THESIS

PREDICTING CONDOR RANGE EXPANSION IN CALIFORNIA TO REDUCE DEVELOPMENT THREATS

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ABSTRACT

PREDICTING CONDOR RANGE EXPANSION IN CALIFORNIA TO REDUCE DEVELOPMENT THREATS

Collisions with wind energy infrastructure is a major cause of wildlife mortality worldwide and especially pose threats to bird and bat populations. Avian species that have associations with habitats that generate strong winds are at higher risk of collision with wind turbines. Critically endangered California condors (*Gymnogyps californianus*) are among species that use areas with high-class winds. As the condor's population growth continues to face challenges, it is imperative that managers working with the California Condor Recovery Program identify and reduce all threats to the species and foster conditions that promote condor recovery. Renewable energy projects, particularly wind energy, pose risks to condors; and new developments within current, documented condor range require planning and consultation with the United States Fish and Wildlife Service. However, industrial-scale wind energy projects in California consider condor flocks in central and southern California separate and statically persisting within their current ranges. This misconception may result in development within condor habitat that is detrimental to range expansion and recovery. In this thesis, I examine factors that influence condor home range sizes, predict where condors are likely to expand their range within identified suitable habitat in California, and assess where the predicted condor range overlaps with areas that generate high-class winds preferred for wind energy development.

My first chapter focuses on estimating annual home ranges of condors and identifying factors that influence home range size. Understanding what intrinsic and extrinsic variables influence condor home ranges can inform management planning and aid in predicting condor range expansion. I used location data collected from condors released in central and southern California to estimate annual condor home range area and assessed twenty-one variables related to individual characteristics, management factors, population dynamics, and habitat suitability to identify strong predictors of home range size. I found that age group, time spent in the wild, age of managing agency, maximum slope, maximum NDVI, distance to water, and road density were significant predictors of annual home range area. On average, adult breeding condors had the smallest home range areas and subadult condors had the largest home range areas. Population size did not affect annual home range size of condors; however, home range size increased the longer a managing agency had been releasing condors.

My objective of the second chapter was to predict condor range expansion in California and identify where there may be conflict between condors and potential wind energy development. Predicting condor range expansion may inform managers of areas to concentrate efforts and resources for management and outreach, as well as identify areas that should be considered during wind energy development planning stages to reduce risks to condor recovery. I used the results from Chapter 1 and a habitat suitability surface to create a tool in which a user can customize the demographics of condor flocks in California sometime in the future and predict the overlapping home ranges of individuals in the flocks. Users can then export the predicted ranges into a GIS program to consider how the overlapping home ranges may be affected by plans for wind energy development and identify possible alternative sites. I

predicted condor range expansion in California under four scenarios: 1) population size and structure stays the same (2019 California population); 2) each flock has 150 individuals with 15 breeding pairs; 3) each flock has a majority of breeding pairs, which maximizes breeding pairs and minimizes sub-adult condors; and 4) each flock has a majority of subadults, which maximizes subadult condors and minimizes breeding pairs. Predicted ranges under different scenarios exhibited high similarity and areas with high-class wind generation overlapped with <10% of predicted condor range under all scenarios. More than 81% of areas with strong winds suitable for energy generation were unaffected by predicted condor range, suggesting there are alternative areas for wind energy development with less risk of conflict with critically endangered California condors.

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SUMMARY

California condors are critically endangered with just over 300 individuals in the wild. Condors narrowly escaped extinction in the early 1980's when the population hit a low of 22 individuals. To save the species, all remaining condors were removed from the wild for a captive breeding program. Since 1992, condors have been released into the wild and the increase in population is seen as a success from a recovery perspective, yet threats to their survival persist. To better understand how condors use their landscapes and help inform management planning, I investigated which individual characteristics, management factors, population dynamics, and environmental variables were associated with annual condor home range size. I used location data collected between 2006 – 2017 from condors released in central and southern California to estimate annual condor home range area and found that age group, time spent in the wild, age of managing agency, maximum slope, maximum NDVI, distance to water, and road density were strong predictors of annual home range area. Adult breeding condors had the smallest home range areas and subadult condors had the largest home range areas. Population size does not affect annual home range size of condors; however, home range size increases the longer a managing agency has been releasing condors. This may potentially be due to more collective information of the landscape that can be transferred between conspecifics. Results from this analysis can be used to inform managers of

areas that need to be included for monitoring and management efforts, as well as, help predict where condors are likely to expand their range.

INTRODUCTION

Population declines and extinctions of species are occurring rapidly throughout the world and experts suggest we are currently undergoing Earth's sixth mass extinction (Clavel et al., 2010; Ceballos et al., 2017). The loss of biodiversity can lead to decreased ecosystem function and health, as well as other direct and indirect consequences (Naeem et al., 2012; Young et al., 2016). Species recovery programs in the United States, created through the Endangered Species Act (ESA), strive to prevent these consequences by protecting and conserving species that are in danger of extinction (USFWS, 1973). The ESA has proven itself successful and only an estimated 2% of species that have been placed under its protection have perished (USFWS, 2011).

One of the main goals of species recovery programs is restoring populations of endangered species to their historic ranges (USFWS, 1973). The reestablishment of populations to previously occupied habitats requires strategic recovery and management plans to prevent extinction and ensure long-term survival of threatened and endangered species (Seddon et al., 2007). These plans often include different actions such as: mitigating threats to species' survival, captive-breeding and reintroduction, monitoring, and outreach programs (Seddon et al., 2007; USFWS, 2011). Species reintroductions and translocations are increasingly used as conservation tools; therefore, understanding species' resource requirements and space-use can better inform monitoring and managing practices and lead to greater recovery program success (Seddon et al., 2007; Margalida et al, 2016; Taylor et al., 2017; Bubac et al., 2019).

Biological requirements of an animal are found within the spatial boundaries of its movement (Burt, 1943; Rivers et al., 2014a). The area in which an animal typically spends its time is defined as a “home range” (Burt, 1943; Seaman and Powell, 1996; Powell and Mitchell, 2012). The home range is a fundamental concept in ecology that helps researchers understand the relationships between animals and their environments (Calenge, 2006). Home ranges are extensions of an individual’s cognitive map that allows it to make decisions that affect its fitness, such as where to find food, mates, and roosting sites (Powell and Mitchell, 2012). Home ranges are also likely to change based on information gathered through experience or learned from others within a population (Powell and Mitchell, 2012).

Most of the world’s vulture species are in danger of extinction (Virani et al, 2011; IUCN, 2020), though they provide important ecosystem services such as decomposition and reduced disease transmission among mammals (Ogada et al., 2012). Included among imperiled vultures is the California condor (*Gymnogyps californianus*), which is critically endangered with just over 300 wild individuals (Mace, 2019). Condors are obligate scavengers and have evolved characteristics to exploit patchily distributed and temporarily available resources (Brodkorb, 1964; Snyder and Snyder, 2005). Among these traits are a 3-meter wingspan for efficient foraging via soaring and keen eyesight for spotting food sources from the air (Snyder and Snyder, 2005). Condors are a long-lived species, reaching sexual maturity around six years-of-age. Condors are typically monogamous and share extensive parental roles—rearing a single chick can take up to a year and a half, thus pairs only breed every other year (Koford, 1953;

Wilbur, 1978, Snyder and Snyder, 2005). Condors are also a social species and like other vultures, can feed and roost in large aggregations (Wilbur, 1978; DeVault, et al., 2003; Snyder and Snyder, 2005; Moleon et al., 2015). Unfortunately, the social disposition of condors also creates challenges to their recovery.

Lead poisoning from the inadvertent ingestion of spent ammunition has been identified as the greatest threat to condor survival today and due to their social nature, one feeding event on a single contaminated carcass can expose multiple condors to lead fragments (Finkelstein et al., 2012; Rideout et al., 2012). However, a multitude of pressures including shooting, egg collecting, habitat loss, and strychnine poisoning contributed to their historical decline (Wilbur, 1978; Finkelstein et al., 2012; Rideout et al., 2012). California condors have been federally listed as critically endangered since the first endangered species list was created in 1967 and the species was the first to have a recovery plan approved by the United States Fish and Wildlife Service (USFWS) under the ESA (USFWS, 1974; Wilbur, 1978). The species narrowly escaped extinction in 1982 when the wild population hit a low of 22 individuals (Snyder and Snyder, 2000). To prevent the disappearance of the species, the USFWS and dedicated biologists captured all remaining wild condors and placed them into zoos for a captive breeding program (Wilbur 1978; Janssen et al. 1986; Wiemeyer et al., 1988; Rideout et al., 2012).

Since 1992, condors have been released back into the wild from release sites in California, Arizona, and Baja Mexico. The species is highly monitored and managed by the California Condor Recovery Program – hereafter referred to as “Program” – a multi-agency collaborative network of zoos, federal and state agencies, and non-profit organizations. Within California, two seemingly distinct flocks exist, in central and southern California, separated by thousands of square kilometers. The extremely small population size and the experimental nature of reintroduction created many unknowns for the Program. How condors would behave in the wild and expand into historic habitat through time were among those uncertainties. Condors currently only occupy a fraction of their historical range in California although many areas remain suitable for occupation (D’Elia et al., 2015).

Condors use a variety of habitats for feeding, roosting, and nesting and can concentrate foraging efforts at different locations at different times throughout the year (Hunt et al., 2006; Meretsky and Snyder, 1992; Rivers et al., 2014a; D’Elia et al., 2015). Condors have been observed exploiting food sources at increasingly farther distances from release sites and managers have assumed that as recovery efforts persist and the wild population matures and becomes more aware of available resources, condor distribution will expand (USFWS, 2013). This assumption is supported by the fact that condors are less likely to be detected and observed feeding on proffered food as flocks increase in size and age (Bakker et al., 2017). However, while individuals are likely to become less dependent on release and feeding sites as flock size and age increases, whether condor ranges increase as a result of the same predictors has yet to be demonstrated.

This chapter aims to understand how population size and demographics are associated with annual home range size of California condors. Which individual characteristics (age group and breeding status, sex, time spent in the wild), management factors (rearing method, age of managing agency, flock), and population changes (flock population size, adult breeding to subadult ratio) are associated with annual home range area? Which environmental covariates previously analyzed to identify suitable habitat (D’Elia et al., 2015) related to soaring conditions and climate (thermal updraft velocity, thermal height, wind speed, winter severity), terrain (maximum slope, terrain ruggedness), landscape productivity (normalized difference vegetation index, distance to water), vegetation characteristics (canopy cover, canopy height, land cover type), and human disturbance (road density, human population density) influence home range area? Identifying how home ranges change as a result of dynamic individual, management, population, and environmental conditions will provide better insight into condor biology and movement. This information is also important for planning management and recovery strategies for this critically endangered species.

Results from this study will help inform managers about factors that are important to condor home range and provide insight into what influences condor range expansion. Managers can use these data to develop management and recovery strategies, especially as management moves from the individual- to population-level.

METHODS

Study Area

My study area included central and southern California. There are three release sites associated with the central California flock which is co-managed by Ventana Wildlife Society (VWS) and Pinnacles National Park (PINN). In central California, condor flocks typically range west along the Big Sur coastline from Monterey to San Luis Obispo Counties and inland throughout San Benito County and parts of western Fresno County. In southern California, condors are managed by the USFWS and typically range throughout the Los Padres National Forest in Santa Barbara and Ventura Counties and the Tehachapi Mountains in Kern County

(Figure 1). Condors use a variety of habitats ranging from rocky outcroppings to redwood forests and pastures on both public and private property.

Figure 1. Condor range in California. Release sites (4 active, 1 inactive) are represented by green stars.

Condor Movement Data Collection and Processing

I used Global Positioning System (GPS) data collected by solar-powered GPS patagial tags mounted on 181 condors during 2003 – 2017. Biologists from PINN, VWS, and USFWS capture condors semi-annually to conduct health evaluations, screen for lead poisoning, and replace radio telemetry and GPS tags. GPS transmitters included Argos GPS PTT-10 (GPS PTT), manufactured by Microwave Telemetry, Inc. (Columbia, MD, USA), and Global System for Mobile Communications (GSM), manufactured by Cellular Tracking Technologies LLC (Rio Grande, NJ, USA). GPS PTT units collected locations every hour, while GPS GSM units had higher temporal resolution, with locations collected up to 1 per minute.

I sub-sampled data collected by GSM transmitters to the first location collected every hour to match the sampling period of GPS PTT transmitters. I used a previously analyzed dataset of GPS locations collected from 2003 – 2013 (Bakker et al., 2017) with additional GPS data downloaded through Movebank.org (Wikelski and Kays, 2017). I considered GPS data collected by an individual condor throughout a calendar year to be a GPS year and the cumulative amount of time a condor collected location data to be a GPS record.

I removed GPS locations with diagnostic errors (HDOP, VDOP, GDOP ≥ 10) and those that were spatially disjunct from the previous and subsequent locations, indicative of outliers (D'Eon and Delparte, 2005; Poessel et al., 2018a). Records were organized by GPS year and only GPS years with at least six months' cumulative data were kept for analyses.

Home Range Estimation

Kernel density estimations (KDE) are a widely accepted method for estimating home range areas (Fleming et al., 2014; Reading et al., 2018; Peron, 2019). KDE work by fitting curved surfaces, called "kernels", over each data point with values highest at the point and decreasing toward the edge of the surface (Silverman, 1976; ESRI, 2019). Kernels are then summed where they overlay, creating a surface of densities by which a home range is estimated. Typically, home ranges are described as the 95% probability distribution of all possible locations of an animal based on its observed locations (Swihart and Slade, 1985; Seaman and Powell, 1996; Laver and Kelly, 2008; Fleming et al., 2015).

However, a problem with traditional KDEs is that locations are assumed to be independent and identically distributed (IID), resulting in underestimations of home range areas as IID observations contain more information than autocorrelated observations (Silverman, 1986; Fleming, et al., 2014; Calabrese et al., 2016). Animal movement data are not independent of each other as they are ordered in space and time; therefore, locations that are closer together in time tend to be closer in space than those farther apart. Accounting for position and velocity autocorrelation through a movement model that best describes movement data more accurately estimates home range areas by appropriately discounting information (Fleming et al., 2015; Calabrese et al., 2016). Then, a more suitable bandwidth can be chosen with which to smooth kernels. Smoothing bandwidths control the spread of each kernel, and therefore, home range estimations are sensitive to the bandwidth used during KDE (Silverman, 1986; Fleming et al., 2015; Calabrese et al., 2016; Peron, 2019).

The continuous-time movement modelling (‘ctmm’) package for R statistical software (Calabrese et al., 2016; R Core Team, 2018) is an open-source software tool that incorporates the various methods needed to produce better home range estimations. The package ‘ctmm’ provides users with the ability to visually inspect movement data to identify patterns indicative of home ranges, fit data to movement models to appropriately account for autocorrelation, define a smoothing bandwidth based on the best movement model, and finally estimate autocorrelated kernel density estimations (Fleming et al., 2015; Calabrese et al., 2016).

Fitting the data to different movement models and selecting the movement model that best describes the data is essential for autocorrelated kernel density estimations. The ‘ctmm’ tool allows users to fit location data to different movement models: independent identically distributed process, Brownian Motion, Ornstein-Uhlenbeck, integrated Ornstein-Uhlenbeck, and Ornstein-Uhlenback Foraging process (Calabrese, et al., 2016). These different movement models incorporate various degrees of autocorrelation and space-use constraints, which are indicative of home ranges. Movement models that exhibit restricted space use and are applicable to home ranges are Ornstein-Uhlenbeck and Ornstein-Uhlenback Foraging process.

I used the web application ‘ctmmweb’ (Dong et al., 2018) to calculate home range areas for each GPS year retained for analyses (Fleming and Calabrese 2015; Calabrese et al., 2016). I followed the standard workflow for the ‘ctmm’ package (Calabrese et al., 2016) in R (R Core Team, 2018) and used default settings and estimations to conduct my home range analyses. The workflow began with visualizing data as scatterplots, empirical variograms, and periodograms, to determine the spatio-temporal structure of the data. Variograms (i.e., plots of semi-variance) visualized the autocorrelation structure of the data to evaluate and identify a range of possible movement models. Using the top movement model, ranked by Akaike’s Information Criteria (Akaike, 1973) corrected for small sample size (AIC_c) (Burnham and Anderson, 2002; Anderson, 2008), ‘ctmm’ calculates an appropriate smoothing bandwidth to estimate a home range area.

Covariate Data Collection and Processing

To identify which factors are associated with home range area, I considered eight intrinsic and 13 environmental variables (Table 1). Intrinsic variables are the biological or ecological characteristics that could influence home range size (Koford, 1953; Snyder et al., 1986; Meretsky and Snyder, 1992; and Rivers et al., 2014a), and I organized these according to individual characteristics, management factors, and population factors. Environmental variables were considered based on potential influence on home range area due to their importance to condor biology and habitat suitability (Koford, 1953; Snyder et al., 1986, Meretsky and Snyder, 1992; Rivers et al, 2014b; D’Elia et al., 2015; Poessel et al., 2018b)

Intrinsic Covariates

Several covariates at the level of the individual are theorized to impact home range size. I combined age and breeding status into one age group variable to consider the slow sexual maturation of condors (Table 1). This also prevented analyzing an incomplete breeding status category separately (i.e., subadults very rarely breed and juveniles never do), which would create biased results. Individuals were categorized as adult breeding (≥ 6 years old and breeding), adult non-breeding (≥ 6 and non-breeding), subadult (3 – 5 years old), or juvenile (0 – 2 years of age). One 5-year-old female was included as a breeding adult based on her known breeding status. Individuals were considered breeding if they were paired and had successfully hatched an egg or fostered a captive-laid egg that hatched during that year. I expected breeding adults to have the smallest annual home range areas as they need to tend to their chicks, which agrees with pre-capture observations of condor movements but conflicts with previous conclusions that both breeding and non-breeding adults have larger monthly home range areas than immatures (Meretsky and Snyder, 1992; Rivers et al., 2014a). Based on my observations and reports of condor movements before all individuals were captured for captive-breeding (Meretsky and Snyder, 1992), I hypothesized that subadults would have the largest home ranges, having gained knowledge of their surroundings and confidence through experience, but no restrictions from breeding behaviors. Male and female condors have similar energetic needs as there are no differences in size and weight (Koford, 1953; Snyder et al., 1986). Though females carry and lay eggs, both sexes take equal roles in parental care (Koford, 1953; Snyder et al., 1986). Because of this, I hypothesized sex would not influence home range size. Most captive-bred individuals are released between 1-2 years of age, but occasionally older individuals are released. Time spent in the wild accounts for how experience in the wild, regardless of age, might affect home range size.

Management characteristics are also thought to affect home range size. Rearing method has been previously shown to be insignificant in relationship to monthly home range size (Rivers et al., 2014a); however, there have been many more successful wild hatched and fledged individuals added to the population since this past work. I included flock (Central versus Southern) rather than managing agency to avoid missing data when a managing agency did not have any GPS records that met my data criteria during a GPS year. Age of managing agency (years since an agency began releasing condors), positively influences condor survival (Bakker et al, 2017). Release sites and their respective managing agencies were established at different times throughout California since 1992, therefore, I included age of managing agency as a fixed variable (Table 1) to account for changes in condor range size as management and recovery programs mature, especially considering how information can be transferred between conspecifics through following more knowledgeable individuals (Dermody et al., 2011; Cortes-Avizanda et al, 2014; Harel et al., 2017).

Finally, I investigated whether population size and demographics are associated with home range size. Condors are social with conspecifics but have been noted to be territorial when nesting (Meretzky and Snyder, 1992). Competition for resources, such as foraging and nesting habitat, can pressure condors to expand their home ranges to decrease intraspecific competition as the population increases. Similarly, I was interested in whether proportion of age groups within a population would influence home range areas due to territoriality between breeding pairs or subadult condors exploring novel areas to occupy. Therefore, I included population size and breeding adult to subadult ratio as additional intrinsic variables.

Due to the heavily managed nature of the Program and small population size, all condors have highly detailed life histories maintained by the USFWS and Program managers, which are recorded in the "California Condor North American Studbook" (Mace, 2019). Data about condor life histories were derived from the condor studbook (Mace, 2019) and supplemented by Program managers (USFWS, PINN, VWS; unpubl. data, 2019).

Environmental Variables

I examined 13 environmental variables (Table 1) previously used to identify suitable condor habitat (D'Elia et al., 2015). I used raster layers capturing environmental variables generated and assessed in this previous habitat study (D'Elia et al., 2015; Table 1). I followed the same categorization of these 13 variables from the previous study as related to soaring conditions and climate, terrain, landscape productivity, vegetation characteristics, and human disturbance (D'Elia et al., 2015). Because a home range reflects the area an animal uses to fulfill biological needs (Burt, 1943; Seaman and Powell, 1996; Powell and Mitchell, 2012), factors used to predict habitat suitability for condors also likely influence condor home range size. Brief descriptions of the environmental variables included from the previous study and how they may affect condor home ranges are provided in the following paragraphs.

Environmental and atmospheric conditions influence the availability of resources and animal movements. Factors related to soaring conditions (thermal updraft velocity, thermal height, and wind speed) can affect the efficacy of condor flight as they search for food and nesting and roosting sites (Koford, 1953; Poessel et al., 2018b). Winter severity could constrain nesting activities which are long in duration; therefore, the size of a home range can be affected by mean minimum temperature (Koford, 1953; D'Elia et al., 2015). Condors use orographic lift to gain altitude while soaring and typically nest in rocky outcrops (Koford, 1953; Poessel, 2018b); therefore, terrain characteristics (e.g., cliffs and terrain ruggedness) are potentially associated with condor home range size.

Other landscape productivity and landcover characteristics may be important factors related to condor home range. Direct measures of carrion available for condors across the landscape are nearly impossible to estimate; however, maximum normalized difference vegetation indices are well-correlated with primary production and correlated with secondary production as well (Oesterheld et al., 1998; Pettorelli et al., 2009; 2011). More specifically, maximum normalized difference vegetation index (NDVI) had a significant positive relationship to deer densities and elk densities throughout the study area during this previous habitat suitability analysis (D'Elia et al., 2015). Condors may use large bodies of freshwater (streams, rivers) for navigation and are attracted to freshwater for bathing; therefore, distance to water may be an important factor for home range size (Koford, 1953; Arizona Condor Review Team, 2002; D'Elia, et al., 2015). To evaluate associations of home range size with vegetation characteristics, canopy cover, canopy height, and land-cover type were assessed. Condor nesting activities have been shown to be sensitive to human activities and disturbance (Koford, 1953; Sibley, 1967; 1969); thus, road density and human population density may help elucidate whether human disturbance affects the sizes of condors' home ranges.

Using the raster surfaces derived during the habitat suitability analysis (D'Elia et al., 2015), I calculated mean or majority values of the environmental variables for all home range estimations using the Zonal Statistics tool in ArcGIS 10.5.1 and ArcGIS Pro (Redlands, California, USA). I used mean values for continuous variables and majority values for categorical variables.

Table 1. Intrinsic[i] and environmental[ii] variables, organized by category, considered during linear mixed model selection to identify factors that influence condor home range size in California.

Variable	**Description**
Individual characteristics	
Age group	Categorical - 4 levels: adult breeding, adult non-breeding, subadult, juvenile. Adult breeding: ≥6 years of age and breeding, adult non-breeding: ≥6 years of age and not breeding, subadult: ≥3 years old and ≤5 years of age, juvenile: ≤2 years of age. *One female individual was 5 years of age and breeding and was included in the adult breeding category
Sex	Categorical - 2 levels: male, female
Time spent in wild	How long an individual has been in the wild from release/wild hatch to end of GPS year, in years

Management characteristics	
Rearing method	Categorical - 2 levels: Wild-hatch, captive-bred and release. Wild hatch includes individuals that were hatched in the wild from captive-laid eggs.
Flock	Categorical - 2 levels: Central CA (condors managed by PINN/VWS), Southern CA (condors managed by USFWS)
Age of managing agency	Age of managing agency at the end of the GPS year, in years
Population factors	
Population size	Number of individuals per flock at end of GPS year
Adult breeding to subadult ratio	Ratio of breeding adult individuals to subadult individuals per flock per GPS year
Soaring conditions and climate	
Thermal updraft velocity	Annual mean velocity of rising air (m/s)
Thermal height	Annual mean thermal height (m)
Wind speed	Categorical - Horizontal wind power class at 50 m above the ground, in 7 classes
Winter severity	Mean minimum winter temperature (^{o}C x 100)
Terrain	
Cliffs	Maximum slope within a 1 km^2 neighborhood (degrees)
Terrain ruggedness	Ratio of a 3-dimensional surface area to planar surface area
Landscape productivity	
Landscape productivity	Average Maximum Normalized Difference Vegetation Index (NDVI)
Distance to water	Euclidean distance to the nearest freshwater (km)
Vegetation characteristics	
Canopy cover	Median canopy cover (%)
Canopy height	Categorical - 5 levels: Bare or very low vegetation (<0.5m), low vegetation (0.5—1m), medium vegetation (1—5m), tall vegetation (>5m), other/non-habitat
Land cover type	Categorical - 10 levels: Non-habitat, perennial ice and snow, developed, bare rock/sand/clay, deciduous forest, evergreen forest, mixed forest, shrubland, grassland/herbaceous/pasture, row crops
Human disturbance	
Road density	Meters of road/km^2
Human density	Humans/km^2

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[i] Intrinsic variables derived from the California Condor North American Studbook (Mace, 2019) with additional information provided by PINN, VWS, and USFWS.

[ii] Original source data for all environmental variable surface layers cited in D'Elia et al., 2015.

Analysis and Modeling

I fitted linear mixed-effects models (LMMs) that combine fixed and random effects as predictors with the ‘lmer’ function with maximum likelihood estimation and Satterthwaithe degrees of freedom in the ‘lme4’ package in R Studio version 1.1.43 (Bates et al., 2015; R Core Team, 2018). Using LMMs allowed me to account for correlations from individuals with repeated measurements of home range estimations over multiple years by including individuals as a random effect. I used maximum likelihood estimation instead of the default restricted maximum likelihood in ‘lme4’ to compare models with different fixed effects using AIC. Maximum likelihood estimation is the more appropriate method to use when comparing error of models containing different fixed effects because this method is not contingent upon the residuals of fixed effects of the models, unlike the restricted maximum likelihood estimation method. I used visual diagnostic plots to check that all model assumptions were met. After calculating summary statistics for my data, I realized that home range areas for the central CA flock during 2004-2005 were considerably larger than home range areas during subsequent years. This was because condors managed by the two different agencies in the central CA flock had not yet found each other and individuals from VWS would frequently visit the southern CA flock. Because I wanted to focus my analysis on home range areas and movement after the VWS and PINN condors began interacting and behaving as one flock, I removed data prior to 2006. This was the year condors managed by VWS and those managed by PINN began intermingling and behaving as a single flock (PINN unpubl. data, 2006).

I then conducted a stepwise model selection to identify variables to include in my final model. I fitted individual models within each subcategory with home range area as the response variable and included Bird ID as a random variable. I retained variables if confidence intervals did not overlap zero, thus displaying an effect on home range area. I assessed Pearson's correlation and multicollinearity between variables that were kept in a single sub-category using the 'cor' and 'vif' functions in R Studio (Fox and Weisberg, 2011; R Core Team, 2018). I considered variables with VIF > 3.0 (Zuur et al., 2010) or $r > 0.70$ to be correlated and kept the variable with the lower AIC for further analyses. Road density and human density were the only pair of variables that showed signs of collinearity and I kept road density for further analyses. Assessing collinearity between variables is an important step because variables that are linearly related reduce the accuracy of coefficient estimates. The remaining variables were then fit to a full model. I used the step function from the 'lmerTest' package in R (Kuznetsova et al., 2017) to eliminate variables from the full model to produce a parsimonious final model that provided the best explanatory power. I used the 'emmean' function with the 'emmeans' package in R (Lenth, 2019) to identify the estimated group mean responses within categorical predictors included in the final model and the significant differences between pairwise comparisons of group means.

RESULTS

I began with 9,720,551 fixes and 660 GPS years from 181 condors. GPS records ranged between a few days to thirteen years in length (median = 3 years). I removed all fixes with diagnostic errors and subset GSM data to match the coarse sampling schedule from GPS-PTT tags. I also only retained GPS years with at least 6 months of cumulative data. After removing data prior to 2006, the sample included 1,538,953 fixes and data from 123 condors (57 from the central CA flock and 66 from the southern CA flock). I used 59 females and 64 males in analyses. Individuals were characterized by age group and breeding status. Due to the length of the study, some individuals transitioned from one age group to the next and between breeding statuses in different GPS years. Overall, I included 105 adult-breeding, 160 adult non-breeding, 87 subadult, and 23 juvenile condor GPS years in my analysis. The sample is representative of the entire California population, including both sexes (59 females, 64 males), and both rearing methods (108 captive-bred, 15 wild-hatch).

Home Range Estimation and Analysis

I estimated a total of 375 home ranges. The median number of home ranges estimated per individual was 2 (range: 1 – 11). All individuals exhibited range residency. Mean home range area was 5,154 km^2 (se = 181 km^2, range = 7.76 – 20,716 km^2). Predictors included in the final model were: Age Group, Time in the Wild, Age of managing agency, Maximum Slope, Maximum NDVI, Distance to Water, and Road Density (Table 2). None of the 95% confidence intervals for the beta estimates contained zero, suggesting all predictors included in the final model had strong effects on home range size. The marginal R^2 value for the final model was 0.65 and the conditional R^2 value was 0.74. These values represent the variation explained by the fixed effects only and the entire model, respectively.

Individual characteristics

Individual characteristics that influence home range size included age group and time spent in the wild. Adult breeding individuals had the smallest mean area for home range (4,348 km^2), and subadults used the largest area on average (6,339 km^2). The mean home range area of juveniles was not significantly different from home range areas of the other age groups, but all other age groups were significantly different from each other (Table 3). With all other variables held constant, time spent in the wild had a moderately strong negative effect on home range area ($\beta_{\text{Time Spent in Wild}}$ = -109.539).

Management Factors

Age of managing agency is the only management factor that affected home range area ($\beta_{\text{Age of managing agency}}$ = 195.012). Keeping everything else constant, home range area increases by ~195 km^2 for every year increase in managing agency's age.

Environmental Covariates

Maximum slope, maximum NDVI, distance to water, and road density were all significant predictors of home range size. Maximum slope and distance to water both had negative effects on home range size, while maximum NDVI and road density had positive effects on home range area. Maximum slope had a strong negative effect on home range size, which decreased by ~348 km^2 with a ~1 degree increase in average maximum slope km^2 scale. Home range area increased by ~130 km^2 as the average value of maximum NDVI per km^2 increases. Home range size decreases by approximately 136 km^2 when the mean distance to water per km^2 increased. Increased road density had a small positive effect on home range ($\beta_{\text{Road Density}}$ = 4.193), with home range increasing by 4.193 km^2 for each m/km^2 increase in road density.

Table 2. Beta estimates and 95% confidence intervals of factors that influence condor home range areas in California. All factors were included in the final model were identified by stepwise model selection. Marginal R^2 value represents variation explained by fixed effects. Conditional R^2 is the variation explained by both fixed effects and random effects Bird ID.

Factor	Beta Estimate	Std. Error	Degrees Freedom	Lower Confidence Level	Upper Confidence Level
Adult Breeding (Intercept)	-16301.657	6172.673	271.619	-28687.354	-4077.249
Adult Non-breeding	809.172	263.453	364.759	291.484	1327.060
Juvenile	1280.218	563.556	359.662	168.623	2389.575
Subadult	1991.275	377.833	371.021	1242.866	2738.699
Time Spent in the Wild	-109.539	34.113	154.322	-179.491	-41.822
Age of Managing Agency	195.012	29.826	196.738	136.131	255.111
Maximum Slope	-347.994	57.702	365.256	-461.380	-234.594
Maximum NDVI	130.071	36.687	226.995	57.483	203.948
Distance to Water	-135.881	30.762	373.102	-196.341	-75.431
Road Density	4.193	0.585	374.963	3.042	5.343

Marginal R^2: 0.65 **Conditional R^2**: 0.74

*Table 3. Mean home range areas (km^2) condors in California by age group. Contrasts from pairwise comparisons depict the difference between home range areas of age groups. Contrasts with * are significantly different.*

Age Group	Adjusted Mean	Std. Error	Degrees of Freedom	Lower Confidence Level	Upper Confidence Level
Adult Breeding	4348	251	275	3854	4842
Adult Non-breeding	5157	208	217	4746	5568
Juvenile	5628	501	364	4642	6614
Subadult	6339	289	326	5770	6908
Contrasts	**Difference**	**Std. Error**	**Degrees of Freedom**	**t-ratio**	**p-value**
Adult Breeding – Adult Non-Breeding*	-809	268	376	-3.019	0.0144
Adult Breeding – Juvenile	-1280	575	379	-2.227	0.1178
Adult Breeding – Subadult*	-1991	385	385	-5.167	<.0001
Adult Non-Breeding – Juvenile	-471	552	375	-0.854	0.8284
Adult Non-Breeding – Subadult*	-1182	352	385	-3.362	0.0047
Juvenile – Subadult	-711	499	385	-1.424	0.4849

DISCUSSION

The California condor is critically endangered and although the population is growing, challenges to condor survival continue to impede the success of recovery efforts. To better understand the relationship between condors and their habitat and help inform management decisions, I estimated annual home range areas of condors and identified intrinsic and environmental factors that influenced annual home range size of condors. I looked at 8 intrinsic and 13 environmental variables and found that age group, time spent in the wild, experience of managing agency, slope, NDVI, distance to water, and road density are all significant predictors of home range size.

Home Range Area and Life Stage

Biological needs of different life stages and varying knowledge of available resources can explain the changes in mean home range area of endangered California condors. Subadults and juveniles (mean = 6,339 ± 289 SE km^2 and mean = 5,628 ± 501 SE km^2, respectively) had larger annual home range areas on average than breeding and non-breeding adult condors (mean = 4,348 ± 251 SE km^2, mean = 5,157 ± 208 SE km^2, respectively; Table 3). These results agree with observations of condors in the wild prior to captivity in 1987 (Meretsky and Snyder, 1992); however, another study found that immature condors (0 – 5 years of age), had smaller monthly home ranges on average than both breeding and non-breeding adults (Rivers et al., 2014a). Different home range sizes corresponding to different age groups are often seen in other vulture and eagle species and are attributed to different fitness priorities—subadults seek to improve chances of survival by exploring the landscape looking for optimal resources, while breeders focus on reproduction and constrain movements to areas around their nests, which are typically within established territories (Kendall et al., 2014; Margalida et al., 2016; Reading et al., 2019).

Incorporating monitoring and outreach activities across populations of subadult and juvenile condors is important to increase chances of survival to sexual maturity and contribution to population recovery. Condors in these two age groups use the largest home ranges yet are still acquiring flight and foraging skills while learning about the surrounding landscapes. Other studies of vultures and raptors also found that immature individuals use the largest home ranges, which are used to find and exploit food sources and maximize survival prospects (Martens et al., 2008; Margalida et al., 2013; Harel et al., 2016; Margalida et al., 2016; Kang et al., 2019). Condors are a long-lived species with delayed sexual maturation, characteristics that contribute to slow population recovery when mortality rates are high (Koford, 1953; Snyder and Snyder, 2005; Ogada et al., 2012). Therefore, including areas used by juveniles and subadults into management plans is imperative to reduce threats to their survival and improve population recovery success (Martens et al., 2008; Margalida et al., 2016).

Breeding condors confine movements to around their nests and have the smallest mean home range area of any age class. Breeding vultures and eagles are commonly found to have smaller home ranges and movements than other age groups (Moss, et al, 2014; Margalida et al., 2016; Reading et al., 2019). Observations of the condor population before the capture of all wild individuals in 1987 also found breeders restricted their movements and visited feeding areas closest to their nests (Meretsky and Snyder, 1992). During breeding seasons, bearded vultures (*Gypaetus barbatus*) and hooded vultures (*Necrosyrtes monachus*) exhibit central-place foraging around nests and individuals maximize food intake at feeding events to balance the trade-offs of nourishment and energy exerted from nesting and foraging efforts (Margalida et al., 2016; Kang et al., 2019; Reading et al., 2019). In contrast, breeding Cinereous vultures (*Aegypius monachus*) also exhibited central-place foraging, yet travelled farther from nest colonies to habitats with richer scavenging opportunities (Carrete and Donazar, 2005). In addition to changes in biological priorities as they age, vultures and condors seemingly retain information about the landscape and prioritize using areas that are energetically profitable, which can also explain why home range area decreases as a condor spends more time in the wild. Other studies have shown that individuals settle into territories as they age and gain information about the landscape (Burt, 1943; Margalida et al., 2016).

Home Range Area and Information Center Hypothesis

The information center hypothesis describes the role communal roosting and social attraction plays as a way of directly and inadvertently gaining information from conspecifics (Bijleveld et al., 2010; Dermody et al., 2011; Cortes-Avizanda et al., 2014; Harel et al., 2017). This hypothesis can help explain why home range areas increase as managing agencies gain years of experience releasing and managing condors. Like other vulture species, condors are social and follow other condors to feeding and roosting sites (Meretsky and Snyder, 1992; Rivers et al., 2014a). However, condors were reintroduced to areas without knowledge of the landscape or conspecifics from which to learn, and during the early years when managing agencies were releasing condors, naïve condors stayed closer to release sites where food was provisioned for them (Rivers et al., 2014a). The life stages before settling into breeding and nesting territories is essential for vultures to maximize chances of survival by exploiting large areas and food resources (Margalida et al., 2016) and monitoring vast expanses increases the likelihood of discovering unpredictable abundances of food (Miller et al., 1965; Meretsky and Snyder, 1992). As bolder individuals discovered roosting, feeding, and nesting habitats farther from release sites, less knowledgeable condors likely followed, and those areas became incorporated into the condor range. When new cohorts are released by different managing agencies, naïve birds can follow the more experienced condors from release sites before exploring new areas of the landscape, which explains why annual home range area increases as managing agencies gain more years of experience with the Program.

Home Range Area and Environmental Variables

Out of the 13 environmental variables assessed, maximum slope, maximum NDVI, distance to water, and road density were retained in the final model and an effect on home range area. Maximum slope was included as a proxy for the presence of cliffs in a home range, which are used by condors for nesting, roosting, and thermal updrafts (Koford, 1953; Snyder et al, 1986; D'Elia et al., 2015; Poessel et al, 2018b). Results from my study indicate that home range size decreases with steeper slope values. Maximum slope proved to be an important variable during the previous habitat suitability analysis, especially when predicting nesting and roosting habitat (D'Elia et al., 2015). Condors typically nest in cavities or ledges on cliffs and roost in trees in mountainous regions (Koford, 1953; Snyder et al.; 1986; Meretsky and Snyder, 1992), and condors often find food in foothills or coastal areas where steep mountains or cliffs meet the ocean (Snyder and Snyder, 2000). Areas with more cliffs contain more suitable habitat for nesting, roosting, and feeding activities; therefore, resources are likely more accessible to condors, resulting in smaller home ranges.

I found that NDVI positively influenced annual home range areas of condors. NDVI was included as an indirect measure of prey availability; larger values of NDVI are correlated with higher ungulate densities in California (D'Elia et al., 2015). Home range size is typically inversely related to food abundance (Marzluff et al., 1997; Maher and Lott, 2000). In my results, home range areas were larger with higher NDVI, which can support more animals. This finding suggests that prey mortality may be a better attraction than prey availability for condors. Ruppell's vultures (*Gyps ruepelli*) and Lappet-faced vultures (*Torgos tracheliotos*) showed similar patterns in Kenya, clustering around migratory herds during dry season when more ungulates perish (Kendall et al., 2014). Hooded vultures (*Necrosyrtes monachus*) also use smaller home ranges during dry seasons, which may be a result of concentrated food availability from prey mortality (Reading et al., 2019). In contrast, turkey vultures (*Cathartes aura*) use breeding areas that have higher values of NDVI than non-breeding areas, with breeding home range areas negatively correlated with NDVI (Dodge et al., 2014). This indicates that prey availability can influence home range size more than prey mortality for some vulture species.

Home ranges with higher mean distances to water were smaller than those with smaller mean distances to water. This is an interesting result as condors are known to be attracted to water sources for bathing (Koford, 1953) and it has been theorized that condors use rivers for navigation (AZ Condor Review Team, 2002). However, it could be that there is more prey mortality in areas farther from fresh water sources, therefore minimizing the need for condors to use larger home ranges. Condors in California use a mix of public and private lands on which there are many active ranching operations (Snyder and Snyder, 2000; Hall et al., 2019). Water troughs and artificial ponds that are present throughout the landscape and continuously used can help explain why home ranges are smaller even though they are seemingly farther from fresh bodies of water.

Home range areas increased by 4.19 km^2 for every increase of km of road per km^2. Condors are somewhat sensitive to human disturbance and are less likely to nest in areas with greater human disturbance (Sibley, 1969; D'Elia et al., 2015). Condors also prefer undisturbed and undeveloped habitats that support grazing operations for cattle, as well as deer or elk (Rivers et al., 2014b; Hall et al., 2019). An increase of road density per home range area could also create more feeding opportunities across a home range due to higher occurrences of wildlife-car collisions; however, it has been shown that black vultures (*Coragyps atratus*) and turkey vultures in north east United States use thermal drafts from roads and prefer foraging on carrion in open habitats with roads, but not on carcasses along roads (Mandel and Bildstein, 2007). Andean condors (*Vultur gryphus*) have also been shown to avoid feeding on carcasses experimentally placed near roads and fed longer and with less vigilant behavior on carcasses far from roads; behaviors suggesting a tradeoff between energy intake and safety (Speziale et al., 2007). Areas with higher road densities may be perceived as dangerous and condors may be willing to traverse more land to find resources in safer areas, resulting in larger home ranges.

Factors not Linked to Home Range Area

While many of variables assessed in this study could seemingly affect home range area, it is most surprising that population size was not influential. As a population grows, condors are detected less frequently, indicating they are ranging farther from release sites (Bakker et al, 2017). However, while condors may be ranging farther from release sites, their annual home range areas are not growing as a function of population growth. Managers have assumed that condor home range area would increase as populations grow due to competition for resources, however that does not appear to be the case. On the contrary, the addition of captive-bred individuals to the population may be impeding annual home range growth due to conspecific attraction .

I did not expect to find a sex effect on home range area as males and females have similar energetic costs and share parental responsibilities (Snyder and Snyder, 2005). Condors typically mate for life and have been observed near their nests throughout the year as they provide considerable parental care to their young (Snyder and Snyder, 2005). Breeding condors share equal responsibility incubating their single laid egg and caring for their hatched offspring, which fledge about 6 months after hatching. They can continue to care for their young up to one year after fledging, which likely contributes to non-breeding adults having smaller home range areas than juveniles and subadults.

Factors not identified as strong predictors of annual home range area cannot be ruled out as influential to condor movement. Future studies may correlate these factors to occurrence distributions instead of home range estimations. My study looked at the space required for condors at a coarse resolution, which may not capture the importance of these variables at a finer spatial or temporal scale.

Management Implications and Areas of Future Research

The results from my analyses can inform Program managers of the factors that influence home range size and areas that should be included in future monitoring and management strategies. These results reflect common understandings of home range areas and animals – young individuals use large areas before settling into smaller home ranges as adults and use habitat that is conducive to nesting, roosting, and foraging activities (Burt, 1943; Meretsky and Snyder, 1992; Moss, et al, 2014; Margalida et al., 2016; Reading et al., 2019). A population with more subadults may see wider-ranging individuals, which may result in lower survival from exposure to risks (Finkelstein et al., 2012; Bakker et al., 2017). Appropriate outreach efforts throughout the aggregated home range areas is advisable to help mitigate threats to condors. That annual home ranges are increasing as managing agencies mature is also an indication that the Program is successful in re-establishing condors to their historic range.

These results can also be used to inform future condor movement studies. Agent-based models simulating condor movement could be parameterized using coefficients from strong predictors identified here. Results from this study can also help predict where condor ranges are likely to expand based on environmental associations and population demographics. This study highlights the need to look at individual movements of condors throughout their home ranges and consider biological and social attractions that can influence these movements.

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Chapter 2– Range Expansion of Critically Endangered California Condors and Overlap with Commercially Valuable Wind

SUMMARY

Collisions with wind energy infrastructure is a major cause of wildlife mortality worldwide and especially pose threats to bird and bat populations. Avian species that have associations with habitats that generate strong winds are at higher risk of collision with wind turbines. Critically endangered California condors (*Gymnogyps californianus*) are among species that use areas with high-class winds. To identify where there is potential for conflict between the expanding condor range and wind energy development, I created a tool to predict and map the overlapping home ranges of customizable condor flocks in California, which were then overlaid with areas of high wind generation. Predicting condor range expansion may inform managers of areas to concentrate efforts and resources for management and outreach, as well as identify areas that should be considered during wind energy development planning stages to reduce risks to condor recovery. I predicted condor range expansion in California under four scenarios: 1) population demography stays the same (2019 California population); 2) each flock has 150 individuals with 15 breeding pairs; 3) each flock has a majority of breeding pairs, which maximizes breeding pairs and minimizes sub-adult condors; and 4) each flock has a majority of subadults, which maximizes subadult condors and minimizes breeding pairs. Predicted ranges under different scenarios exhibited high similarity and areas with high wind generation overlapped with <10% of predicted condor range under all scenarios. More than 81% of areas with commercially valuable winds were unaffected by predicted condor range, suggesting there

are alternative areas for wind energy development with less risk of conflict with critically endangered California condors.

INTRODUCTION

As the human population continues to grow, human-wildlife conflicts have become more frequent. Among those conflicts are strike risks that wind turbines pose to avian and other volant species. Bird mortalities from wind turbines in the contiguous United States are estimated to be in the hundreds of thousands every year (Loss et al., 2013). With the increase of electricity generated from renewable sources, bird and bat mortality due to collision with wind turbines will likely increase (Smallwood and Bell, 2020). The United States hopes to have 20% of its total energy generated from wind power by 2030 (US Dept. of Energy, 2008) and many states are taking initiatives to harvest more renewable energy as well. The state of California currently produces approximately a quarter of its energy from renewable sources (EIA, 2017); however, the Clean Energy and Pollution Reduction Act of 2015 (California Senate Bill 350) requires that California electricity generated from renewable sources must increase to 50% by December 31, 2030, suggesting that more wind energy farms are to be constructed.

Managers and researchers have conducted surveys to identify which volant species are at risk in the presence of wind farms. Avian species that deploy migratory strategies, have associations with habitats that generate high wind potential, and have moderate dispersal rates, result in significantly higher collisions with wind turbines (Thaxter et al., 2017). Large soaring birds, such as raptors, storks, and vultures, have high risk and rates of collision with turbines due to their use of wind generated from mountainsides, high wing loading, and low maneuverability (Katzner et al., 2017; Thaxter et al., 2017; Poessel et al., 2018a). Wind turbines can also cause habitat fragmentation, displacement, or reduced breeding success (Smith and Dwyer, 2016). There are even greater consequences to species that cannot offset losses of individuals in a population due to low reproductive rates. Among species with traits that are especially sensitive to conflicts with wind turbines and energy farms is the critically endangered California condor (*Gymnogyps californianus*).

The California condor is the largest avian scavenger of North America with evolved characteristics to exploit patchily distributed and temporarily available resources (Brodkorb, 1964; USFWS, 1974; Snyder and Snyder, 2005). Among these traits are keen eyesight and a 3-meter-wingspan used to travel large distances looking for carrion (Snyder and Snyder, 2005). Like other large soaring birds, condors take advantage of meteorological and environmental conditions that produce thermal and orographic updrafts to sustain flights of long durations (Poessel et al., 2018b). Condors are a long-lived species, reaching sexual maturity around six years-of-age and reproducing one chick every two years, when breeding is successful (Koford, 1953; Snyder and Snyder, 2005). These traits make condors more vulnerable to collisions with wind turbines and sensitive to losses in their population.

While there are currently no records of fatalities of condors attributed to collisions with wind turbines, managers recognize the potential threat wind energy facilities pose to condors as the species expands their range (USFWS, 2013). The California condor population comprises just over 300 individuals in the wild. Condors are highly monitored and managed by the California Condor Recovery Program– hereafter referred to as the “Program” – a multi-agency collaborative network of zoos, federal and state agencies, as well as non-profit organizations.

While numbers of condors have been slowly increasing throughout the years, threats to condor survival are still present and the wild population is supplemented by releases of captive-reared individuals (Finkelstein et al., 2012; Rideout et al., 2012; Kelly et al., 2015; Bakker et al., 2017). As obligate scavengers, condors are reliant on carcasses they find on the landscape. Unfortunately, the inadvertent ingestion of spent ammunition in some of the carcasses condors feed on causes lead poisoning to be the largest cause of death in adult condors (Finkelstein et al., 2012; Rideout et al., 2012). Because mortality rates exceed those necessary for stable and increasing wild populations (Kelly et al., 2015), identifying and minimizing all threats to condor survival is a priority of Program managers.

Managers monitor individual condor movements with visual observations, radio telemetry, and Global Positioning System (GPS) units to understand where condors spend their time and why. These tracking strategies can also help provide insight about the health of an individual, recover deceased condors, and identify threats to condor survival. However, as the Program matures, condors are expected to move further away from release sites, use larger home ranges, and adopt more wild behaviors (Bakker et al., 2017). While this shift in behavior is considered a success from a recovery standpoint, it makes condors more vulnerable to threats to their survival. Predicting where and when condors will occupy suitable habitat in California can help inform monitoring and management strategies aimed at mitigating potential constraints to condor recovery.

In this chapter, my objective was to predict condor range expansion in California to identify where there is conflict between condors and potential wind energy development. Less than half of suitable habitat for condors is currently occupied (D’Elia et al., 2015), but as the

Program matures and individual home ranges increase in size (Chapter 1), more of this habitat is likely to be used. Results from this chapter may inform managers of areas to concentrate efforts and resources for management and outreach, as well as identify areas that are likely to be re-occupied by critically endangered California condors which should be considered during wind energy development planning stages. To reach this objective, I created a predictive tool using information learned about annual condor home ranges (Chapter 1) and a condor habitat suitability surface (D'Elia et al., 2015).

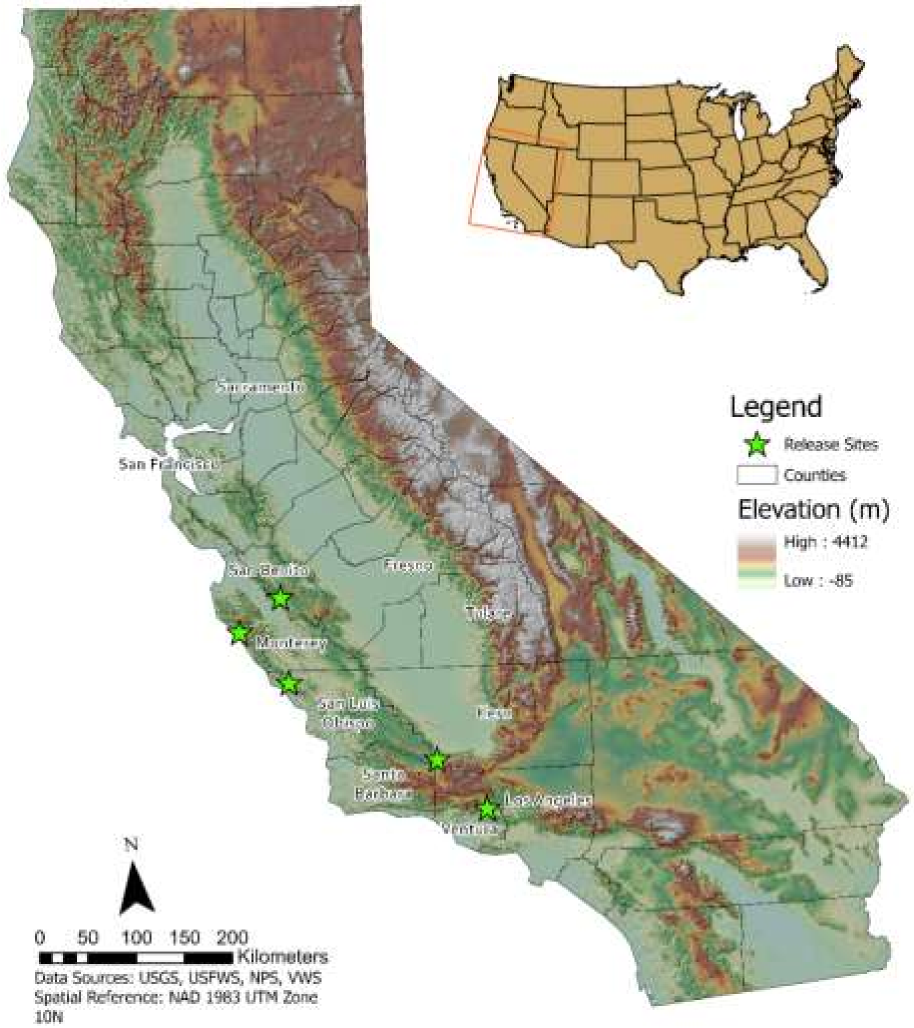
METHODS

Study Area

The study area included California, where three agencies manage five release sites (4 active and 1 defunct) in central and southern California (Figure 2). In central California, two release sites along the Pacific coast are operated by Ventana Wildlife Society (VWS) and one approximately 50 kilometers inland of the coast is managed by Pinnacles National Park (PINN). Due to the proximity of these three release sites, all condors in central California are co-managed and monitored as a single flock by both managing agencies. In southern California, condors are managed by the United States Fish and Wildlife Service (USFWS) and are released out of Bitter Creek National Wildlife Refuge. A release site at Hopper Mountain National Wildlife Refuge continues to be part of the core use areas of condors in southern California, even though it is no longer in operation.

In central California, condors typically range west in the mountainous regions along the Big Sur Coastline from Monterey to San Luis Obispo counties and inland throughout San Benito

County and parts of western Fresno County. In southern California, condors typically range throughout the Los Padres National Forest in Santa Barbara and Ventura Counties and the Tehachapi Mountains in Kern County (Figure 2). California condors are not known to travel over ocean, therefore, the Channel Islands and other islands off the coast of California were excluded from our study.



Data Sources: USGS, USFWS, NPS, VWS
Spatial Reference: NAD 1983 UTM Zone 10N

Figure 2. Map of area included to predict condor range expansion in California. Condor release sites are represented by green stars.

Predictive Tool

To predict where condors are likely to expand their range, we created a predictive tool consisting of two models in Netlogo version 6.1.1 (Wilensky, 1999). Netlogo is a, “multi-agent programmable modeling environment” and is typically used for programming agent-based models (Wilensky, 1999). Agent-based models simulate the actions and interactions of individuals in a system and assess how processes at the individual-level produce phenomena at the system-level (Huston et al., 1988). The models in my predictive tool differ from agent-based models in that while I am programming individual entities to execute specific functions and actions, individuals do not interact, adapt, or learn.

The overarching goal was to create a tool that allows users to customize population demographics of the condor flocks in California sometime in the future and predict the overlapping home ranges of the flocks. Users can then consider ways that the overlapping home ranges may be affected by plans for wind energy development and identify possible alternative sites. Two models were developed, with the first model not intended for general use, but necessary to create input that is used in the second model. The first tool builds an ordered list of potential roost site locations and patches around them, that if all were incorporated into a home range, would yield an area larger than any observed range. The second tool uses that list and home range estimates derived from findings in Chapter 1 to define home ranges of the appropriate area and overlay all ranges.

Model 1

The purpose of the first model is to populate a habitat suitability surface (D’Elia et al., 2015) with the potential roost sites, convert the coordinates from a projected coordination system (UTM) to patch coordinates in Netlogo, and set the rules by which home ranges grow. Rules by which home ranges grow determines how patches within the model are incorporated into home ranges starting at the potential roost site location. I created three main parameters that can be adjusted by a user to change the pattern by which the home ranges grow within the habitat suitability layer. The first parameter, “Highest-patches-selected”, is the number of patches that are selected around the perimeter of the growing home range to incorporate all patches within a certain radius of itself into the home range. The “Radius-of-placed-cells” parameter adjusts the radius of a circle of cells that gets added to the home range as it grows. Finally, a “Home-range-complexity” parameter determines how strictly home ranges expand into the areas with the highest habitat suitability score. Home range complexity can be set incrementally from 0 to 1, with 0 allowing total randomness of cells around the perimeter for selection, and 1 allowing only the patches with the highest habitat suitability scores to be selected.

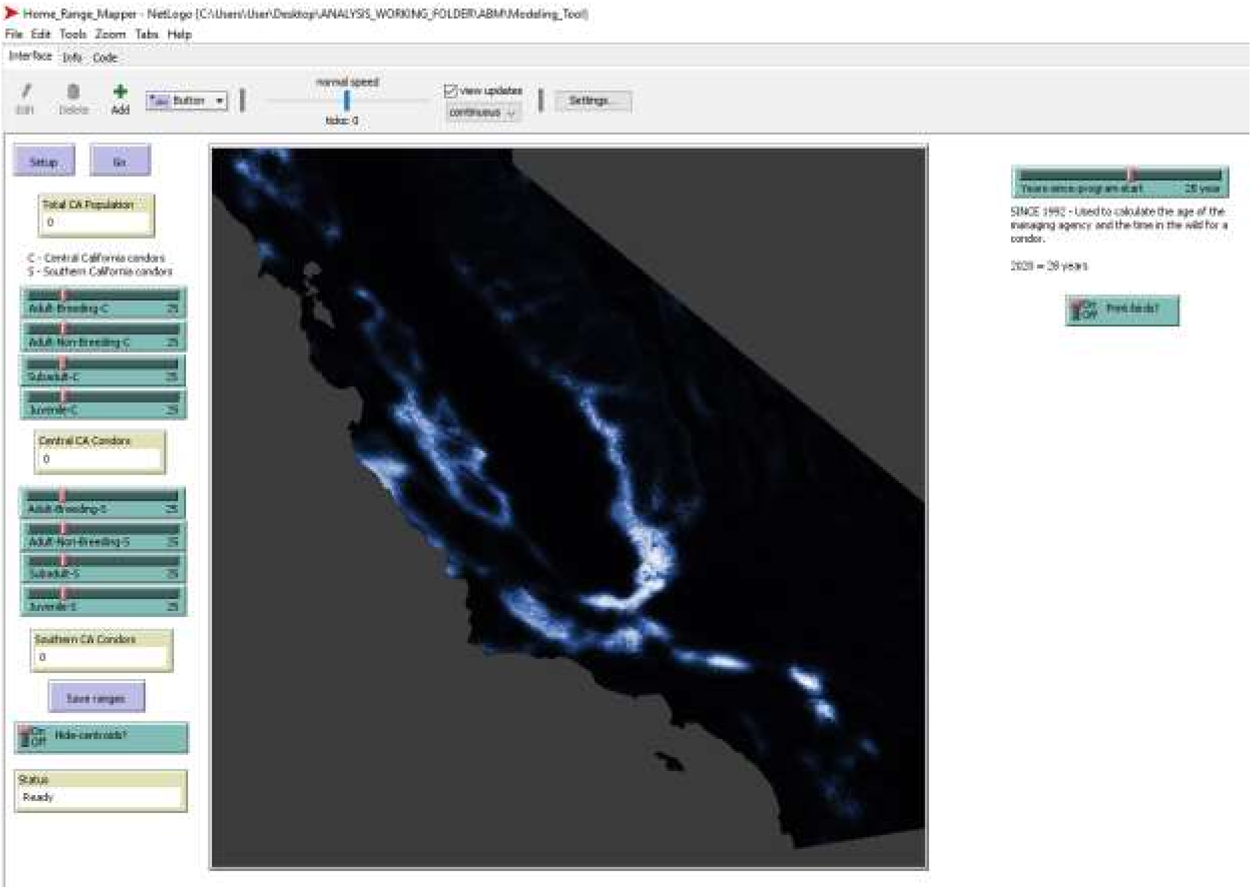
The model space is a two-dimensional representation of California. Each patch represents one square kilometer and is attributed with a habitat suitability score (D’Elia et al., 2015) and color. Patches change color to signify that they are a part of a home range. During the model setup, agents called “birds” are created on patches with potential roost sites and this roost site patch and all neighboring patches become a part of the home range. All eight patches on the perimeter of the roost site then incorporate all patches within the specified radius into the home range. From this point until the home range accumulates 30,000 patches (or km^2), the number of patches set by "Highest-patches-selected" with the highest habitat suitability scores around the perimeter incorporate all patches within the specified radius.

To emulate the shape of home ranges estimated in Chapter 1 of my thesis, I set "Highest-patches-selected" to 10, "Radius-of-placed-cells" to 14, and "Home-range-complexity" to 0.75, allowing patches with the highest habitat suitability score around the perimeter to be selected 75% of the time. The other 25% of the time, any ten random patches along the perimeter of the home range were selected. These values were determined through trial and error, adjusted until the appearance of final home ranges were visually similar to observed home ranges. The parameters used to grow the home ranges, along with the potential roost site locations, their patch (x, y) coordinates, and ordered lists of coordinates of all patches that sum to the 30,000 km^2 home ranges for each were then saved as a text file that is used in the second model.

Model 2

The second model estimates and maps condor home ranges into suitable habitat using a linear model (Eq. 1) that explains the relationship between home range area and various predictor variables (Chapter 1). A user determines how many condors of each age group (breeding adult, non-breeding adult, subadult, juvenile) in both the central and southern California flocks to estimate home ranges for, as well as how many years will have passed since 1992 (when the Program began releasing condors) via sliders on the user interface (Figure 3). Condors of each age group are generated and assigned a numerical identifier that is matched with a potential roost site with the same identifier. Condors assume the environmental variable values that the roost sites own, which allows the home range areas to be calculated for every condor using Eq. 1 (see Chapter 1 for sources and units for explanatory data). Home ranges are then mapped within the suitable condor habitat in California.

Home Range Area (km^2) = Age Group (Intercept) - 109.5392 (Time Spent in the Wild) + 195.0115 (Age of Managing Agency) - 347.9939 (Maximum Slope) + 130.0706 (Maximum NDVI) - 135.8813 (Distance to Water) + 4.1928 (Road Density) Eq. 1



ticks: 0

☑ view updates

continuous

Total CA Population
0

C - Central California condors
S - Southern California condors

Adult-Breeding-C 25

Adult-Non-Breeding-C 25

Subadult-C 25

Juvenile-C 25

Central CA Condors
0

Adult-Breeding-S 25

Adult-Non-Breeding-S 25

Subadult-S 25

Juvenile-S 25

Southern CA Condors
0

Hide-centroids?

Status
Ready

Years-since-program-start 28 year

SINCE 1992 - Used to calculate the age of the managing agency and the time in the wild for a condor.

2020 = 28 years

Figure 3. User interface of Model 2 used to predict and map condor range expansion in California.

Home Range Origins and Estimates of Model Parameters

To grow home range areas into suitable habitat, I generated 500 random points for each flock, for a total of 1,000, to be used as origins of home ranges. I generated points within the combined core areas of the central and southern California flocks observed during 2017 using the Create Random Points tool in ArcGIS version 10.6.2 (ESRI, Redlands, California, USA). Core areas are described as regions within home ranges that are used more extensively than expected under a uniform random distribution of use (Powell, 2000). Age of managing agency was determined for each managing group using the “Years Since Program Start” slider on the user interface by subtracting five and eleven from the amount of years set on the slider, as those are how many years VWS and PINN began releasing condors after the USFWS did in 1992, respectively. Year zero represents 1992.

The amount of time a condor spent in the wild was randomly assigned to a condor based on its age group. Juveniles can be born in the wild or released from captivity, therefore they can be assigned between 0 – 2 years of time spent in the wild. Most condors are released between 1 and 2 years of age, but there are individuals that are released as subadults and adults, so subadults can have between 1 and 5 years spent in the wild. Breeding and non-breeding adults could be assigned a uniform random value between one year and the age of its managing agency for its time spent in the wild.

Estimated Environmental Variables

Because original values for environmental variables were averaged over estimated home ranges in Chapter 1, I needed values for: maximum slope, maximum NDVI, distance to water, and road density to estimate home range sizes using Eq. 1 in the predictive model. To get these values, I created circular buffers (area = 5,153 km^2) around the generated random points to represent the mean home range area averaged across all age groups. I clipped the circular home ranges to the coast of California, so no area was over the ocean, then calculated the mean values of each environmental variable per km^2 for every circular home range using the Zonal Statistics tool in ArcGIS. I then saved all origin coordinates (UTM) and their corresponding environmental variable values in a text file.

Model Evaluation

To test the efficacy of the predictive tool, I compared the observed and predicted home range areas of condors wearing GPS units during the two final years included in the study (2016 and 2017), as well as the two subsequent years following the study (2018 and 2019). I estimated the annual home range areas of condors for 2018 and 2019 using the same methods as in Chapter 1. Using the number of individuals in each age group per flock collecting location data during a given year, I used Model 2 to predict the total area of overlapping home ranges. Then, I compared observed and predicted merged home range areas using the Fuzzy Kappa Statistic (K_{fuzzy}) calculated with the Map Comparison Kit version 3.2.3 (Research Institute for Knowledge Systems, 2011, Bhv, NL). K_{fuzzy} is the fuzzy-set equivalent of the Kappa statistic (Hagen, 2003). Whereas the Kappa statistic rates pairs of cells as discrete values of equal (0) or unequal (1), fuzzy-based map comparisons account for gradients of similarity between cells, based on the cell values of their neighbors, resulting in continuous values between 0 (distinct) and 1 (identical; RIKS, 2003). K_{fuzzy} combines the common cell-by-cell Kappa statistic (Cohen, 1960) and fuzzy-based map comparisons based on fuzzy-set calculation (Zadeh, 1965) to produce a statistic wherein, “the expected percentage of agreement between two maps is corrected for the fraction of agreement statistically expected from randomly relocating all cells in both maps” (Visser and de Nijs, 2006). Results from the map comparison is a comparison map, which details cell-by-cell agreement in increments from 0—1, a K_{fuzzy} statistic that summarizes the agreement in a single number, and the Average Similarity score, which is simply the mean similarity of all the cells in the map.

Scenarios

I predicted condor range expansion under 4 different scenarios thirty-eight years since the Condor Recovery Program began releasing condors in the wild in 1992. The first scenario predicted overlapping condor ranges if the California population maintained the same demographics as the most recent published population estimate (USFWS, 2020). During 2019, the central California flock reported: 10 breeding adults, 53 non-breeding adults, 24 subadults, and 18 juveniles (Welch, PINN, pers. comm, 2020). The southern California flock reported: 6 breeding adults, 49 non-breeding adults, 29 subadults, and 19 juveniles (Aster, USFWS, pers. comm, 2020). The second scenario predicted condor home ranges of 150 condors (30 breeding adults, 40 non-breeding adults, 40 subadults, and 40 juveniles) in each flock. I used 150 individuals with 30 breeding adults because those are included as delisting criteria, in addition to self-sustaining populations with positive growth rates, in the Condor Recovery Plan (USFWS, 1996). The final two scenarios were predicted to examine how the total area of overlapping ranges may be affected by the proportions of age groups with the largest and smallest mean home range areas in a population. Because breeding adult and subadult condors have the smallest and largest home range areas on average (4,348 km^2 and 6,339 km^2, respectively; Chapter 1), I predicted home range areas of populations with a majority of breeding adults and a minority of subadults (70 breeding adults, 35 non-breeding adults, 10 subadults, 35 juveniles). I also predicted home ranges of the reverse scenario: 10 breeding adults, 35 non-breeding adults, 70 subadults, and 35 juveniles. The overlapping ranges were saved as ASCII files for use in ArcGIS Pro version 2.5.0 (ESRI, 2020).

GIS Analysis

I calculated the overlapping area of predicted condor ranges and commercially valuable wind of all four scenarios using the Intersect tool in ArcGIS Pro. I used a dataset from the National Renewable Energy Laboratory (NREL) that classifies wind at 50 meters above ground level. Of the 7 wind classes, areas with class ≥ 3 (i.e., high-class winds, with speeds > 6.4 m/s) are considered commercially valuable and suitable for wind energy development (NREL, 2015; Poessel et al., 2018a). I then used the overlapping ranges to calculate the percent area of predicted overall condor range that has potential conflict with wind energy development and the percent area of landscapes with commercially valuable wind that is unaffected by predicted condor range.

RESULTS

Predictive Tool

The cumulative area of overlapping condor home ranges predicted by the model generally reflected the cumulative area of overlapping observed home ranges estimated from GPS data collected by condors wearing GPS tags during 2016 – 2019. Map comparisons between the observed and predicted areas produced K_{fuzzy} values between 0.6 – 0.9 (Table 4). My lowest K_{fuzzy} value (0.6) was from the comparison between the observed and predicted condor range during 2019. This statistic was improved by removing an extreme outlier from one subadult condor from the central California flock that had a very large home range area (89,937.17 km^2) during that year (mean home range area = 5,965.88 ± 1,182.85 km^2; Figure 4). After removing the outlier, I compared the updated observed area of overlapping home ranges and predicted overlapping area and achieved a K_{fuzzy} value of 0.9 (Table 4).

Table 4. Map comparisons of predicted and observed cumulative area of overlapping condor home ranges in California. Comparisons with Fuzzy Kappa values closer to 1 are for surfaces that are more similar, whereas Fuzzy Kappa values closer to 0 are more different.

Year	Fuzzy Kappa	Average Similarity
2016	0.810	0.969
2017	0.896	0.980
2018	0.719	0.942
2019	0.627	0.903
2019 (outlier removed)	0.903	0.982

Predicted Scenarios and Commercially Valuable Wind

I predicted condor range expansion in California under four scenarios: 1) population demography stays the same (2019 California population); 2) each flock has 150 individuals with 15 breeding pairs; 3) each flock has majority breeders, which maximizes breeding pairs and, minimizes sub-adult condors; and 4) each flock as majority subadults, which maximizes subadult condors and minimizes breeding pairs (Figure 5). The mean area of the predicted merged ranges was 63,814 km^2 (SE = 13,434 km^2, min = 60,232 km^2, max = 66,856 km^2). Predicted merged condor ranges in central and southern California did not overlap in any scenarios, though they were connected in most by one or two ranges. Predicted ranges under different scenarios exhibited high similarity, with K_{fuzzy} values between 0.61 – 0.88 and Average Similarity values of 0.93 – 0.98 (Table 6). The predicted range for the same population demographics was the most dissimilar when compared with maps of the other predicted scenarios (K_{fuzzy} = 0.61 – 0.67, Average Similarity = 0.93 – 0.94). All other scenarios were fairly similar to each other with K_{fuzzy} values between 0.87 – 0.88 and Average Similarity values between 0.97 – 0.98. Commercially valuable wind overlapped with <10% predicted condor range under all scenarios (Table 5). I also found that >81% of commercially valuable wind was unaffected by predicted condor range under all scenarios (Table 5).

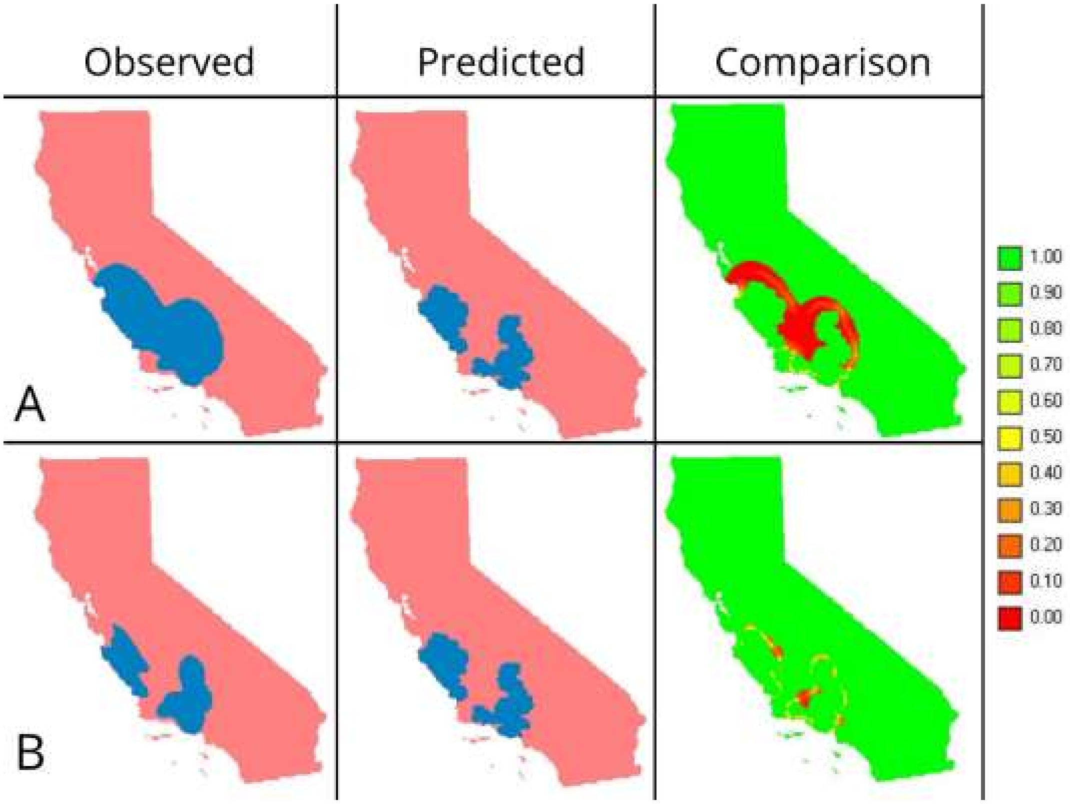


Figure 4. Map comparisons between observed and predicted overlapping condor ranges during 2019 with (A) and without an extreme outlier (B). For observed and predicted maps, colors represent categories of cells – pink cells do not contain condor range, blue cells contain condor range. The green to red color gradient in the comparison maps indicate the level of fuzzy similarity between the observed and predicted maps. A value of 1.0 (green) corresponds to total similarity and a value of 0.0 (red) corresponds to total dissimilarity. Values in yellow shades (around 0.5) point to some similarity in both observed and predicted maps.

Table 5. Predicted merged condor range areas in square kilometers and percent overlap with commercially viable wind.

Scenarios	**Predicted Condor Range Area (km^2)**	**Viable Wind Area (km^2)**	**Wind and Condor Range Intersection Area (km^2)**	**Overlap with Condor Range (%)**	**Overlap with Viable Wind (%)**
Same population demographics (2019)	60,232	33,494	5,994	9.95	17.90
150 condors and 15 breeding pairs per flock	66,856	33,494	6,228	9.32	18.59
Majority breeders	61,449	33,494	5,891	9.59	17.59
Majority subadults	66,719	33,494	6,003	9.00	17.92
Mean	63,814		6,029	9.46	18.00
Standard Deviation	2,688		142	0.41	0.42
Standard Error	1,344		35	0.10	0.11

Table 6. K_{fuzzy} (dark gray) and Average Similarity (light gray) values of pairwise map comparisons between predicted condor ranges assessed using Map Comparison Kit v. 3.2.3 (RIKS, 2011) .

	Same Pop	Delist	Breeders	Subadults
Same Pop	1.00	0.61	0.67	0.62
Delist	0.93	1.00	0.88	0.87
Breeders	0.94	0.98	1.00	0.88
Subadults	0.93	0.97	0.98	1.00

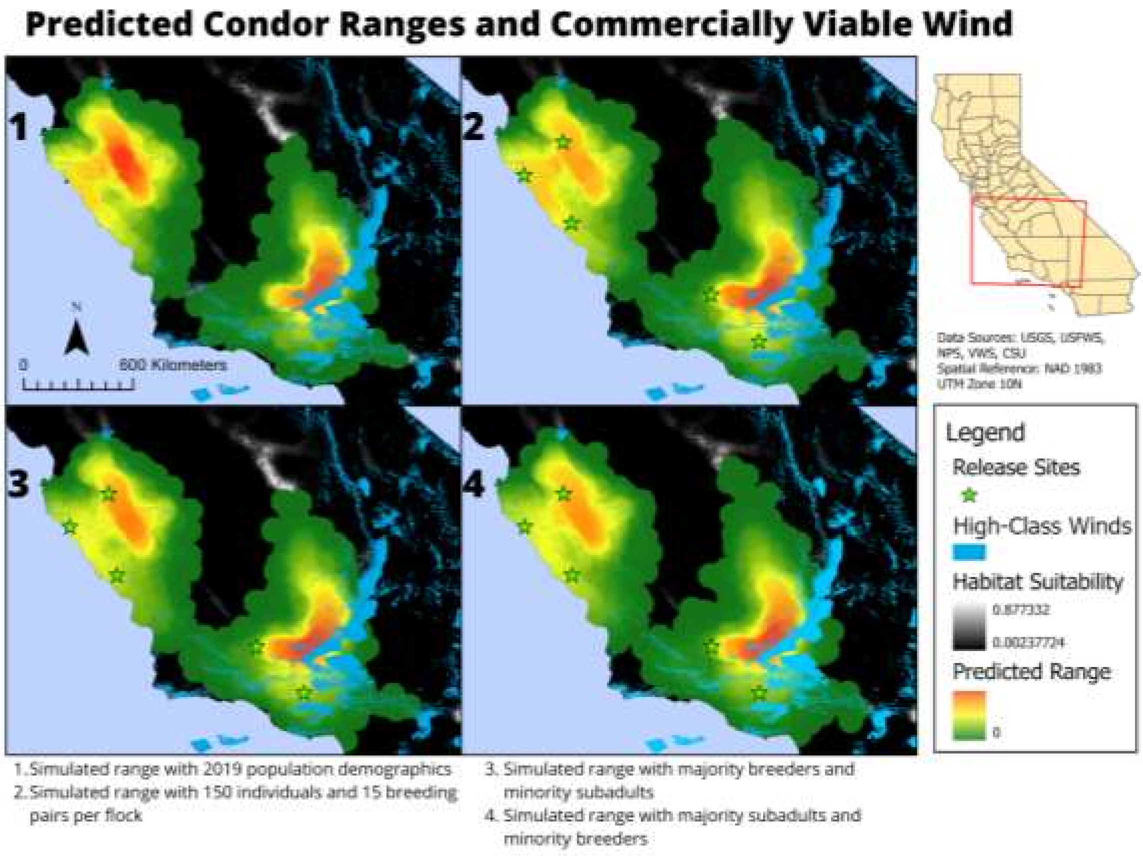


Figure 5. Predicted merged condor ranges in California, 38 years after USFWS began releases. Warmer colors depict overlapping home ranges and the upper limit of overlapping ranges varied for each scenario (from 1 to 4): 71, 115, 116, 129. Lighter shades of gray depict higher habitat suitability scores (D'Elia et al., 2015).

DISCUSSION

Predictive Tool

I created a predictive tool to estimate condor home range areas and map them throughout suitable habitat in California. I used modified agent-based models with non-interacting agents to create our predictive tool. While the tool is useful for predicting the overall area of overlapping home ranges of hypothetical condor populations, it does not include simulations of extremely large home range areas of individuals exhibiting exploratory movements which may be a significant limitation. Exploratory movements are typically made by subadult individuals to find and exploit food sources and maximize survival prospects (Margalida et al., 2013, 2016; Harel et al., 2016; Martens et al., 2018; Kang et al., 2019). However, if areas visited during large distance movements are not considered during siting and planning stages of wind turbines, development in those areas may place immature individuals at a higher risk of mortality before they can contribute to population recovery. Therefore, developing a tool in the future that includes areas used by juveniles and subadults exhibiting exploratory movements and with extremely large home ranges is imperative to reduce threats to their survival and improve population recovery success (Margalida et al., 2016; Martens et al., 2018).

Predicted condor ranges may be conservative in area due to the constrained area of potential roost sites used as origins of home ranges. The predictive tool uses potential roost sites that were randomly generated within suitable roosting habitat of condor core areas during 2017.

Scenarios

Predicted overlapping condor home range areas were very similar under every scenario and map comparisons produced K_{fuzzy} values between 0.61 – 0.88 and Average Similarity values of 0.93 – 0.98 (Table 6). All predicted scenarios were set 38 years after the USFWS began releasing condors in 1992, with 150 individuals in each flock and different amounts of individuals per age group for every scenario except for the scenario with the same population demographics as 2019. While individual characteristics and management factors, population dynamics, and environmental variables affect home range size (Chapter 1), pairwise map comparisons between all predicted scenarios indicate that different demographics do not appear to have large effect on the cumulative area of overlapping condor ranges with the same population size. With the values of the home range growth parameters set in Model 1, predicted ranges mainly followed the mountainous regions throughout central and southern California and did not cover the Central Valley. This pattern was expected as condors use rough topography to gain altitude for soaring large distances to look for patchily distributed food sources and tend to avoid flat areas that do not produce strong updrafts (Poessel et al., 2018a; Poessel et al., 2018b) and reflects patterns of observed home ranges (Chapter 1).

Condor Range Expansion and Commercially Valuable Wind

I found that <10% of condor ranges in all predicted scenarios overlapped with commercially viable wind and that <19% of commercially viable wind overlapped with predicted condor range. While there was very little difference in size and shape of predicted ranges with different demographics during the same year (Figure 5), all possible areas of overlap between predicted condor ranges and high-class winds should be considered during siting and planning stages for wind energy development to reduce the likelihood of conflict between condor range expansion and turbines. Thoughtfully selecting sites for development is especially important because wind turbine curtailment efforts of wind farms in operation have been shown ineffective in reducing mortality in birds from collision with turbines, though they are successful in reducing mortality in bats (Smallwood and Bell, 2020). Condors are even more vulnerable to collisions with turbines given the species' 3-meter wingspan, heavy wing-loading, and low maneuverability. In addition, when condors do use areas that generate winds of high-classes that are required for energy development, they have been shown to fly at altitudes that place them within the rotor-swept zone of turbines 39% of the time (Poessel et al., 2018a). The development of wind farms in areas condors are likely to use in the future places an additional stressor on the survival of a critically endangered species that is already threatened by lead poisoning. Fortunately, there are many alternative areas where developers can construct turbines that are less likely to impact condor survival, especially if placed a distance away from ridgelines with strong orographic updrafts (Poessel et al., 2018a).

Management Implications and Future Studies

The tool I created for predicting condor range expansion can be useful to Program managing agencies by providing a resource they can use for prioritizing monitoring and management needs and strategies. Because the population is so small, managers track individual condors in their flock on a daily basis. However, as the population grows, monitoring individuals will become increasingly difficult, especially as condors use areas that are inaccessible to managers. Additionally, estimating when condors from the central and southern California flocks will likely overlap in range can help managers plan for changes in approaches to monitoring and management. Predicted overlapping home ranges in central and southern California connected in all scenarios with 150 individuals per flock; however, range densities indicate there was no notable overlap of individual home ranges from central and southern California. This suggests that for the scenarios I predicted, the two flocks will likely remain separate and managers can continue monitoring as usual, though individuals may take exploratory forays into areas occupied by condors from the other flock.

Condors are a social species, an attribute not directly simulated in our predictive tool, which uses non-interacting agents. How the attraction of condors to conspecifics may influence condor range expansion is important for managers to include in conversations with wind energy developers. Like other avian scavengers, condors are attracted to conspecifics and gain information about habitat quality by following more experienced individuals (Meretsky, 1992; Bijleveld et al., 2010; Dermody et al., 2011; Cortés-Avizanda et al., 2014; Rivers et al., 2014; Harel et al., 2017). Therefore, the use of areas that are likely to be developed by just a few condors can attract more condors to those areas. Additionally, it may be that there is a minimum threshold of condors that travel between central and southern California before it is deemed a safe practice and becomes a more regular behavior.

New release sites and the presence of captive-bred condors being held before release, can alter condor movements by attracting wild individuals to the new release sites. In 2015, when condors were first released at San Simeon, several adults from the central California flock began visiting the new release site and surrounding area almost immediately (personal observation). The following year, a pair nested near the new site, the first to nest in San Luis Obispo County in over 60 years (VWS, 2015). The attraction of wild condors to captive-bred individuals in holding pens at release sites, also likely contributes to why core areas remain constrained around the release sites.

Overlapping core areas of the central and southern California condor flocks may be better indicators than overlapping home ranges of the two flocks mixing. Core areas reflect the regions within condor home ranges that are used more heavily than other areas in the home range (Powell, 2000). Therefore, overlapping core areas would illustrate true interaction between the two flocks, whereas overlapping home ranges only indicate that at some point in time, condors from the two flocks have visited the same area. Future studies might want to create a similar tool that estimates the overlapping core areas to better predict when the two condor flocks will merge. Allowing home range origins to generate from core areas that also increase through time may also simulate more accurate representations of home range areas predicted farther into the future. Home ranges predicted in this model grow from origins constrained to the combined core areas observed in 2017 and effectively predicted overlapping home ranges that were very similar to overlapping ranges observed during 2016 – 2019. While home range areas predicted in the near future likely originate from a similar core area, home ranges predicted for condor populations farther into the future likely use larger core areas and may be conservatively represented using the current model.

The model created for this study did not include interacting agents that could influence or alter the size of home ranges estimated and mapped throughout suitable habitat in California. Future iterations of this model could be made more complex by programming social interactions, randomized exploratory movements of subadults, and changes in home range areas based on these stochastic events. While adding modifications to the predictive tool can provide insight into how social attraction and extreme movements affect condor range expansion, our tool is useful for predicting the overlapping area of average condor home ranges for individuals in different age groups and identifying where there is likely to be conflict with potential wind energy development.

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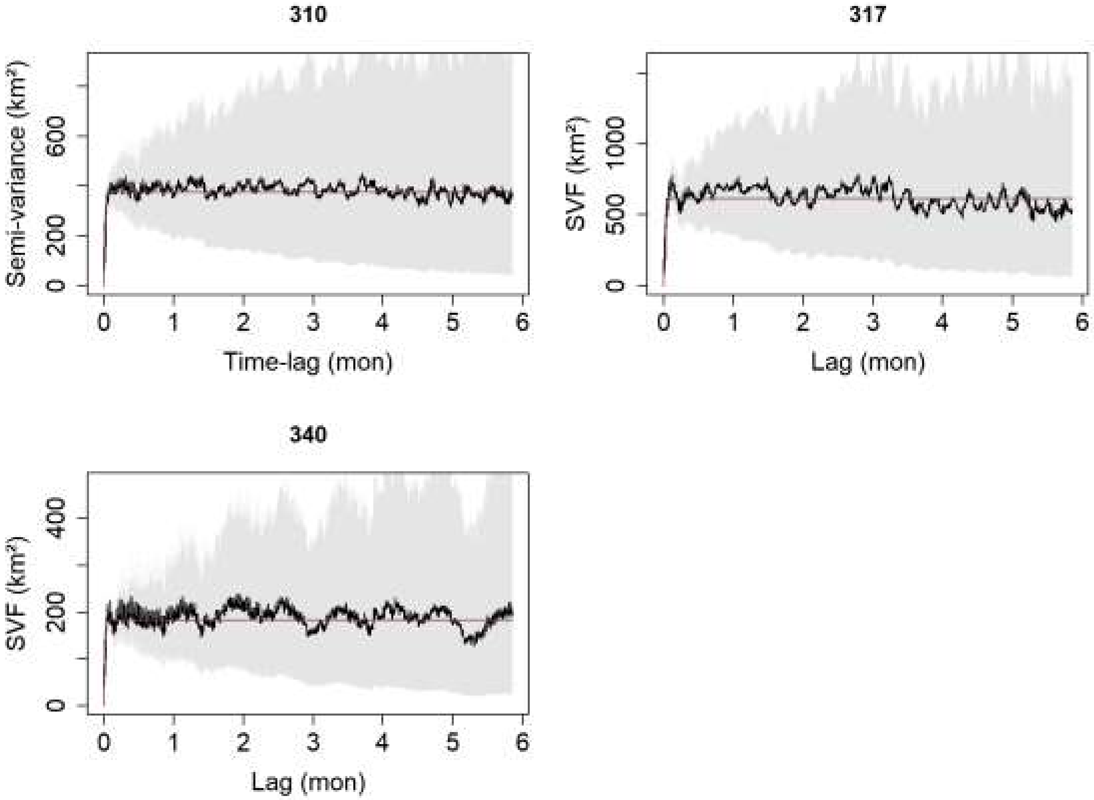
APPENDICES

Supplemental Methods 1.1. Descriptions of Movement Models

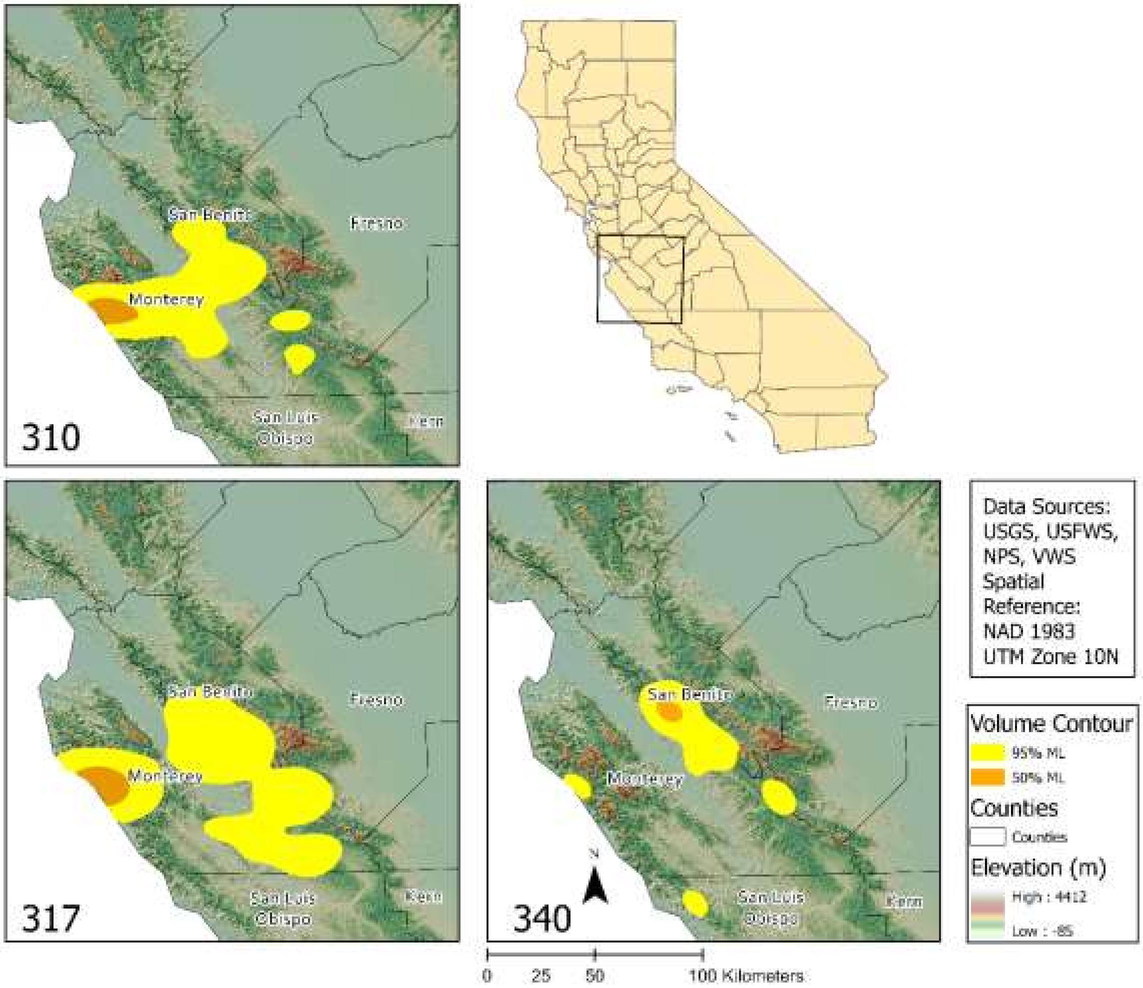
Independent identically distributed (IID) process assumes no correlation between positions and velocities, thus is not generally known as a movement model, but is an assumption of location data when using standard kernel density estimation. Brownian motion (BM) describes regular diffusion with position autocorrelation, but no velocity autocorrelation and no constraint of space (Calabrese et al., 2016). Ornstein—Uhlenbeck (OU) model includes spatial correlation, both position autocorrelation and a constrained space use (Uhlenbeck and Ornstein, 1930; Calabrese et al., 2016). The integrated OU (IOU) is like BM, but features autocorrelated velocities (Johnson et al., 2008; Calabrese et al., 2016). Finally, the Ornstein—Uhlenbeck Foraging (OUF) process accounts for position and velocity autocorrelations and a tendency to remain in the same area (Fleming et al., 2014, 2015; Calabrese et al., 2016). Movement models that exhibit restricted space use and are applicable to home ranges are OU and OUF processes.



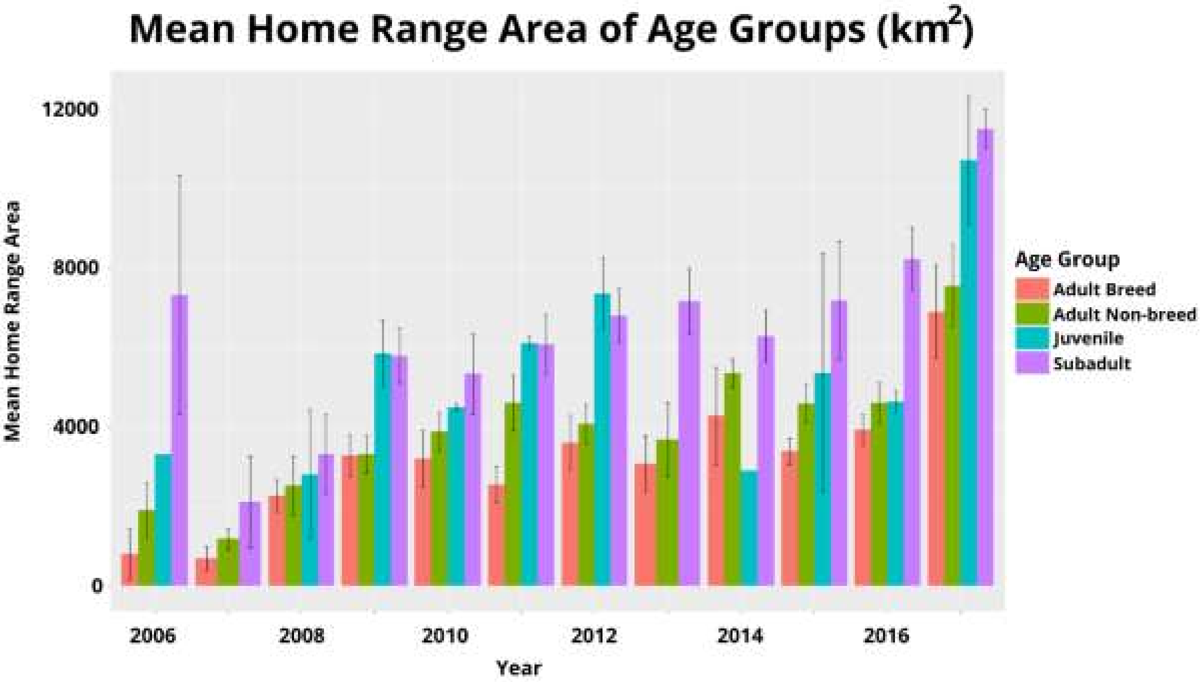
Supplementary Figure 1.1. Empirical variograms of the location data of condors 310, 317, and 340 during 2017 produced using the 'ctmmweb' shiny app (Dong et al., 2018). Empirical variograms visualize the autocorrelation structure of location data by plotting the semi-variance in positions as function of the time lag separating observations (Fleming et al., 2014; Calabrese et al., 2016). Variograms that eventually reach an asymptote are indicative of a range-resident animal.

Supplementary Table 1.1. All movement models fitted to location data of condors 310, 317, and 340 during 2017 using the 'ctmmweb' shiny app (Dong et al., 2018).

Bird ID	Model type	AIC$_c$	DOF mean	DOF area	DOF speed	Area (km^2)	Area CI (km^2)	t [position]	t [velocity]	speed (km/day)	speed CI (km/day)	t
310	OUF anisotropic	0	290.623	533.287	1014.056	5359.5	(4914.22 - 5823.82)	48675.57	1066.585	305.24	(295.84 - 314.63)	NA
310	OU anisotropic	353.918	221.279	423.008	0	5292.78	(4800.36 - 5808.91)	65993.38	NA	NA	NA	NA
310	OUF isotropic	1238.248	260.288	491.435	1538.696	7105.72	(6491.29 - 7747.54)	54621.26	1203.098	292.86	(285.54 - 300.17)	NA
310	OUf anisotropic	1853.875	948.108	1591.035	3755.455	4148.92	(3947.54- 4355.25)	NA	NA	297.88	(293.11 - 302.64)	6526.668
317	OUF anisotropic	0	186.73	339.129	2260.885	8976.2	(8046.17 - 9956.36)	68698.61	1771.631	251.24	(246.06 - 256.42)	NA
317	OUF isotropic	570.517	175.436	327.165	3316.261	11485.7	(10274.7 - 12763.19)	73488.33	2078.403	244.23	(240.07 - 248.38)	NA
317	OU anisotropic	855.974	127.241	242.034	0	8402.27	(7376.99 - 9493.3)	107904.97	NA	NA	NA	NA
317	OUf anisotropic	1421.453	618.989	1010.964	3562.443	7210.33	(6772.66 - 7661.51)	NA	NA	275.4	(270.88 - 279.93)	8969.821
340	OUF anisotropic	0	272.72	517.52	474.041	2988.33	(2736.38 - 3251.21)	46105.05	832.9907	259.73	(248.04 - 271.41)	NA
340	OU anisotropic	176.237	220.878	430.562	0	2961.93	(2688.73 - 3248.16)	58467.83	NA	NA	NA	NA
340	OUF isotropic	782.934	272.5	517.924	675.249	3366.67	(3082.93 - 3662.72)	46060.03	923.7775	250.52	(241.07 - 259.96)	NA
340	OUf anisotropic	1844.314	890.931	1553.149	3755.215	2410.3	(2291.91 - 2531.64)	NA	NA	234.38	(230.63 - 238.12)	6143.472



Supplementary Figure 1.2. Home range and core areas of condors 310, 317, and 340 represented by the 95% (yellow) and 50% (orange) volume contours of autocorrelated kernel density estimations. Home ranges and core areas were estimated using the 'ctmmweb' shiny app (Dong et al., 2018).



Supplementary Figure 1.3. Mean home range areas and standard error of condors by age group in California for years 2006 – 2017. Home ranges are 95% autocorrelated kernel densities estimated using the 'ctmmweb' shiny app (Dong et al., 2018).

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Supplementary Methods 2.1. Overviews, Design Concepts, and Details (ODD) for Model 1

1. Overview
    a. Purpose: Populate habitat suitability surface (D'Elia et al., 2015) with potential roost site locations, convert site location coordinates from a geographical coordination system (UTM) to patch coordinates in Netlogo, set the rules by which home ranges grow, and create ordered list of roost site locations and surrounding patches that, if all incorporated into a home range, would yield an area larger than any observed range. This ordered list of roost site locations and patches is to be used in Model 2.
    b. Entities, state variables, and scales:
        i. Entities: Patches, birds.
        ii. State variables:
            1. Patches have (x, y) coordinates, color, and conductance from combined activity layer of suitable habitat (D'Elia et al., 2015). Higher conductance = better habitat for condors. Patches change color and contribute to individual home range area.
            2. Birds have ID, x-dim and y-dim (corresponding to UTM coordinates).
        iii. Scales:
            1. Spatial scale – California, mainly central and southern CA. All patch x, y coordinates in NetLogo correspond to NAD1983 UTM Zone 10N.
                1. 1 patch = 1 km^2
            2. Temporal scale – Model time does not correspond to real time scale.
                1. Time step = 1 roost site location converted from UTM to patch coordinates and 30000-patch home range area mapped
    c. Process overview and scheduling
        i. Setup: Sets up model.
            1. Set-up landscape – import combined condor activity habitat suitability layer (D'Elia et al., 2015).
            2. Assign patches conductance based on suitability.
            3. Roost site coordinates in UTM are matched to model patch coordinates and placed on map.
            4. A bird sprouts at each roost site.
        ii. Go: Runs model.
            1. Do-One: For every bird -

            1. Patch where bird has sprouted (the roost site) turns yellow, becomes part of home range
            2. All patches in 14-patch radius (or Radius-of-placed-cells from slider) become part of home range – patch coordinates of roost site and total area of home range saved to text file
            3. If random number generated between 0 – 1 is < 0.75, then 10 patches (or Highest-Patches-Selected from slider) on edge of home range with highest conductance values add patches within 14-patch radius to home range
            4. If random number generated between 0 – 1 is > 0.75, then any 10 patches on edge of home range add patches within 14-patch radius to home range
            5. The coordinates of each selected patch and the total area of the home range (after all patches in radius are incorporated into the home range) is saved to the text file.
            6. Process repeats until home range is ≈ 30000 km^2
            7. Text file with ordered list of potential roost site locations, surrounding patch coordinates, and cumulative areas is saved to folder.
        iii. Sliders: Home-range-complexity, Radius-of-placed-cells, Highest-patches-selected
            1. Home-range-complexity: determines how strictly home range grows into patches with highest conductance (suitability) values
            2. Radius-of-placed-cells: determines size of radius of patches to add to home range
            3. Highest-patches-selected: determines how many patches on the edge of the home range to select as centers of radius
        iv. Counters: Condor, Home range size (km^2)
            1. Condor: Counts how many condor home ranges have been mapped
            2. Home range size: Displays the size of home range currently being mapped
2. Design Concepts
    a. Basic principles – Basic principles – Animals typically have spatial boundaries within which they seek to fulfill biological needs to increase survival and fitness. This spatial boundary is called a “home range”. Ecological niche models identify habitat that is suitable for animals based on species’ associations with environmental variables. I used a habitat suitability surface developed for condors (D’Elia et al., 2015) to simulate condor range expansion throughout habitat suitable for condors.

   b. Emergence – How and where individual home ranges grow and spread based on home range growth rules is a key output of this model.
   c. Adaptation – Individuals do not have adaptive traits or decision-making behaviors. All traits, states, and actions are results of user input and programmed parameters.
   d. Objectives –from Populate habitat suitability surface (D'Elia et al., 2015) with potential roost site locations, convert site location coordinates from a geographical coordination system (UTM) to patch coordinates in Netlogo, set the rules by which home ranges grow, and create ordered list of roost site locations and surrounding patches that, if all incorporated into a home range, would yield an area larger than any observed range. This ordered list of roost site locations and patches is to be used in Model 2.
   e. Learning – Individuals do not interact and learn.
   f. Prediction – Individuals cannot predict future conditions.
   g. Sensing – All decisions made for home range growth is programmed, thus individuals do not use sensing.
   h. Interaction – Individuals do not interact with each other.
   i. Stochasticity – Stochasticity in the model is based on the random number generated used for home-range-complexity; i.e., how strictly home range growth adheres to patches with highest suitability scores.
   j. Collectives – Birds are separated by flock, thus can only be assigned potential roost sites within the core areas of their assigned flock.
   k. Observation – The text file saving potential roost site and surrounding patch coordinates and cumulative home range areas are saved to a text file, which is used as input for Model 2.
3. Details
   a. Initialization – The initial state of the model world has a habitat suitability surface that is not yet populated with potential roost site locations. The user specifies Home-range-complexity, Radius-of-placed-cells, and Highest-patches-selected. I ran the model with parameters set at 0.75, 14, and 10, respectively.
   b. Input Data - The base layer of the model comes from the combined activity ecological niche model developed by D'Elia et al. (2015). Two .csv files containing the potential roost site locations are imported to use as origins of home ranges.
   c. Submodels
      i. Do-One: See Process overview and scheduling above for description.

Supplementary Methods 2.2. Overview, Design Concepts, and Details (ODD) for Model 2

1. Overview
    a. Purpose: To estimate and map condor home range areas based on suitable habitat identified by D'Elia et al. (2015) and linear mixed model from home range analysis (Punzalan, et al., 2020).
    b. Entities, state variables, and scales:
        i. Entities: Patches, condors, centroids.
        ii. State Variables:
            1. Patches have (x, y) coordinates, color, and conductance from combined activity layer of suitable habitat (D'Elia et al., 2015). Higher conductance = better habitat for condors. Patches change color and contribute to individual home range area.
            2. Condors have ID, age group, intercept (based on age group), time spent in the wild, manager, managing agency age, slope, NDVI, distance to water, road density, and home range area. Condors do not interact or change age groups or states during any time step.
            3. Centroids have ID, x-coordinate, y-coordinate, area-list, slope, NDVI, distance to water, road density, home range area.
        iii. Scales:
            1. Spatial scale – California, mainly central and southern CA. All patch x, y coordinates in NetLogo correspond to NAD1983 UTM Zone 10N.
                a. 1 patch = 1 km^2
            2. Temporal scale – Model maps out annual home ranges.
                a. 1 model run = 1 year.
    c. Process overview and scheduling
        i. Setup: Sets up model.
            1. Reset world and counters.
            2. Check if model world file exists
                a. If it does exist, import world file with landscape and centroid information.
                b. If it does not exist, Create world file:
                    i. Set-up landscape – import combined activity ENM conductance layer (D'Elia et al., 2015).
                    ii. Set-up centroids –
                        1. Create 500 centroids in central CA core area and 500 centroids in southern CA core area

            from “Ordered_Patch_Neighborhood.txt” file created in Make_Home_Ranges model.
            2. Assign environmental variables to centroids by matching centroid ID to ID in “Enviro_Vars_Core.txt”.

ii. Go: Runs model.
    1. Clear/reset condors.
    2. Set-up condors
        a. Creates number of condors in each age group and flock set by sliders on interface.
        b. Clear condors
            i. Reset the environmental variable values.
    3. Define condors
        a. Ratio of central CA condors = .40 PINN to .60 VWS.
        b. Condors get environmental variable values
            i. Randomly assign centroid-identifier based on flock (1-500 for central CA, 501-1000 for southern CA).
            ii. Get values for environmental variables from centroid with centroid-id that matches centroid-identifier.
        c. Intercept assigned based on condor’s age group
        d. Time in wild randomly assigned based on condor’s age group (0 to 3 for juveniles, 1 to 5 for subadults, 0 to Age-of-Agency for adults).
        e. Age of agency set based on assigned Agency and Years-since-program-start slider.
        f. Home-range-km2 calculated using linear mixed model equation from Punzalan et al. (2020).
    4. Condors find centroids with matching centroid-identifier and assign the centroid with home range area.
    5. Centroids plot-one-range
        a. Patch with matching centroid ID asks 10 patches with highest conductance within 14-patch radius to turn green.
        b. If random number generated between 0 – 1 is < 0.75, then 10 patches (or Highest-Patches-Selected from slider) on edge of home range with highest conductance values add patches within 14-patch radius to home range
        c. If random number generated between 0 – 1 is > 0.75, then any 10 patches on edge of home range add patches within 14-patch radius to home range

            d. Process repeats until home range is ≈ area of estimated home range
        6. All ranges are painted in world.
    iii. Save Ranges (Optional)
        1. Push “Save-Ranges” button
        2. Overlapping ranges are exported as file for input into geodatabase.
        3. .txt -> copy raster -> define projection NAD 1983 UTM Zone 10N.

2. Design Concepts
    a. Basic principles – Animals typically have spatial boundaries within which they seek to fulfill biological needs to increase survival and fitness. This spatial boundary is called a “home range”. Ecological niche models identify habitat that is suitable for animals based on species’ associations with environmental variables. D’Elia et al. (2015) identified suitable habitat for condors based on 3 activities: feeding, roosting, and nesting and found that < 30% of modeled nesting habitat and <40% of modeled roosting and feeding habitat were occupied. To predict where condors are likely to expand their range, we identified factors that are associated with annual condor home range. We then used the resulting linear mixed model to predict the sizes of individual condors and mapped them out into the combined activity ecological niche model developed by D’Elia et al (2015).
    b. Emergence – How home ranges overlap and spread throughout California is the emerging property we are evaluating in this model.
    c. Adaptation – Individuals do not have adaptive traits or make decisions. All traits, states, and actions are results of user input and programmed parameters.
    d. Objectives – Annual home ranges of condors are mapped based on the size of their home range (determined via linear mixed model), the location of their centroid, and the suitability of surrounding area (determined by ecological niche model/conductance layer).
    e. Learning – Individuals do not interact and learn.
    f. Prediction – Condors do not predict future conditions.
    g. Sensing – Condors home ranges grow based on assigned values of age, breeding status, environmental variables of potential site location and list of patches from Model 1; therefore, condors do not use sensing.
    h. Interaction – Condors do not interact with each other. Condors, patches, and centroids only interact by exchanging biological and environmental values to calculate home range area, which is used to grow home range into ecological niche model.
    i. Stochasticity – The stochasticity in the model results from which centroid and its associated environmental variables.

    j. Collectives – Condors are separated by flock, so they can only be assigned centroids within the core areas of their assigned flock.
    k. Observation – Predicted ranges can be saved and imported into ArcGIS (or other geographic information system) for analysis.

3. Details
    a. Initialization – User specifies the number of condors within each age group and flock, as well as, how many years since the Condor Recovery Program started in 1992. Corresponding centroids and environmental variables are randomly assigned to condors at the start of each model run.
    b. Input Data – The base layer of the model comes from the combined activity ecological niche model developed by D'Elia et al. (2015). The centroids were randomly generated within the minimum convex polygon of core areas of condors from the central and southern CA flocks wearing GPS tags during 2017, then converted to Netlogo patch coordinates in Model 1. Mean environmental variable values were calculated for circular buffers with 40.5 km radius around centroids in ArcGIS Pro version 2.5.0 (ESRI, 2020) using aggregated environmental layers generated by D'Elia et al. (2015).
    c. Submodels
        i. Linear mixed model from home range analysis (Chapter 1): Home Range Area (km^2) = Age Group (Intercept) + -109.5392 $\beta_{\text{Time Spent in the Wild}}$ + 195.0115 $\beta_{\text{Age of Managing Agency}}$ + -347.9939 $\beta_{\text{Maximum Slope}}$ + 130.0706 $\beta_{\text{Maximum NDVI}}$ + -135.8813 $\beta_{\text{Distance to Water}}$ + 4.1928 $\beta_{\text{Road Density}}$
            a. Intercept values for age groups: Juvenile = -15021.4, Subadult = -14310.4, Adult non-breeding = -15492.5, Adult breeding = -16301.7