Applying circuit theory and landscape linkage maps to reintroduction planning for California Condors

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Abstract

Conservation practitioners are increasingly looking to species translocations as a tool to recover imperiled taxa. Quantitative predictions of where animals are likely to move when released into new areas would allow managers to better address the social, institutional, and ecological dimensions of conservation translocations. Using >5 million California condor (*Gymnogyps californianus*) occurrence locations from 75 individuals, we developed and tested circuit-based models to predict condor movement away from release sites. We found that circuit-based models of electrical current were well calibrated to the distribution of condor movement data in southern and central California (continuous Boyce Index = 0.86 and 0.98, respectively). Model calibration was improved in southern California when additional nodes were added to the circuit to account for nesting and feeding areas, where condor movement densities were higher (continuous Boyce Index = 0.95). Circuit-based projections of electrical current around a proposed release site in northern California comported with the condor's historical distribution and revealed that, initially, condor movements would likely be most concentrated in northwestern California and southwest Oregon. Landscape linkage maps, which incorporate information on landscape resistance, complement circuit-based models and aid in the identification of specific avenues for population connectivity or areas where movement between populations may be constrained. We found landscape linkages in the Coast Range and the Sierra Nevada provided the most connectivity to a proposed reintroduction site in northern California. Our methods are applicable to conservation translocations for other species and are flexible, allowing researchers to develop multiple competing hypotheses when there are

uncertainties about landscape or social attractants, or uncertainties in the landscape conductance surface.

Introduction

Endangered species reintroductions and translocations are important and increasingly applied conservation interventions to save species from extinction and facilitate their recovery [1, 2]; but, failure rates can be high when not properly planned [2–4]. For most species, a key determinant of success is identification of the reintroduction landscape, which considers ecological, social, and institutional dimensions [5, 6]. This can be particularly important for species that have large home ranges and those that have the potential to cause human-wildlife conflict.

A priori identification of the reintroduction landscape via modeling species' movement probabilities away from release sites has important conservation implications for (1) defining areas where regulatory protections may be needed, (2) quantifying whether there will be sufficient ecological resources for the reintroduced population, (3) identifying and quantifying threats, (4) identifying barriers or restrictions to movement and colonization, and (5) predicting gene flow and future metapopulation connectivity. This is particularly critical for wide-ranging species where simply identifying breeding areas or local conditions in the immediate vicinity of the reintroduction site is insufficient. When paired with habitat linkage or population dynamics models, predicting movement probabilities away from reintroduction sites can also provide information necessary for identifying habitats in need of protection [6–8], comparing likely costs and outcomes of various reintroduction scenarios [9], and for helping to define and quantify recovery targets [10].

The California condor (*Gymnogyps californianus*) is a critically endangered species with a global population of <350 free-flying individuals. Ongoing efforts to restore the species to its former range in southern and central California, Baja California, and Arizona have been well-chronicled [11–13]. However, condors are still reliant on human intervention for survival and population growth primarily due to the continued use of lead ammunition, which condors ingest when scavenging on dead animals or gut piles left in the field [13, 14]. California condors remain absent from large portions of their historical range although planning efforts are underway to restore them to the Pacific Northwest via a new release site in northern California [15].

California condors are a good case-study for modeling the geographic extent of the reintroduction landscape because they can undertake long daily flights from nests or roosts to find carrion, and their movements have been closely monitored at multiple sites for many years [12, 16]. Around the proposed reintroduction site in northern California, nesting, roosting, and feeding habitats are relatively expansive and in close juxtaposition [17]. However, existing habitat models do not account for distances from release sites, habitat connectivity, nor landscape resistance to movement [17]. Furthermore, existing models that were trained and tested with data from condors using terrestrial features did not account for differences in activity-specific habitat selection by condors during flight [17]. Connectivity modeling using circuit theory [18] is one tool that has been used for assessing the likelihood of species' recolonizing an area [19], identifying habitat connectivity between occupied sites and reintroduced populations [20], and for understanding why reintroduced populations have not colonized apparently suitable habitats [21]. We propose that circuit theory can also be useful in predicting the dispersion of condors from reintroduction sites.

Our goals were to: (1) develop a habitat model to predict landscape conductance (the inverse of landscape resistance) across the study area, based on the relative likelihood of

occurrence of condors in flight around existing release sites in southern and central California; (2) use electrical circuit theory and our model of landscape conductance to empirically derive and test a spatially-explicit working hypothesis delineating the area of predicted landscape occupancy around release sites, and (3) map habitat connectivity between modeled core nesting areas around the proposed northern California release site and existing release sites. We expect our model of condor movement probabilities around a new reintroduction site to be useful for recovery planning and intend to test and update this model as we acquire new movement data. Our methods are broadly applicable to conservation translocations for other species where sufficient data exists to produce a reliable landscape conductance surface.

Methods

Study area

Our study area included California, Oregon, and Washington, USA (32˚-49˚N and 114˚-124˚W). Within the study area, the current range of the California condor is limited to the mountainous regions of southern and central California where reintroductions are ongoing at four release sites: one in southern California operated by the U.S. Fish and Wildlife Service, two in central California along the Pacific coast operated by Ventana Wildlife Society, and one in central California operated by Pinnacles National Park. There are also two release sites outside of the study area: one in Baja California, and one in northern Arizona. A new release site, which is the focus of this study, has been proposed for northern California, near the Oregon border (see Fig 1).

Major mountain ranges are oriented along a north-south axis and include the Coast Ranges, the Cascade Mountains, and the Sierra Nevada. Wide valleys, including the Central Valley in California and the Willamette Valley in Oregon, separate the Coast Ranges from interior mountain ranges. The Tehachapi Mountains in southern California and the Klamath and Siskiyou Mountains in northern California and southern Oregon connect the inland and coastal mountain ranges. The climate ranges from Mediterranean in southern and central coastal California to temperate rainforest in coastal areas of northern California, Oregon, and Washington. Precipitation and temperature are highly variable along elevation and latitudinal gradients in interior portions of the study area, resulting in large variation in ecological communities.

Landscape conductance surface

We developed a map of relative landscape conductance for California condors in flight by modeling the relationship of environmental covariates to known locations of condors aloft. Specifically, we used MaxEnt version 3.3.3k, 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 [22–24]. Presence-only models, such as MaxEnt, are preferred over presence/absence models in nonequilibrium situations, including when modeling expanding populations of imperiled species [25]. MaxEnt models can be conservatively interpreted as a relative index of environmental suitability, where higher index values depict better conditions for the species [22]; in this case, better conditions for the occurrence of condors in flight. We focused our analysis at the landscape-scale with a 1 km^2 spatial grain given that our ultimate goal was to identify landscape-scale connectivity and movement probabilities. We trained and tested models using data from the background area (see Fig 1) but projected them to the entire study area. We built simple models given the large spatial extent and coarse-resolution of the spatial data and to avoid overfitting the model to the training region, which would likely degrade its performance when we project it to novel geographic areas [26].
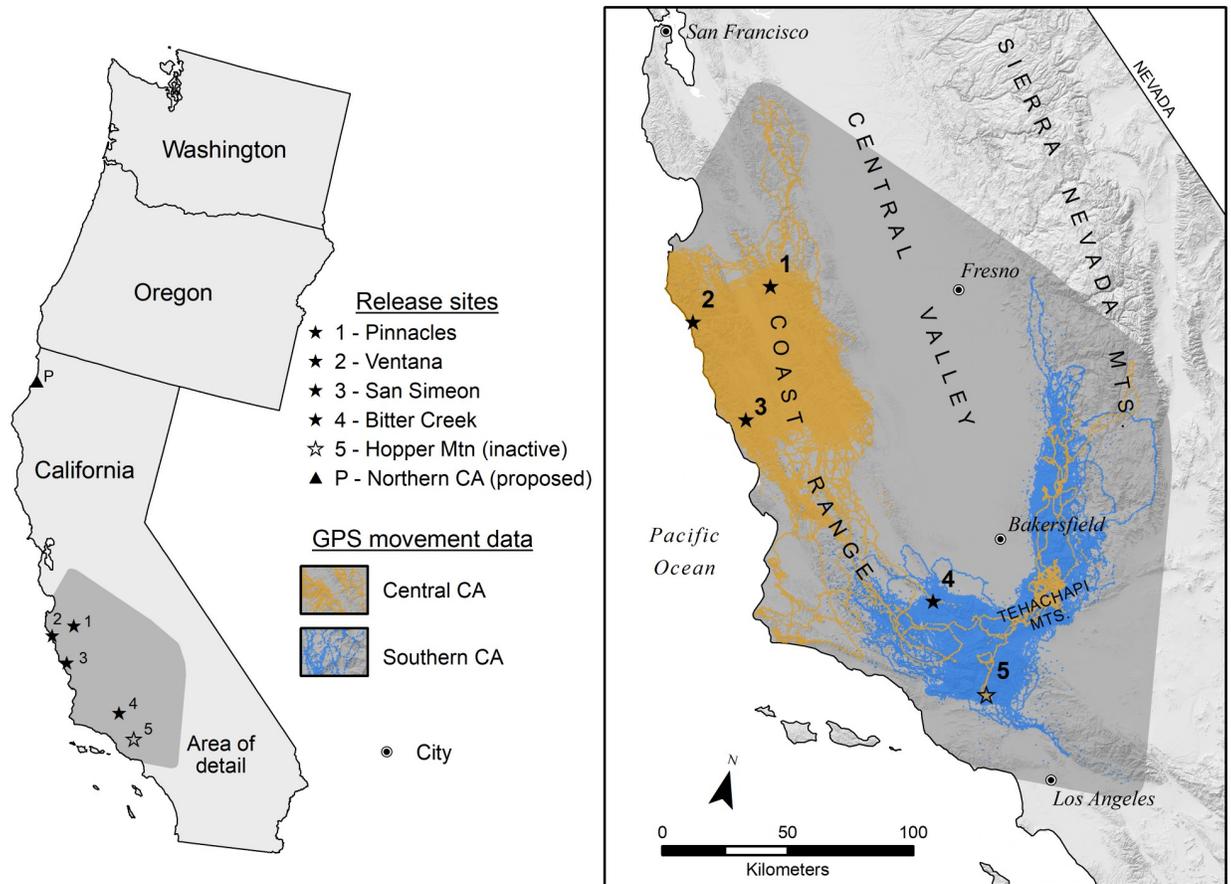
Fig 1. Study area, background area for developing a California condor landscape conductance surface (dark gray), in-flight California condor locations (July 2013-May 2017), and release sites.

Condor occurrence data. We downloaded, from Movebank (www.movebank.com), raw condor locations of all California condors equipped with Global System for Mobile Communications (GSM)/Global Positioning System (GPS) transmitters in the southern and central California flocks. This included occurrence data spanning July 2013-May 2017 for 75 individual condors: 29 from central California release sites (1,939,737 GPS points), and 46 from the southern California release site (3,453,959 GPS points) (Fig 1). The occurrence data included juveniles and adults (breeding and non-breeding) of both sexes, as well as captive-reared and wild-fledged individuals (S1 Table). GSM/GPS transmitters were patagial-mounted and deployed on a subset of the condor population during routine handling [27]. GSM/GPS transmitters record location, altitude, and accuracy data every 2–30 minutes and transmit these data to a GSM network or Code-Division Multiple Access (CDMA) network. We filtered raw GPS data using the following procedure:

1. We selected only those points with reliable GPS fixes ("proofed" = 1) that likely represented condors in flight ("speed" > 2.78 meters per second (m/s) and < 30.0 m/s). Below we refer to our filtered data as movement points because we based all of our analyses on occurrence points from condors in flight.

2. We removed points that were located offshore. We also removed points within 5 km of existing release sites and the Hopper Mountain National Wildlife Refuge (NWR) flight pen

(a former release site which is occasionally used to trap condors) because the frequency of condor movement within these areas is artificially inflated by periodic baiting to recapture condors for health screenings and to replace transmitters. Free-flying condors are also attracted to these sites when captive condors are held in the flight pens prior to release. We chose 5 km based on inspection of frequency plots, which showed a marked decline in the number of movement points at this distance.

3. MaxEnt requires that occurrence points are independent, as autocorrelation can lead to a biased model. We can minimize bias from autocorrelated GPS locations by rarifying data at regular time intervals over a relatively long period [28, 29]. Therefore, we further filtered our occurrence dataset to include only one randomly selected movement point per individual condor, per day, for all days that GPS positions were available. This resulted in 22,251 filtered points for southern California and 6,839 filtered points for central California (S1 Table). Given the multi-season and multi-year dataset, as well as the ability of individuals to move long distances, condors in our study had the potential to access various landscapes throughout the annual cycle. Thus, occurrence datasets were sufficient to describe the landscape-scale ecological relationship between condors in flight and environmental covariates.

Background data.   MaxEnt requires that the user specify a background (i.e., area available for the species to select) against which one compares covariate values at occurrence points [22, 24]. We created MaxEnt models within the environmental and geographic space of the background area, but projected models across the entire study area. Choice of an appropriate background sample is crucial to avoid sample selection bias and, consequently, poor performing models [30]. We generated a background area by defining a convex hull around all condor movement points (see **Condor Occurrence Data**, above), buffering the resulting polygon by 10 km to account for the area outside of the strict hull boundary that was presumably available for condors to select, and clipping the polygon to the coastline. We then produced 10,000 random points within the buffered convex hull to serve as background data (see Fig 1). We used 10,000 points, as previous work has shown this is sufficient to represent the range of environmental conditions across large study areas [31]. To match the condor occurrence dataset, we excluded background points from the area within 5 km of each release site and the Hopper Mountain NWR flight pen.

Environmental covariates.   As obligate soaring birds, California condors rely on upward air movement for staying aloft [32, 33]. When lift is favorable due to winds deflecting off mountains, or due to thermal updrafts, condors can move long distances expending limited energy. From an evolutionary perspective, this ability for obligate scavengers to move long distances with minimal energy expenditure is a critical adaptation to finding carrion—an ephemeral resource [34, 35]. Therefore, we hypothesized that upward air movement influences landscape conductance for condors. We also hypothesized that condor movements are constrained by the distribution of terrestrial habitats (e.g., areas of low percent tree canopy cover, low human disturbance, high primary productivity, rugged terrain, and steep slopes).

In developing our MaxEnt models, we considered seven covariates related to thermal updrafts, terrain (a proxy for orographic lift), terrestrial condor habitat, and human disturbance (Table 1). We selected covariates based on published species-habitat associations [17, 33, 36–38], species-habitat models developed for other vultures [39–43], and the availability of GIS data at the appropriate spatial scale spanning the entire study area. For covariates we suspected to be correlated with landscape-scale habitat selection (i.e., at a larger scale than our spatial grain of 1 km^2) we summarized focal statistics within a 10 km neighborhood (Table 1). We used a 10 km neighborhood recognizing that large vultures in-flight have the visual acuity

Table 1. Covariates used in developing a California condor landscape conductance surface.

Covariate	Description	Data Source
Thermal Updraft Velocity	Annual mean velocity of rising air (m/s)	Regional Atmospheric Soaring Prediction Maps (http://www.drjack.info/RASP/index.html)
Terrain Ruggedness	Ratio of 3-dimentional surface area to planar surface area within a 10 km neighborhood	The National Map Small-Scale Collection (https://nationalmap.gov/small_scale/mld/elev100.html) processed with DEM Surface Tools for ArcGIS 10 (http://www.jennessent.com/arcgis/surface_area.htm)
Slope	Mean slope (degree)	The National Map Small-Scale Collection (https://nationalmap.gov/small_scale/mld/elev100.html)
Tree Canopy Cover	Median tree canopy cover (%)	National Land Cover Database 2011 (http://www.mrlc.gov/nlcd2011.php)
Terrestrial Habitat	Density of terrestrial habitat within a 10km neighborhood	Derived from California condor nesting and feeding models [17]. We used focal statistics in ArcGIS 10 to calculate the mean amount (km^2) of terrestrial habitat (presence of either nesting or feeding habitat) within 10km of each cell.
Road Density	meters of road/km^2 within a 10km neighborhood	Data Basin (http://databasin.org/datasets)
Human Population Density	humans/km^2 within a 10 km neighborhood	2010 TIGER/Line Census Data (https://www.census.gov/geo/maps-data/data/tiger-data.html)

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to perceive landscape features and resources (at a resolution as small as 2 m) at distances of up to 10 km [44, 45].

To identify correlated covariates, which might reduce model interpretability, we assessed multicollinearity among covariates by calculating univariate pairwise Spearman correlation coefficients (r_s) based on values of each variable at condor movement points in each modeling region. If two covariates had $r_s > 0.70$, we retained only one of the pair to aid in interpretation of model results, retaining the covariate that had greater biological meaning.

Model selection and settings. We developed several *a priori* hypotheses describing the relationship between condor movement and covariates based on our knowledge of obligate soaring birds, and condors specifically, and created MaxEnt models for each hypothesis (Table 2). We evaluated our models using 5-fold cross-validation. We calculated several measures of model performance on the data withheld for testing for each fold, including mean values of regularized training Gain, test AUC, and AIC [22, 46]. We then averaged these measures across folds. We selected the model with the lowest mean AIC as the best performing model that we then projected to the remainder of the study area. We used the logistic output of this projection as a measure of relative landscape conductance for California condors. We considered whether non-linear transformations of our species distribution model output

Table 2. Mean relative contribution of covariates (%), and measures of model performance for a California condor landscape conductance surface (Some columns in the upper portion of the table do not sum to 100 due to rounding).

Covariate	Model 1	Model 2	Model 3	Model 4	Model 5
Slope	9.8	10.1	10.0	92.0	100
Terrain Ruggedness	0.2	0	0.1	0.1	0
Thermal updraft velocity	0.5	0.5	- -	8.0	- -
Tree canopy cover	0.8	0.7	0.8	- -	- -
Modeled terrestrial habitat	88.6	88.6	89.1	- -	- -
Human population density	0	- -	- -	- -	- -
Road density	0	- -	- -	- -	- -
Model Performance Measures					
AIC	125413	125418	125440	148034	152022
Regularized Training Gain	1.48	1.48	1.47	0.68	0.60
Test AUC	0.91	0.91	0.91	0.81	0.80

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might produce more accurate conductance surface [47]; but, we retained a simple linear relationship because our occurrence data consisted of condors that were in-flight and moving.

For model settings, we used only linear and quadratic features, set the maximum number of model iterations to 5,000, implemented clamping, and did not remove duplicate presence records or add occurrence data to the background.

Circuit theory and condor movement

We defined three modeling regions to predict condor movements, centered on existing or proposed release sites: (1) southern California, with an existing release site at Bitter Creek NWR, (2) central California, with existing release sites at Pinnacles National Park, the Santa Lucia Mountains adjacent to Big Sur, and the mountains near San Simeon, and (3) northern California, with a proposed release site in the Bald Hills of Redwood National Park (Fig 1). Modeling regions included all areas within 350 km of the above release sites. We chose 350 km to encompass the farthest Euclidean distance of condors from release sites in our occurrence data. This distance was uncorrected for topography because condors in flight can skirt topographic relief.

Within each modeling region, we used Circuitscape software v 4.0 to model California condor movement through the landscape [48]. Circuitscape uses algorithms from electrical circuit theory to model connectivity, treating landscapes as resistance (or conductance) surfaces where one can model patterns of animal movement as electrical current between sources and destinations across a resistor [18]. When one considers combinations of sources and destinations, the result is a continuous map of electrical current and voltage across all possible routes in the network [18].

Electrical current in Circuitscape is ecologically interpreted as the net probability of movement between a source and a destination through a resistance or conductance surface [18]. The conductance surface for our analyses was the logistic output of the MaxEnt model described above. We defined the source of electrical current as points centered on existing release sites within each modeling region. Given our lack of knowledge about the destination of condors, we generated points representing ground nodes at 10 km intervals along the edges of our modeling regions (i.e., along a 350-km buffer that encircled the respective release sites). We placed ground nodes in all directions away from the release sites to avoid directionality bias. Our ground nodes extended beyond our study area and landscape conductance values, meaning we needed to assign conductance values to grid cells outside of the study area, including the Pacific Ocean, Nevada, and Baja California. Large vultures avoid, or have difficulty, crossing large bodies of water [49–51]; therefore, we assigned the minimum conductance value observed in our study area to the Pacific Ocean. Given the unknown conductance in terrestrial areas in Nevada and Baja, we assigned all cells in these areas the median conductance value observed in our study area; we used median values to provide a constant surface for electrical flow outside of the study area rather than for estimating net movement probabilities in these areas.

We ran Circuitscape in Advanced Mode, iteratively connecting each source node to each ground node within each modeling region. This allowed us to model condor net movement probabilities in all directions away from release sites across the network, creating individual current maps for each source-ground node connection in the network for each of the three modeling regions. For each modeling region, the mean of the individual current maps provided a direction-neutral connectivity map. The default units of electrical current maps were amperes (A), which we converted to milliamps (mA) by multiplying outputs by 1,000 so we

could work with simpler numbers. To assess the relationship of electrical current to the prevalence of condors in flight, we extracted the electrical current values to condor movement points and plotted the reverse cumulative frequency of these values in 1 mA intervals. We used a reverse cumulative frequency plot, as we were interested in how the frequency of condor movements might attenuate in relation to electrical current.

We assessed the degree to which mean electrical current related to the predicted/expected ratio of condors moving after their release (from release sites, which we treated as sources of electrical current) using the continuous Boyce Index and Predicted/Expected (P/E) curves produced by the ECOSPAT package in R [52, 53]. Given known biases around ground nodes [54], we limited our evaluation of the models to within 300 km from release sites. The continuous Boyce index and continuous P/E curves calculated in ECOSPAT are presence-only and threshold-independent measures that provide information on model resolution and predictive performance across the spectrum of habitat suitability values (or, in our case, electrical current values) within each modeling region [52, 53]. Boyce index values vary from -1 to +1, with values closest to +1 indicating a model where predictions were consistent with the distribution of the movement points. Values close to zero indicate that the model is not different from a random model, and negative values indicate an incorrect model. An ideal model would have a P/E curve that was linear and positive, where electrical current was proportional to the probability of use by released condors in flight.

Landscape connectivity of reintroduction sites

We evaluated landscape connectivity for California condors between the proposed release site and existing release sites in California using Linkage Mapper v. 2.0.0 [55]. Linkage Mapper uses a landscape resistance surface and a map of core areas to identify least-cost paths between core areas [55]. Our resistance surface was the inverse of the conductance surface described above (1 /Conductance) [18]. We defined core areas as generalized nesting habitat patches by reclassifying D'Elia et al's [17] logistic map of relative nesting habitat suitability into a binary output using a threshold value of 0.04 [17], and removing all patches smaller than $10km^2$. We then built network and map linkages using the cost-weighted network adjacency method in Linkage Mapper to identify core areas to connect, dropping corridors that intersected with core areas. Linkages were visualized using cost-weighted distances, where higher values represent weaker connectivity among modeled nesting habitat patches.

Results

Landscape conductance surface

Our habitat suitability model of condors in flight generally aligned with the current and recent historical distribution of the species. Given the high relative contribution of terrestrial habitat to our in-flight model (see Table 2), factors that most influenced that model (i.e., areas of high topographic relief, low percentage of tree canopy cover, and high landscape productivity [17]) were most favorable to condor movements and therefore more likely to be occupied by condors in flight. Our model predicted that areas over deserts, dense forests, and wide flat valleys were less likely to be occupied by condors in flight. Correlation coefficients of univariate pairs of environmental covariates were all below 0.70; therefore, no covariates were removed prior to development of an in-flight condor habitat model. The model with the lowest AIC, and therefore the one that we selected to represent our conductance surface, was the model that included all covariates (Table 2).
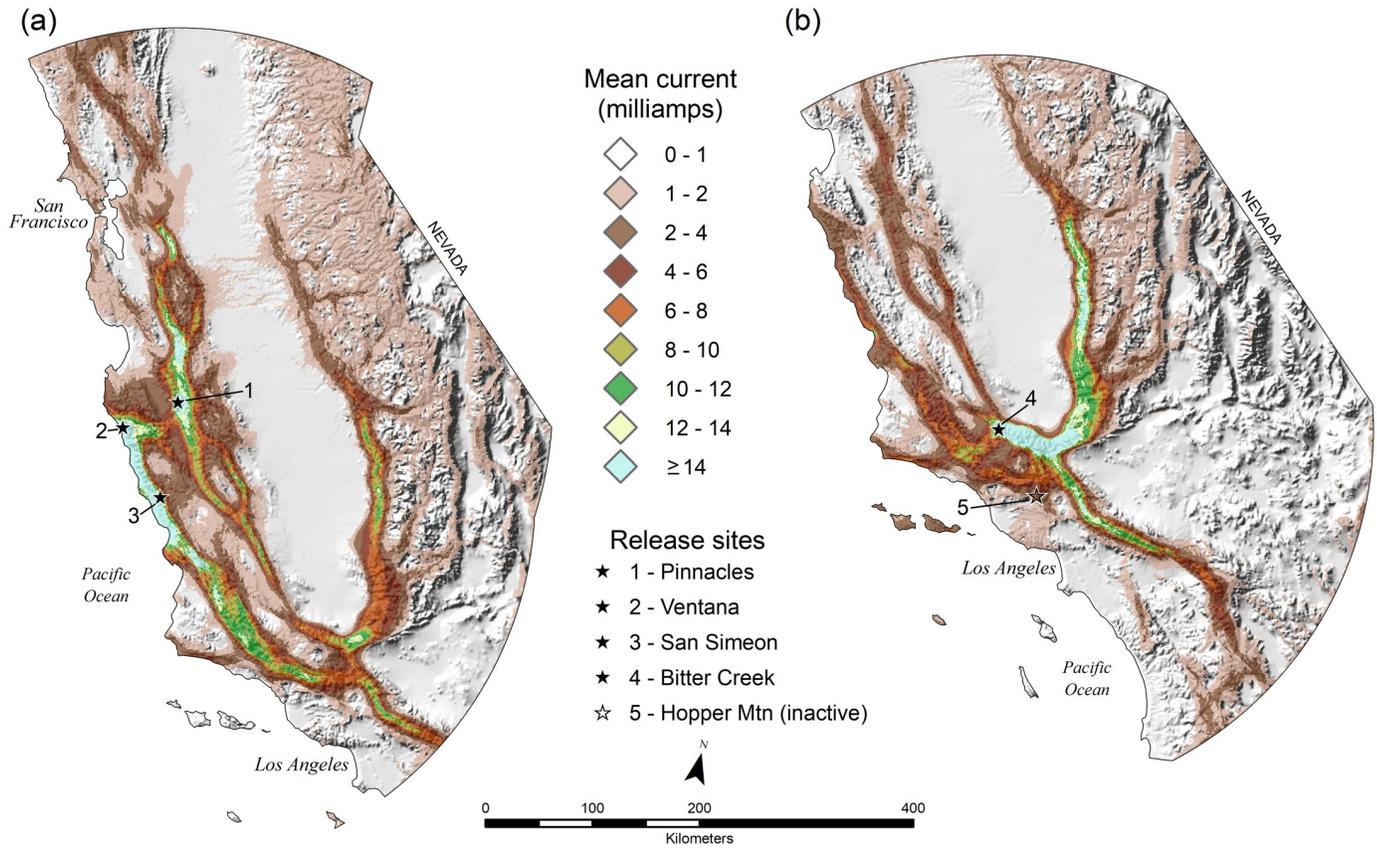
Fig 2. Mean electrical current for California condor circuit theory models in (a) central California and (b) southern California, USA.

Circuit theory and condor movement

Mean electrical current generated via Circuitscape (1,166 source-ground connections, 220 for southern California, 726 in central California, and 220 in northern California) was well calibrated with the known pattern of condor movement in southern and central California (Figs 2 and 3). The continuous Boyce Index for electrical current in southern California was 0.86 and in central California was 0.98 (Fig 3). A spike in the P/E plots, between approximately 20 and 40 mA in southern California, corresponds with a higher than expected density of condor movement points in the Tehachapi Mountains. We suspected this was because Hopper Mountain NWR, an area where condor nesting activity is concentrated and where baiting and trapping occurs—had an extremely high frequency of condor movement that was unaccounted for in our model. This prompted us to conduct a *post-hoc* analysis to determine whether adding prior information on destination nodes within the circuit—representing condors moving from release sites to areas of high use at Bitter Creek NWR, the Tehachapi Mountains, and Hopper Mountain NWR—would improve model fit. Specifically, we used Circuitscape to develop a new current map based on pairwise connections between the release site (i.e., the source node) and the center of two high-use areas noted above (i.e., ground nodes). We then overlaid the new map with the original map of electrical current and took the maximum value of the two surfaces. We found that accounting for movement to these high-use areas via our *post-hoc* analysis, improved the continuous Boyce Index from 0.86 to 0.95, and smoothed out the spike in the P/E curve (Fig 3).
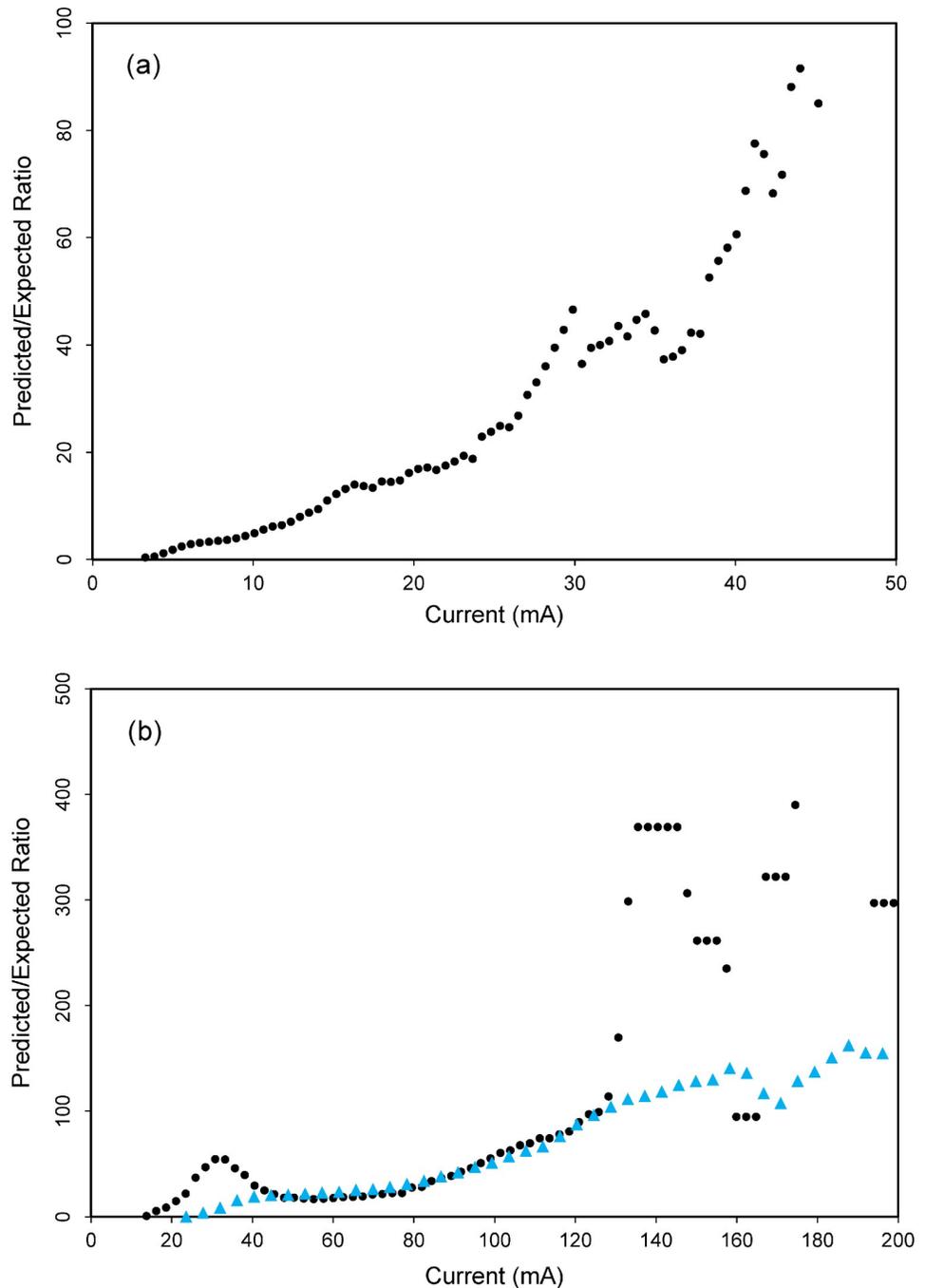
Fig 3. Continuous predicted/expected plots of electrical current models for California condors in (a) central California and (b) southern California, USA. Blue triangles in (b) represent the predicted/expected plot when Hopper Mountain National Wildlife Refuge and the Tehachapi Mountains were added as additional ground nodes in the electrical circuit.

The number of condor movement points attenuated away from release sites, concordant with the attenuation of electrical current (Fig 4). Reverse cumulative frequency plots of condor movement declined roughly linearly, with approximately 93–98 percent of movement points contained within areas ≥2 mA (Fig 4). In northern California, our model of electrical current
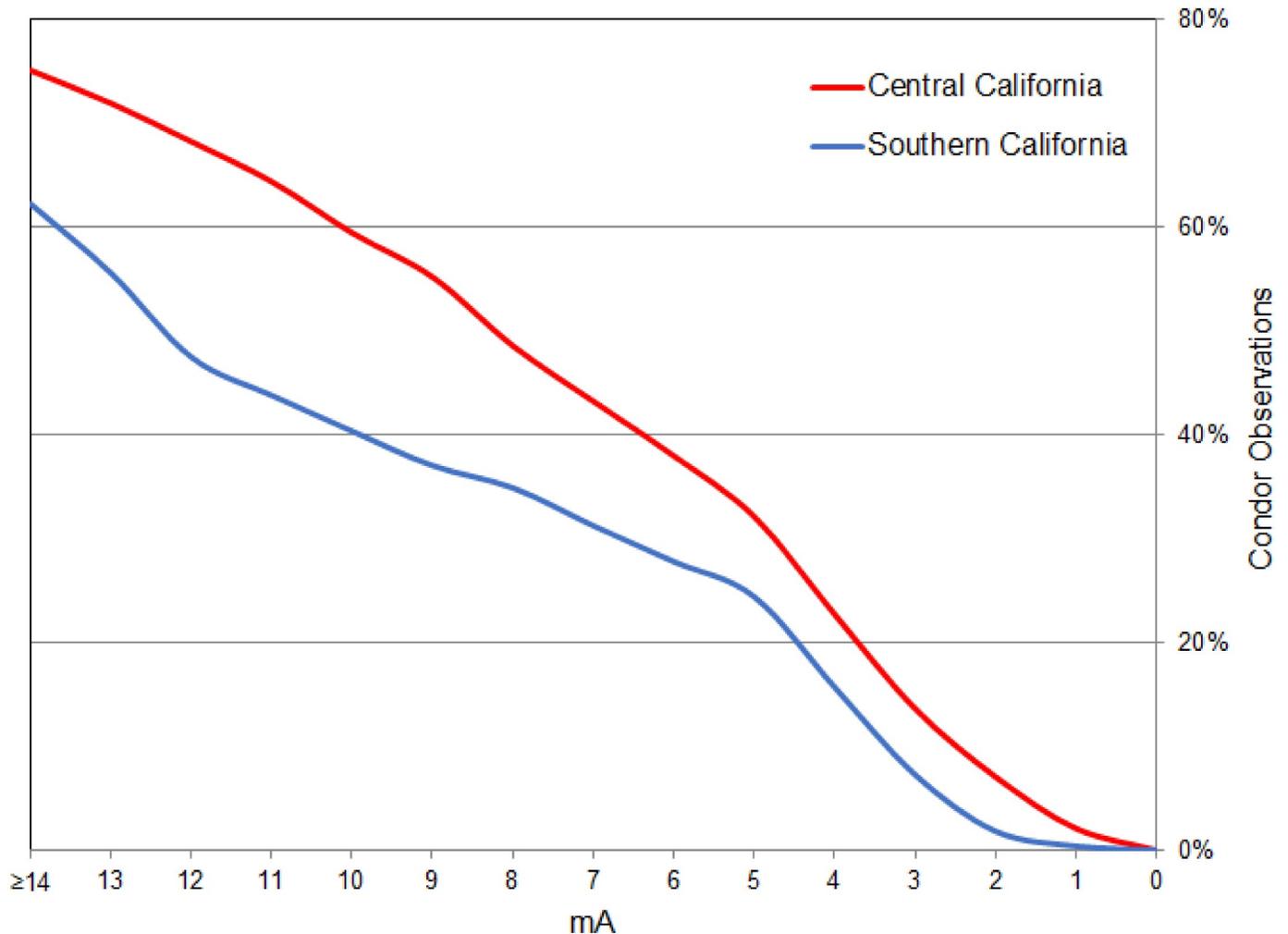
Fig 4. Reverse cumulative frequency plot of in-flight California condor locations (July 2013-May 2017) in relation to electrical current for the southern and central California modeling regions, USA.

predicted that condor movements would likely be initially most concentrated in northwestern California and southwest Oregon (Fig 5). Specifically, areas likely to encompass >90 percent of condor movements were generally concentrated in the Klamath, Siskiyou and North Coast Ranges (including the King Range), extending south to Bodega Bay, inland to the Mt. Shasta region, and north to the Umpqua Valley.

Landscape connectivity of reintroduction sites

Our cost-weighted distance linkage network provided a useful visualization of areas of high and low connectivity among modeled nesting habitat patches. Our linkage network consisted of 305 modeled nesting habitat patches that met the minimum size criteria of 10 km² (Fig 6). Linkage mapper produced a network of 553 least-cost-path links between nesting habitat patches, with a mean cost-weighted distance of 177.6 (in cost units, not geographic distance). Areas of high cost-weighted distance between core nesting areas near the proposed release site and the existing release sites included the San Francisco Bay area (mean cost-weighted distance among two links = 753.5) and the northern Sierra Nevada mountains (cost-weighted
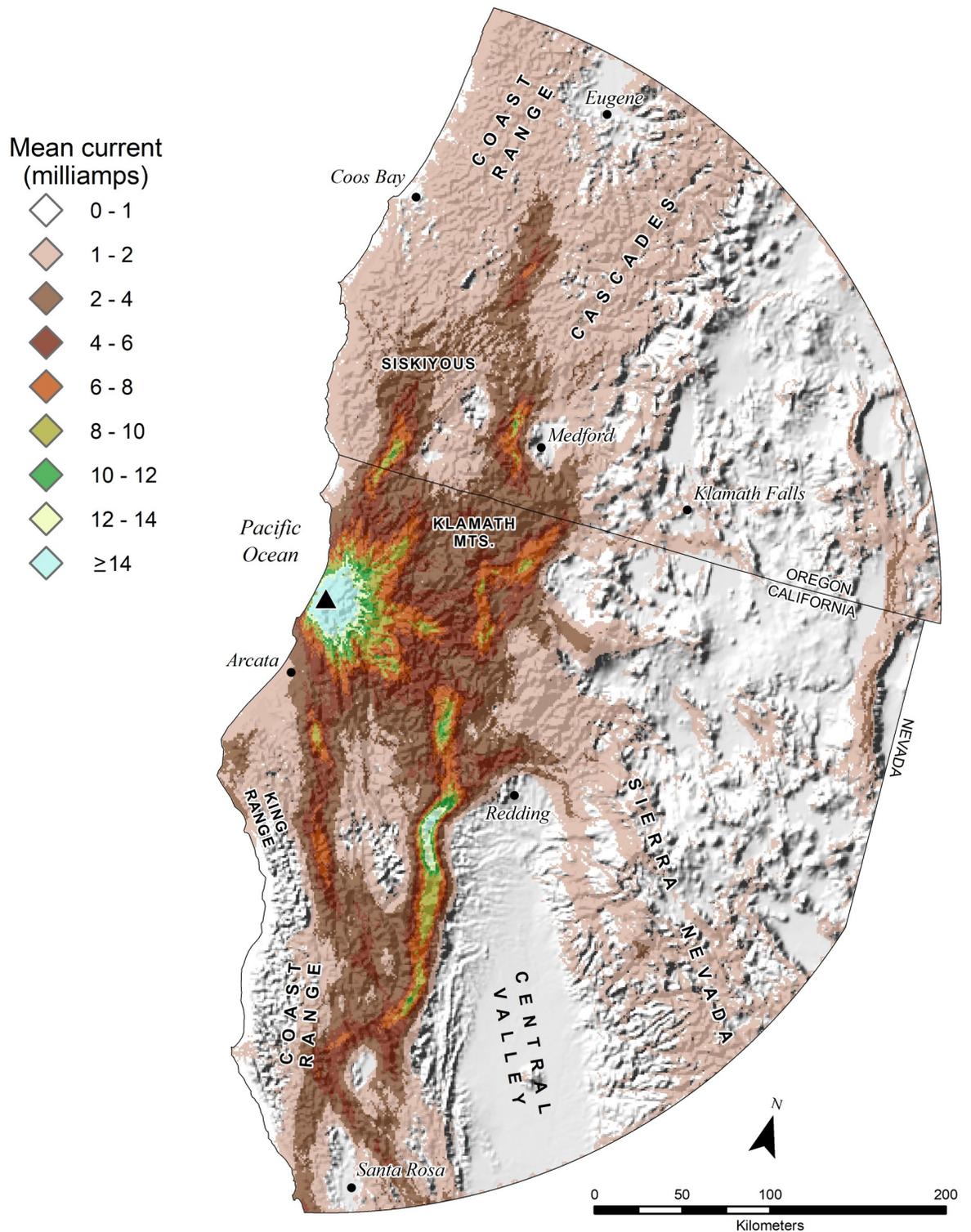
Fig 5. Mean electrical current for a California condor circuit theory model around a proposed release site (▲) in northern California, USA.
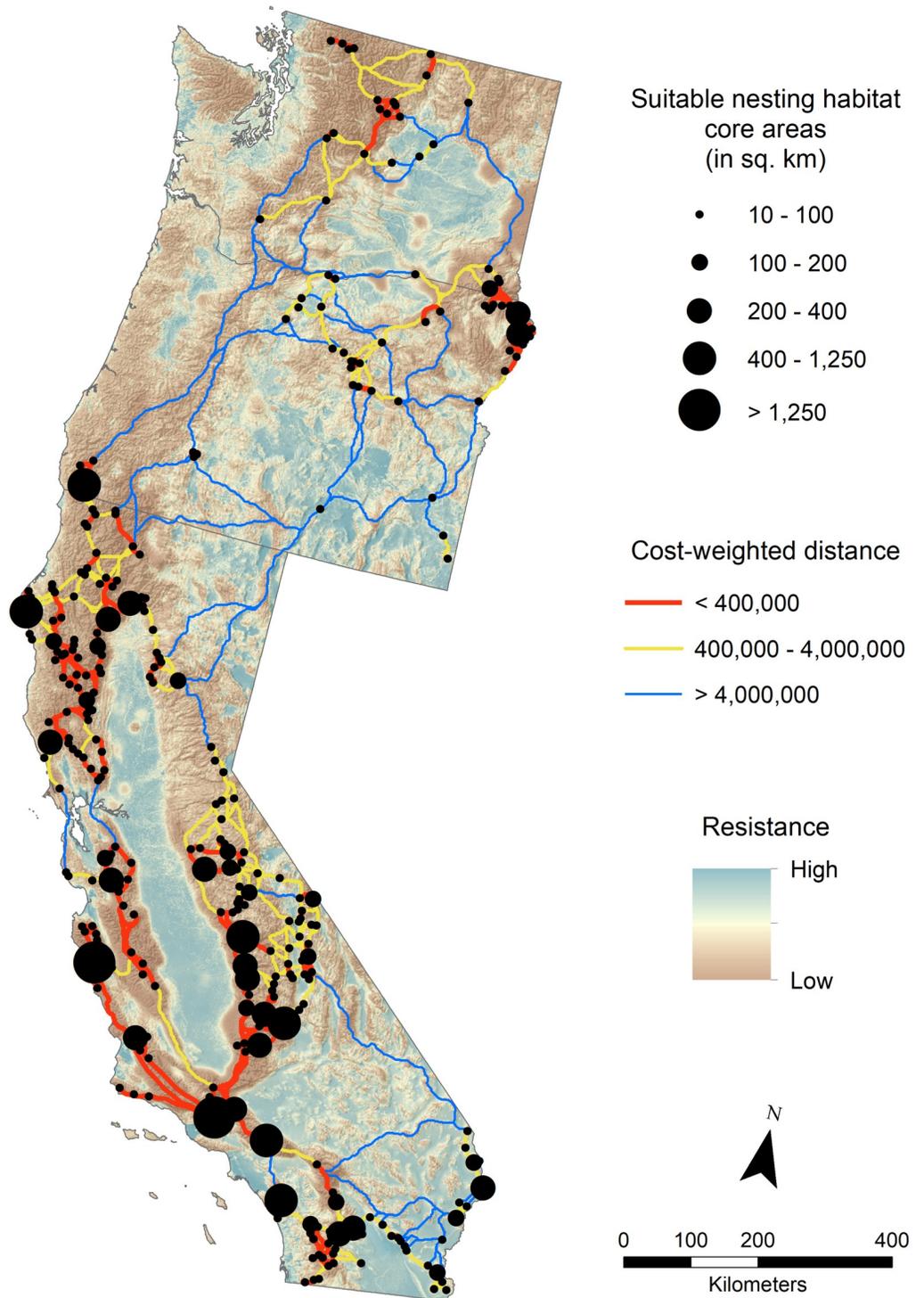
Fig 6. Least-cost-path linkages between California condor modeled core nesting habitats (≥ 10 km^2) in Washington, Oregon, and California, USA. For display purposes, core nesting habitats are represented as points and linkages between large core nesting habitats were snapped to points through core nesting habitats while maintaining their least-cost path distances.

distance = 428.3). We found an even higher cost-weighted distance between core nesting areas near the proposed release site in southwest Oregon and core nesting areas in northern and eastern Oregon (mean cost-weighted distance > 1,000).

Discussion

### Landscape conductance surface

As we predicted, our models indicated that condors showed an affinity for moving over terrestrial nesting or feeding habitats and over areas with moderate to steep slopes. They also showed strong avoidance of wide, flat valleys and areas of low primary productivity where ungulate densities were relatively low. This makes ecological sense, as we would expect condors in flight to spend most of their time searching for food in areas of slope-lift in open or semi-open habitats, patrolling nesting territories, or commuting between nesting and feeding areas. It is also intuitive that condors would be less likely to travel across expansive flat areas where they risk being grounded, or through areas where food densities are low. We recognize the possibility that some valleys may become accessible to condors when summer thermals provide sufficient lift for sustained soaring flight. It is also possible that some areas with low annual average productivity may occasionally be attractive to condors due to seasonal movements of native ungulates or livestock.

Contrary to our expectations, annual thermal updraft velocities appeared relatively unimportant to the relative frequency of moving condors. This may partially be a function of our use of a covariate for thermal lift that is based on average values across the annual cycle. Others have found significant relationships between meteorological variables and condor space use at finer temporal scales [33, 38], suggesting that landscape resistance to condor movements is dynamic, and meteorological "gates" between different parts of the landscape likely emerge and vanish throughout the year. Seasonal models using the techniques we describe here could help elucidate these temporal changes in condor space-use across the annual cycle.

We predicted significant areas of suitable in-flight condor habitat around the proposed northern California release site. It is important to emphasize that our predictions are based on a species distribution model that is inherently correlative, rather than process-based [56]; and therefore, represents a working hypothesis based on data from other regions. Several studies have highlighted the potential hazards of projecting species distribution models into novel areas [57–60]. Yet, when constructed with careful consideration of a species' ecology, distribution models remain a transparent, quantifiable, and repeatable method for developing and testing hypotheses about potential habitat in occupied regions. Projecting models to novel areas can be reliable enough for effective decision-making provided that the data and models are reasonable and any correlations across covariates are stable through the temporal and geographic domains for which the predictions are made [58, 61]. Falsification or support for our hypotheses will be possible through evaluating whether our models are correlated with the distribution of condors once a population is established in northern California.

We limited our analysis to a small subset of ecologically relevant covariates and smooth response curves, as is recommended for large spatial extents [26, 62]. Thus, our results represent relative habitat suitability at the landscape scale and were not intended to elucidate finer-scale habitat selection. Future efforts to develop landscape conductance surfaces could explore this finer-scale habitat selection by: (1) using a hierarchical approach [63] with a smaller spatial grain; (2) including environmental covariates on seasonal or real-time wind direction and speed in relation to topographic features; (3) including seasonal or real-time meteorological conditions; and, (4) including direct measures of terrestrial and marine food availability. In addition, separating occurrence points into categories of movement (e.g., linear soaring,

gliding, and circular soaring), or specific parts of a species' life cycle [64], might also improve our ability to make finer-scale predictions [51, 65–67].

Species distribution models are grounded in the ecological theory that species distributions are determined, at least in part, by environmental covariates and that reasonable approximations for these covariates can be estimated [62]. Therefore, it is important to acknowledge potential weaknesses in the species-environmental covariate relationship when interpreting species distribution model outputs. Our covariate for terrestrial habitat, which had the highest percent relative contribution to our conductance surface, likely underestimated feeding habitats along the coast for three reasons: (1) our model of feeding habitat was based on a higher proportion of observed inland feeding occurrences than coastal feeding occurrences, (2) the coastal feeding occurrences were limited to a small section of coastline near the Big Sur reintroduction site and may not represent the full range of suitable coastal feeding conditions, and (3) we did not include direct or indirect covariates representing coastal food availability (e.g., distribution of marine mammal haul-outs or marine mammal strandings) or on-shore winds [17]. Thus, relative habitat suitability and conductance values along the immediate coast are likely biased low and should be viewed with caution. Our experience suggests that coastal areas with relatively consistent diurnal onshore winds and steep slopes are likely to be favorable to condor movement and may be an important corridor for north-south travel, at least in certain seasons. In addition, use of sea breezes deflecting off terrain or sea breeze fronts has been documented in other large soaring birds [49, 68, 69].

Our terrestrial habitat covariate likely underestimated nesting habitat in forests given the higher prevalence of cliff and cave nesting condors in our dataset, and our covariates did not include direct measures to predict the distribution of potential nesting trees. Thus, areas of the northern California coast along the redwood belt, with concentrations of large redwood trees suitable for nesting, and areas of the Sierra Nevada with groves of giant Sequoias or other nesting habitat, may be more connected than depicted in our models. Studies of other large soaring vultures suggest they are more frequently observed in open or semi-open habitats than in densely forested habitats while foraging [29, 70, 71]. This is likely due to their reliance on vision for finding food, rather than olfaction [72]. Whereas areas of dense trees may not be used by condors in southern and central California in greater proportion to their availability [38], this pattern may not hold as the distribution of condors expands into areas of the historical range where nest trees are more widely available, or where nesting and foraging areas are separated by forests (see [73]).

The redwood coast has an exotic humid climate and is perhaps the most famous example of a cloud-connected coastal ecosystem for its high incidence of summertime fog [74]. We considered including a covariate that accounted for fog in our in-flight condor models, expecting that areas of extensive and frequent fog might inhibit condor movements due to decreased visibility. However, data limitations precluded evaluation of seasonal differences in fog frequency, duration, or intensity. If finer scale datasets become available, we recommend including seasonal fog characteristics for future modeling efforts, as we suspect it may play a role in space use at these finer scales. Daily and hourly changes in wind patterns due to temperature gradients and terrain (e.g., surface wind, sea breeze, slope wind, valley wind, and mountain wind; see [75, 76]) also may be important in understanding finer-scale landscape conductance; therefore, their inclusion in finer-scale species distribution models for the California condor should be considered.

Circuit theory and condor movement

We found that electrical current was correlated with condor movement around existing reintroduction sites. Our models were able to discriminate between areas condors were likely to

move or avoid because of the great variation in environmental covariates that had significant relationships to landscape conductance in our modeling regions. For species where landscape conductance around the release site lacks significant variation, circuit theory models may offer little advantage over simple Euclidean distances and focusing on finer-scale habitat attributes may be necessary to understand these colonization patterns [20].

We developed simple electric circuits where the only source of individuals was at the release sites and we systematically placed grounds around the release sites assuming no directional bias. However, we recognize that there may be opportunities to improve our model of net movement probabilities by incorporating additional electrical sources and grounds of specific "strengths" (amps and resistances, respectively; see [48]). For example, in addition to reintroduction sites, one could specify nesting areas likely to be used by the reintroduced population as additional potential sources of individuals, with the strength of the source scaled relative to the productivity of the nesting habitat. It may also be prudent to specify source-node strengths for individual release sites depending on the number of animals released or the amount of time that the release site has been in operation—factors that are highly correlated for condors [77]. If information on likely destinations (e.g., important feeding areas or overnight roosting sites) were available, one could place grounds with specific resistance values within the modeling regions to improve upon our directionally naïve models. Adding sources and destinations may be important when breeding grounds are concentrated or where there are other attractants that affect a large proportion of the population. For example, our model in southern California underpredicted net movement probabilities around Hopper Mountain NWR and in the Tehachapi Mountains. We were able to significantly improve model performance by including additional ground nodes in these areas. While increasing model complexity can come at a cost of less generalization to novel environments, it may be useful for modelers to experiment with various configurations and strengths of possible attractants within their modeling region to assess the potential impact of these sources and attractants on predicted movement probabilities of the translocated species.

Unexplored in our analyses are the location of nearby release sites and the role of social tradition or social attraction in condor movements (see [78, 79]). Our anecdotal observations suggest that opening a new release site within commuting distance of an existing release site is a significant attractant to California condors. For example, when condors were first released at San Simeon in 2015, multiple adults from Big Sur began frequenting the San Simeon area almost immediately. Two individuals from Big Sur nested in the vicinity of the new release site shortly thereafter—something reintroduced condors had not done previously despite approximately 20 years of reintroductions at Big Sur [80, 81]. Social attraction from establishment of new release sites has also been observed in condors in southern California and in other vulture reintroduction programs in Europe [82, 83]. In addition, social attraction may play a role in the expansion of vulture populations as individuals discover new nesting or feeding areas. While our models focus on the relationship of condor movements to landscape features, they do not account for social tradition or social attraction. Future efforts to account for these factors may improve predictive capabilities.

More sophisticated analytical and simulation models are available that can produce results similar to, or in some cases superior to, those produced by circuit theory [18]. Unlike individual-based movement models and agent-based models (e.g., [84]), circuit theory models do not depict individual selection of locations during movement or exploration *per se* (see [85]) and do not account for intra- or interspecific competition [86], settlement patterns [87, 88], temporal scale, Allee effects [89], or sex- or age-specific habitat use, selection, or movement. Despite these shortcomings, they are relatively easy to construct, require minimal parameterization, and can be useful on their own or as a building block for individual-based simulations. Thus,

circuit theory models may be an effective intermediate step prior to the more involved modeling of individual movements [18] and can provide insights into the appropriateness of a resistance/conductance surface prior to its use in an individual-based model. Further, individual-based models typically require data on movement step distance, turning angles, and related motion parameters to vary by habitat conditions and by sex and age class of the individual (e.g., [90, 91]). Circuitscape requires essentially none of this, while still providing a reasonable approximation of how animals may radiate from a translocation site.

Landscape connectivity of reintroduction sites

Identifying how, and to what extent, a translocated population of animals might be ecologically connected or disconnected with existing populations is of central importance in planning reintroductions and conservation translocations. In most cases, there is an explicit goal of connecting populations to form or maintain a metapopulation with adequate gene flow (e.g., [92, 93]). However, for some species there are legal reasons for having initial separation between translocated populations and existing populations—for example, if a threatened or endangered species is reintroduced as an experimental population under the ESA [94]. There may also be a desire to keep populations separate to reduce disease transmission risk [95], or when the genetic risks of connectivity outweigh the benefits [96].

Our habitat linkage maps for condors generally agree with the existing and historical distribution of condors and the anticipated movement pathways of condors that follow large north-south mountain ranges in California. They are also concordant with the available genetic information from the historical population, which did not reveal any geographically isolated mtDNA haplotypes from the Pacific Northwest to Baja California, Mexico [97]. High cost-weighted distance between modeled nesting habitats across the San Francisco Bay area and across the forests of the northern Sierra Nevada indicates relatively high landscape resistance to condor movement between these areas. However, given the distances condors can travel [27, 98], it is unlikely these areas will significantly restrict gene flow once a population becomes established in the Pacific Northwest. Our linkage model indicates that connectivity between core nesting areas around the proposed release site is most restricted to the north and east. However, we need more data on nesting habitats and movement patterns in dense forests before drawing reliable conclusions regarding landscape connectivity through the forested regions of northern California, Oregon, and Washington [17]. We emphasize that habitat and population linkages are dynamic, and that further work to evaluate seasonal changes in habitat and population connectivity are likely to reveal changes across the annual cycle that are not evident in our predictions that rely on annual averages.

Conservation translocations are adaptive challenges in that they are complex and require solutions that blend technical expertise with social values [99]. Managers need objective predictions of where animals are likely to move once released to effectively communicate with stakeholders and to proactively mitigate threats. Our case study of California condors shows that circuit-based models are a potential useful tool for managers to consider when planning conservation translocations.

Supporting information

S1 Table. California condors outfitted with Global System for Mobile Communications transmitters or GPS transmitters from July 2013 to May 2017, California, USA.
(DOCX)

Acknowledgments

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