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Activity-specific ecological niche models for planning reintroductions of California condors (*Gymnogyps californianus*)

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ABSTRACT

Ecological niche models can be a useful tool to identify candidate reintroduction sites for endangered species but have been infrequently used for this purpose. In this paper, we (1) develop activity-specific ecological niche models (nesting, roosting, and feeding) for the critically endangered California condor (*Gymnogyps californianus*) to aid in reintroduction planning in California, Oregon, and Washington, USA, (2) test the accuracy of these models using empirical data withheld from model development, and (3) integrate model results with information on condor movement ecology and biology to produce predictive maps of reintroduction site suitability. Our approach, which disentangles niche models into activity-specific components, has applications for other species where it is routinely assumed (often incorrectly) that individuals fulfill all requirements for life within a single environmental space. Ecological niche models conformed to our understanding of California condor ecology, had good predictive performance when tested with data withheld from model development, and aided in the identification of several candidate reintroduction areas outside of the current distribution of the species. Our results suggest there are large unoccupied regions of the California condor's historical range that have retained ecological features similar to currently occupied habitats, and thus could be considered for future reintroduction efforts. Combining our activity-specific ENMs with ground reconnaissance and information on other threat factors that could not be directly incorporated into empirical ENMs will ultimately improve our ability to select successful reintroduction sites for the California condor.

1. Introduction

The saga of saving the California condor (*Gymnogyps californianus*) from the brink of extinction by combining vigorous field efforts with aggressive captive breeding and releases is legendary in the field of conservation biology (reviewed by Snyder and Snyder, 2000). Yet, California condors are still one of the most critically endangered birds in the world, and are completely absent from the northern half of their historical range. Furthermore, there is no overall strategy for planning future reintroductions to recover a viable metapopulation (Walters et al., 2010; D'Elia and Haig, 2013). Nonetheless, the condor recovery program has gathered extensive data on condor nest biology (Snyder et al., 1986), movement ecology (Meretsky and Snyder, 1992; Hunt et al., 2007) and primary mortality factors (Rideout et al., 2012) via a scientific program of inquiry into population declines, captive breeding, and the subsequent release of California condors into a variety of environments, from the deserts of Arizona to the coast of California. These efforts have increased the number of captive condors available for release, and vastly improved our understanding of condor ecology and the primary threats to their survival and recovery. Thus, there is an expanded foundation upon which to develop a long-range vision of condor recovery—a vision that embraces a more complete assessment of available habitat over a wider area of the condor's historical range and identifies opportunities for additional recovery areas and potential reintroduction sites (Walters et al., 2010).

Ecological niche models (ENMs) are a potentially powerful tool for helping to identify additional recovery areas and reintroduction sites (Martínez-Meyer et al., 2006; Osborne and Seddon, 2012) as they provide a quantitative and spatially-explicit framework for

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describing the relationship between biological and physical properties of the landscape and a species' ecological and geographic distribution (Guisan and Zimmermann, 2000). ENMs have a wide range of applied uses in ecology including: understanding the ecological requirements or biogeography of species, finding new species or populations, identifying and prioritizing reintroduction sites, conservation planning and reserve design, predicting species invasions, predicting the effects of climate change or habitat loss, and for integrating information on movement ecology and demography to predict metapopulation dynamics in a spatially-explicit framework (reviewed by Peterson, 2006; Franklin, 2009; Peterson et al., 2011).

Despite their widespread use in ecology relatively few studies have used ENMs to identify species' reintroduction sites (reviewed by Peterson et al., 2011; Osborne and Seddon, 2012). Martínez-Meyer et al. (2006) introduced the idea of using ENMs to identify and prioritize reintroduction sites for California condors, but presented their results as conceptual because they did not categorize occurrence data by activity type and did not include environmental covariates in their model that were likely to be important to condor habitat selection. Categorizing occurrence data by activity type and developing separate activity-specific ENMs is crucial for developing reliable spatial models for California condors because they use different environments for different activities. This approach is likely to provide increased predictive precision over pooling occurrence data for any species that fulfills critical survival and reproductive functions in divergent habitats.

In this paper we build on the conceptual approach presented in Martínez-Meyer et al. (2006) and develop functional models for identifying candidate reintroduction areas for California condors through: (1) producing and testing the accuracy of activity-specific (i.e., nesting, roosting, and feeding) ENMs using environmental covariates that are linked to condor biology; (2) projecting ENMs throughout most of the recent historical range of the species to identify areas that are ecologically suitable but unoccupied; and (3) integrating activity-specific models with information from movement ecology studies and condor biology to identify areas that are predicted to be ecologically suitable but unoccupied. Model results can help focus field surveys to further evaluate release site suitability and may identify potential recovery areas for the California condor in unoccupied areas of its historical range that have not yet been fully considered.

2. Materials and methods

2.1. Study area

Our study area included California, Oregon, and Washington, USA (Fig. 1). Within the study area the current range of the California condor is limited to southern and central California where three captive release programs are in operation. Condors were extirpated from the northern half of their historical range, which once extended to British Columbia, Canada, early in the twentieth century (D'Elia and Haig, 2013).

2.2. Ecological niche models

Many algorithms are available for constructing ENMs (Guisan and Zimmermann, 2000; Elith and Graham, 2009; Elith and Leathwick, 2009). We used MAXENT, a maximum entropy-based machine learning computer program that estimates the probability distribution of a species' occurrence based on a given set of environmental constraints (Phillips et al., 2006). We selected MAXENT because it does not require absence data, it allows for categorical and continuous environmental data, and because it is in a class of models known as generative models that outperform discriminative methods when modeling with presence-only data (Elith et al., 2006, 2011; Phillips and Dukík, 2008). MAXENT models can be conservatively interpreted as a relative index of environmental suitability or relative density, where higher index values depict better conditions for the species (Phillips et al., 2006).

Despite their relatively good performance and ease of use, critics of presence-only ENMs warn against numerous pitfalls, including: use of questionable occurrence data (Lozier et al., 2009); overfitting models by failing to implement species-specific tuning (Anderson and Gonzalez, 2011; Warren and Seifert, 2011); ignoring spatial dependency in model evaluation (Veloz, 2009); misinterpreting outputs as occurrence probability, failure to consider sampling bias or detection probabilities in data acquisition, and misinterpretation of model evaluation statistics (Yackulic et al., 2013). We attempted to navigate these pitfalls through (1) screening of occurrence data, (2) using model selection procedures, (3) evaluating the impact of spatial dependency on model performance, (4) interpreting outputs as a relative measure of suitable habitat rather than occurrence probabilities, (5) adjusting for sampling bias in model development, and (6) using and interpreting multiple model evaluation statistics.

2.2.1. Condor occurrence data

Presence-only niche models require species' occurrence locations. Because condors use different habitats for nesting, roosting, and feeding (Koford, 1953), we partitioned condor occurrence data into these three activities and generated separate occurrence datasets for each activity (Fig. 1). Activity-specific occurrence data spanning the time period from 1960–2011 were obtained from a variety of reliable sources (see Appendix A). All occurrence data were filtered to remove duplicate records and occurrence locations with a positional precision of <1 km.

2.2.2. Environmental covariates

To develop ENMs, we considered 13 predictor variables (i.e., covariates) related to soaring conditions and climate, terrain, landscape productivity, vegetation characteristics, and human disturbance (Table 1; see Appendix B). We selected covariates based on published information on species-habitat associations (Koford, 1953; Snyder et al., 1986; Meretsky and Snyder, 1992), species-habitat models developed for other vultures (e.g., Donázar et al., 1993; Poirazidis et al., 2004; García-Ripollés et al., 2005; Gavashelishvili and McGrady, 2006; Mateo-Tomás and Olea, 2010; Rivers et al., 2014), and the availability of GIS data at the appropriate spatial scale spanning the entire study area (i.e., California, Oregon, and Washington). Although covariates related to vegetation characteristics and human disturbance were temporally mismatched with some of the older condor occurrence data, the general patterns of land use and vegetation types in the southern California and Sierra Nevada mountains have remained relatively constant over the last few decades (e.g., Raumann and Soulard, 2007; Soulard et al., 2007). Therefore, we assumed this potential source of error was unlikely to significantly affect model results.

2.2.3. Background data

MAXENT requires that the user specify the background (i.e., area available for the species to select), against which covariates at the occurrence points will be compared (Phillips et al., 2006; Phillips, 2007; Elith et al., 2011). Ten-thousand random points within 180 km of California condor nests (farthest documented movement by a nesting condor away from a nest (Meretsky and Snyder, 1992)) were generated to serve as background data. Islands off the coast of California were excluded from the background sample as condors are not known to travel across the ocean to these areas.

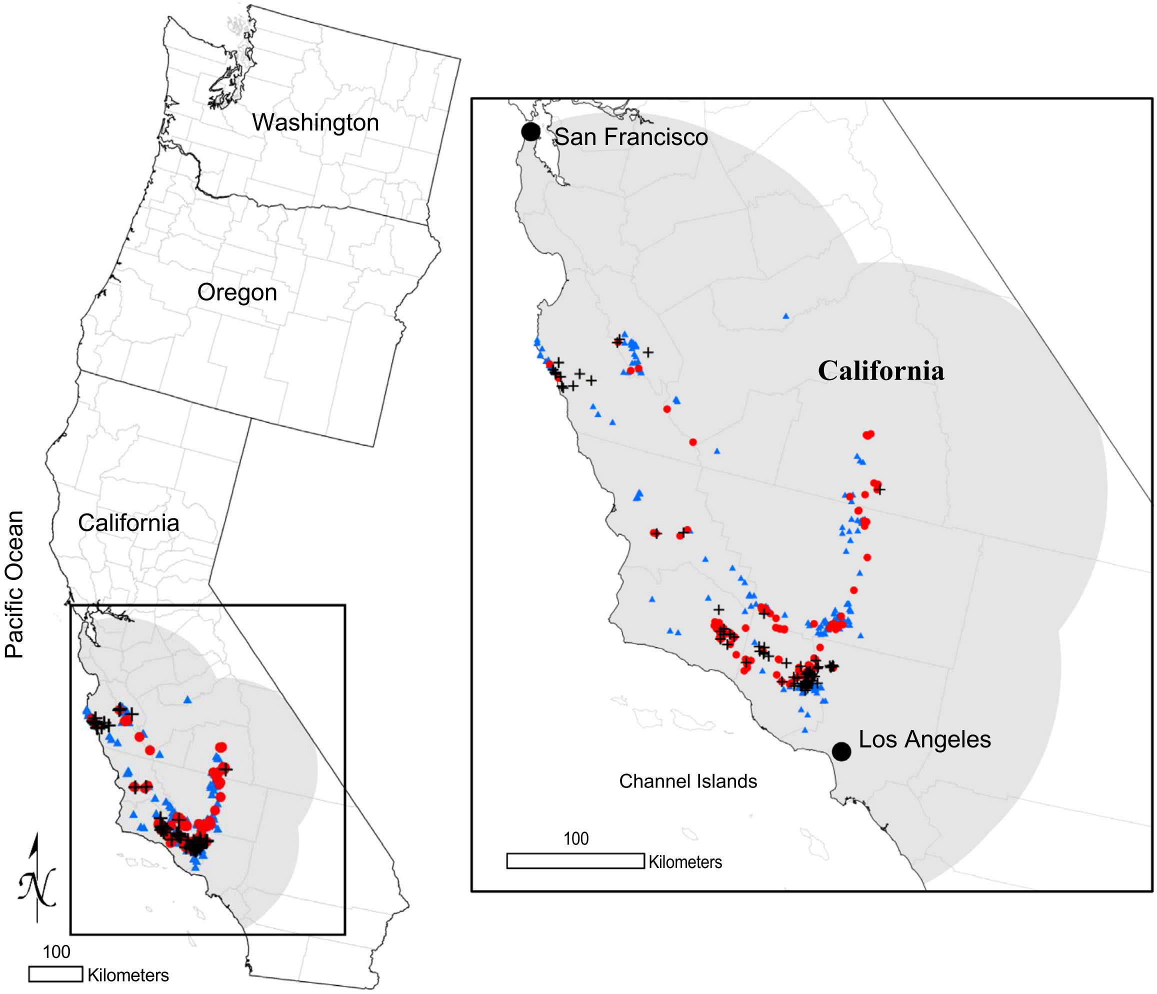

Fig. 1. Study area (left) and California condor nest (black crosses), roost (red circles) and feeding (blue triangles) occurrence data used in model development and evaluation. The gray zone is the area from which background data were selected for ecological niche model development, and which encompasses the current range of the species in southern California.

We assumed no bias in survey effort for nests or roosts as researchers have conducted extensive searches for these activity locations since the 1960s (Sibley, 1969; Snyder et al., 1986). Bias in survey effort for feeding locations led us to develop a separate set of background points for the feeding ENM. These points were selected from the same spatial extent as the nesting and roosting background sample, but approximated the frequency distribution of distance of feeding locations to roads (74.6% of points were within 1 km of a road, 19.7% were within 1–2 km, 5.2% were within 2–3 km, and 0.5% were >3 km from a road). Matching the sampling bias in our occurrence data and background data provides a better measure of the difference between the distribution of occurrences and that of the background and should therefore provide better predictive performance (Phillips et al., 2009).

2.2.4. Correlated environmental covariates

We assessed multicollinearity among covariates by calculating univariate pair-wise Spearman correlation coefficients (r_s) based on values of each variable at condor occurrence points. If two covariates had $r_s > 0.70$, we retained only one of the pair to aid in interpretation of model results. Thermal height and thermal updraft velocity were the only pair of covariates that exceeded this r_s value. We removed thermal height from further consideration and retained thermal updraft velocity.

2.2.5. Spatial scale

Condors select habitats at a variety of spatial scales, from coarse-grained selection of mountain ranges to fine-grained selection of a particular nest cliff or cave (Stoms et al., 1993). The accuracy of the available occurrence data and resolution of some of the environmental predictor variables led us to construct our models with a resolution of 1 km^2, summarizing mean values of some covariates within 10 km of each cell using focal statistics in ArcGIS (see Table 1). These spatial scales matched the intent of our research, which was to identify candidate release areas to include in follow-up ground surveys where finer-scale habitat features could be assessed.

2.2.6. Model settings and model selection

MAXENT (version 3.3.3a) was run with a convergence threshold of 10^{-5} and a maximum of 5000 iterations. We implemented bootstrap resampling with 20 replicates, holding out 25% of the samples for testing in each run of the model. MAXENT is in a school of models known as algorithmic models which treat the true model as an unknown, potentially complex, reality that is difficult or impossible to truly estimate (Warren and Seifert, 2011). As such, MAXENT models may be vulnerable to overfitting and may not perform well without implementing appropriate measures to limit their complexity (Phillips et al., 2006; Dudík et al., 2007). To limit model complexity and avoid overfitting, we used an information

Table 1
Covariates used to develop California condor nesting, roosting, and feeding ecological niche models.

Covariate	Description	Data source
Soaring conditions and climate		
Thermal updraft velocity[a]	Annual mean velocity of rising air (m/s)	Regional Atmospheric Soaring Prediction Maps (http://www.drjack.info/RASP/index.html)
Thermal height[a]	Annual mean thermal height (m)	Regional Atmospheric Soaring Prediction Maps (http://www.drjack.info/RASP/index.html)
Wind speed	Horizontal wind power class at 50 m above the ground (category)	National Renewable Energy Lab High Resolution Wind Resources Data (http://www.nrel.gov/rredc/wind_resource.html)
Winter severity	Mean minimum winter temperature (°C × 100)	PRISM Climate Data (http://www.prism.oregonstate.edu)
Terrain		
Cliffs	Maximum slope within a 1 km^2 neighborhood (degrees)	National Atlas (http://nationalatlas.gov)
Terrain ruggedness[a]	Ratio of 3-dimensional surface area to planar surface area (see Jenness, 2004)	National Atlas processed with Jenness (2004)
Landscape productivity		
Landscape productivity[a]	Average Maximum Normalized Difference Vegetation Index (maxNDVI) 2006–2010	USGS Remote Sensing Phenology Data (http://phenology.cr.usgs.gov)
Distance to water	Euclidean distance to the nearest freshwater (stream river, lake, or reservoir)	National Atlas (http://nationalatlas.gov)
Vegetation characteristics		
Canopy cover	Median canopy cover (%)	National Land Cover Database 2006 (http://www.mrlc.gov/index.php)
Canopy height	Majority mean height (category)	LANDFIRE 2001 (http://landfire.cr.usgs.gov)
Land cover type	Majority land cover type (category)	National Land Cover Database 2006 (http://www.mrlc.gov/index.php)
Human disturbance		
Road density[a]	km of road/km^2	Data Basin (http://databasin.org/datasets)
Human population density[a]	humans/km^2	2010 Census Data (http://www.census.gov/geo/maps-data/)

[a] Covariate calculated using mean values within a 10 km radius moving window of each 1 km^2 cell.

theoretic approach (Akaike, 1974; Burnham and Anderson, 2002) to select the best of a series of models with different levels of complexity (i.e., varying levels of MAXENT's regularization parameter (β = 1, 5, 10, and 15) and the types of environmental features, using ENMTools (Warren et al., 2010; Warren and Seifert, 2011). Regularization acts as a penalty function in MAXENT where increasing values of β reduces the number of parameters entered into the model (Phillips et al., 2006). In addition to varying the regularization parameter, we varied the complexity of the models by using two different sets of environmental features: (1) autofeatures, which allows models to fit up to five continuous environmental features (linear, quadradic, product, threshold, and hinge) and categorical features, with the more complex features only available when sample sizes are large enough (Phillips and Dukík, 2008); and, (2) manually limiting the model to categorical, linear, and quadratic features, which constrained MAXENT to simpler models at larger sample sizes (Phillips et al., 2006). A total of eight models (each with 20 replicates) of varying levels of complexity were run for each activity type. The ENM for each activity type with the lowest median AIC_c was selected as the most parsimonious model that best fit the data (see Appendix C). We used AIC_c in an attempt to balance the need to predict specific model fit to the training data against the generality that enables reliable prediction outside of areas where the model was trained (Elith and Leathwick, 2009; Merow et al., 2014).

2.2.7. Projecting models

A model trained on occurrence data and environmental covariates in one geographic location can be projected across geographic space by applying it to those same environmental covariates in another area or over a broader geographic distribution (Phillips and Dukík, 2008). Because we sought to project the models outside of the area used to train the model we implemented 'clamping', a method in MAXENT that ensures the response curves do not get extrapolated beyond the values observed at presence locations (i.e., the response curves are clamped, or fixed, at the maximum or minimum observed values; Elith et al., 2010). We also implemented a multivariate environmental similarity surface analysis to evaluate where novel environmental conditions existed in the projection layer (Elith et al., 2011). Novel conditions were defined as those with at least one covariate beyond the range of values encountered in the occurrence or background data (see Elith et al., 2011). Implementing clamping and excluding novel environments from projections allowed us to transfer the model in *geographic space* while not extrapolating beyond the *environmental space* where the species has been observed (see Peterson et al., 2011).

2.2.8. Niche similarity

The degree of similarity among the activity-specific ENMs was calculated using Warren et al.'s (2010) similarity statistic (I) in ENMTools, where a value of 0 indicates no overlap in suitability and 1 indicates complete overlap in suitability. We then tested the hypothesis that activity-specific niches were identical to one another using pairwise niche identity tests in ENMTools (see Warren et al., 2010). Pairwise identity tests pool occurrence data for each pair of activity-specific niches, randomize the identity of the occurrence data, and extract two new samples of equal size to the original samples for each model replicate. These new samples are then used to generate a pair of ENMs in MAXENT for each replicate model, and ENMTools uses predicted suitability scores from these ENMs to obtain a distribution of overlap scores between activity-specific niches drawn from a shared distribution (Warren et al., 2010). Twenty-five replicates were run for each pair of activities and z-scores were calculated to test whether activity-specific niches were statistically different from one another ($P \leqslant 0.05$). We also generated maps of niche similarity and calculated pairwise percentages of niche intersection (Appendix D). Percent niche intersection was calculated as: $x/((\text{area of niche}_1 + \text{area of niche}_2) - x)$, where x is the area of niche intersection.

2.3. Model evaluation

ENM performance can be evaluated with a number of statistics and it is often instructive to assess model performance using more than a single metric because each quantifies a different aspect of predictive performance (Elith and Graham, 2009; Elith and Leathwick, 2009). Accordingly, we assessed model performance using several different metrics: Gain (Phillips, 2005), Overall Accuracy, Sensitivity, Specificity, Kappa (κ) and Area Under the Receiver Operating Characteristic Curve (AUC) (Fielding and Bell, 1997) (see Appendix E for details). In addition to evaluators based on presences and pseudoabsences, we calculated the continuous Boyce index $B_{\text{cont}(0.1)}$, an evaluator based only on the presence data, and plotted predicted/expected curves for each ENM using the procedures developed by Boyce et al. (2002) and refined by Hirzel et al. (2006) (see Appendix E for details).

Examination for plausibility of model results is especially important when extrapolating in geographic or environmental space (Elith et al., 2010). Therefore, in addition to measures of model performance, we examined other outputs produced by MAXENT, including jackknife plots, variable importance, response curves, and suitability maps to ensure they were producing results that were plausible given our understanding of condor habitat selection (see Rivers et al., 2014) and the recent historical distribution of the species.

2.3.1. Spatial autocorrelation

The evaluation statistics we calculated assume spatial independence of samples (Fielding and Bell, 1997). When occurrence data are spatially dependent, randomly partitioning the data into test and training data may result in an overly optimistic assessment of model accuracy because of the proximity of training sites to test sites and spatial autocorrelation in the environment (Veloz, 2009). To examine spatial autocorrelation in model results, we calculated Moran's Index (I) coefficients for model residuals at multiple lag distances (10–200 km at 10 km intervals) for each activity-specific niche model, developed correlograms, and tested for significance ($P \leqslant 0.05$) (Legendre and Fortin, 1989; see Appendix F). Calculations were performed in ArcMap 10.0 using the Incremental Spatial Autocorrelation Tool. Occurrence data were then *thinned* by removing all points within 5 km of one another and the analyses were rerun to examine the change in model evaluation statistics. We chose 5 km for data thinning because this approximated the maximum distance we could thin the data to produce models where the number of parameters did not exceed the number of occurrence points. We did not attempt to incorporate spatial dependency into final model predictions, as doing so is not recommended when making predictions outside the area used to train the model (Dormann et al., 2007); rather, thinned models were used only to evaluate the effect of spatial dependency on model performance.

2.4. Identifying candidate reintroduction areas

We assumed that condor reintroductions would be more successful in areas predicted to have the highest suitability of nesting, roosting, and foraging habitats that were proximal to one another and were relatively expansive. To determine these areas we calculated a measure of relative suitability for establishing a reintroduction site using the following procedure:

1. Nesting, roosting, and feeding ENMs were transformed to binary rasters using a threshold value that maximized κ.
2. Using these three binary maps to mask the logistic rasters, we calculated the sum of the logistic raster values within a 50 km radius of each cell using focal statistics in ArcGIS. We used 50 km as this was the distance to which condors typically restrict their movements from nests (Meretsky and Snyder, 1992).
3. Outputs from these three rasters were then added together using the raster calculator and the output grid was scaled from 0 to 1 using the following calculation:

$$\text{Grid value} = (x - \min\ x)/(\max\ x - \min\ x)$$

where x is the sum of nesting, roosting, and feeding logistic values within 50 km of each cell, and min x and max x represent the minimum and maximum value of x observed in the study area.

3. Results

For each of the three condor activities, we developed models that had excellent accuracy at predicting test data and were good at discriminating between used and available sites (Table 2). Models were well calibrated, with the predicted-to-expected ratio of evaluation points increasing as habitat suitability scores increased (Appendix G). Test gain (a measure of model performance on data withheld for testing; see Appendix E) was similar to training gain (a measure of model performance on data used to train the model) in all three models (Table 2), suggesting that the models were not overfit to the training data.

According to our models, approximately 11%, 14%, and 23% of the currently-occupied range of the condor in southern California (approximated by the background area) is comprised of suitable nesting, roosting, and feeding habitat, respectively. Models predicted nesting, roosting, and feeding habitat in 8%, 7%, and 14% of the entire study area, respectively. Of the total area modeled by each activity-specific niche, the currently occupied range contained only 27% of the modeled nesting habitat, 36% of modeled roosting habitat, and 34% of modeled feeding habitat within the study area (Appendix D).

Activity-specific ENM residuals had significant spatial autocorrelation (see Appendix F). Thinning data by removing points within 5 km of one another reduced spatial autocorrelation (see Appendix F). Thinned models retained high predictive performance, despite severe reduction in sample size (Table 2). $B_{\text{cont}(0.1)}$ was sensitive to reductions in sample size (Table 2) due to the lack of sufficient data to adequately evaluate a large number of categories, but P/E curves retained relatively good form in thinned models (Appendix G).

All activity-specific niche models (Fig. 2) were statistically different from one another. Nest and roost ENM predictions had the highest similarity of the ENMs ($I = 0.85$, $z = -3.73$, $P < 0.001$). Roost and feeding ENMs had similarity statistic $I = 0.70$ ($z = 8.48$, $P < 0.001$), whereas the nest and feeding ENMs were the least similar of the models ($I = 0.54$, $z = -23.04$, $P < 0.001$). Pairwise percent overlap of the ENMs showed 46% overlap for nest and roost ENMs, 20% overlap for roost and feeding ENMs, and 16% overlap for nest and feeding ENMs (Appendix D).

The importance of environmental covariates differed among condor activities (Fig. 3; Table 3). The importance of each covariate is calculated by MAXENT during model training by tracking improvement in model fit with incremental changes in coefficient values during model optimization (Phillips, 2005). These incremental improvements are summed and normalized to calculate the percent contribution of each environmental covariate for each model run. Terrain features contributed most among covariates in

Table 2
Model characteristics and measures of predictive accuracy for California condor ecological niche models.

Measures	Models with all data			Spatially-thinned models		
	Nesting	Roosting	Feeding	Nesting	Roosting	Feeding
Model characteristics						
Training data (n)	75	107	187	27	40	53
Test data (n)	24	35	94	8	13	17
Logistic threshold	0.04	0.13	0.15	0.09	0.13	0.28
Accuracy measures						
Overall accuracy	0.93	0.94	0.83	0.93	0.93	0.86
Sensitivity	0.98	0.97	0.90	0.97	0.95	0.84
Specificity	0.88	0.91	0.77	0.89	0.91	0.88
Cohen's Kappa (κ)	0.86	0.88	0.67	0.86	0.86	0.72
Boyce Index$_{\text{cont}(0.1)}$	0.88	0.92	0.95	0.55	0.68	0.59
Test AUC	0.98	0.95	0.91	0.98	0.93	0.90
Training gain	2.84	2.02	1.56	2.62	1.77	1.57
Test gain	2.87	1.98	1.56	2.82	1.75	1.38

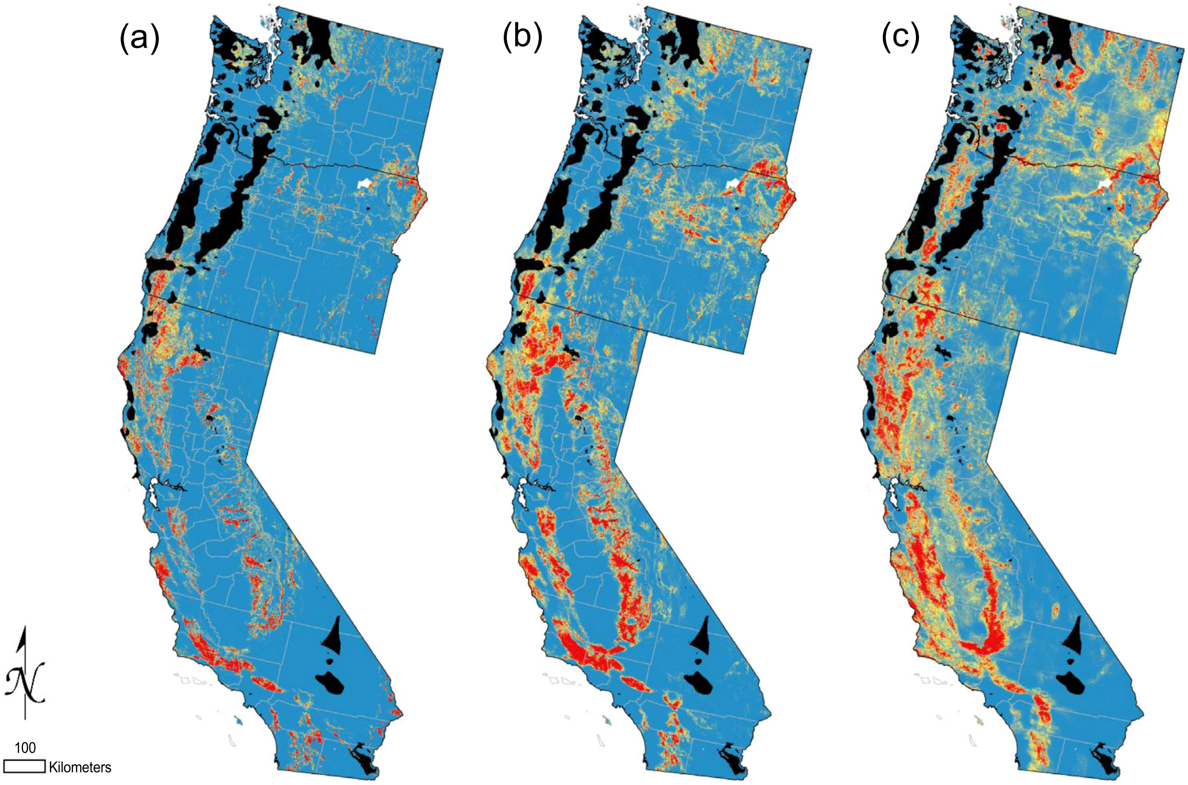

Fig. 2. California condor (a) nesting, (b) roosting, and (c) feeding ecological niche models. Warmer colors represent areas identified by the models as having higher relative suitability. Black areas represent areas with environmental conditions not encountered during model training.

predicting condor nesting and roosting habitat, while landscape productivity and vegetation characteristics had the largest contribution to the feeding model (Fig. 3; Table 3).

Our reintroduction model aligned well with the current and recent historic distribution of California condors in southern California (Fig. 4). Outside of southern California, our model predicts that northwestern California and southern Oregon and the Hell's Canyon region have the most expansive areas of modeled nesting, roosting, and feeding habitat that are proximal (Fig. 4).

4. Discussion

Selection of appropriate release sites is a key element of reintroduction science (Seddon et al., 2007) and is fundamental to a successful reintroduction project (Griffith et al., 1989), especially with species such as the California condor that have slow reproductive cycles and expensive breeding and rearing costs. For these species, decisions on release sites have substantial and lasting ecological, financial, and regulatory implications (Snyder et al., 1996). Our results suggest that ENMs can be useful in reintroduction planning as >70% of predicted nesting habitat for the California condor and >60% of predicted roosting and feeding habitat is outside of the species' current range within the study area (Figs. 2 and 4).

Our ENMs for the California condor make sense ecologically. Condors are known to nest in cliffs in remote areas (Koford, 1953; Snyder et al., 1986; Meretsky and Snyder, 1992) and our nest models predicted suitable habitat in areas containing cliffs and low

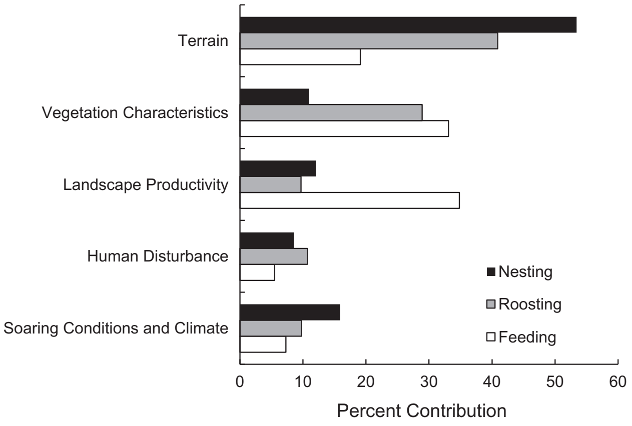

Fig. 3. Average percent contribution of covariate categories for California condor nesting, roosting, and feeding models.

Table 3
Average percent contribution of covariates for California condor ecological niche models.

Covariate	Nesting	Roosting	Feeding
Soaring conditions and climate			
Thermal updraft velocity	1	4	3
Wind speed	1	2	2
Winter severity	13	4	3
Terrain			
Cliffs	52	37	18
Terrain ruggedness	2	4	1
Landscape productivity			
Landscape productivity	5	7	28
Distance to water	7	3	7
Vegetation characteristics			
Canopy cover	4	20	3
Canopy height	4	4	7
Land cover type	3	5	23
Human disturbance			
Road density	8	10	2
Human population density	1	1	4

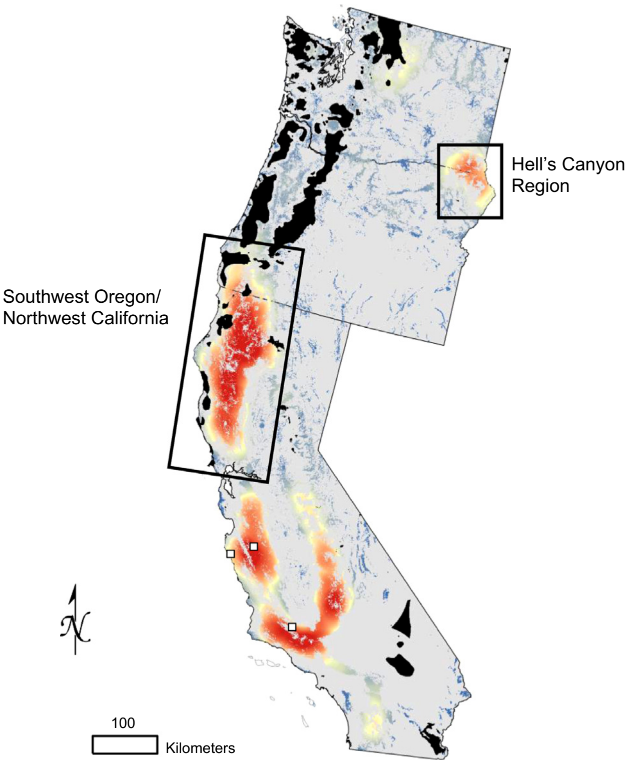

Fig. 4. California condor reintroduction suitability map. Warmer colors indicate areas of higher relative suitability for establishing a reintroduction site. Gray areas are outside of predicted nesting, roosting, and feeding habitat. Black areas represent areas with environmental conditions not encountered during model training. White boxes represent current release sites.

road density. Condors typically roost in trees in mountainous areas and our roost ENM predicted suitable roosting habitat in areas with steep slopes and trees. Feeding condors are typically found in mountain foothills or at coastal sites where steep mountains meet the ocean, where primary productivity is high, and ungulates or marine mammals are concentrated (Snyder and Snyder, 2000). Similarly, our feeding ENM predicted suitable habitat in areas with moderate to steep slopes in areas that had high primary productivity.

To date, most distribution and habitat models for vultures have not disentangled specific activities at occurrence points (e.g., Donázar et al., 1993; Hirzel and Arlettaz, 2003; Martínez-Meyer et al., 2006; Rivers et al., 2014); or, they have examined only a single activity type (e.g., nest sites; see Poirazidis et al., 2004; García-Ripollés et al., 2005; Gavashelishvili and McGrady, 2006; Mateo-Tomás and Olea, 2010), despite recognition that separating activity types can be useful for highly mobile species that use distinct environments for specific activities (Guisan and Thuiller, 2005; Martínez-Meyer et al., 2006). We found that separating niche models for the California condor into activity types was informative, as condors use different habitats for nesting, roosting and feeding (Figs. 2 and 3; Table 3; Appendix D). Therefore, our activity-specific models offer a more precise depiction of the condor's use of ecological niche space than models with pooled occurrence data and provided a more refined view of the interspersion and juxtaposition of various condor habitats in geographic space. This information is essential when selecting a reintroduction site for a species that requires different, but proximal, ecosystems to survive and reproduce.

In addition to being useful in identifying potential release areas, this increased model precision will be useful in: (1) identifying activity-specific threats (e.g., identifying areas where exposure to toxins, such as lead (Finkelstein et al., 2012) or anticoagulant rodenticides (Thomas et al., 2011), may be high) and areas to prioritize threat reduction measures; (2) targeting non-lead ammunition education programs, or identifying areas to dispose of uncontaminated carcasses where they might provide an additional food resource (see Mateo-Tomás and Olea, 2010); (3) identifying areas to survey for historical nest sites (Snyder and Snyder, 2000); or, (4) developing models of habitat connectivity and metapopulation persistence over time. Future niche modeling efforts for other highly vagile species should consider activities separately, especially when those activities occur in different environments. Activity-specific niche modeling also may be useful for less mobile species if a species is using different environments for discrete activities that are essential for the species' survival and reproduction, and occurrence data and environmental data relevant to that species are available at a spatial resolution sufficient to associate these discrete activities with particular environments.

As with all biological models, we recommend caution in interpreting our results, as variability in natural systems, errors in data used to develop the model, and uncertainty in model structure and scale can increase the uncertainty of model results (Pauly and Christensen, 2006). Our modeling effort has taken steps to reduce this uncertainty by testing our models against data withheld from model development, averaging multiple model runs, incorporating multiple spatial scales based on the species' biology, and using model selection to find the most parsimonious model that best fit the data. The relatively good predictive performance of our models—even when models were significantly thinned to reduce spatial dependency of the training and test data—and their alignment with our knowledge of condor ecology and historical distribution suggests that, despite the uncertainties inherent in predictive modeling, they should be useful for prioritizing ground reconnaissance surveys for California condor reintroduction sites.

Our models could not directly incorporate the primary threat to California condor survival and recovery—lead poisoning from spent ammunition (Finkelstein et al., 2012). Because lead poisoning is currently preventing the establishment of self-sustaining condor populations at all existing release sites (Walters et al., 2010), consideration of voluntary or regulatory measures to reduce or remove this threat will be important when weighing whether future reintroduction efforts are likely to substantively contribute to recovery of a viable condor metapopulation.

4.1. Areas for further research

A key assumption of ENMs is that the species is at equilibrium with their environment (Elith and Leathwick, 2009). This assumption was violated by our condor dataset which spanned a period of population collapse and then reestablishment through reintroductions. Despite this lack of equilibrium, correlative models currently remain one of the only methods of forecasting distributions (Elith and Leathwick, 2009) and tests of presence-only ENMs for other recovering species that were not at equilibrium with their environment have shown that ENMs can produce useful results despite the violation in this assumption (e.g., Cianfrani et al., 2010). In addition, condors are highly mobile and retained the ability to select habitats throughout their recent geographic range (i.e., the background area) during the time when occurrence data were collected. Whether or not our models will retain strong predictive performance across geographic space when projecting outside of the current range is an open question. It is encouraging that predictions generally align with our understanding of condor habitat selection and their historical distribution (D'Elia and Haig, 2013). Predictive accuracy of California condor models when projected in geographic space could be tested with data from populations outside of our study area (e.g., in Arizona and Utah), which could inform how robust our models are to violating the assumption of equilibrium.

Traditional niche models based on all occurrences throughout the annual cycle cannot reflect the dramatic seasonal shifts in space use sometimes observed in wildlife populations (e.g., Peterson et al., 2005). Our activity-specific habitat models did not consider temporal variation in habitat use that some have suggested occurs in California condors (Meretsky and Snyder, 1992; Johnson et al., 2010). Developing seasonal habitat models (e.g., Edrén et al., 2010; Rivers et al., 2014) may be useful to delineate areas used intermittently or more intensely during certain times of the year. Projecting season-specific models to new regions might also help identify areas with seasonal opportunities or limitations that are not apparent in time-invariant niche models.

Rivers et al. (2014) found that, along the central California coast, coastal habitats were especially important, probably as a result of the availability of marine mammal carcasses and the availability of consistent onshore winds that facilitate soaring flight. We contemplated developing a separate activity-specific niche model for coastal feeding given obvious differences in inland versus coastal feeding environments. However, we chose not to given the limited area within which coastal foraging currently occurs (<30 km stretch of coastline). As condors expand their range and additional coastal feeding occurrence data become available, separating coastal foraging occurrences from inland foraging occurrences could improve the predictive performance of our feeding model. Those planning reintroduction efforts should consider that coastal feeding sites are underrepresented in our feeding model and that coastal covariates were not included, meaning that there are likely areas of coastline that are suitable for condor feeding, but which are not modeled as suitable.

Overlaying additional threat factors, or factors that associate positively with condor habitat use that could not be directly incorporated into empirical ENMs, is likely to provide information critical to selecting a successful reintroduction site. Factors that could further inform release-site selection include: (1) logistical considerations, (2) land ownership patterns and land conservation status, (3) low-flying aircraft flight routes, (4) wind turbines, (5) distribution of large trees that could provide additional nesting habitat, (6) distribution and density of food, (7) the degree to which threats have been eliminated or abated (e.g., lead ammunition), and (8) heterospecific competition and density of nest predators. Failure to consider these factors could result in selecting suboptimal or even unsuitable release sites. We recommend future analyses consider combining our ENM models with the factors above, and explicitly account for relative suitability (see Appendix G), relative importance of each ENM, and uncertainty in model predictions using a spatially explicit conservation prioritization framework such as Marxan (Ball et al., 2009) or Zonation (Moilanen et al., 2005); or using a Bayesian network approach (e.g., Laws and Kesler, 2012).

5. Conclusions

Our modeling results suggest that California condors currently occupy <30% of modeled nesting habitat, and <40% of modeled roosting and feeding habitat within the study area, implying that there may be significant opportunities for further reintroductions (Fig. 4). Reintroduction projects typically assume that the last place a species was observed is the best place for a reintroduction, but this is not always true (e.g., White et al., 2012). Our results suggest that at least two geographic regions in the unoccupied northern portion of the historical range of the condor have retained environmental conditions that, in the absence of additional threats not included in our models, appear to be conducive to condor nesting, roosting, and feeding.

Modeling species with ranges that are in flux, including species being considered for reintroduction, is a delicate art (Elith et al., 2010). Our analyses suggest that ENMs can be useful for reintroduction planning as long as care is taken to incorporate important aspects of a species' ecology. Outputs from our models can be integrated with movement data (see Nathan et al., 2008) to configure future individual-based models, analyze metapopulation viability and population connectivity, and identify areas of potential conflict between development and habitat conservation. Our approach, which separately models specific activities, has applications for other species and reintroduction programs where it is routinely assumed (often incorrectly) that individuals fulfill all their needs for survival and reproduction within a single environmental space.

ENMs developed for reintroduction planning are subject to change based on the availability of new information. As new reintroduction sites for condors are established, models can be rigorously tested and updated with new data gained from these release efforts (e.g., Cianfrani et al., 2010; Cook et al., 2010; Rinnhofer et al., 2012). Ultimately, accumulation of new data across a number of release sites will increase our ability to identify remaining areas of unoccupied but suitable habitat and develop area-specific models to tease apart differences in the use of environmental space across geographic regions (Bamford et al., 2009). Such an approach will facilitate a more complete picture of

California condor space use and will contribute to designing a strategic and effective rangewide recovery strategy.

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Appendices A–G. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2015.01.002.

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