



RESEARCH ARTICLE

Spatial patterns in occupancy and reproduction of Golden Eagles during drought: Prospects for conservation in changing environments

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ABSTRACT

We used a broad-scale sampling design to investigate spatial patterns in occupancy and breeding success of territorial pairs of Golden Eagles (*Aquila chrysaetos*) in the Diablo Range, California, USA, during a period of exceptional drought (2014–2016). We surveyed 138 randomly selected sample sites over 4 occasions each year and identified 199 pairs of eagles, 100 of which were detected in focal sample sites. We then used dynamic multistate modeling to identify relationships between site occupancy and reproduction of Golden Eagles relative to spatial variability in landscape composition and drought conditions. We observed little variability among years in site occupancy (3-yr mean = 0.74), but the estimated annual probability of successful reproduction was relatively low during the study period and declined from 0.39 (\pm 0.08 SE) to 0.18 (\pm 0.07 SE). Probabilities of site occupancy and reproduction were substantially greater at sample sites that were occupied by successful breeders in the previous year, indicating the presence of sites that were consistently used by successfully reproducing eagles. We found strong evidence for nonrandom spatial distribution in both occupancy and reproduction: Sites with the greatest potential for occupancy were characterized by rugged terrain conditions with intermediate amounts of grassland interspersed with patches of oak woodland and coniferous forest, whereas successful reproduction was most strongly associated with the amount of precipitation that a site received during the nesting period. Our findings highlight the contribution of consistently occupied and productive breeding sites to overall productivity of the local breeding population, and show that both occupancy and reproduction at these sites were maintained even during a period of exceptional drought. Our approach to quantifying and mapping site quality should be especially useful for the spatial prioritization of compensation measures intended to help offset the impacts of increasing human land use and development on Golden Eagles and their habitats.

Keywords: Golden Eagle, *Aquila chrysaetos*, wind energy, occupancy, reproduction, drought

Patrones espaciales en ocupación y reproducción de *Aquila chrysaetos* durante la sequía: perspectivas para conservación en ambientes cambiantes

RESUMEN

Usamos un diseño de muestreo a gran escala para investigar los patrones espaciales en ocupación y éxito reproductivo de parejas territoriales de *Aquila chrysaetos* en las Montañas Diablo, California, durante un período de sequía excepcional (2014–2016). Evaluamos 138 sitios de muestreo durante cuatro ocasiones cada año e identificamos 199 parejas de águilas, 100 de las cuales fueron detectadas en sitios de muestreo focales. Luego usamos un enfoque de modelado dinámico multiestado para identificar las relaciones entre la ocupación del sitio y la reproducción de *A. chrysaetos* con la variabilidad espacial en la composición del paisaje y las condiciones de sequía. Observamos poca variación entre años en la ocupación del sitio (media de 3 años = 0.67), pero la probabilidad anual estimada de reproducción exitosa fue relativamente baja durante el período de estudio y disminuyó de 0.39 (EE = 0.08) a 0.18 (EE = 0.07). Las probabilidades de ocupación del sitio y reproducción fueron sustancialmente mayores en los sitios de muestreo que estuvieron ocupados por los individuos reproductivos exitosos en el año previo, indicando la presencia de sitios que fueron usados de manera consistente por las águilas reproductivas exitosas. Encontramos fuerte evidencia de una distribución espacial no azarosa tanto en ocupación como en reproducción – los sitios con el mayor potencial de ocupación estuvieron caracterizados por condiciones accidentadas del terreno, con cantidades intermedias de pastizales intercalados con parches de bosques de roble y coníferas, mientras que la reproducción exitosa estuvo más fuertemente asociada con la cantidad de precipitación que recibió un sitio durante el período de anidación. Nuestros resultados resaltaron las contribuciones de los sitios reproductivos productivos y ocupados consistentemente para con la productividad global de las poblaciones reproductivas locales, y mostraron que tanto la ocupación como la reproducción en estos sitios se mantuvieron incluso durante un período de sequía excepcional. Nuestro enfoque de cuantificar y mapear la calidad del sitio debería ser especialmente útil para la priorización espacial

de medidas de compensación destinadas a ayudar a contrarrestar los impactos del aumento del uso de la tierra y del desarrollo sobre *A. chrysaetos* y sus hábitats.

Palabras clave: *Aquila chrysaetos*, energía eólica, ocupación, reproducción, sequía

INTRODUCTION

In territorial birds, individuals occupying different habitats may experience varying probabilities of survival or reproduction depending on the amount and availability of resources within the area that they occupy (Ferrer and Donazar 1996, Balbontín et al. 2003, Sergio and Newton 2003). As a consequence, individuals that occupy the most productive areas (i.e. those with greater availability of resources and minimal disturbance) should be less affected by fluctuating environmental conditions, show less variability in occupancy and breeding success, and make a disproportionate contribution to long-term population productivity. Analyzing spatial patterns in occupancy and reproduction for territorial species is, therefore, an important step in conservation planning so that environmental features that contribute to site quality can be identified, measured, and, if possible, managed (Dunning et al. 1995, Whitfield et al. 2004, Martin et al. 2009, Lee and Bond 2015). However, site quality can be temporally and spatially dynamic as a result of natural or anthropogenic disturbances that influence an area's capacity to consistently support occupancy and reproduction. Broad-scale and flexible sampling approaches are needed to reliably identify and track dynamics in site quality, particularly in landscapes subject to high (or increasing) levels of environmental variation.

Golden Eagles (*Aquila chrysaetos*) are a long-lived, widely distributed raptor species of mounting conservation concern because they are especially sensitive to environmental changes associated with increases in human land use and development. Recent demographic analyses have been consistent in showing that any additive mortality posed by an increase in anthropogenic threats is likely to trigger population declines or exacerbate any declines that may be ongoing (USFWS 2016, Tack et al. 2017, Wiens et al. 2017). Monitoring trends in occupancy and breeding success of Golden Eagles at broad spatial scales could help land managers to proactively identify the environmental conditions associated with site quality so that conservation efforts can be strategically prioritized in areas that make disproportionate contributions to population persistence (e.g., Sergio and Newton 2003, Hipkiss et al. 2014). Nonetheless, monitoring the occupancy and reproduction of Golden Eagles at broad spatial scales can be logistically challenging and expensive.

Recent advances in survey design and interpretation of distributional data have made species-level monitoring at broad spatial scales considerably more feasible and cost

effective than in the past (Noon et al. 2012, Rossman et al. 2016). In particular, sampling designs associated with monitoring sites (e.g., a territory or other predefined area) can be a useful approach to investigate population dynamics and evaluate how landscape features or human land use might influence those dynamics (MacKenzie et al. 2006, 2012, Martin et al. 2009). Individuals of many species may be difficult to detect, depending on physiographic conditions or the period of the breeding cycle, so strong inference from site occupancy studies requires accounting for imperfect detection (i.e. failure to detect the species when it is present). Failing to account for imperfect detection can lead to inaccurate estimates of state variables such as the proportion of sites that are occupied or used, the proportion of sites with successful reproduction, or species abundance (MacKenzie et al. 2006, Nichols et al. 2007, Guillera-Aroita et al. 2014). Methods are now well developed for using detection–nondetection data to estimate dynamics in site occupancy and reproduction, while accounting for imperfect detection (Nichols et al. 2007, MacKenzie et al. 2009, 2012, Lee and Bond 2015). Dynamic multistate modeling considers multiple biologically relevant states, such as breeding or nonbreeding, which provides an especially useful framework for investigating occupancy and reproduction by accounting for the potential effects of the previous year's occupancy status (i.e. vacant, occupied with no young, or occupied with young). This is relevant because the likelihood of a site being occupied or supporting reproduction in a given year could be either lower or higher when young were produced in the previous year because of site-specific resource depletion (Pulliam and Danielson 1991), or, alternatively, because of the site's capability to support more consistent resources or higher-quality individuals (Sergio et al. 2009, Lee and Bond 2015). In the case of Golden Eagles, this framework can be used to estimate, analyze, and map spatial patterns of occupancy and reproduction. Such information is particularly useful for conservation policy that aims to maximize reproductive success and maintain stable breeding populations (Bald Eagle Protection Act of 1940 (16 U.S.C. 668–668d, 54 Stat. 250) as amended, USFWS 2013).

We used detection–nondetection data collected under a multistate occupancy survey design framework to identify spatial patterns in site quality of Golden Eagles, where occupancy and reproduction were considered measures of quality. Our study was conducted during a period of exceptional drought in the northern Diablo Range of west-

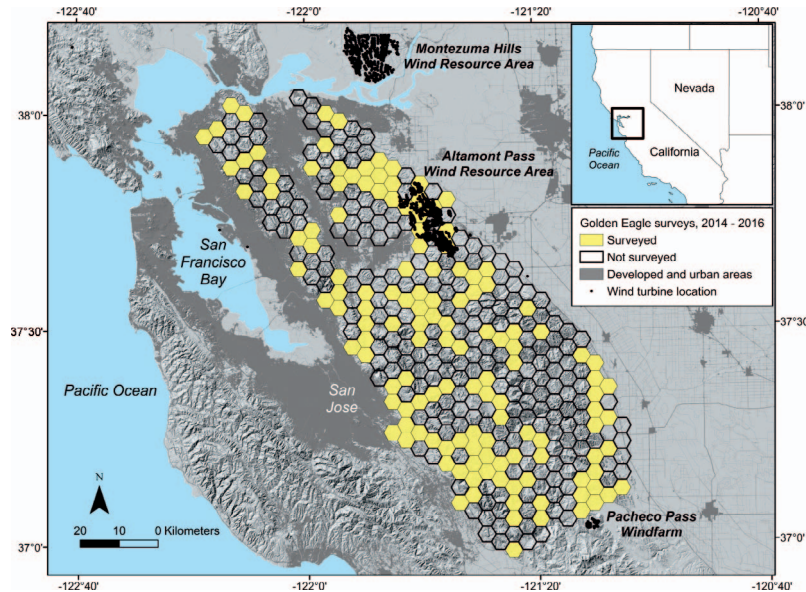


FIGURE 1. The Diablo Range study area of west-central California, USA, including the distribution of 138 randomly selected survey sites (1,385-ha hexagons highlighted in yellow) that were repeatedly searched each year from 2014 to 2016 for evidence of occupancy and reproduction by Golden Eagles. We also show the distribution of operational wind energy facilities in the study region.

central California, USA, a region that supports one of the densest known breeding populations of Golden Eagles in North America (~ 54 pairs per 1,000 km^2 ; Wiens et al. 2015, Hunt et al. 2017). This region includes the Altamont Pass Wind Resource Area (APWRA), where previous reports have indicated that ~ 65 Golden Eagles are killed annually by collisions with wind turbines (Smallwood and Thelander 2008). Thus, our goal was not only to characterize broad-scale patterns in quality of breeding sites for Golden Eagles, but also to consider how such patterns might be used within a management context to help offset the highly localized source of mortality associated with wind energy production in our study area. Our specific objectives were to: (1) examine potential sources of variation in the probability of detection, occupancy, and reproduction, (2) develop predictive spatial models of occupancy and reproduction, and (3) provide recommendations to improve strategies for identifying and monitoring the site quality of Golden Eagles at broad spatial scales.

METHODS

Study Area

The 5,170 km^2 study area was located in the northern Diablo Range of west-central California (approximate site center: 37.497889°N, 121.610394°W; Figure 1). We delineated this area based on movements of resident Golden Eagles radio-tagged within the vicinity of the APWRA during 1994–2000 (Hunt 2002, Hunt et al. 2017). The

study area ranged from 0 m to 1,333 m above mean sea-level elevation and was dominated by chaparral and California oak woodland communities, with stands of coniferous forest appearing above 1,200 m. The northern portion of our study area was mostly grassland, with occasional rocky outcroppings and widely scattered stands of oak (*Quercus* spp.), eucalyptus (*Eucalyptus* spp.), California foothill pine (*Pinus sabiniana*), Coulter pine (*P. coulteri*), and California buckeye (*Aesculus californica*). Grasslands with scattered patches of oak (oak savannah) descended to the agricultural flatlands of the San Joaquin Valley to the east, and the study area was bounded to the west and southwest by highly developed urban areas and cities extending from Berkeley and the San Francisco Bay southward to San Jose. Vegetation types were more diverse in the central portion of our study area, which included a high density of oak woodlands interspersed with chaparral, sage scrub, and open grassland. The region had a Mediterranean climate characterized by hot, dry summers and cool, wet winters. Average annual rainfall was 389 mm, with most precipitation occurring between September and April (U.S. Climate Data, <http://www.usclimatedata.com>). The average high temperature was 23°C. Land use consisted of private ranchlands with livestock grazing, in addition to state and county lands that received varying levels of cattle grazing and recreational use. The APWRA was located in the northeastern portion of the study area (see Smallwood and Thelander (2008) and Hunt et al. (2017) for additional details about APWRA), and 2 other wind energy facilities (Montezuma Hills Wind Resource

Area and Pacheco Pass) were located on the periphery (Figure 1).

Sampling Design and Eagle Surveys

Our study area included all areas in public or private ownership, but we excluded the densely populated urban areas of the San Francisco Bay area and the agricultural fields of the San Joaquin Valley from our sampling scheme because Golden Eagles radio-tagged in our study area were rarely observed using these landscapes (Hunt 2002). Surveys could not be performed in all areas potentially occupied by eagles in the study area due to budget constraints, logistical considerations, and limited access to private lands. Consequently, we used a probabilistic sampling approach to infer estimates of site occupancy and reproduction by territorial pairs of Golden Eagles. Areas targeted for repeated surveys of Golden Eagles were randomly selected from a grid of 373 equally sized (1,385 ha) hexagonal cells overlaid on the study area (total area = 516,844 ha; Figure 1). The size of each survey hexagon corresponded to the estimated mean size of the annual core-use area of territorial Golden Eagles radio-tagged in the study area (~1,385 ha). Thus, under our sampling design, a 'site' was defined as a 1,385-ha hexagonal area that had the potential to be occupied by ≥ 1 territorial pair of Golden Eagles during the breeding season.

We followed the general recommendations of Driscoll (2010) and Pagel et al. (2010) for surveys of Golden Eagles. Based on approximate transition dates between stages in the breeding cycle of Golden Eagles in our study area (Hunt 2002), we partitioned surveys within years using 4 developmental stages of the breeding season: courtship (December 15–February 28), incubation (March 1–April 30), the nestling period (May 1–June 15), and the fledgling period (June 16–July 30). Each time period represented a survey occasion in our analysis. On each survey occasion, observers established observation points on selected ridges and hilltops that provided views of the entire focal sampling plot. Observers then searched for evidence of occupancy and reproduction by territorial pairs of eagles for up to 4 hr per observation period per survey using binoculars and high-powered (40–50 \times) spotting scopes. Some sites required surveys spaced <5 days apart to achieve complete coverage. We used a multistate occupancy framework for surveys (Nichols et al. 2007, MacKenzie et al. 2009, 2012), wherein the goal was to characterize the focal sample site as being in 1 of 3 possible observation states: (1) no territorial pair of eagles detected (state 0); (2) ≥ 1 territorial pair detected but no evidence of successful nesting observed (state 1); or (3) ≥ 1 territorial pair detected with evidence of successful reproduction (state 2). When possible, we classified eagles as juveniles, subadults, or adults based on visible plumage characteristics (Bloom and Clark 2001, Kolar and Wiens 2017). A

sample site was classified as unoccupied (state 0) if no eagles were observed, or if ≥ 1 eagles were observed that were not demonstrating nesting or territorial behaviors. A sample site was considered to be occupied by a territorial pair of eagles (state 1) if we observed: (1) a male and female copulating, undulating, perching together, or attacking intruders, or (2) an incubating eagle on a nest, young nestlings in a nest, or a female with a brood patch. We attributed detections of territorial pairs to sample sites by mapping activity centers of pair observations (i.e. a used nest, locations of fledglings, or focal area of copulations, territorial displays, and perches). We surveyed sites with pair detections during mid-June to late July to determine the number of young fledged, after most nestlings were $>80\%$ of average fledging age (~56 days old; Driscoll 2010). A site was accorded successful reproduction (state 2) if ≥ 1 nestlings or fledglings of this age were observed (Steenhof et al. 1997, Kochert et al. 2002, Steenhof and Newton 2007). We recorded failed nesting attempts in cases in which evidence of nesting was found (e.g., incubating female) but no young were produced. We omitted failed nesting attempts as an additional state in our analysis because that would have demanded larger sample sizes and was beyond the scope of our study.

Characteristics of Sample Sites

Anticipating spatial and temporal heterogeneity in estimates of occupancy and reproduction—through study design and by collecting data on relevant covariates to model existing variation—is essential for good performance of site-occupancy models (MacKenzie et al. 2006, 2009). Accordingly, we quantified a small set of site-specific covariates to explore potential sources of variation in landscape occupancy and reproduction of Golden Eagles (Table 1).

Vegetation cover and terrain. We predicted that landscape conditions, including primary vegetation type (grassland, forest, or scrubland) and terrain, could influence the occupancy and reproduction of Golden Eagles because prey detection and hunting success are most often associated with rugged, open landscapes (Marzluff et al. 1997, Kochert et al. 2002, McIntyre et al. 2006, Singh et al. 2016). California ground squirrels (*Otospermophilus beecheyi*) were the predominant prey of Golden Eagles in our study region (Carnie 1954, Hunt et al. 2017) and were widespread and numerous, especially in grasslands and open oak woodlands (Grinnell and Dixon 1918, Fitch 1948). Other important prey included black-tailed jackrabbits (*Lepus californicus*) and desert cottontails (*Sylvilagus audubonii*). We used the National Oceanic and Atmospheric Administration's Coastal Change Analysis Program (C-CAP) regional land cover map to characterize the distribution of vegetation types in our study area (NOAA 2010). The map included 29 categories

TABLE 1. Site characteristics considered in dynamic multistate occupancy models of detection, occupancy, and reproduction of Golden Eagles in the Diablo Range, California, USA, 2014–2016.

Site characteristic	Description	Mean value (SD)	Min–Max
Grassland	Areas dominated by graminoid or herbaceous vegetation, generally >80% of total vegetation (NOAA 2010).	0.44 (0.29) ^a	0.02–0.99
Scrub	Areas dominated by shrubs <5 m tall, with shrub canopy >20% of total vegetation cover. Included tree shrubs and young trees in early successional stage (NOAA 2010).	0.17 (0.21) ^a	0.00–0.84
Forest	Areas dominated by trees generally >5 m tall and >20% of total vegetation cover. Included deciduous, evergreen, and mixed species (NOAA 2010).	0.29 (0.21) ^a	0.00–0.78
Topographic roughness (TRI)	Mean terrain ruggedness, where larger values indicate greater terrain heterogeneity, or more rugged areas. Calculated as the difference between the elevation value of each cell of a 30-m resolution digital elevation model and the mean of the 8-cell neighborhood surrounding each focal cell.	78.9 (30.8)	6.1–162.0
pptEN	Mean amount of precipitation (mm) during the early nesting period (December 1 to March 31).	294.3 (67.6)	35.6–489.8
pptBR	Mean amount of precipitation (mm) during the brood-rearing period (April 1 to June 30).	45.9 (7.5)	14.5–73.8
ppt _{t-1}	Mean amount of precipitation (mm) in the year (January 1 to December 31) prior to the current year's breeding season.	234.2 (53.0)	125.6–365.9
Tmax	Mean maximum temperature (°C) during brood-rearing (April 1 to June 30).	23.9 (2.0)	19.4–29.6

^a Values expressed as the proportion of a 1,385-ha sample site used to survey eagles.

of land cover (21 of which occurred in our study area) and was produced for the Pacific coastal region of California using 30-m resolution satellite imagery. Extensive field sampling, validation, and standard quality-control review procedures were used in developing the map (NOAA 2010). We combined existing land cover types into 3 general categories that we hypothesized would be important sources of spatial variation to territorial pairs of eagles: open grassland, scrub and shrub vegetation, and forest cover (Table 1).

Topography interacts with wind conditions and vegetation cover to influence the movements and foraging tactics of Golden Eagles (McLeod et al. 2002, Katzner et al. 2012, Watson et al. 2014). To evaluate how terrain features might influence the landscape occupancy patterns of Golden Eagles, we used ArcGIS 10.1 (ESRI, Redlands, California, USA) and a 30-m resolution digital elevation model (DEM) to estimate mean terrain ruggedness (TRI) for each sample site (Riley et al. 1999). Terrain ruggedness was calculated as the difference between the elevation value of each 10-m cell of the DEM and the mean of the 8-cell neighborhood surrounding the focal sampling cell within each 1,385 ha survey hexagon. We considered TRI to be a measure of terrain heterogeneity among sites, where larger values indicated greater heterogeneity, or a more rugged area (Table 1).

Drought conditions. Our study was conducted during the most severe multiyear drought to have affected the region in the past 1,200 yr (Griffin and Anchukaitis 2014, Mann and Gleick 2015). Central and southern California

experienced the lowest precipitation totals in the observed climate record, the effects of which were amplified by record high temperatures. Drought can strongly affect the population demography of raptors, especially their reproduction (Newton 1998, Macías-Duarte et al. 2004, Cruz-McDonnell and Wolf 2016). Associations between drought and reductions in reproduction are typically explained by the combined effects of reduced rainfall and increased air temperature on primary production and prey populations, whereby breeders may forgo nesting, suffer more nesting failures, or raise fewer young in years of low precipitation (Hustler and Howells 1990, Wichmann et al. 2003). We predicted that the hot, dry conditions associated with drought in our study area could have limited the primary productivity of grasslands, availability of prey, and, ultimately, reproduction of Golden Eagles. We further predicted that drought-related effects could have been spatially variable in our study area because of differences among sites in vegetation cover, elevation, terrain, and coastal proximity, which could have resulted in highly localized patterns of rainfall (Daly et al. 2008).

To investigate our predictions, we obtained spatial data on precipitation and maximum temperature from PRISM maps (PRISM Climate Group, Oregon State University, Corvallis, Oregon, USA; <http://prism.oregonstate.edu>). PRISM maps were raster-based digital maps with 4-km² spatial resolution representing mean monthly temperature (°C) and total monthly precipitation (mm) developed from local weather station data and a DEM (Daly et al. 2008). Weather variables in our analysis included maximum

mean temperature during the brood-rearing period (late incubation, nestling, and early fledgling; April 1 to June 30), and total precipitation calculated for 3 different time periods: (1) the year prior to the current year's breeding season (January 1–December 31); (2) early nesting (courtship, nest building, and incubation; December 1 to March 31); and (3) brood-rearing. We obtained site-specific estimates of total precipitation and mean maximum temperature by computing the average values of PRISM raster cells within each sample site in ArcGIS 10.1.

Data Analysis

Detection, occupancy, and reproduction of territorial pairs. We created detection histories for 138 of 373 sites that were randomly selected for repeated surveys of Golden Eagles. Sites were typically surveyed 3–4 times each year (mean number of visits per site per year = 3.2). Time intervals in which surveys could not be completed because of weather or logistical constraints were coded as missing observations (MacKenzie et al. 2012). We analyzed detection histories with dynamic multistate occupancy models in program MARK (White and Burnham 1999) to estimate detectability and the probability of a site being vacant (state 0) or occupied by unsuccessful (state 1) or successful (state 2) breeders. We followed the model parameterization used by MacKenzie et al. (2009, 2012), where ψ_1 was the probability that a sample site was occupied in the first year of the study, and R_1 was the probability that successful reproduction occurred at a site in the first year, given that the site was occupied (i.e. state 2). For subsequent years, similar probabilities were defined that could vary by state in the previous year, where ψ_{xi} was the probability that a given site was occupied in year i , conditional upon state ($x = 0, 1$, or 2) in the previous year ($i - 1$), and R_{xi} was the probability that successful breeders were present in year i , conditional upon state in the previous year. Detection probabilities also followed the MacKenzie et al. (2009) parameterization, where $p1_{ik}$ was the probability of detecting occupancy during survey k , given that the site was occupied with no successful reproduction in year i , $p2_{ik}$ was the probability of detecting occupancy during survey k , given that the site was occupied by a pair of eagles that successfully reproduced in year i , and δ_{ik} was the probability of correctly identifying successful reproduction (observing young) at a site, given that the site was occupied and reproduction had occurred. Primary assumptions were that: (1) the occupancy status of sample sites did not change during the breeding season, (2) detection histories among sites were independent, and (3) there were no false positives for higher-order states (i.e. if successful breeding was observed [state 2], the true state of the site could not be 0 or 1; MacKenzie et al. 2009).

Model development and selection. We developed and ranked a suite of candidate models using a sequential

approach to model selection, similar to that used by MacKenzie et al. (2012), Lee and Bond (2015), and Tempel et al. (2016). Each model represented a competing hypothesis about the effects of time and spatial covariates on probabilities of detection, occupancy, and reproduction. Our strategy was to examine time- and state-specific variation in each model parameter first, then determine support for site-specific covariates toward explaining any existing temporal or spatial variation. We used this approach to avoid fitting an excessive number of possible models, which could lead to ambiguous results. We selected the best model at each stage of the analysis using Akaike's information criterion adjusted for small sample size (AIC_c), and used the selected model with the lowest AIC_c in subsequent stages. We evaluated the strength of evidence for each model using differences in AIC_c (ΔAIC_c) and AIC_c weights (Burnham and Anderson 2002). At each stage of the analysis, the model with the lowest AIC_c was cross-checked against competitive models (those with $\Delta AIC_c \leq 2.0$) from the previous stage to ensure that we apportioned variation correctly among model parameters. We examined maximized log-likelihood ($-2\ln L$) and model deviance values to ensure that ΔAIC_c values were not solely a result of adding additional, uninformative parameters (Arnold 2010). We also gauged the strength of evidence for competing models based on the degree to which 95% confidence intervals (95% CI) of covariate slope coefficients overlapped zero. Competitive models with covariate coefficients that had a 95% CI that did not include zero were considered to have the strongest support. The modeling procedure included 6 sequential stages:

- (1) We assessed within- and among-year variation in probabilities of detection ($p1$, $p2$, δ) while holding occupancy and reproduction parameters at their most general structure, {state*year}. We considered 9 alternative models in which detection probabilities were constant over occupancy states and survey periods (i.e. breeding stages), varying between occupancy states but constant over survey periods, or varying with occupancy state, survey period, and year. The probability of observing young (δ) was modeled as time-dependent, but we fixed δ_1 and $\delta_2 = 0$ in all models because it was not possible to observe fledged young during the first 2 survey periods within a year.
- (2) We determined how the availability of historical data on nest locations and the amount of forest cover at sample sites influenced detection probabilities. In our study area, some of our focal sample sites ($n = 32$ sites in 2014) had historical data on the locations of eagles and their nests from a previous study (Hunt 2002), whereas the remaining sites had not been previously

surveyed and had no historical information. Observers used historical nest locations to facilitate searches during surveys, so we anticipated that the probability of detecting territorial eagles and their young would be greater at sites where such information was available. To account for this potential source of heterogeneity in detection, we used a spatial covariate that allowed detection rates to vary between sample sites with and without historical data (i.e. the covariate was 1 if historical data were available for a site and 0 otherwise). This covariate was updated annually to include newly discovered nests. We anticipated that historical data on nest locations would have a greater effect on detecting breeders (p_2) and their young (δ) than on detecting nonbreeders (p_1) based on preliminary findings from surveys conducted in 2014 (Wiens et al. 2015). We also predicted that the amount of forest cover in a sample site could have a negative influence on detectability because Golden Eagles in our study area nested almost exclusively in oak and pine trees, which often obscured observations of adults and young during surveys, especially in sites with more extensive forest cover.

- (3) We determined whether the previous year's reproductive state was correlated with the current year's occupancy and reproductive state while describing detection probabilities according to the best model structure from steps 1 and 2. We predicted that sites occupied by successful breeders in the previous year would have greater probabilities of occupancy and reproduction in the current year than sites without successful breeders in the previous year. The mechanisms underlying this hypothesis include the possibility that such sites were of high quality, or sources (Pulliam 1988) in that they made relatively large contributions to overall population productivity relative to other sites (Runge et al. 2006, MacKenzie et al. 2009). Alternatively, if the probability of occupancy or reproduction was lower at sites where reproduction had occurred previously, that might suggest resource depletion, or an energetic cost of raising young imposed on the following year's breeding effort (Lee and Bond 2015). We ranked an additional 5 candidate models in which current year's occupancy and reproduction were either constant over occupancy states (i.e. the effect of year only) or dependent upon the previous year's state (i.e. model {state + year}).
- (4) We examined the potential effects of terrain and vegetation conditions on the probability of occupancy. We considered 4 site-specific covariates: terrain ruggedness (SD of mean elevation), and the proportion of site with grassland, forest, or scrubland vegetation cover types (Table 1). We predicted that occupancy would be positively associated with increasingly rough

terrain conditions and the amount of grassland cover within survey sites, and negatively associated with the amount of forest and scrubland cover types (Crandall et al. 2015, Nielson et al. 2016). We modeled the effects of grassland and forest cover separately because these effects were negatively correlated with one another. We considered a nonlinear (quadratic) relationship between grassland and occupancy because we posited that sites with too little or too much grassland could limit opportunities for foraging or nesting.

- (5) We investigated how drought conditions influenced reproduction. Previous studies of Golden Eagles conducted near the APWRA showed that the proportion of pairs that attempted to nest varied among years (presumably in response to environmental variation), whereas territory occupancy did not (Hunt et al. 2017). As a consequence, we chose to model drought conditions separately from and prior to the effects of terrain and vegetation conditions on reproduction. We predicted that there would be time- and site-specific effects of drought on reproduction, such that the amount of precipitation that a site received would be positively correlated with reproduction, and the mean maximum temperature would be negatively associated with reproduction (Steenhof et al. 1997, Watson 2010, Reynolds et al. 2017). We predicted that years with greater amounts of precipitation during drought would positively affect reproduction in the following breeding season. We also considered a model with both precipitation and temperature, which represented a hypothesis that these effects had an additive influence on reproduction.
- (6) We examined how terrain and vegetation conditions influenced the probability of reproduction. We predicted that there would be site-specific, vegetation-related effects on reproduction, such that the amount of grassland would be positively related to reproduction, whereas scrubland or forest vegetation types (which could hamper prey availability or foraging success) would be negatively correlated with reproduction. We assessed an additional 6 candidate models in this final stage of model selection.

We used the final, top-ranked model to project annual estimates of occupancy and reproduction across the landscape on the grid of hexagonal sample sites that covered the entire study area (Figure 1). For sample sites that were not surveyed, we estimated unconditional probabilities of occupancy and reproduction at site i based on covariate values associated with the site (MacKenzie et al. 2006). For sites that were surveyed, we estimated conditional probabilities at site i based on covariate values and site-specific detection histories. We used ArcGIS 10.3 (ESRI, Redlands, California, USA) for this analysis.

TABLE 2. Survey effort, detections of Golden Eagles, and evidence of reproduction found during multistate occupancy surveys conducted in the Diablo Range, California, USA, 2014–2016.

	2014	2015	2016	Years combined
Sites surveyed	133	134	136	403
Sites with ≥ 1 territorial pairs detected	88	89	89	266
Sites with nesting attempt detected	20	24	27	71
Sites with successful nest detected	17	15	20	52
Total fledged young detected	22	19	30	71
Observed occupancy ^a	0.66	0.66	0.65	0.66
Observed nesting rate ^{a,b}	0.15	0.18	0.20	0.18
Observed nesting success ^{a,b}	0.13	0.11	0.15	0.13
Young fledged per occupied site	0.25	0.21	0.34	0.27
Young fledged per successful site	1.29	1.27	1.50	1.37

^a Observed (naïve) estimates do not account for imperfect detection during surveys.^b Does not include 1 of 2 pairs that nested in the same sample site in 2015 and 2016.

RESULTS

We searched 138 sample sites up to 4 times per site annually from 2014 to 2016 and recorded 2,674 detections of individual Golden Eagles: 1,728 (65%) adults, 352 (13%) subadults, 257 (10%) juveniles (i.e. first-year birds, including nestlings and fledglings), and 337 (13%) eagles of unknown age. We mapped the activity centers of ≥ 1 territorial pairs of eagles in 90 (65%) of 138 sample sites surveyed. The total number of territorial pairs detected in focal sample sites varied little among years (range = 88 to 89 pairs; Table 2). Based on mapped locations of used nests and activity centers of paired eagles, 81 (90%) of 90 occupied sample sites were occupied by 1 pair during the study, 8 (9%) were occupied by 2 pairs, and 1 (1%) site included the nests and activity centers of 3 different pairs of eagles (\bar{x} = 1.11 pairs detected per sample site). During annual surveys we detected as many as 99 additional territorial pairs with activity centers that fell outside the boundary of a focal survey site (i.e. ancillary detections). Thus, in total, we detected as many as 199 pairs of eagles, 100 of which were located in focal sample sites in at least one year and included in occupancy analyses. We found evidence of successful reproduction (≥ 1 fledgling detected) at 15–20 sample sites annually (Table 2). The mean number of fledglings detected per successful nest over the 3-yr study was 1.37 (\pm 0.07 SE; range = 1.27 to 1.50). A total of 20 (27%) of 73 observed nesting attempts apparently failed during the incubation or early nestling stages for unknown reasons.

Detection of Territorial Pairs and Their Young

We provide model selection results (stages 1–6) in Appendix Table 4. The best model of among- and within-year variation in detection probabilities was $\{p1(\text{survey}) p2(.) \delta(\text{year} + \text{survey})\}$, which indicated that:

(1) the probability of detecting eagles that were nonbreeders or unsuccessful ($p1$) declined from 0.91 (\pm 0.03 SE) to 0.38 (\pm 0.06 SE) during the breeding season (Figure 2A); (2) the probability of detecting successful breeders ($p2$) remained constant over time at 0.88 (\pm 0.03 SE; Figure 2A); and (3) the probability of observing young at occupied sites (δ) varied among years and among survey occasions (Figure 2B, Appendix Table 5). Availability of historical data on nest locations (HD) had a strong and positive effect on the probabilities of detecting successful breeders ($p2$) and observing young (δ ; Figure 2B), but this effect was not strongly associated with the detection of nonreproductive pairs ($p1$). A model that included the effect of forest cover on δ was competitive ($\Delta\text{AIC}_c = 0.29$), but the slope coefficient for this effect overlapped zero ($\hat{\beta} = -1.68$, 95% CL = $-4.02, 0.65$), indicating relatively weak support for this parameter. The overall best model of detection probability was $\{p1(\text{survey}) p2(\text{HD}) \delta(\text{year} + \text{survey} + \text{HD})\}$, which we retained when modeling occupancy and reproduction.

Occupancy and Reproduction

Influence of previous year's occupancy state. Reproductive status at a sample site in the previous year was a consistent predictor of the current year's occupancy and reproductive status. The top-ranked model examining the effects of previous year's occupancy status, $\{\psi(\text{state}) R(\text{state} + \text{year})\}$, indicated that there was annual variation in reproduction (but not occupancy), and that the pattern of variation depended upon reproductive status at the site in the previous year (Appendix Tables 4 and 5). Probabilities of occupancy and reproduction estimated under the top-ranked model were consistently greater at sites that were occupied by reproductive eagles in the previous year as compared with sites that were vacant or occupied by nonreproductive eagles; the probability of occupancy was 0.17 (\pm 0.04 SE), 0.87 (\pm 0.05 SE), and 0.96 (\pm 0.03 SE) for

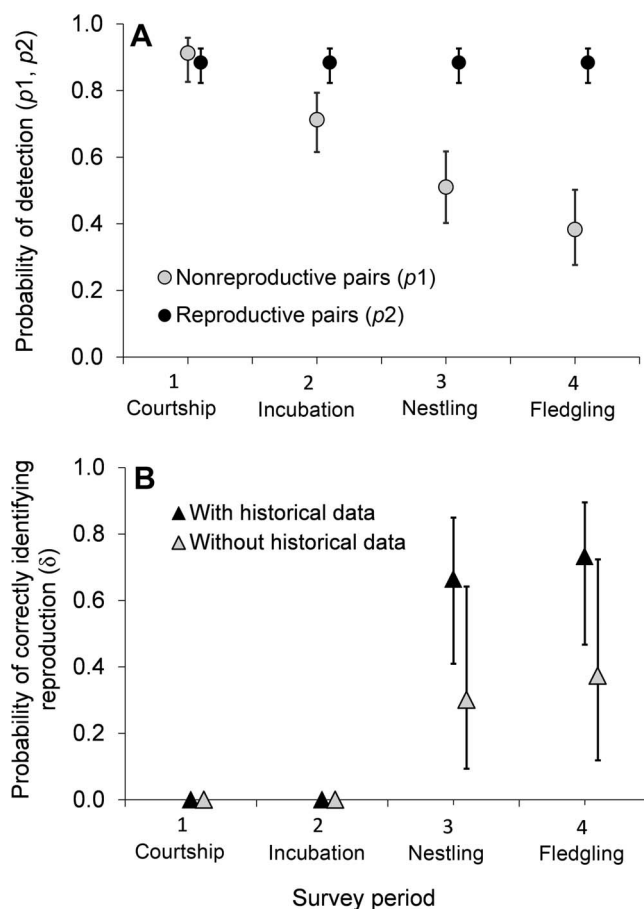


FIGURE 2. Within-season change in (A) the probability of detecting territorial pairs of Golden Eagles that successfully produced young or did not, and (B) the probability of correctly identifying successful reproduction (i.e. observing young that were present) at sites with and without historical data available on locations of previously used nests in the Diablo Range, California, USA, 2014–2016. Vertical lines represent 95% confidence intervals. Parameter estimates are from the top-ranked multistate model (Appendix Table 4).

sites that in the previous year were vacant, had nonreproductive eagles, or had reproductive eagles, respectively. On average, the probability of reproduction was $0.08 (\pm 0.05 \text{ SE})$, $0.10 (\pm 0.02 \text{ SE})$, and $0.72 (\pm 0.03 \text{ SE})$ for sites which in the previous year were vacant, had nonreproductive eagles, or had reproductive eagles, respectively.

Influence of landscape conditions and weather. Top models that included the influence of landscape attributes and weather covariates on occupancy and reproduction outperformed models without these spatial covariates ($\Delta\text{AIC}_c = 4.87$ to 13.54 ; Appendix Table 4). The overall top-ranked model for occupancy, $\{\psi(\text{state} + \text{TRI} + \text{grassland}^2 + \text{scrub})\}$, indicated that state-dependent occupancy was positively influenced by terrain ruggedness (Figure 3A), had a nonlinear (quadratic) relationship with grassland (Figure 3B), and was negatively influenced by the

TABLE 3. Derived estimates, with standard errors (SE) and lower (LCL) and upper (UCL) 95% confidence limits, for the probability of occupancy and successful reproduction by Golden Eagles in the Diablo Range, California, USA, 2014–2016. Annual estimates are from the top-ranked dynamic multistate occupancy model (Appendix Table 4); covariates were held constant at their median values.

Parameter and year	Estimate	SE	LCL	UCL
Probability of occupancy				
2014	0.678	0.041	0.592	0.753
2015	0.755	0.041	0.666	0.827
2016	0.799	0.052	0.668	0.883
Probability of successful reproduction (≥ 1 young fledged)				
2014	0.389	0.084	0.241	0.561
2015	0.200	0.070	0.097	0.371
2016	0.179	0.071	0.077	0.362

amount of scrubland vegetation cover (Appendix Table 5). When we replaced the generic effect of ‘year’ in the previous best model of reproduction with the annual covariate for total amount of precipitation during brood-rearing, a better (lower AIC_c) model was attained. The overall top-ranked model for reproduction, $\{R(\text{state} + \text{pptBR} + \text{grassland})\}$, showed that successful breeding was positively influenced by the additive effects of mean precipitation during brood-rearing and amount of grassland vegetation (Figure 4). A closely competing model ($\Delta\text{AIC}_c = 0.32$) included a negative effect of scrubland on reproduction ($\hat{\beta} = -5.93$, 95% CI = -11.56 to -0.30). High amounts of forest cover were negatively associated with both occupancy and reproduction, but this effect was relatively weak compared with the effect of grassland vegetation cover. Estimates of parameters derived from the top model (Table 3) showed that there was little variability among years in occupancy (3-yr mean = 0.74), and that the annual probability of reproduction declined from $0.39 (\pm 0.08 \text{ SE})$ to $0.18 (\pm 0.07 \text{ SE})$. We cross-checked competitive models from previous modeling stages against the final, best-supported model, but none of these ‘post hoc’ models were competitive ($\Delta\text{AIC}_c > 8.0$).

Projected site-specific parameter estimates from the final model illustrated a patchy and nonrandom distribution of occupancy and state-dependent reproduction of Golden Eagles (Figure 5). The final model predicted lower reproduction in areas in the southeastern portion of the study area that received relatively little rainfall (Figure 5). The most contiguous areas of consistently greater probabilities of occupancy and reproduction among years were in the northern and northwestern portions of the study area, and included the APWRA.

DISCUSSION

Our study used a broad-scale, randomized sampling design to characterize patterns of spatial and temporal variation

in detectability, site occupancy, and reproduction in a population of Golden Eagles exposed to a variety of natural and anthropogenic stressors in the northern Diablo Range of west-central California. Three general findings came out of our study. First, probabilities of site occupancy and reproduction were substantially greater at sites that were occupied by successful breeders in the previous year, indicating the presence of sites that were consistently used by successfully reproducing pairs of eagles. Second, our analysis and results provided strong evidence for nonrandom spatial distribution in site quality of Golden Eagles, as measured by occupancy and reproduction. Spatial variation in these parameters was best explained by differences among survey sites in vegetation cover, terrain conditions, and the amount of rainfall that a site received during the nesting period. Third, the probability of detecting territorial pairs during surveys was <1.0 and varied with time of the breeding season, as did the probability of observing young at sites with reproductive pairs. Imperfect detection of eagle pairs and their young resulted in notable differences (0.02–0.13 among years) between naïve estimates of the proportion of sites with successful reproduction and model-based estimates. Our findings highlight the contribution of consistently occupied and productive breeding sites to the local population, and showed that occupancy and reproduction at these productive sites was maintained even during a historically severe drought period. Our approach to monitoring site occupancy and reproduction offered the opportunity to quickly detect the environmental conditions that contribute to site quality for Golden Eagles at broad spatial scales. This information can help local resource managers to recognize and maintain high-quality areas that make disproportionate contributions to population productivity and persistence.

Spatial Patterns in Site Quality

Site quality, as reflected by spatial variation in occupancy and successful reproduction, may affect individual fitness and contribute to density-dependent reproduction, with strong implications for population limitation (Ferrer and Donazar 1996, Sergio and Newton 2003, Hunt et al. 2017). In long-lived raptors such as Golden Eagles, a key feature of site-dependent population limitation is that a relatively small number of breeding sites may sustain a large population through source–sink dynamics (Newton 1991, Sergio and Newton 2003, Hipkiss et al. 2014). As in many other raptor species, the breeding segment of Golden Eagle populations is buffered by segments of floating, non-territorial individuals that can quickly fill territory vacancies as they arise (Hunt 1998). The basis for the ‘floater’ adaptation is that waiting for access to a high-quality territory confers higher fitness than accepting a substandard one, the threshold of site acceptance being the promise of replacement-rate reproduction over the

individual’s lifetime (Kokko and Sutherland 1998). Variation in site quality can also sustain eagle populations that have declined to the point of losing their floater buffer, as long as source sites remain (Ferrer and Donazar 1996, Hunt et al. 2017).

Our analysis indicated an overall high and consistent proportion of sample sites that were occupied by pairs of Golden Eagles (3-yr mean = 0.74). By projecting modeled estimates across the study area (Figure 5), we illustrated that the spatial pattern of pair occupancy was not uniform, and that few areas had a consistently high probability of successful reproduction during the study. Areas with a relatively greater probability of occupancy were patchily distributed relative to landscape conditions (i.e. more rugged terrain with intermediate amounts of open grassland vegetation). In addition, reproduction was markedly greater at sites with successful breeders in the previous year (Figure 4), indicating the presence of sites that were consistently occupied by successfully reproducing eagles during the study. This finding was similar to that of Martin et al. (2009), who used dynamic multistate occupancy modeling to show that long-term (1988–2007) reproduction of Golden Eagles at historical breeding territories in interior Alaska, USA, was also associated with the previous year’s reproductive status. The effect of previous year’s occupancy state was less pronounced in that study relative to ours, but differences in study design and duration make direct comparisons difficult. Regardless, these findings do support the hypothesis that certain sites acted as sources (Pulliam 1988), in that they consistently made disproportionately large contributions to overall population productivity relative to other sites (Runge et al. 2006, MacKenzie et al. 2012). Inferences in our study were based on sites, not individual eagles, so it was unclear if sites with consistent reproduction were influenced more by the site’s physiographic conditions, or if older, more experienced individuals with greater reproductive abilities occupied areas with better and more consistent resources (e.g., Carrete et al. 2006). As long-lived, fiercely territorial birds with strong fidelity to breeding sites and mates (Kochert et al. 2002), Golden Eagles are expected to show a positive correlation between individual and site quality if intrinsically superior or more experienced individuals settle in and retain sites with relatively greater availability of resources (Łomnicki 1988, Sergio et al. 2009).

Our finding that occupancy was positively associated with rugged and open grasslands was consistent with that of several other studies that investigated relationships between landscape conditions and finer-scale patterns of resource use by Golden Eagles. Topography, in particular, is a highly relevant component of the landscape that interacts with wind conditions and vegetation cover to promote space use, prey availability, and foraging tactics of

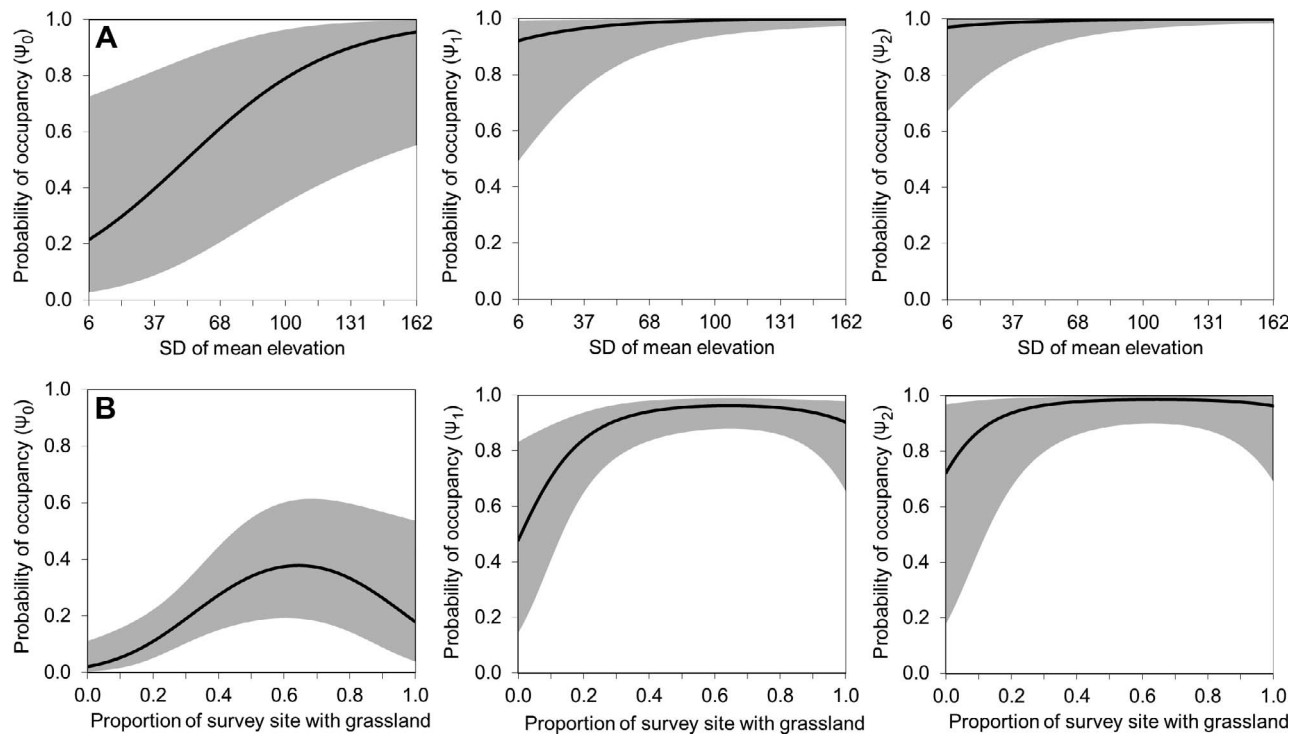


FIGURE 3. Dynamic probability of site occupancy by territorial pairs of Golden Eagles in the Diablo Range, California, USA, 2014–2016, relative to (A) terrain ruggedness (SD of mean elevation), and (B) the amount of grassland at survey sites that were either vacant (ψ_0), had nonreproductive pairs (ψ_1), or had reproductive pairs (ψ_2) in the previous year. Shaded regions represent 95% confidence intervals. Estimates are from the top-ranked multistate model (Appendix Table 4).

Golden Eagles (McLeod et al. 2002, Katzner et al. 2012, Watson et al. 2014). Based on seasonal radio-tracking data collected in southern Idaho, USA, LeBeau et al. (2015) found that terrain ruggedness and slope strongly influenced habitat use by adult Golden Eagles. In south-central Montana, USA, Golden Eagles most often used rugged terrain in shrub and grasslands, although Crandall et al. (2015) noted that daily nest survival was negatively associated with terrain ruggedness. These studies emphasized the likely importance of a mix of selected features, especially relative to locations of used nests during the breeding season. Occupancy by pairs of eagles in our study was also greatest at sites with intermediate amounts of grassland and forest vegetation, as shown by the strong support in our analysis for a unimodal (convex) relationship between occupancy and amount of grassland. Our analysis also indicated a negative, albeit somewhat weak, association between the proportion of scrubland vegetation cover at a site, occupancy, and breeding success. Large patches of scrub, which dominated sites in the central portion of our study area, included chaparral shrubs 2–5 m tall that may ultimately limit prey availability and foraging opportunities of eagles.

Previous studies that have examined sources of variation in the reproduction of Golden Eagles have

shown that pairs nest more often and produce more fledglings when their primary prey is abundant and weather conditions are favorable (Tjernberg 1983, Steenhof et al. 1997, Kochert et al. 2002, McIntyre and Schmidt 2012). Few pairs attempted to nest during our study, and even fewer successfully produced young. Observed (naïve) estimates of annual nest success ranged from 0.11 to 0.15, and were substantially lower than those observed during previous, territory-based surveys of Golden Eagles completed within 30 km of the APWRA during 1994–2000 (range = 0.33 to 0.65; Hunt et al. 2017). Unlike previous studies of Golden Eagles (Watson 2010), we found little evidence that the amount of precipitation that a site received during winter, or during the prior year, influenced the current year's reproduction. Rather, our analysis and results provided strong support for the hypothesis that the amount of precipitation that a site received during brood rearing was most important. In our study, rainfall that did occur during the drought period was highly localized and patchy, and we observed grassland vegetation in these areas (and presumably the California ground squirrels in these areas) to respond rapidly. We caution, however, that we lacked pre- and post-drought data for our study, and that too much rain could also potentially have a negative influence on

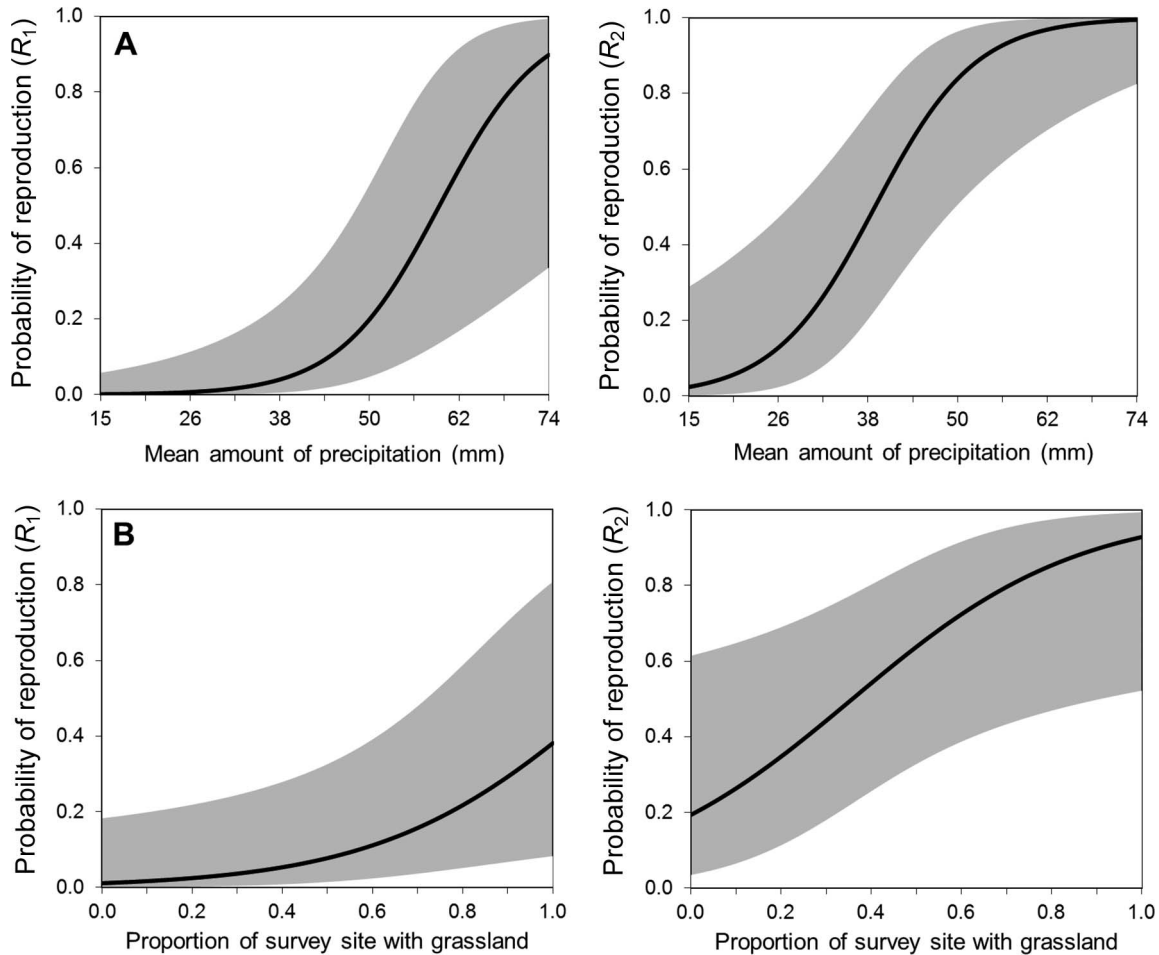


FIGURE 4. Dynamic probability of successful reproduction by territorial pairs of Golden Eagles in the Diablo Range, California, USA, 2014–2016, relative to (A) the mean amount of precipitation (mm) during the brood-rearing period (March–July), and (B) the amount of grassland at survey sites that had nonreproductive pairs (R_1), or reproductive pairs (R_2) in the previous year. Shaded regions represent 95% confidence intervals. Estimates are from the final top-ranked multistate model (Appendix Tables 4 and 5).

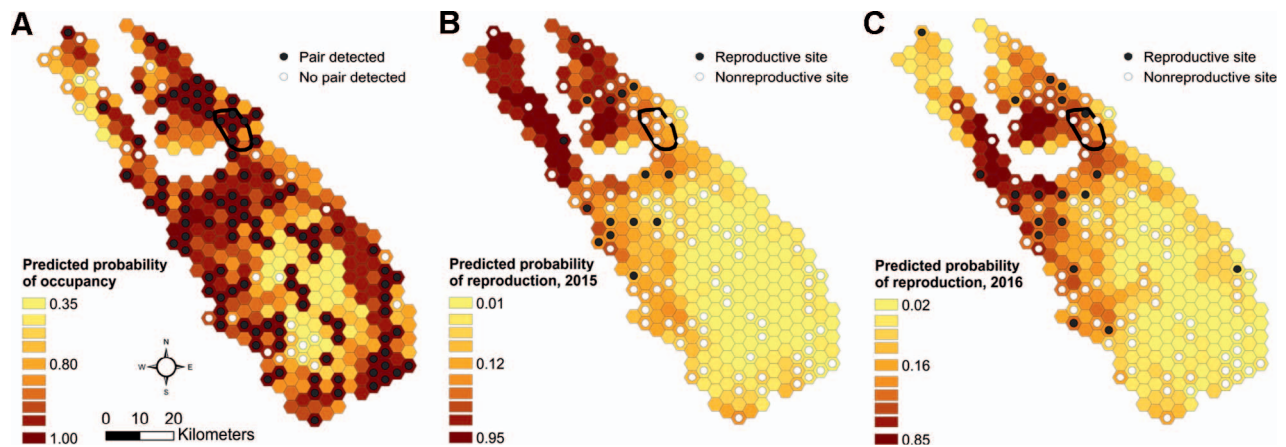


FIGURE 5. Spatial distribution of the predicted probability of (A) site occupancy, (B) successful reproduction in 2015, and (C) successful reproduction in 2016 for territorial pairs of Golden Eagles in the Diablo Range, California, USA. Predicted values are from the top-ranked multistate model (Appendix Table 4). The black polygon shows the location of the Altamont Pass Wind Resource Area.

reproduction if adult foraging or prey populations are negatively affected by cold, wet conditions (Dawson and Bortolotti 2000, Sergio 2003). In addition, the previous year's precipitation can influence annual grassland species composition through lagged effects (Dudney et al. 2017), which in turn could influence reproduction and abundance of California ground squirrels (Fitch 1948). Such processes suggest that the long-term relationship between annual precipitation and reproduction may be nonlinear (quadratic) in our study area.

The spatial covariates that we selected to represent environmental conditions relevant to Golden Eagles and their prey likely missed many of the fine-scale features that may influence occupancy and breeding success, but the strong support for these effects in our analysis demonstrated clear associations between landscape structure, distribution of territorial pairs, and spatial patterns of reproductive success. This finding has important implications for conservation planning for Golden Eagles, as it highlights a linkage between landscape composition and population vital rates—a connection relevant to understanding fitness consequences of changes to site quality, source–sink dynamics, and other aspects of metapopulation dynamics relevant to management (Pulliam 1988, Runge et al. 2006).

Maximizing Detectability of Golden Eagles and Their Young

Our findings emphasize the importance of accounting for imperfect detection in studies of occupancy and reproduction of Golden Eagles. The pattern of variation in detectability that we observed has 3 main implications for researchers and land managers to consider for optimizing monitoring strategies for this species. First, estimated detection probabilities for breeding vs. nonbreeding territorial pairs of eagles diverged considerably as the breeding season progressed (Figure 2A). This finding showed that seasonal changes in territorial behaviors associated with nesting (e.g., undulation displays) can strongly influence an observer's ability to detect pairs of eagles during surveys. The probability of detecting territorial pairs during surveys of occupied sample sites in our study (mean = 0.88 and 0.63 for reproductive and nonreproductive pairs, respectively) was similar to that estimated for Golden Eagles during aerial surveys in Alaska (0.68; Booms et al. 2010, also see Martin et al. 2009), and Wyoming (0.60–0.67; Olson et al. 2015). Golden Eagles are large, conspicuous birds with highly visible territorial displays, but our finding that detection probability during a single survey was <1 indicates that multiple surveys are required to reliably detect territorial pairs that are present, especially pairs that are nonreproductive. In our study, detection probability was greatest in the early stages of breeding, when all territorial pairs were

most heavily engaged in courtship behaviors and territorial displays that made them readily observable. Reproductive pairs continued these displays throughout the breeding season, whereas nonnesting or unsuccessful pairs may have expanded their use of the landscape, or decreased the frequency of territorial behaviors that facilitated their detection. This finding underscores the importance of conducting surveys early in the breeding season to determine the occupancy status of territorial pairs.

Second, the detection probability of reproductive pairs increased when observers used historical data on previously used nest locations to locate eagles during surveys. Golden Eagles often reuse alternative nest structures within their territories (Kochert and Steenhof 2012, Millsap et al. 2015), so the ability to integrate historical information into our surveys and analysis of detection was a major advantage of our approach that reduced the amount of unexplained heterogeneity in the survey data. Detection probability was also negatively influenced by the amount of forest cover at a sample site. However, this effect was relatively weak, perhaps because our measure of forest cover was coarse in that it did not account for fine-scale attributes of forest patches that could have influenced the visibility of Golden Eagles (e.g., tree height or tree density).

Finally, we found that the probability of observing young at sites with successful nesting (δ) was highly variable, both spatially and through time. Correct identification of sites with successful reproduction varied across space and among years, and also changed within years as young eagles fledged from their tree nests and became more visible to observers. In 2014, for example, our analyses indicated that successful breeding by territorial pairs was correctly identified only about half the time when naïve, uncorrected survey data were used. In contrast, the probability of observing young had increased by 2016, such that naïve and model-based estimates were more similar in that year. The magnitude of difference between naïve and model-based estimates of reproduction in some years suggests that estimates of fecundity and population trends derived from data collected during remote surveys of Golden Eagles could also be biased low. Our results are consistent with those of other studies which have shown imperfect and variable detection of Golden Eagles, which suggests that estimation approaches like those used here may provide more accurate and reliable assessments of reproduction than those that ignore underlying uncertainties associated with determination of breeding status.

Prospects for Conservation Planning

Golden Eagles are exposed to a variety of threats of increasing frequency and distribution, including direct mortality from electrocution by power lines, collisions with

vehicles and human-created structures such as wind turbines, and poisoning or other types of human persecution (USFWS 2016, Hunt et al. 2017). Indirect threats to Golden Eagles include loss of foraging habitats or decreases in prey availability associated with human land use, including urbanization, agriculture, and energy development (Kochert et al. 2002). The development of wind-power and solar facilities, in particular, is expected to increase dramatically in habitats occupied by Golden Eagles, and the threats associated with energy development have the potential to negatively affect population trajectories (USFWS 2016, Wiens et al. 2017). Conservation plans for Golden Eagles exposed to renewable energy development include monitoring of population trends so that regulatory officials can determine the appropriate number of permits to issue for take requests by renewable energy projects while maintaining stable or increasing breeding populations (USFWS 2013, 2016). Detecting changes in vital rates of a wide-ranging, long-lived species such as the Golden Eagle, however, is strongly limited by the cost and logistical challenges associated with monitoring. Our study indicates that a randomized sampling design coupled with estimation of breeding state and associated detection probabilities, as defined by Nichols et al. (2007) and MacKenzie et al. (2009, 2012), can be an efficient approach to estimate and map trends in occupancy and site quality of Golden Eagles.

Conservation policy is often aimed at managing landscape change, either through restoration, mitigation, or protection. Therefore, identifying linkages between landscapes, climate, and population vital rates is a key objective in the development of conservation policy aimed at managing species sensitive to changes in human land use and climate (Lawler et al. 2010, Hole et al. 2011, Reynolds et al. 2017). To meet this objective, resource managers need to maintain or improve sites that are of high quality and resilient to environmental change, rather than focusing on poor sites while unknowingly allowing key areas to deteriorate (Dias 1996, Sergio and Newton 2003, Nielson et al. 2016). Our study has provided quantitative information on spatial patterns of occupancy and reproduction of Golden Eagles in the vicinity of a large wind-energy facility, the APWRA, during a historically severe drought. During this presumably lean time for eagles, areas with the greatest likelihood of occupancy by successful breeders were relatively small, patchily dispersed, and strongly influenced by spatially variable weather patterns. Our results suggest that losing some of these high-quality patches could lower mean productivity across the entire landscape, especially in years when population productivity is low. This does not mean that moderate or poor-quality sites occupied by eagles are not relevant to population persistence, as these sites are likely to play a significant role in source–sink dynamics within

the study population. In our study area, the quality of a site for eagles may change or be exacerbated through time, especially given the negative impacts of increasing drought severity on oak woodlands (Asner et al. 2016) and the multitude of potential effects of climate change on grassland ecosystems (Chaplin-Kramer and George 2013).

Identifying spatial patterns in site quality and its correlates is an important precursor to understanding the demographic spatial structure of a study population, and represents a step toward conservation policy that aims to maximize habitat occupancy and maintain stable breeding populations. In Sweden, for example, local regulatory officials generally prevent wind energy development within 2 km of known used nests of Golden Eagles, but sites considered to be of higher quality (i.e. breeding territories with a history of relatively greater occupancy and reproductive output) have a larger proposed protection zone of 4 km (Hipkiss et al. 2014). In our study area, similar protective measures could be considered for all known Golden Eagle nesting sites, but areas that we identified in the broader landscape with a high likelihood of recent reproduction, rugged terrain, and intermediate amounts of open grassland could receive enhanced protection from management actions that modify foraging habitats or create disturbances or hazards to nesting adults. This approach would be especially well suited to developing and locating conservation banks (Bunn et al. 2014) as a means of pooling mitigation resources and protecting areas of the greatest ecological value to Golden Eagles.

Conservation actions that reduce the impacts of human-caused disturbance or mortality on Golden Eagles will most likely be site specific. Proposed compensation measures considered to minimize, mitigate, and offset sources of mortality risk include: (1) power-pole retrofitting and use of raptor-safe new power poles to reduce the risk of electrocutions; (2) clearing high-risk highways and roads of carcasses to reduce the frequency of vehicle collisions with eagles feeding on carrion; (3) preservation of existing habitats important to nesting and foraging; and (4) habitat restoration in disturbed areas to enhance prey availability (Allison et al. 2017). Compensation measures must be sufficient to offset all major sources of anthropogenic mortality to ensure meeting a goal of stable or increasing breeding populations, yet little is known about the effectiveness of these proposed conservation actions, much less where such actions should be focused to benefit eagles the most. Assessments based on recent occupancy and reproductive output of Golden Eagles can provide an efficient and accurate measure of the relative contribution of specific sites or breeding areas to population growth, which offers the opportunity for land managers to prioritize conservation efforts in areas that support high

levels of reproduction and make disproportionate contributions to population persistence.

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Ethics statement: This research was conducted in compliance with the *Guidelines to the Use of Wild Birds in Research*.

Author contributions: J.D.W., W.G.H., M.R.F., and D.A.B. formulated the questions; P.S.K. and T.H. collected data and supervised research; J.D.W. and P.S.K. analyzed the data; and all authors wrote the paper.

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APPENDIX TABLE 4. Ranking of dynamic multistate occupancy models used to characterize variation in occupancy (ψ), reproduction (R), and probabilities of detection (p_1 , p_2 , δ) for Golden Eagles in the Diablo Range, California, USA, 2014–2016. Model selection results are shown for each stage of the parameter modeling process.

Model selection stage and candidate models ^a	ΔAIC_c ^b	AIC _c weight	K	Deviance
1. Within- and among-year variation in detection probabilities (p_1 , p_2 , δ) {All models with $\phi(\text{state})$ $\psi(\text{state} \times \text{year})$ $R(\text{state} \times \text{year})$ }				
$p_1(\text{survey})$ $p_2(.)$ $\delta(\text{year} + \text{survey})$	0.00 ^c	0.68	23	1458.12
$p_1(\text{survey})$ $p_2(\text{year})$ $\delta(\text{year} + \text{survey})$	2.50	0.19	25	1456.09
$p_1(\text{year} + \text{survey})$ $p_2(.)$ $\delta(\text{year} + \text{survey})$	4.24	0.08	25	1457.83
$p_1(\text{survey})$ $p_2(\text{survey})$ $\delta(\text{year} + \text{survey})$	5.52	0.04	26	1456.82
$p_1(\text{survey})$ $p_2(.)$ $\delta(\text{survey})$	9.57	0.01	21	1472.18
$p_1(\text{year} + \text{survey})$ $p_2(\text{year} + \text{survey})$ $\delta(\text{year} + \text{survey})$	11.49	0.00	30	1453.52
$p_1(\text{year} \times \text{survey})$ $p_2(\text{year})$ $\delta(\text{year} \times \text{survey})$	25.12	0.00	35	1455.29
$p_1(\text{year} \times \text{survey})$ $p_2(\text{year} \times \text{survey})$ $\delta(\text{year} \times \text{survey})$	40.17	0.00	44	1448.14
$p_1(.)$ $p_2(.)$ $\delta(\text{year} + \text{survey})$	77.93	0.00	20	1542.77
$p(.)$ $\delta(\text{year} + \text{survey})$	101.71	0.00	19	1568.76
2. Influence of historical nest data and forest cover on detection {All models with $p_1(\text{survey})$ $p_2(.)$ $\delta(\text{year} + \text{survey})$ }				
$p_1(\text{survey})$ $p_2(\text{HD})$ $\delta(\text{year} + \text{survey} + \text{HD})$	0.00 ^d	0.32	25	1447.19
$p_1(\text{survey})$ $p_2(\text{HD})$ $\delta(\text{year} + \text{survey} + \text{HD} + \text{forest})$	0.29	0.28	26	1445.20
$p_1(\text{survey})$ $p_2(\text{HD})$ $\delta(\text{year} + \text{survey})$	1.77	0.13	24	1451.23
$p_1(\text{survey} + \text{HD} + \text{forest})$ $p_2(\text{HD} + \text{forest})$ $\delta(\text{year} + \text{survey} + \text{HD} + \text{forest})$	1.96	0.12	29	1439.94
$p_1(\text{survey})$ $p_2(\text{HD})$ $\delta(\text{year} + \text{survey} + \text{forest})$	2.18	0.11	25	1449.37
$p_1(\text{survey} + \text{HD})$ $p_2(.)$ $\delta(\text{year} + \text{survey})$	5.51	0.02	24	1454.98
$p_1(\text{survey})$ $p_2(.)$ $\delta(\text{year} + \text{survey})$ <i>Top model, step 1</i>	6.40	0.01	23	1458.12
$p_1(\text{survey} + \text{HD} + \text{forest})$ $p_2(.)$ $\delta(\text{year} + \text{survey})$	7.78	0.01	25	1454.97
$p_1(\text{survey} + \text{forest})$ $p_2(.)$ $\delta(\text{year} + \text{survey})$	8.44	0.00	24	1457.91
$p_1(\text{survey})$ $p_2(\text{forest})$ $\delta(\text{year} + \text{survey})$	10.86	0.00	25	1458.05
3. Effect of occupancy (ψ) and reproductive state (R) in previous year {All models with $p_1(\text{survey})$ $p_2(\text{HD})$ $\delta(\text{year} + \text{survey} + \text{HD})$ }				
$\psi(\text{state})$ $R(\text{state} + \text{year})$	0.00 ^e	0.51	20	1454.43
$\psi(\text{state} + \text{year})$ $R(\text{state} + \text{year})$	2.13	0.18	21	1454.33
$\psi(\text{state})$ $R(\text{state})$	2.15	0.18	19	1458.79
$\psi(\text{state} \times \text{year})$ $R(\text{state} \times \text{year})$ <i>Top model, step 2</i>	4.01	0.07	25	1447.19
$\psi(\text{state} + \text{year})$ $R(\text{state})$	4.30	0.06	20	1458.73
$\psi(\text{state})$ $R(\text{year})$	8.95	0.01	18	1467.80
$\psi(\text{year})$ $R(\text{year})$	84.79	0.00	17	1545.83
4. Influence of topography and vegetation on occupancy {All models with $R(\text{state} + \text{year})$ $p_1(\text{survey})$ $p_2(\text{HD})$ $\delta(\text{year} + \text{survey} + \text{HD})$ }				
$\psi(\text{state} + \text{TRI} + \text{grassland}^2 + \text{scrub})$	0.00 ^f	0.61	24	1431.92
$\psi(\text{state} + \text{TRI} + \text{grassland}^2)$	2.07	0.22	23	1436.25
$\psi(\text{state} + \text{grassland}^2)$	3.22	0.12	22	1439.65
$\psi(\text{state} + \text{TRI} + \text{scrub})$	6.27	0.03	22	1442.70
$\psi(\text{state} + \text{scrub})$	6.72	0.02	21	1445.38
$\psi(\text{state} + \text{grassland})$	10.29	0.00	21	1448.96
$\psi(\text{state} + \text{TRI} + \text{grassland})$	10.84	0.00	22	1447.27
$\psi(\text{state})$ <i>Top model, step 3</i>	13.54	0.00	20	1454.43
$\psi(\text{state} + \text{TRI})$	15.36	0.00	21	1454.02
$\psi(\text{state} + \text{forest})$	15.60	0.00	21	1454.27
$\psi(\text{state})$	15.68	0.00	19	1458.79
5. Influence of climate on occupancy and reproduction {All models with $\psi(\text{state} + \text{TRI} + \text{grassland}^2 + \text{scrub})$... $p_1(\text{survey})$ $p_2(\text{HD})$ $\delta(\text{year} + \text{survey} + \text{HD})$ }				
$R(\text{state} + \text{pptBR})$	0.00 ^g	0.63	24	1427.04
$R(\text{state} + \text{pptBR} + \text{Tmax})$	2.06	0.23	25	1426.83
$R(\text{state} + \text{year})$ <i>Top model, step 4</i>	4.87	0.06	24	1431.92
$R(\text{state} + \text{pptEN})$	5.56	0.04	24	1432.61
$R(\text{state} + \text{Tmax})$	6.14	0.03	24	1433.19
$R(\text{state} + \text{pptEN} + \text{Tmax})$	6.97	0.02	25	1431.74
$R(\text{state} + \text{ppt}_{t-1})$	7.97	0.01	24	1435.02
6. Influence of topography and vegetation on reproduction {All models with $\psi(\text{state} + \text{TRI} + \text{grassland} + \text{scrub})$... $p_1(\text{survey})$ $p_2(\text{HD})$ $\delta(\text{year} + \text{survey} + \text{HD})$ }				
$R(\text{state} + \text{pptBR} + \text{grassland})$	0.00 ^h	0.36	25	1419.58
$R(\text{state} + \text{pptBR} + \text{scrub})$	0.32	0.30	25	1419.90
$R(\text{state} + \text{pptBR} + \text{grassland}^2)$	1.82	0.14	26	1419.12
$R(\text{state} + \text{pptBR} + \text{TRI} + \text{grassland})$	2.28	0.11	26	1419.58
$R(\text{state} + \text{pptBR} + \text{TRI})$	3.58	0.06	25	1423.16
$R(\text{state} + \text{pptBR})$ <i>Top model, step 5</i>	5.19	0.03	24	1427.04

APPENDIX TABLE 4. Continued.

^a ψ_1 = the probability that a sample site was occupied in the first year of the study, R_1 = the probability that successful reproduction occurred at a site in the first year, given that the site was occupied (i.e. in state 2). ψ_{xi} = the probability that a given site was occupied in year i , conditional upon state ($x=0, 1$, or 2) in the previous year ($i-1$), and R_{xi} = the probability that successful breeders were present in year i , conditional upon state in the previous year; $p1_{ik}$ = the probability of detecting occupancy during survey k , given that the site was occupied with no successful reproduction in year i , $p2_{ik}$ = the probability of detecting occupancy during survey k , given that the site was occupied by a pair of eagles that successfully reproduced in year i , δ_{ik} = the probability of correctly identifying successful reproduction (observing young) at a site, given that the site was occupied and reproduction had occurred (MacKenzie et al. 2009, 2012). Time effects modeled as constant (.) or varying with survey occasion (survey), or year. Spatial covariates included the site-specific availability of historical nesting locations (HD), proportion of sample site with grassland, forest, or scrub cover, terrain ruggedness (TRI), mean amount of precipitation during the early nesting (pptEN) or brood-rearing (pptBR) periods or during the year (January 1–December 31) prior to the current year's breeding season (ppt_{*i-1*}), and mean maximum temperature during the brood-rearing period (Tmax).

^b AIC_c = Akaike's information criterion for small sample size; ΔAIC_c = difference between the AIC_c value of each model and the model with the lowest AIC_c ; K = number of parameters included in the model.

^c AIC_c of the top model = 1507.04.

^d AIC_c of the top model = 1500.64.

^e AIC_c of the top model = 1496.63.

^f AIC_c of the top model = 1483.09.

^g AIC_c of the top model = 1478.22.

^h AIC_c of the top model = 1473.03.

APPENDIX TABLE 5. Logit-link parameter estimates and 95% confidence limits from the top-ranked dynamic multistate occupancy model developed for Golden Eagles in the Diablo Range, California, USA, 2014–2016.

Model parameter ^a	Description	Estimate	95% CL	
			Lower	Upper
ψ_1 (Intercept)	Initial site occupancy	0.297	−0.664	1.258
R_1 (State)	Initial reproduction	0.448	−0.587	1.484
ψ (Intercept)	Occupancy intercept	−0.990	−4.447	2.466
ψ (State 0)	Occupancy, state 0	−4.799	−6.872	−2.725
ψ (State 1)	Occupancy, state 1	−1.049	−3.436	1.339
ψ (TRI)	Occupancy slope, terrain ruggedness effect	0.028	0.005	0.051
ψ (grassland)	Occupancy slope, linear grassland effect	10.902	3.239	18.564
ψ (grassland ²)	Occupancy slope, nonlinear (quadratic) grassland term	−8.445	−15.120	−1.770
ψ (scrub)	Occupancy slope, linear scrubland effect	−2.578	−5.485	0.329
R (Intercept)	Reproduction intercept	−7.662	−12.985	−2.339
R (State 0)	Reproduction, state 0	−3.651	−7.647	0.345
R (State 1)	Reproduction, state 1	−3.041	−5.484	−0.597
R (grassland)	Reproduction slope, linear grassland effect	4.073	0.420	7.726
R (pptBR)	Reproduction slope, linear effect of precipitation during brood-rearing	0.150	0.050	0.251
$p1$ (Intercept)	State 1 detection intercept	−0.478	−0.963	0.008
$p1$ (Survey 1)	State 1 detection, survey period 1	2.822	1.925	3.720
$p1$ (Survey 2)	State 1 detection, survey period 2	1.385	0.765	2.006
$p1$ (Survey 3)	State 1 detection, survey period 3	0.518	−0.092	1.128
$p2$ (Intercept)	State 2 detection intercept	1.090	0.375	1.805
$p2$ (HD)	State 2 detection slope, historical data effect	0.942	0.097	1.788
δ (Intercept)	Delta intercept	−0.521	−2.005	0.963
δ (2014)	Delta, 2014	−0.776	−2.017	0.465
δ (2015)	Delta, 2015	−0.803	−1.984	0.379
δ (Survey 3)	Delta, survey period 3	−0.324	−1.166	0.518
δ (HD)	Delta slope, historical data effect	1.527	0.470	2.585

^a ψ_1 = initial probability of occupancy for territorial pair of eagles in nonreproductive (state 1) and reproductive (state 2) states during the first year of the study; ψ_{xi} = the probability that a given site was occupied in year i , conditional upon state ($x=0, 1$, or 2) in the previous year ($i-1$); R_{xi} = the probability that successful breeders were present in year i , conditional upon state in the previous year; $p1_i$ = the probability of detecting ≥ 1 nonbreeding or unsuccessful territorial pairs in year i ; $p2_i$ = the probability of detecting successful breeders in year i ; and δ_i = the probability that young were observed, given detection of occupancy in year i (MacKenzie et al. 2009, 2012). Time effects modeled as constant (.) or varying with survey occasion (survey), or year. Spatial covariates included the site-specific availability of historical nesting locations (HD), proportion of sample site with grassland, forest, or scrub cover, terrain ruggedness (TRI), and mean amount of precipitation during the brood-rearing (pptBR) period.