preadult survival (−31%, 44%) and fecundity (−23%, 22%) had substantial effects on total population size. The population model was also sensitive to changes in immigration and emigration, and values used to determine resource acquisition (Table 2). Proportional changes in our parameterization of territory size and OHV disturbances had relatively little influence on model output (≤5%). Models that assumed a closed population (no immigration or emigration) went to zero individuals during time steps 150–250 in all simulations, indicating a heavy dependence on immigration to maintain numbers of breeding eagles in the landscape.

Emergent Population Dynamics. We observed variation in the size, distribution, and age structure of the simulated population over time (Fig. 4), which can be attributed to dynamics emerging from interactions among the demographic and environmental processes included in the model. Size, distribution, location, and annual occupancy rates of breeding territories emerged from spatial and temporal variation in availability of suitable nesting habitats and prey resources. Distribution of food resources changed over time following use and replenishment of prey resource values at hexagons used by foraging individuals among time steps. Resource acquisition was another emergent property of the model that varied with an eagle's location, territorial status, age class, home-range size, and competition with other simulated eagles. Spatial output of the baseline model included the projected landscape distribution of high versus low quality breeding sites, as determined by breeding territories with the greatest reproductive output and fewest deaths over 150 yr of simulation (Fig. 5).

Potential Effects of Renewable Energy Development. All scenarios representing different levels of risk of future renewable energy development resulted in a significant population decline (Table 3, Fig. 6). The worst-case scenario, which assumed that
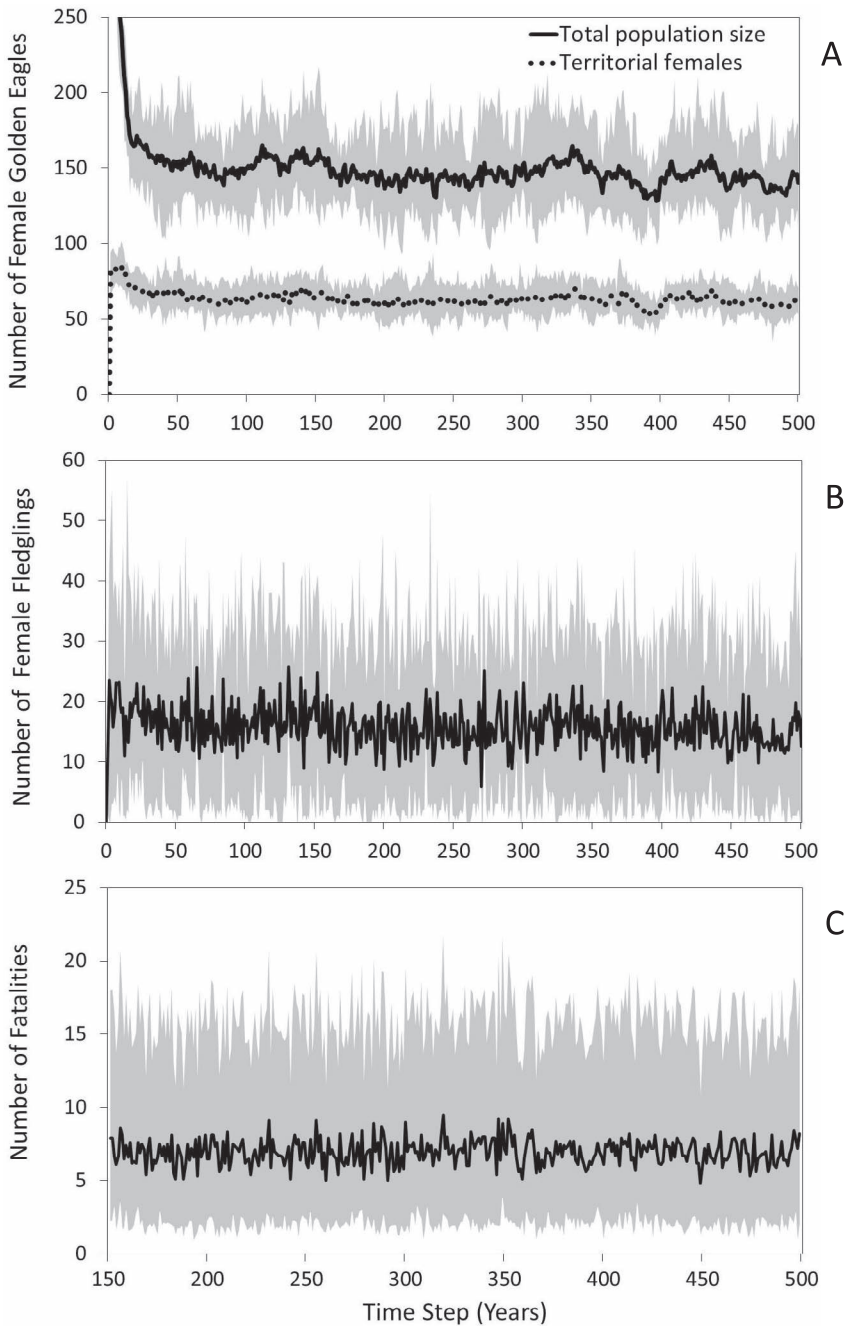
Figure 4. Output from the stable, baseline population simulation model for Golden Eagles in the Desert Renewable Energy Conservation Plan area of southern California, U.S.A, including: (A) total population size and number of territorial females, (B) number of female fledglings produced, and (C) number of fatalities from collisions with wind-turbines, powerline electrocutions, or collisions with vehicles during time steps 150–500. Black lines show median values from 10 replicate simulations, each conducted over 500 time steps (years); shaded areas indicate maximum and minimum values (A, B), or 95% confidence intervals (C).

Table 1. Mean values of output demographic parameters obtained from the stable, baseline demographic model developed for Golden Eagles in the Desert Renewable Energy Conservation Plan area, California, as compared to empirical estimates from local and regional field studies. Simulated values were calculated from 10 replicates of the last 350 yr of 500-yr simulations.

PARAMETER	SIMULATED DATA		OBSERVED DATA[a]		
	MEAN	SD	VALUE	95% CI	SOURCE
Population size (number of female Golden Eagles)					
Total population size	145.0	20.4	67.5	20–170	A
Occupied territories (no. territorial females)	62.2	8.1	74.0	—	B
Territory density (occupied territories per 1000 km^2)	6.8	1.1	8.1	—	B
Juveniles	15.2	10.0	39.0	—	B
Subadults (2nd–4th yr)	39.7	10.7	—	—	
Floaters (non-territorial adults and 4th yr subadults)	27.4	7.8	—	—	
Fecundity (mean number of young per territorial female)	0.34	0.21	0.35	0.105–0.705	C
Survival					
Juvenile survival	0.76	0.19	0.70	0.66–0.74	D
2nd yr survival	0.78	0.20	0.77	0.73–0.81	D
3rd yr survival	0.85	0.17	0.84	0.79–0.88	D
4th yr survival	0.85	0.14	0.87	0.84–0.89	D
Adult survival	0.87	0.04	0.87	0.84–0.89	D
Cause of death					
Collisions and electrocution	0.20	0.09	0.19	—	E
Other anthropogenic and natural sources	0.80	0.11	0.81	—	E
Movement and space use					
Territory size (km^2)	44.9	7.6	16.1	6.3 – 25.9	F
Adult home range size (km^2)	489.4	59.6	307.8	133.7 – 480.5	F
Preadult home range size (2nd to 4th yr eagles; km^2)	665.0	121.8	307.8	133.7 – 480.5	F
Juvenile dispersal distance (km)	134.2	25.4	151.0	74.7 – 227.5	G
Population growth rate (λ)	1.003	0.082	—	—	

[a] Key to observed data sources: (A) estimated from aerial line-transect surveys conducted in the DRECP area in 2012 (George et al. 2014). We divided published estimates by two to get total abundance of females, assuming a 1:1 sex ratio; (B) estimated from helicopter survey of nests used by Golden Eagles in the DRECP area in 2012 (Latta and Thelander 2013); (C) estimated from a Bayesian gamma regression model with field-based measures of productivity from five long-term studies in the western U.S. (Tack et al. 2017); we divided estimates by two to get fecundity values; (D) estimated from band-recovery data collected in the western U.S. from 1968 to 2013 (U.S.F.W.S. 2016); (E) estimated from fatalities of satellite-tagged Golden Eagles in the western U.S. (U.S.F.W.S. 2016; proportions recalculated from Table 8); (F) estimated from mean monthly 95% convex hull home ranges from eight Golden Eagles marked with GPS-GSM transmitters (Braham et al. 2015); (G) estimated from 63 juvenile Golden Eagles marked with satellite transmitters in the southwestern U.S. (Murphy et al. 2017).

fatality rates of simulated eagles would increase in DFAs by 0.0077 with a concurrent 25% reduction in prey availability, caused the most precipitous and significant decline (66% decline in post-disturbance population size; Fig. 6). Contrary to expectations, a scenario with a relatively low increase in site-specific fatality (0.0027) and no effects on prey availability resulted in a similar decline in population size relative to a scenario with a moderate increase in fatality (0.0047) plus a 25% reduction in prey availability (Table 3). This result emerged because ranging behavior of simulated eagles was largely determined by prey availability. Thus, when prey values declined in disturbed areas (i.e., simulating degradation of foraging habitats), so did the use of

these areas by foraging eagles. A scenario with moderate effects of development, but coupled with conservation actions (i.e., a 99% reduction in mortality risk in Planned Conservation Areas), resulted in the smallest population decline of the four scenarios considered, but the decline was still notable (33% decline in post-disturbance population size). Mean post-disturbance population size under the scenario with conservation actions was significantly greater than a similar scenario without conservation actions (Table 3).

DISCUSSION

We developed, documented, and assessed a spatially explicit, individual-based simulation model for a local population of Golden Eagles exposed to

Table 2. Sensitivity of the stable, baseline demographic model for Golden Eagles in the Desert Renewable Energy Conservation Plan area, California, to incremental changes in uncertain model parameters. We expressed model sensitivity as the percent change in size of the simulated population relative to the stable baseline population model when uncertain model parameters were proportionally increased or decreased by the amount shown.

PARAMETER	MEDIAN POPULATION SIZE[a]	SD	PERCENT CHANGE FROM BASELINE MODEL
Adult survival			
10% increase	300	32.1	110%
10% decrease	81	12.5	−43%
Preadult survival			
10% increase	206	29.6	44%
10% decrease	99	24.3	−31%
Fecundity			
10% increase	175	21.4	22%
10% decrease	110	20.0	−23%
Immigration			
10% increase	175	21.2	22%
10% decrease	105	18.3	−27%
Emigration			
10% increase	124	17.5	−13%
10% decrease	166	27.1	16%
Prey resource acquisition			
20% increase (prey rich)	166	23.8	16%
20% decrease (prey poor)	113	15.5	−21%
Territory size			
10% increase	144	19.1	1%
10% decrease	138	19.2	−3%
OHV disturbance			
Inactive (no disturbance)	146	21.5	2%
20% greater impact	136	21.5	−5%

[a] Median population size estimated from the baseline model was 143.0 ± 20.4 (SD) female Golden Eagles.

threats associated with rapid increases in renewable energy development. Our study provided initial insights into the effectiveness of using such models to identify possible population responses of Golden Eagles to renewable energy development relative to other sources of anthropogenic (or natural) mortality. We found that the simulated population of Golden Eagles had behavior consistent with life-history traits and population demography of natural populations, especially with respect to studies conducted on breeding populations in the desert regions of the American Southwest. We showed that complex interactions between highly mobile individuals, the distribution of their resources, and site-specific changes in land use could be effectively represented within a virtual modeling environment. We further show that simulated increases in the future occurrence and distribution of anthropogenic stressors resulted in alternate population trajectories for Golden Eagles. The simulation model we developed here should be a particularly useful tool for researchers and land managers wanting to explore how proposed site-specific management actions may affect a local breeding population of eagles, or for evaluating spatial conservation options.

Recently, U.S.F.W.S. (2016) compiled information on population size and trend of Golden Eagles, generated estimates of recent survival and fecundity rates, and used these data in matrix population models to forecast future population trends and the ability of Golden Eagles in the western U.S. to withstand additional mortality. Their analysis suggested that any increases in mortality to current populations will either exacerbate the potential for future declines, or steepen the rate of any current declines (U.S.F.W.S. 2016). Results from our population simulation model were consistent with these findings, as additional mortality associated with future disturbance scenarios led to a significant decline in population size. A limitation of traditional matrix population models is that they do not readily accommodate threats that act on individuals at varying spatial scales, so they cannot easily identify the importance of specific landscape locations in sustaining populations (Munns 2006, Schumaker et al. 2014). Our study demonstrated how such insights can be gained from individual-based, spatially explicit population models. Each simulated eagle in our model possessed traits that varied in time and space relative to age, resource availability, disturbances, or territorial status. Emergent population dynamics from our simulation model illustrated how survival, reproduction, and population trends of Golden Eagles depended on complex interactions among spatial, demographic, and environmental sources of variation. This analytical framework contrasted sharply with traditional projection matrix models in which such interactions must be parameterized and stipulated in advance, and then used to guide the outcome of abundance and distribution of a study population.

Achieving correspondence between output of our population model and observed field data was a critical step in validating the forecasting capabilities of our model. Population size and distribution, breeding parameters, mortality processes, and move-
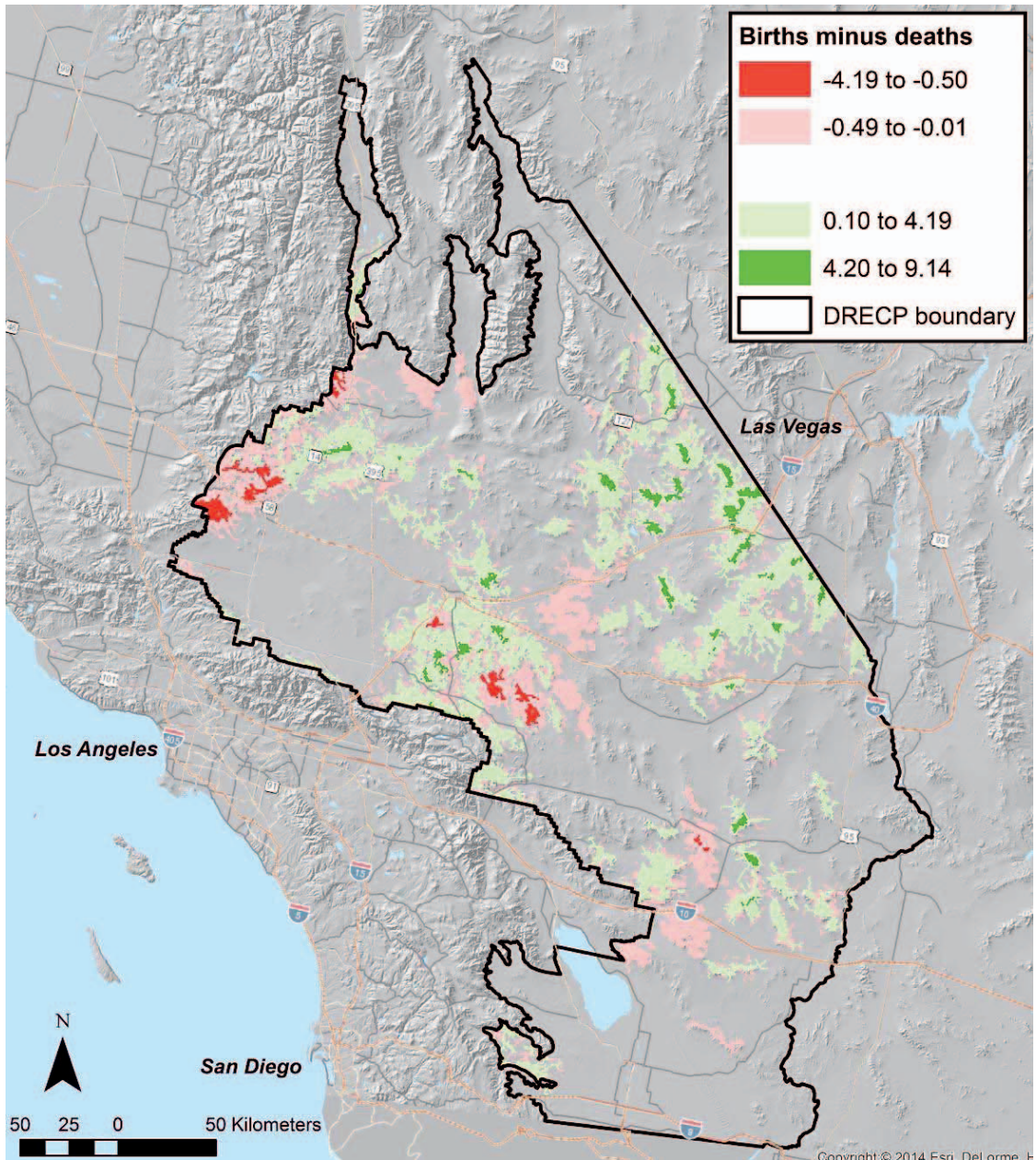
Figure 5.   Predicted spatial distribution of long-term productivity and mortality at breeding territories of Golden Eagles in the Desert Renewable Energy Conservation Plan area of southern California, U.S.A. We show the mean number of births minus deaths per 1-km^2 in home ranges established by simulated eagles during 150 time steps (years) and 10 replicate simulations of the stable, baseline population model. Source habitats appear in green, sink habitats appear in red.

Table 3. Estimates of mean pre- and post-disturbance population sizes from replicate simulations of different hypothesized effects of renewable energy development on Golden Eagles in the Desert Renewable Energy Resource Area, CA U.S.A. Pre- and post-disturbance means were calculated from time steps 149–199 and 450–500, respectively, over 10 replicate simulations of each risk scenario.

Risk Scenario[a]	Potential Maximum Fatality Rate	Pre-disturbance Population Size			Post-disturbance Population Size			ANOVA[b]	
		Mean	SD	Min–Max	Mean	SD	Min–Max	$F_{1,1019}$	P
Low	0.0054	145.5	18.4	110–205	83.2	12.1	53–124	4090.4	<0.001
Moderate	0.0074	146.0	20.5	96–213	85.7	11.4	60–122	3365.4	<0.001
Severe	0.0104	149.6	21.5	95–217	53.0	7.3	35–80	9223.2	<0.001
Moderate with conservation	0.0074	140.4	20.9	93–205	93.1	14.8	63–189	1738.8	<0.001

[a] Risk scenarios included an increase in mortality risk of 0.0027 above baseline levels in Development Focal Areas (DFAs) and no effect on prey availability (low effect), an increase in mortality risk of 0.0047 above baseline levels and a 25% reduction in prey availability within DFAs (moderate effect), an increase in mortality risk of 0.0077 above baseline levels and a 25% reduction in prey availability within DFAs (severe effect), and an moderate increase in mortality risk (0.0047) and a 25% reduction in prey availability within DFAs, but coupled with a 99% reduction in mortality risk within Planned Conservation Areas (moderate effect with conservation).

[b] Analysis of variance (ANOVA) comparison of pre- and post-disturbance population size means.

ment behaviors of the simulated population were generally consistent with empirical field studies of Golden Eagles. Our simulations produced a steady-state mean population size in the study area of 145 females (290 individuals total, assuming a 1:1 sex ratio), which was somewhat larger than an estimate (135 individual females) from aerial surveys conducted in the study area by George et al. (2014), but well within the 95% confidence interval of their estimate (41 to 340 female eagles, assuming a 1:1 sex ratio). As noted by George et al. (2014), however, the precision of their estimate of population size was poor, and it was possible that prey and eagle numbers were depressed in the study area during their surveys because of severe drought conditions. Additional surveys are needed to determine population size with greater precision under a broader range of environmental conditions. Such information could be used to validate and refine estimates of population size in our simulation model, thereby increasing its predictive capabilities.

Based on our sensitivity analysis, changes in adult survival had the greatest proportional influence on relative population size. This finding was similar to that of Whitfield et al. (2004) and Tack et al. (2017), who used demographic models to show that even small changes in adult survival of Golden Eagles had disproportionately strong effects on population grown rate (λ). Collectively, these findings suggest that conservation efforts focused on improving adult survival should make disproportional contributions to maintaining relatively stable population trajectories. We also found that changes in preadult

(juvenile and subadult) survival had pronounced effects on local population size, and that immigration and emigration of nonbreeding individuals played a large role in stabilizing localized population trends. Thus, while our results are consistent with other studies in that adult survival should be the most important demographic parameter for the population dynamics of Golden Eagles, an exclusive focus on this parameter in a conservation context overlooks the potentially strong controlling influences that preadult survival and dispersal movements may have in stabilizing local breeding populations. In our simulations, immigration from outside the study region and natal dispersal within the study area acted jointly to sustain a local breeding population that would otherwise decline to extinction. This finding illustrated how the local population could appear stable only because of sustained immigration from outside of the DRECP area, which emphasizes the importance of a broad-scale perspective to conservation and research of Golden Eagles (also see Katzner et al. 2017). Preadult Golden Eagles pass through a highly nomadic phase of dispersal in which specific, yet disparate areas may be intensively used (Soutullo et al. 2006, Poessel et al. 2016, Murphy et al. 2017). Our findings show that identifying these areas and implementing site-specific conservation measures aimed at mitigating mortality sources could make disproportionate contributions to long-term stability of local and regional populations. In practice, this means allowing surrounding areas to produce dispersing eagles
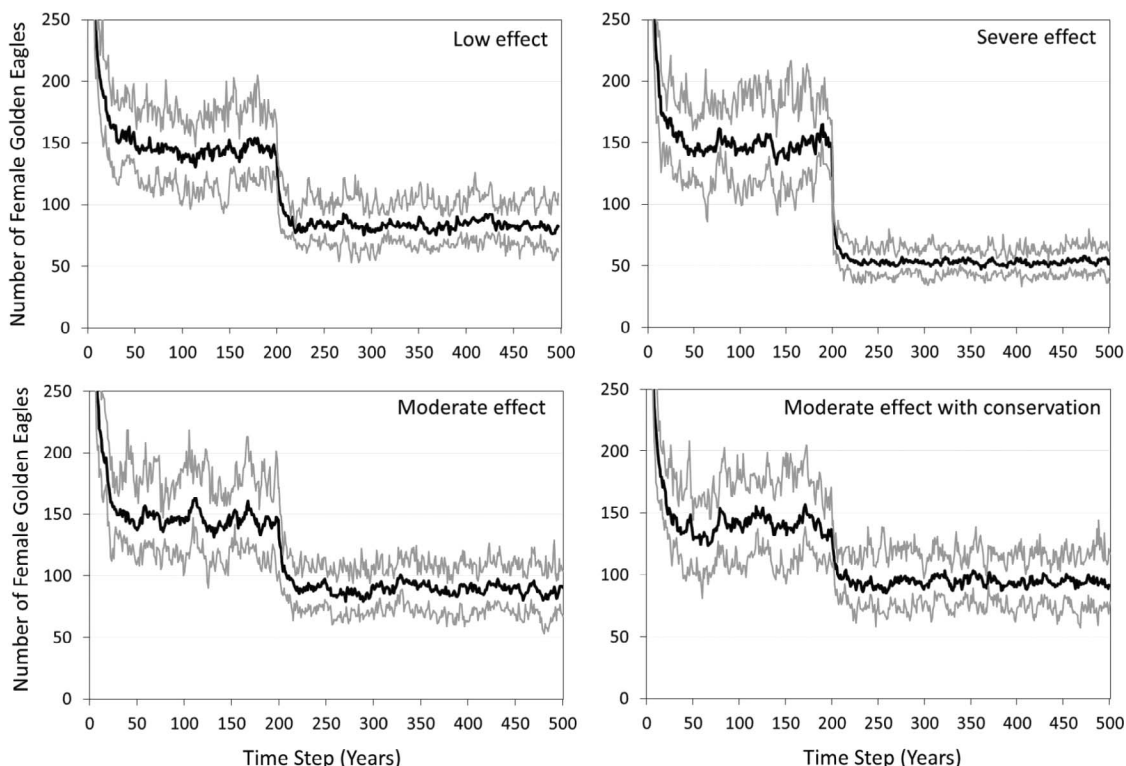
Figure 6.   Predicted population response of Golden Eagles in the Desert Renewable Energy Conservation Plan area of southern California, U.S.A., to four different risk scenarios associated with planned energy development, including: an increase in mortality risk of 0.0027 in Development Focal Areas (DFAs) with no effect on prey availability (low effect), an increase in mortality risk of 0.0077 in DFAs with a 25% reduction in prey availability (severe effect), an increase in mortality risk of 0.0047 in DFAs with a 25% reduction in prey availability (moderate effect), and the moderate effect scenario coupled with a 99% reduction in mortality risk in Planned Conservation Areas (moderate effect with conservation). Black lines show median values from 10 replicate simulations, each conducted over 500 time steps (years); grey lines indicate maximum and minimum values.

while minimizing disturbance and mortality sources at the most productive breeding sites.

Decreasing mean reproductive output had a disproportionately large effect on relative size and distribution of the simulated population of eagles. This result supports management strategies that work toward mitigating low productivity caused by decreases of main prey species, or by reducing human disturbances in breeding and foraging sites to help offset increases in fatality rates elsewhere in the landscape (CEC 2014). Our parameterization of disturbance effects to nesting Golden Eagles caused by OHVs had little effect on population size and distribution. Other studies suggest that OHVs can have substantial negative effects on nesting success of Golden Eagles via increased human disturbance and subsequent nest abandonment (Steenhof et al.

2014). We did not observe any pronounced effects of OHVs in our model, but our study included possible disturbances at designated OHV sites only, whereas actual use and associated impacts of OHVs may be more widespread (e.g., remote trails near nesting sites; Spaul and Heath 2016). As with other uncertainties of our model, disturbances caused by recreational activities may be greater than what we recognized and future work could build upon our model to more fully explore the consequences of such effects.

Potential Effects of Renewable Energy Development. Future renewable energy development under the DRECP includes the construction of wind turbines, solar collection fields, power lines, and roads, which are anticipated to result in the loss of foraging habitats, breeding territories, and individ-

ual Golden Eagles via increased fatality rates (Pagel et al. 2013, Brown 2014, CEC 2014). Our case study is among the first to investigate how increases in renewable energy development could interact with other limiting factors to affect population dynamics of Golden Eagles, and how conservation planning areas might be most effectively placed to offset anticipated negative effects. We found that even small increases in mortality risk to simulated eagles within planned development sites had negative consequences for future population trajectories. This result was not particularly surprising, especially given the juxtaposition of highly suitable nesting habitats and prey resources (Fig. 1A, B) relative to areas targeted for future development of renewable energy infrastructure (Fig. 1D). In our simulation model, this spatial pattern created a dynamic in which territorial eagles, in particular, suffered increased mortality as they encountered risks from newly constructed powerlines, wind turbines, and roads in established territories and home ranges. Given that our population model was especially sensitive to relatively small changes in preadult and adult survival, even small increases in mortality of these stages led to a disproportionately large and negative effect on the future number of breeding females in the landscape.

Our population model provided us with a broadly applicable conceptual framework within which to explore how relative population size and distribution of both breeding and nonbreeding Golden Eagles could be affected by site-specific sources of mortality associated with current and future renewable energy projects. We evaluated a small and relatively simplistic set of risk scenarios to demonstrate the ecological applications of our modeling framework in a conservation planning context. A more detailed analysis would have included a wider range of potential changes in land use on foraging habitats and prey populations, or effectiveness of specific mitigation actions (e.g., seasonal curtailment of wind turbines, power pole retrofitting to reduce electrocutions) in offsetting anticipated increases in fatality rates in DFAs. Nonetheless, even in our low-risk development scenario, the DRECP failed to meet its target conservation goal of a stable or increasing breeding population of Golden Eagles. This result suggests that rapid management actions may be required to meet established conservation goals.

Effectiveness of proposed conservation actions. Conservation actions that reduce the effects of human-caused mortality to Golden Eagles will most likely be site specific. Proposed management options considered for conservation of Golden Eagles under the DRECP included: (1) seasonal curtailment of wind turbines to reduce blade-strike collisions, (2) power pole retrofitting and use of raptor-safe new power poles to reduce the risk of electrocutions, (3) clearing high-risk highways and roads of carcasses to reduce frequency of vehicle collisions with eagles feeding on carrion, and (4) habitat restoration in disturbed areas (CEC 2014). We explored the possible benefit of these proposed conservation actions to Golden Eagles by reducing site-specific mortality rates in designated Conservation Planning Areas. A comparison of models with and without conservation actions showed that site-specific reductions in mortality risk helped to offset the negative effects to the population caused by an increased fatality rate in newly developed areas. It remains unclear whether such reductions in localized fatality rates are within the reach of management, but our analysis clearly illustrated the relative benefits of possible site-specific conservation actions.

The effects of wind turbines on birds, and possible mitigation measures, have been studied increasingly in recent years (Marques et al. 2014). Currently, little is known regarding the numbers of Golden Eagles that are killed each year by collisions with existing wind turbines in the study region (Pagel et al. 2013, Lovich 2015). The DRECP calls for up to 20,000 megawatts of renewable energy in the plan area (CEC 2014), which requires construction of new transmission lines to carry that energy. Utility structures such as power poles and powerlines can pose a major threat to eagles through electrocutions and collisions (Lehman et al. 2007, Dwyer et al. 2014). Mortality associated with scavenging on road-killed carcasses has also been documented throughout the species' geographic range, and can be a substantial source of anthropogenic mortality (Hunt 2002). Compensation for the loss of breeding areas and individuals must be sufficient to offset all of these effects to ensure a stable or increasing population, yet little is known about the effectiveness of proposed compensation measures. Our approach to assessing the effectiveness of possible site-specific conservation actions should be particularly useful for prioritizing specific locations for research and conservation.

Model Uncertainties and Refinement. As is common for many wide-ranging, long-lived raptor species, empirical data on stage-specific vital rates

and movement were lacking for Golden Eagles in our study system. Sparse field data can impart bias and imprecision to estimates of population size derived from mechanistic demographic models such as ours. However, for wide-ranging, difficult-to-study species, a precise estimate of the rate of population decline is of less use than a reliable assessment of the relative efficacy of two or more management strategies for slowing or reversing that decline (Schumaker et al. 2014). We further emphasize that the modeling framework we presented here is extendable, not only in space, but also in terms of adding more biological detail from field studies. Sources of parameter uncertainty in our model stemmed from implicit assumptions made during development, which facilitates tractability and future assessment of these uncertainties within an analytical context. For example, we developed a female-only model that does not account for pair interactions and behavioral (e.g., Allee) effects on population vital rates—effects that are often associated with small population size and low density (Keitt et al. 2001). Sensitivity of the model to these and other assumptions could be explored by developing alternative and more complex model structures. Nonetheless, increasing realism also entails greater model complexity, and too many input parameters and submodels can confound interpretation and communication of results.

Uncertainty regarding model structure and vital rates for our study system is likely to persist, especially because many demographic traits of Golden Eagles are difficult and expensive to measure directly. Our sensitivity analysis helped to address uncertainties about which demographic parameters had the strongest influence on population trajectories. Relatively small changes to some parameters (e.g., survival, fecundity, immigration, resource acquisition) resulted in disproportionately large effects on population size, indicating areas of focus for future monitoring, research, and management. For example, genetic analyses (Rudnick et al. 2005, Doyle et al. 2014) and use of camera traps for individual mark-recapture studies are promising methods that could be used to improved estimates of stage-specific movement patterns and adult and preadult survival in our study area. Our model also identified ecological relationships of disproportionate influence that could be prioritized within a monitoring framework, particularly with respect to habitat quality as affecting survival and successful reproduction, and nesting habitat and prey avail-

ability as affecting breeding and foraging success. Better empirical estimates of these relationships could improve the realism and predictive capabilities of our model. In addition, the sensitivity of our model to changes in immigration and emigration rates suggested that larger simulations conducted at broader spatial scales are needed to capture the importance of wide-ranging movements of preadult eagles (Murphy et al. 2017) in maintaining demographic stability among localized populations.

Applications for Conservation and Management. Our study demonstrates the novel use of a visual and quantitative tool to map, conceptualize, and forecast potential population responses of Golden Eagles to disturbances caused by renewable energy development or other anthropogenic stressors. The management-relevance of our modeling approach stems from its use of dynamic resource and disturbance maps of actual landscapes as principal drivers influencing simulated biological, ecological, and behavioral mechanisms that determine long-term population dynamics. We demonstrated this capability by evaluating whether the established conservation goals of the DRECP are likely to be met under a range of different risk scenarios. Variability in model output showed that the spatial distribution of breeding territories relative to future, site-specific threats strongly influenced adult and subadult mortality processes, and consequentially, total population size. This result highlights the value of using flexible tools for risk assessment that incorporate spatially dependent processes when determining potential consequences of management and other activities to Golden Eagles.

In territorial species, individuals occupying different habitats may experience different probabilities of survival or reproduction depending on the amount and availability of resources within the area they occupy (Ferrer and Donázar 1996, Balbontín et al. 2003). In our model, spatial patterns of site quality emerged from dynamic linkages between survival, reproduction, and the distribution of threats and resources in each simulated eagle's home range. Mapped output from the model illustrated how some breeding territories contributed more to maintaining long-term stability in population size than others: territories in the eastern portion of the DRECP essentially acted as sources (births outnumbered deaths), whereas breeding territories in the north and southwest acted as sinks (deaths outnumbered births; Fig. 5). Differences among breeding sites in productivity has been

documented in empirical studies of Golden Eagles (e.g., Hipkiss et al. 2014), and was an emergent property of our model resulting from spatial variability in food supply, disturbances, and competition with other simulated eagles. In this respect, the model predicted specific areas that may contribute disproportionately to long-term productivity of the local eagle population, thereby providing a guide for prioritizing future monitoring and conservation efforts.

Our work represents an important next step in the longer-term goal of developing modern, defensible forecasting models in general, and for demographic modeling of Golden Eagles in particular. Spatially explicit, individual-based models provide a context to better understand the population dynamics that emerge from decisions that individuals make as they interact with complex and variable landscapes. Our modeling framework offers researchers and decision makers the opportunity to: (1) make informed choices about what specific areas should be prioritized for conservation, (2) synthesize biological data to evaluate potential demographic responses to site-specific management and development actions, (3) determine the likelihood that implementation of a particular management strategy will meet established conservation goals, and (4) investigate the importance of broad-scale population processes, such as metapopulation dynamics, that are difficult and costly to study in a wide-ranging species like the Golden Eagle.

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Appendix. Input values used to parameterize an individual-based, spatially explicit simulation model in program HexSim for Golden Eagles in the Desert Renewable Conservation Plan area of southern California, U.S.A.

EVENT CATEGORY	PARAMETER	STAGE CLASS[a]	VALUE
Territory prospecting and establishment	Minimum nesting habitat score to establish territory	S3, S4, A	18
	Target nesting habitat score	S4, A	40
	Maximum area explored to meet target	S4, A	50 km^2
		S3	200 km^2
	Dispersal distance (if nesting habitat score < 18)	S3, S4, A	54–107 km
	Maximum number of dispersal moves if unsuccessful	S4, A	5
		S3	3
Foraging and resource acquisition	Home-range size	S4, A	≤500 km2
		J, S2, S3	600–800 km2
	Prey resource acquisition target	A	400
		S2, S3, S4	350
		J	300
	Prey resource class (% of resource target acquired in home range)	J, S2, S3, S4, A	Low (<40%)
			Medium (40–89%)
			High (≥90%)
Reproduction	Expected fecundity (mean, min, and max values of Poisson distribution)	A	0.40, 0, 3
		S4	0.17, 0, 3
	Prey resource class coefficient	S4, A	Low (multiply expected by 0.75)
			Medium (multiply expected by 1.00)
			High (multiply expected by 1.25)
	OHV exposure (% overlap of OHV area and territory)	S4, A	≥85%
Dispersal movements	Juvenile dispersal (1st-yr movement distance)	J	90–175 km
	Emigration (parameterized as additional mortality)	J, S2	0.10–0.12
	Immigration (annual introductions)	Random (1–5 yrs old)	15 individuals per year
Survival	Survival rates by stage and prey resource class	J	Low (0.70)
			Medium (0.74)
			High (0.80)
		S2	Low (0.70)
			Medium (0.77)
			High (0.80)
		S3, S4	Low (0.82)
			Medium (0.85)
			High (0.87)
		A	Low (0.85)
			Medium (0.87)
			High (0.89)

[a] Stage classes included juveniles (J), 2nd-yr subadults (S2), 3rd-yr subadults (S3), 4th-yr subadults (S4), and adults (A; eagles ≥5 yr old).