The Journal of Wildlife Management 1–13; 2021; DOI: 10.1002/jwmg.22052

Research Article

Combining Occurrence and Habitat Suitability Data Improve Conservation Guidance for the Giant Kangaroo Rat

ALYSSA E. SEMERDJIAN,[1,2] *Humboldt State University, 1 Harpst Street, Arcata, CA 95521, USA*
H. SCOTT BUTTERFIELD, *The Nature Conservancy, 201 Mission Street #4, San Francisco, CA 94105, USA*
ROBERT STAFFORD, *California Department of Fish and Wildlife, PO Box 6360, Los Osos, CA 93412, USA*
MICHAEL F. WESTPHAL, *U.S. Bureau of Land Management, 940 2nd Avenue, Marina, CA 93933, USA*
WILLIAM T. BEAN,[3] *Humboldt State University, 1 Harpst Street, Arcata, CA 95521, USA*

ABSTRACT Identifying high-quality habitat (i.e., areas with resources and conditions suitable to support long-term species persistence) is a priority for conservation, but estimating habitat quality is expensive and time consuming. Instead managers often rely on occurrence data or models of habitat suitability, but these data are only proximally related to individual and population persistence on the landscape. In most habitat suitability modeling studies, researchers treat the model as a hypothesis and the occurrence data as the truth. But occurrence does not always correlate with habitat as expected; therefore, occurrence data may be unreliable. We propose that suitability models and occurrence data be given equal weight to highlight areas of disagreement for future demographic study. To highlight this approach, we used the giant kangaroo rat (*Dipodomys ingens*) as a case study because their distinct burrow mounds allow for remote monitoring of short-term presence and long-term persistence. We conducted trapping, manned aerial surveys, and aerial imagery surveys in the San Joaquin Desert in California, USA, between 2001 and 2017 and compared the results to an existing habitat suitability model to provide estimates of long-term persistence based on the presence of burrow mounds made by giant kangaroo rats. We treated areas of positive agreement as priorities for habitat conservation and areas of negative agreement as areas managers could ignore. Remaining areas should be prioritized for additional occupancy and demographic studies. From an initial area of 17,385 km^2, we identified 668 km^2 of currently occupied high-quality habitat. Of this, just 135 km^2 was on private land and therefore requiring protection. We classified 1,498 km^2 (8.6%) for additional research. Of that area, 744 km^2 was flagged for additional occupancy surveys. Our 3 data sets disagreed over 754 km^2, suggesting a need for further demographic studies to reveal important population-habitat relationships for the species in those areas. This approach can be useful as part of any habitat conservation exercise for prioritizing protection or targeting future demographic studies.

KEY WORDS aerial imagery, endangered species, giant kangaroo rat, Heteromyidae, live trapping.

Conservation of high-quality habitat (i.e., areas with resources and conditions suitable to support long-term species persistence) is a foundation for recovery of sensitive species (Murphy and Noon 1992, Alagona 2013). Ideally, managers would prioritize protection based on habitat quality: allocating resources to habitat that is high quality rather than habitat that is low quality (i.e., environmental conditions that allow for species survival but not reproduction or persistence; Krausman and Morrison 2016). Measures of habitat quality, particularly range-wide, are rarely available. As a substitute, managers frequently rely on 1 of 2 complementary sets of data for prioritizing habitat conservation, depending on what is available: occurrence data and habitat suitability estimates derived from habitat suitability models (Garshelis 2000). In habitat suitability models, occurrence data are defined as spatially explicit records of animal presence. We define habitat suitability models broadly to include any statistical model that relates species occurrence data (with or without true absences) to environmental covariates (Guisan and Zimmerman 2000). The outcome of these models is a prediction of suitability (i.e., the relative probability of presence; Johnson et al. 2006, Phillips and Elith 2013). Occurrence data and habitat suitability models relate to more direct measures of habitat quality (and are more easily obtained), but both present problems that interfere with a manager's ability to identify high-quality habitat.

Received: 13 February 2020; Accepted: 9 March 2021

[1]*E-mail: aes495@humboldt.edu*
[2]*Current affiliation: Department of Integrative Biology, Oregon State University, 3110 Cordley Hall, Corvallis, OR 97331, USA*
[3]*Current affiliation: California Polytechnic State University, San Luis Obispo, 1 Grand Avenue, San Luis Obispo, CA 93407, USA*

Occurrence data on its own provides little information beyond that an animal was present at a given location at a particular time. As an extreme example, stranding events (i.e., the zone of corpse removal; Gaston 2003) would serve as poor records for blue whale (*Balaenoptera musculus*) habitat conservation. In fact, animals occur in low-quality habitats for a myriad of reasons. Animals may have incorrectly assessed habitat quality (i.e., ecological traps; Battin 2004). Individuals in variable environments may be present in currently low-quality habitat because of demographic lags (Bissonette and Storch 2007), and stochastic demographic processes may result in habitat temporarily unoccupied (Eriksson 1996). Dispersing individuals may be recorded in low-quality habitat that they must pass through to get to a suitable location. Finally, individuals may occur in low-quality habitat because of emigration from nearby populations with net positive growth rates (i.e., ecological sinks; Pulliam 1988). Nevertheless, managers continue to rely on occurrences to guide and assess conservation planning (U.S. Fish and Wildlife Service [USFWS] 1998, 2010). This is in part because, depending on the methods, occurrence data can be relatively quick and inexpensive to collect, which is ideal given the limited resources managers typically have to operate. These data are also easy to share and can be made readily available. These data sets are sometimes collated over a broad timespan by a variety of observers using a variety of survey methods (e.g., the California Natural Diversity Database). Data that is not collected systematically comes with inherent limitations, so managers should consider what these data can and cannot reveal about habitat (Garshelis 2000).

Recognizing the limitations of using occurrence data on its own, researchers have developed various statistical approaches, including habitat suitability models, to relate broad patterns of occurrence to underlying habitat features (Morrison et al. 2006). Habitat suitability models suffer additional problems of interpretation. Among other reasons, these models may also perform poorly because they do not account for detection probability (MacKenzie et al. 2002), do not address suitability at appropriate temporal or spatial scales, or do not account for biological processes such as dispersal or metapopulation dynamics (Guisan and Thuiller 2005). Despite these many limitations, habitat suitability models generally provide surprisingly accurate predictions of relative probability of presence. That is, when considering data independent of those used to construct the model, areas of predicted high suitability tend to have proportionally more occurrences than areas of low predicted suitability (Johnson et al. 2006). Researchers have reported that habitat suitability models do not accurately reflect habitat quality (Weber et al. 2017, Dallas and Hastings 2018). Specifically, areas of predicted low suitability are rarely high quality, but areas of predicted high suitability do not necessarily reflect high-quality habitat (Weber et al. 2017). Although habitat suitability models may be more useful than occurrence data alone for conservation planning, researchers generally urge that predictions be treated as hypotheses rather than truth (Araújo and Peterson 2012, Guisan et al. 2013).

Most researchers that rely on habitat suitability models for conservation planning do treat them as hypotheses, against which they test (ideally) independently collected occurrence data to assess model performance (Boone and Krohn 2002). In this approach it can be difficult to determine whether an area that was predicted to be high-quality habitat, but where the target species is absent, represents a flaw in the model or a situation where the model is correct and the animal was absent because of dispersal limitations, demographic decline, or other factors that limit occurrence (Araújo and Peterson 2012, Guisan et al. 2013). Conversely, an area predicted to be low quality may have animals present in the form of sinks or traps, but again without further investigation it can be hard to tell whether the model was incorrect. In short, in a typical model assessment framework, it may be impossible to distinguish between cases where the model was right and the occurrence data wrong and vice versa (Wiens 2002). Therefore we suggest that, when possible, managers instead rely on multiple sets of evidence for habitat conservation planning (i.e., treating predictions from habitat suitability models and independently collected occurrence data as equally likely to be true). In this approach, areas of positive agreement (i.e., predicted high suitability where animals are present) should be prioritized for conservation, whereas areas of negative agreement (i.e., predicted low suitability where animals are absent) should have low priority. Areas of disagreement, rather than being discarded as places where the model was wrong, should instead be treated as opportunities for additional research. Unoccupied but predicted high-quality habitat could be considered as locations for species reintroductions, or, if suitability referred to climatic suitability alone, could represent targets for habitat restoration (D'Elia et al. 2015, Stewart et al. 2019, Bryant et al. 2020). Areas that are occupied but not predicted as habitat might be sinks, or they might represent areas of incorrect model inference. All of these areas would likely provide high-value opportunities for additional research on habitat requirements for the species.

We use the giant kangaroo rat (*Dipodomys ingens*) as a case study to illustrate our approach. Giant kangaroo rats, endemic to the San Joaquin Desert of California, USA, are listed as endangered under the United States and California Endangered Species Acts, primarily because of habitat loss (USFWS 1998, California Department of Fish and Wildlife [CDFW] 2016). Giant kangaroo rats construct burrow mounds that, over time, create topographic heterogeneity (Grinnell 1932). In addition, giant kangaroo rats clip vegetation around their burrow mounds while gathering seed heads to cache, creating a conspicuous pattern of bare ground with vegetation remaining in between burrow mounds (Bean et al. 2012). The presence of vegetation clipping is apparent enough to be used to document changes in the species' distribution using manned aerial surveys (Bean et al. 2012). Aerial survey data distinguish between giant kangaroo rat presence and absence in the year assessed and provide greater coverage, including assessment of private land, compared to live trapping, although with less spatial precision (Bean et al. 2012). These burrow mounds are uniquely identifiable and easily distinguished from mima mounds, which, in the San Joaquin Valley, are thought to be a long-term result of pocket gopher activity (*Thomomys* spp.; Reed and Amundson 2007), and burrows created by California ground squirrels (*Otospermophilus beecheyi*), which are the most visually similar sign made by any sympatric species, based on their size, shape, and dispersion pattern (Grinnell 1932, Williams 1992). Specifically, burrow mounds made by giant kangaroo rats are circular or slightly ovoid, 3–6 m in diameter and uniformly spaced approximately 3–6 m apart (Williams and Kilburn 1991). By contrast, California ground squirrel burrow systems tend to have smaller individual circles of burrows connected by multiple runways, creating a neural network appearance. Like burrow mounds made by giant kangaroo rats, mima mounds are typically round. Both the size and spacing of mima mounds are variable, but those aspects typically distinguish them from burrow mounds made by giant kangaroo rats, which for the most part fall within a predictable and uniform range for size and spacing and, depending on the time of year, are devoid of vegetation in contrast to the surrounding area (Fig. 1).

Giant kangaroo rats are able to re-colonize areas that had once been used as farmland (Bean et al. 2012). Based on an assessment of aerial imagery and time since recolonization, we estimated that giant kangaroo rat construction of burrow mounds can take approximately 4–10 years until they reach the point of being visible from the air (A. E. Semerdjian, Humboldt State University, unpublished data). A long-term exclosure experiment in the Carrizo Plain National Monument, Santa Margarita, California, demonstrated that burrow mounds made by giant kangaroo rats can persist for ≥10 years after removal of kangaroo rats (Prugh and Brashares 2012). Density of burrow mounds correlates with long-term habitat quality (Bean et al. 2014). Therefore, the presence of these uniquely identifiable burrow mounds, which require years of continual occupancy to develop, better represents long-term giant kangaroo rat persistence and high-quality habitat than occurrence data or a habitat suitability model alone.

The goal of this study was not to test the accuracy of a single method but to compare and contrast available evidence of long-term persistence, current occurrences, and habitat suitability estimates to prioritize habitat conservation for an endangered species. Locations with the highest value for conservation are those with observations of burrow mounds made by giant kangaroo rats, confirmed recent occurrence, and high habitat suitability. Locations with no burrow mounds made by giant kangaroo rats, no confirmed recent occurrences, and low habitat suitability do not need to be considered for giant kangaroo rat conservation. Areas where long-term and current occurrence data disagree, or where occurrence status is not as expected given habitat suitability estimates, will guide future research regarding giant kangaroo rat habitat requirements

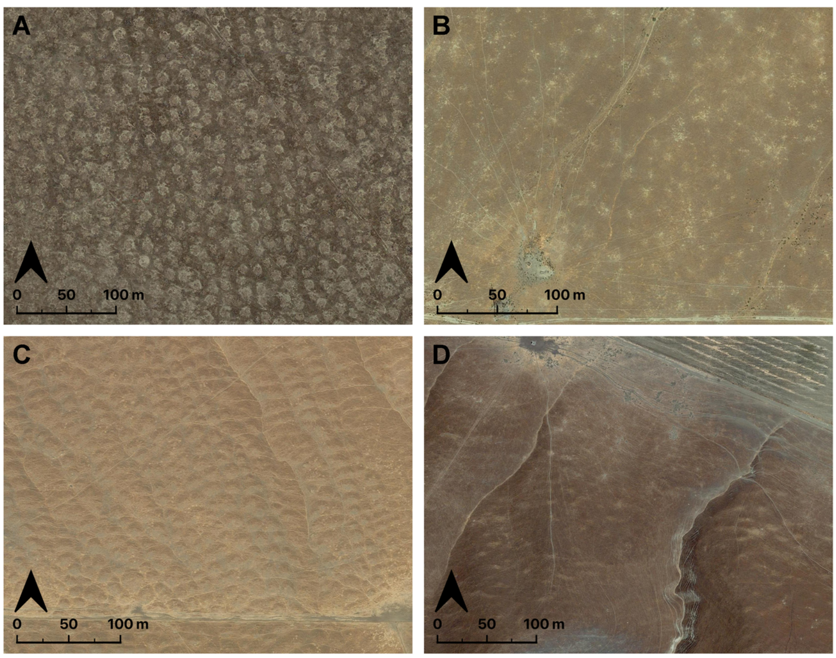

Figure 1. Example of different soil disturbances found within the range of the giant kangaroo rat. A) Core giant kangaroo rat habitat. Burrows are present as uniformly spaced with roughly 20 m between each burrow. Carrizo Plain National Monument, California, USA (35.1305, −119.7356). B) California ground squirrel burrows and cattle sign; soil disturbance is less circular and not evenly spaced. California ground squirrel burrows often connected by runways, cattle feeding sign often with clear paths leading to a central location such as a trough. Wind Wolves Preserve, California (35.0338, −119.1497). C) Probable mima mounds. Mound size variable. They are typically spaced close together with no distinction between vegetation on and between mounds. Wind Wolves Preserve, California (34.9901, −119.2315). D) Topographic features often seen on steep hillsides. Features are wider than they are round and are often connected by livestock paths. South of Avenal, California (35.9643, −120.1360). The imagery in the figure was taken in 2021. Image source: Google Earth (Google, Mountain View, CA, USA).

and demographics. We expected that much of the study area would not need to be considered for conservation, but there would be high priority locations, including some areas that were already being managed for the species and some that were not. We also expected that there would be areas where the data disagreed, especially around the edges of established colonies. Along with providing guidance for the conservation of giant kangaroo rats, we ultimately aimed to illustrate the value of treating habitat suitability predictions and occurrence data on equal footing for wildlife management in general.

STUDY AREA

The giant kangaroo rat's historical range, combined with a 10-km buffer area, covered 17,385 km^2 of the San Joaquin Desert in California. The San Joaquin Desert has a Mediterranean climate characterized by warm, dry summers with high temperatures occurring from June to September, and cool, wet winters with low temperatures and most rainfall occurring from December to March (Germano et al. 2011). Precipitation was low in our study area ($\bar{x}$ annual precipitation ~25 cm/yr) and the average annual minimum and maximum temperatures ranged between 3.7°C and 26.1°C, respectively (PRISM Climate Group 2004). The San Joaquin Desert is ringed by the California Coast Range to the west, the Sacramento-San Joaquin River Delta to the north, the Sierra Nevada mountain range to the east, and the Tehachapi range to the south. Our study area primarily consisted of the flat valley floor, but also contained parts of the surrounding mountain ranges, including elevations between 9.4 m to 519.1 m above sea level (PRISM Climate Group 2004). The San Joaquin Desert is a biodiversity hotspot home to dozens of sensitive, endemic species (Germano et al. 2011) and was historically dominated by sparse desert shrublands and alkali flats before the introduction of non-native annual grasses and widespread conversion to agriculture and energy development (Griggs et al. 1992, Williams 1992, USFWS 2010; Fig. 2). There are 5 species of Heteromyids with overlapping ranges within the San Joaquin Desert. Giant kangaroo rats are fiercely competitive and often at least partially exclude the other species where they are abundant (Prugh and Brashares 2012). Giant kangaroo rats were the dominant small mammal in parts of our study area, whereas California ground squirrels were dominant in others. During our study, pockets of relatively undisturbed giant kangaroo rat habitat persisted in the San Joaquin Desert, though much of their historical range was used for agriculture, energy extraction, and livestock production. The USFWS identified 6 regions of population persistence for giant kangaroo rats, all within the San Joaquin Desert. They are the Ciervo-Panoche Natural Area in Fresno and San Benito counties, Kettleman Hills in Kings County, San Juan Creek in San Luis Obispo County, the Carrizo Plain in San Luis Obispo and Kern counties, a large space that includes Lokern Ecological reserve in western Kern County, and the Cuyama Valley in San Luis Obispo and Santa Barbara counties (Fig. 2; USFWS 2010). The data for our study was collected between 2007 and 2017.

METHODS

We compiled and compared 3 independent data sets to assess occurrence and habitat suitability for the giant kangaroo rat. First, we combined trapping data and data collected during manned flight surveys to determine contemporary occurrences of giant kangaroo rats. Second, we visually assessed aerial and satellite imagery for evidence of burrow mounds made by giant kangaroo rats. Third, we obtained a model of habitat suitability for giant kangaroo rats trained with occurrence data from before their widespread decline (Rutrough et al. 2019) to identify areas of agreement and disagreement with these estimates of occurrence.

We livetrapped giant kangaroo rats between 2010 and 2017. The majority of trapping occurred within the 2 largest populations in the Carrizo Plain and the Ciervo-Panoche Natural Area (Bean et al. 2014, Alexander et al. 2019, Semerdjian 2019, Widick and Bean 2019). We baited Sherman XL live traps (H.B. Sherman Traps, Tallahassee, FL, USA) with millet-based birdseed and checked traps for 3–5 nights/site during summer. In all cases, we designed the number of traps and number of nights at each site to ensure detection probability was >0.99 (Semerdjian 2019). We identified captured animals to species and either marked them with individually numbered ear tags, or with permanent markers. All handling adhered to protocols under a USFWS Recovery permit (TE37418A-3), a California Scientific Collecting Permit (SC-11135), and Humboldt State University Animal Care protocols (p13/14.W.109-A and 16/17.W.96-A).

We used several plot arrangements to detect giant kangaroo rats during the 8 years of trapping. We selected many sites trapped from 2013–2017 as part of other research to collect genetic samples, and these were targeted to known or suspected giant kangaroo rat locations. The entire set of sites, therefore, was not randomly or systematically distributed, and our trapping results do not represent an estimate of giant kangaroo rat prevalence—a far higher proportion of our trapping sites had giant kangaroo rats present than would be expected from a random sample of the landscape. At all trapping locations, field crews visually assessed an area approximately 250 m in diameter for giant kangaroo rat burrows. The ability of field observers to predict giant kangaroo rat presence based on burrow appearance and other signs is high (Williams 1992, Bean et al. 2012, Semerdjian 2019); therefore, these trapping efforts represent an estimate of giant kangaroo rat presence or absence, at the time of trapping, within an approximately 250-m radius of trap locations. The majority of trapping occurred on public lands; we also accessed private lands with permission.

We conducted manned aerial surveys using a Cessna 185 aircraft (Cessna, Wichita, KS, USA) opportunistically in subsets of the species' range in August, September, or October 2001, 2006, 2010, 2011, 2016, and 2017. Pilots

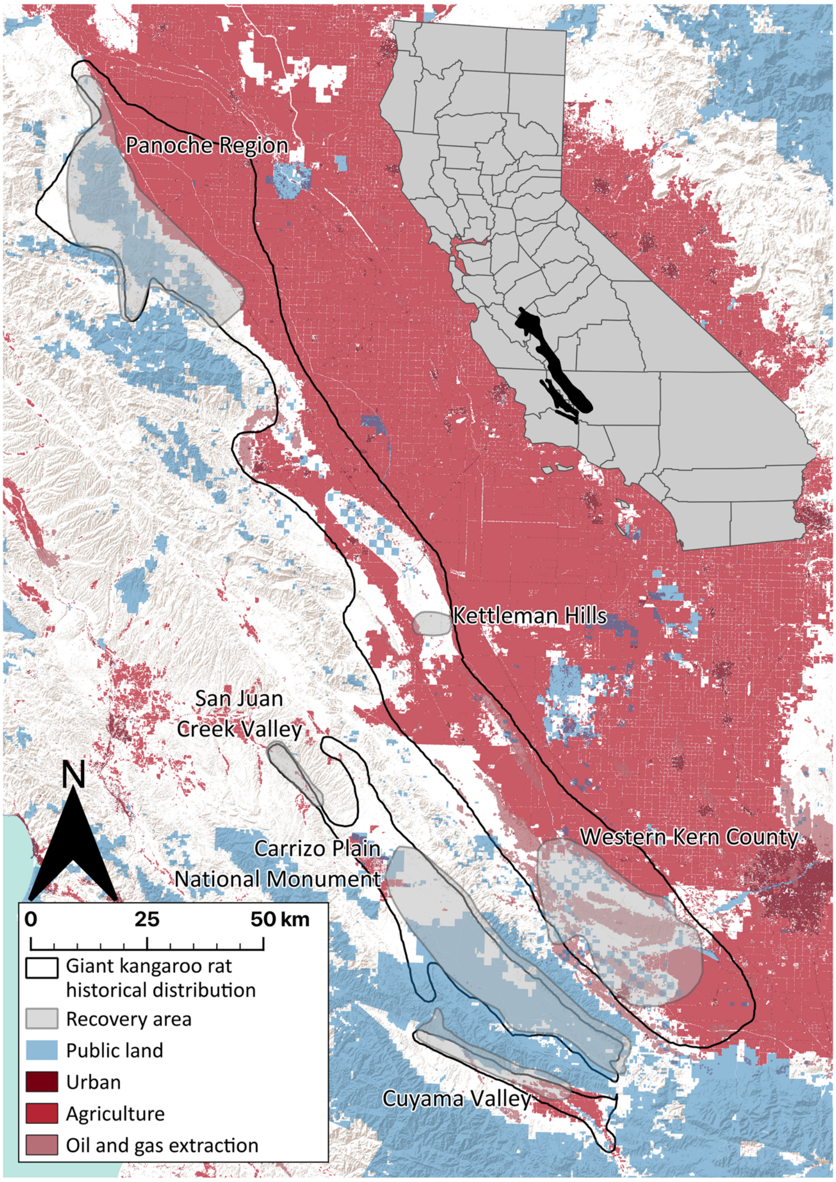

Figure 2. Currently accepted historical range for the giant kangaroo rat in San Joaquin Valley, California, USA, along with land conversions encroaching on the range, and public land and recovery areas identified as important conservation locations for the species. The giant kangaroo rat's historical range is outlined in black (Williams 1992) and areas referenced in the species recovery plan (USFWS 2010) are in gray and have corresponding labels. Public lands in shown in blue (California Protected Area Database 2017). Urban development and agriculture as of 2011 are shown in dark and medium red, respectively (Homer et al. 2015), and oil and gas extraction sites that are active or in the process of being built as of June 2018 are in light red (California Division of Oil, Gas and Geothermal Resources 2016). Basemap sources: Esri, United States Geological Survey, National Oceanic and Atmospheric Administration.

flew surveys in straight-line transects spaced approximately 800 m to 1 km apart, 250 m above ground level, and 145 km/hour. Two observers looking out opposite side windows of the plane recorded global positioning system locations whenever the plane entered or exited an area with active giant kangaroo rat sign as determined by vegetation clipping on burrow mounds. We generated areas of occurrence by connecting straight-line distances between global positioning system points and buffering these lines by 500 m on each side (Bean et al. 2012).

We systematically inspected satellite and aerial imagery for signs of burrow mounds made by giant kangaroo rats. We created a set of 1-km^2 cells within a 10-km buffer of the historical range (Williams 1992). For the survey, we used default basemap imagery available at the time in ArcGIS (Esri, Redlands, CA, USA), consisting of high-resolution National Agriculture Imagery Program aerial imagery from 2014 and lower-resolution Satellite Pour l'Observation de la Terre satellite imagery from 2008. We recruited observers through the Wildlife Department at Humboldt State University. They attended a 2-hour training focused on distinguishing burrow mounds made by giant kangaroo rats from other soil disturbances and then we gave them a testing data set to review. We required these observers to achieve a total accuracy score >90% before reviewing additional imagery. Observers scored each randomly assigned cell for evidence of giant kangaroo rat burrow mound presence or absence and confidence, ranging from 1 (low confidence) to 5 (high confidence). At least 2 observers assessed each cell independently. If the 2 observers agreed on burrow mound presence or absence, we scored the cell according to their assessment. A. E. Semerdjian, W. T. Bean, or a third observer (A. Rutrough) who had prior experience with this method and the species in the field reviewed observations in which the 2 primary observers disagreed on whether they observed burrow mounds (Rutrough et al. 2019). We considered only cells with average confidence scores ≥3 in further analysis.

For each 1-km^2 cell, we noted whether at least 2 observers detected giant kangaroo rat burrows, and calculated the mean confidence score from all observers. We used a MaxEnt model designed by Rutrough et al. (2019) to quantify habitat suitability throughout our study area. The model used presence points derived from giant kangaroo rat burrow detections in aerial imagery dating before 1960, before the species' range was reduced by agricultural expansion, to model the giant kangaroo rat's fundamental niche (Rutrough et al. 2019). Mean annual precipitation, slope, and percent silt were the predictors in their model, which was quite accurate, with a Boyce index of 0.96 calculated from an independent data set. Rutrough et al. (2019) projected this model using modern climatic values to estimate current abiotic habitat suitability for giant kangaroo rats. We used estimates from the modern projection to assign binary values of high quality or low quality to each of our 1-km^2 cells using the maximum sensitivity plus specificity threshold (Bean et al. 2012), with values calculated using the PresenceAbsence package in R (Freeman and Moisen 2008, R Core Team 2018).

We also assigned each cell a value based on trapping and manned aerial survey records—we coded cells where we trapped giant kangaroo rats or where we saw evidence of active burrow mounds during the manned flight surveys as recently present, cells where we trapped but did not capture giant kangaroo rats and where manned flight surveys did not occur or did not detect giant kangaroo rats as absent, and the rest of the cells as not surveyed. We coded cells with multiple trapping locations as present if ≥1 of the trapping locations had a giant kangaroo rat.

We compared the results from the habitat suitability model from Rutrough et al. (2019) to our imagery survey assessment of burrow mounds. We expected that if observers were able to distinguish burrow mounds made by giant kangaroo rats from other landscape features there would be few burrow mounds in predicted low-quality habitat. We also expected that there would be areas predicted as high quality but with no sign of giant kangaroo rat occurrence, largely because the habitat suitability model did not account for developed areas, and therefore many places that were predicted by the model to be high-quality habitat would not have burrow mounds present because of land conversion.

We assessed the relationships between estimated high and low-quality habitat, locations where giant kangaroo rat sign was detected or absent in the imagery survey, and locations where giant kangaroo rats or their sign were detected or absent during manned flight surveys and trapping using chi-square tests. All tests only considered pairings where absence data was available, meaning that we did not include regions where we did not trap and where we did not detect giant kangaroo rat burrows during manned flight surveys.

Finally, we assessed our independent sources of data to prioritize research and management actions. We divided the data into 5 categories (Table 1). The first category was a priority for habitat conservation; these were areas that were classified as high quality, had visible signs of

Table 1. Summary of agreement across 3 sets of independent data related to giant kangaroo rat habitat and occurrence in San Joaquin Valley, California, USA. Habitat quality is drawn from a habitat suitability model estimating the species' historical fundamental niche. The imagery survey represents occurrence of visible burrow mounds made by giant kangaroo rats, an indicator of long-term persistence, from imagery from 2008 and 2014. Manned flights and trapping were evidence of giant kangaroo presence during the years that the surveys occurred: 2001, 2006, 2010, 2011, 2016, and 2017 for the manned flights and 2010 to 2017 for trapping.

Category	Habitat quality[a]	Imagery survey	Flights or trapping	Interpretation	Number of 1-km^2 cells	% of total number of 1-km^2 cells
1	High	Present	Present	High priority conservation	668	3.86
2	High	Present	None	High priority conservation with surveys to confirm presence	744	4.30
3a	High	Present	Absent	Translocation site or no longer high quality	16	0.09
3b	High	Absent	Present	Expanding population or soil restricts mound construction	438	2.53
3c	Low	Absent	Present	Sinks, traps, or dispersal	193	1.11
3d	Low	Present	Present	Model wrong	33	0.19
3e	Low	Present	Absent	Imagery survey error	4	0.02
3f	Low	Present	None	Surveys needed to confirm image survey or model error	70	0.40
4	High	Absent	None	Possible restoration areas	7,831	45.22
5a	Low	Absent	Absent	No management action needed	30	0.17
5b	Low	Absent	None	Likely no management action needed	7,359	42.50

[a] High-quality habitat is defined here as environmental conditions predicted to allow for the long-term persistence of species, and low-quality habitat is defined here as environmental conditions that are not predicted to allow for species persistence (Krausman and Morrison 2016).

burrow mounds in aerial imagery, and giant kangaroo rats were present in either traps or their sign was detected during manned aerial surveys. The second category may also be prioritized for conservation but only after additional surveys to verify current giant kangaroo rat occurrence; these areas were predicted high quality and had visible sign of burrow mounds, but no trapping had occurred and manned surveys were not performed (or did not identify signs of active burrows). The third category was prioritized for additional demographic research. These areas had some disagreement among the model, the aerial surveys, and the trapping. Specifically, these areas had giant kangaroo rats present but were predicted low quality, had giant kangaroo rats present and were predicted high quality but with no visible sign of burrow mounds, or were predicted high quality and had visible sign of burrow mounds, but we did not capture giant kangaroo rats when we trapped. The fourth category consisted of areas that were predicted high quality, but giant kangaroo rats were absent, and had no sign of burrow mounds in the aerial imagery. These areas may be low priority for research but might serve an important role for restoration in the future. The final category were areas that were predicted low quality, had no sign of burrow mounds, and the cells had not been trapped or no giant kangaroo rats were present. We calculated the area of each category found on public or private lands, and within or outside spaces designated as recovery areas for giant kangaroo rats by the USFWS. Preservation of recovery areas are important to the down-listing process for the species, with each area having its own threats and criteria for protection (USFWS 2010).

We further divided areas of disagreement into 6 subcategories (Table 1). We categorized sites predicted to be low quality with giant kangaroo rats recently present and with signs of burrow mounds from the aerial surveys—signifying long-term persistence—as incorrectly predicted by the model (i.e., the model was wrong). We categorized sites predicted to be high quality with giant kangaroo rats recently present but no sign of burrow mounds as habitat where giant kangaroo rats have not, or cannot, build burrow mounds. This could be due to soil constraints or recent (<10 yr) population expansion. We considered sites predicted to be low quality with giant kangaroo rats recently present and no signs of burrow mounds to be sinks, traps, or temporary or dispersal habitat. We considered sites predicted to be high quality with giant kangaroo rats absent and signs of burrow mounds to be either no longer high quality, or sites warranting further study into whether giant kangaroo rats have been permanently extirpated, and if so why. These sites could be potential translocation areas pending close investigation into why giant kangaroo rats are no longer present. We considered areas predicted to be low quality with giant kangaroo rats absent but with signs of burrow mounds to be errors in the aerial survey data—places where observers misclassified soil disturbance as burrow mounds made by giant kangaroo rats. Finally, areas predicted to be low quality with giant kangaroo rat burrows present in aerial imagery but with no further data available are locations in need of further surveys to determine whether the disagreement is due to an error in the habitat suitability model or the imagery survey. We had no additional data sources to evaluate these categories but instead present them as opportunities for future research to resolve disagreements among the data sets.

RESULTS

Trapping occurred in 4 of the 6 regions recognized in the giant kangaroo rat species recovery plan (Fig. 3). We caught giant kangaroo rats at 190 of the 279 plots in the Ciervo-Panoche region, 3 of the 9 plots in the Kettleman Hills, 6 of the 7 sites in the San Juan Creek area, and 91 of the 108 sites set in the Carrizo Plain. We did not trap in western Kern County and the Cuyama Valley because of difficulties obtaining landowner permission; however, we did trap in a few areas outside of the known giant kangaroo rat distribution. We caught giant kangaroo rats at 4 of the 9 sites set north of the Carrizo Plain National Monument, and east of the San Juan Creek area. We did not catch any giant kangaroo rats at the 9 sites at Wind Wolves Preserve, or at the 9 sites at Bitter Creek National Wildlife Refuge, both in Kern County. Active giant kangaroo rat burrow mounds covered 1,118.56 km^2 during manned aerial surveys in the Carrizo Plain, Ciervo-Panoche Natural Area, and areas in and around the Kettleman Hills Recovery Area (Fig. 3).

Observers reviewed aerial imagery covering 17,385 km^2 of the San Joaquin Desert. Of these, 5.3% ($n = 922$) required a third observer because of disagreement among the first 2 observers. Burrow mounds made by giant kangaroo rats were absent with a confidence score ≥3 in 89.39% of the cells, occurrence of burrow mounds was uncertain (<3) in 4.53%, and burrow mounds were present with a confidence score ≥3 in 6.07% of the cells. Of the 9,697 km^2 predicted high quality, 1,428 km^2 (14.73%) had signs of burrow mounds made by giant kangaroo rats. Of the 1,535 km^2 that had burrow mounds visible in the imagery surveys, 93.02% were found in areas predicted high quality by the model. Of the 7,691 km^2 predicted low quality, 7,582 km^2 (98.58%) had no sign of burrow mounds.

Associations between categories were all significantly different from random (habitat quality and imagery surveys: $n = 17{,}385$, $\chi^2_3 = 12{,}043$, $P < 0.001$; habitat quality and manned flight surveys or trapping data: $n = 2{,}689$, $\chi^2_3 = 2{,}330.6$, $P < 0.001$; and imagery and manned flight surveys or trapping data: $n = 2{,}689$; $\chi^2_3 = 2{,}331.5$, $P < 0.001$). The majority of the study area had no sign of burrow mounds but was predicted high quality (47.56%) or low quality (39.70%; Fig. 4; Table 1). Areas predicted as high quality with signs of burrow mounds and giant kangaroo rats recently present comprised 3.86% of the study area; of those, 533 out of 668 (79.79%) were on public land, and 537 (80.39%) were within the designated recovery areas. Areas predicted as high quality with signs of burrow mounds and giant kangaroo rats absent during trapping, or

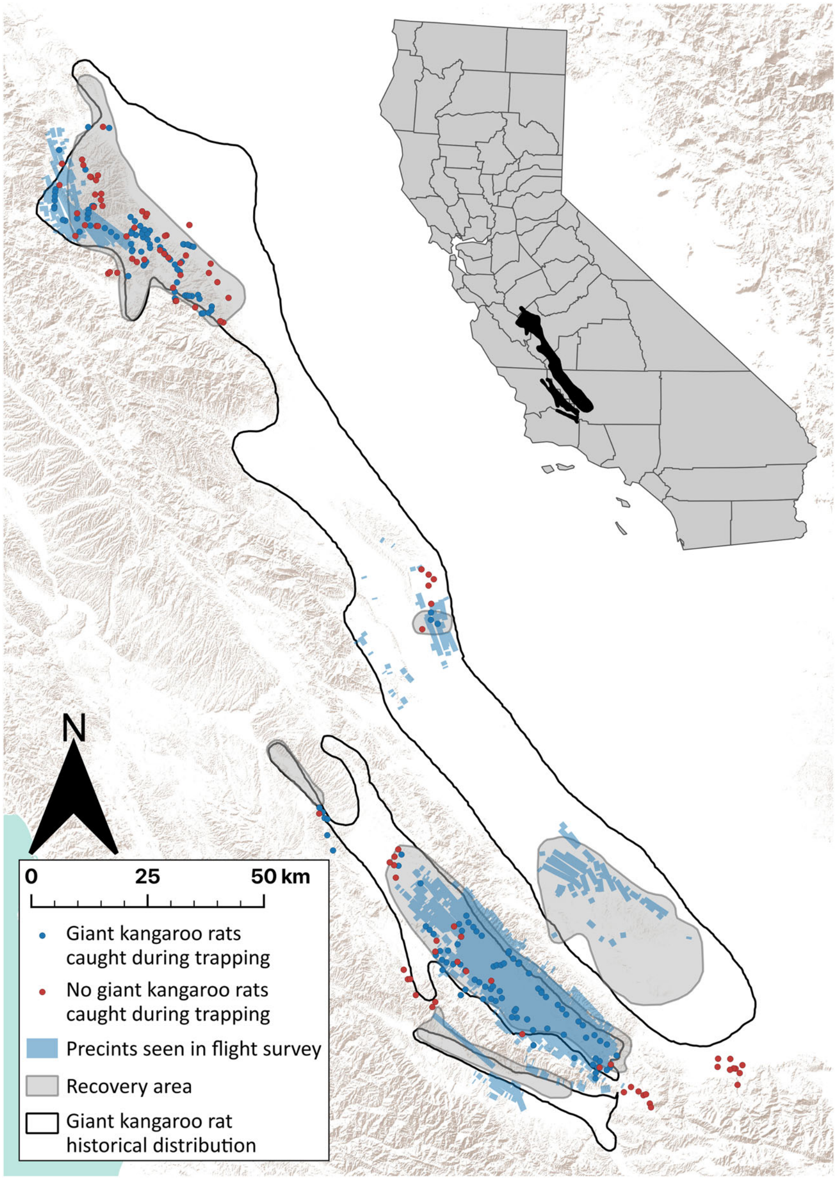

Figure 3. Blue polygons represent locations where we saw giant kangaroo rat burrow mounds during manned flight surveys, which took place in 2001, 2006, 2010, 2011, 2016, and 2017 in San Joaquin Valley, California, USA. Dots indicate sites trapped between 2010 and 2017. Blue dots are sites where we caught giant kangaroo rats; red dots are sites where we did not. Areas referenced in the species recovery plan (USFWS 2010) are shaded in gray with corresponding labels. Basemap sources: Esri, United States Geological Survey, National Oceanic and Atmospheric Administration.

with no further survey data available, comprised 4.37% of the study area; of those, 192 out of the 760 (25.26%) were on public land, and 237 (31.18%) were within designated recovery areas.

Areas of disagreement represented another 4.34% of the study area (Table 1, category 3), with 424 out of 684 (61%) on public land, and 399 (58.33%) in designated recovery areas. There were 33 1-km^2 cells (0.19% of study area) predicted low quality but with giant kangaroo rats and burrow mounds present and 438 1-km^2 cells (2.53% of the study area) that were predicted to be high-quality habitat with giant kangaroo rats present but no sign of burrow mounds. These areas were primarily in the Carrizo Plain and Ciervo-Panoche, with a notable population in the central portion of the range on private land. Sites with giant kangaroo rats present but predicted low quality and no sign of burrow mounds comprised 1.11% of the study area; these sites were exclusively found on the periphery of the Carrizo Plain and Ciervo-Panoche populations. There were 16 1-km^2 cells (0.09% of study area) representing sites where we trapped and did not catch kangaroo rats though the area was predicted high quality and burrow mounds were visible. Sites with burrow mounds visible but predicted low quality and no giant kangaroo rats present comprised 0.02% of the study area; most of these sites were at the edge of the historical range. The final 0.40% of the study area contained cells in predicted low-quality habitat where burrow mounds were detected but no trapping or manned flight survey data was available. These cells are scattered throughout the study area, with the biggest cluster in the southern portion of the

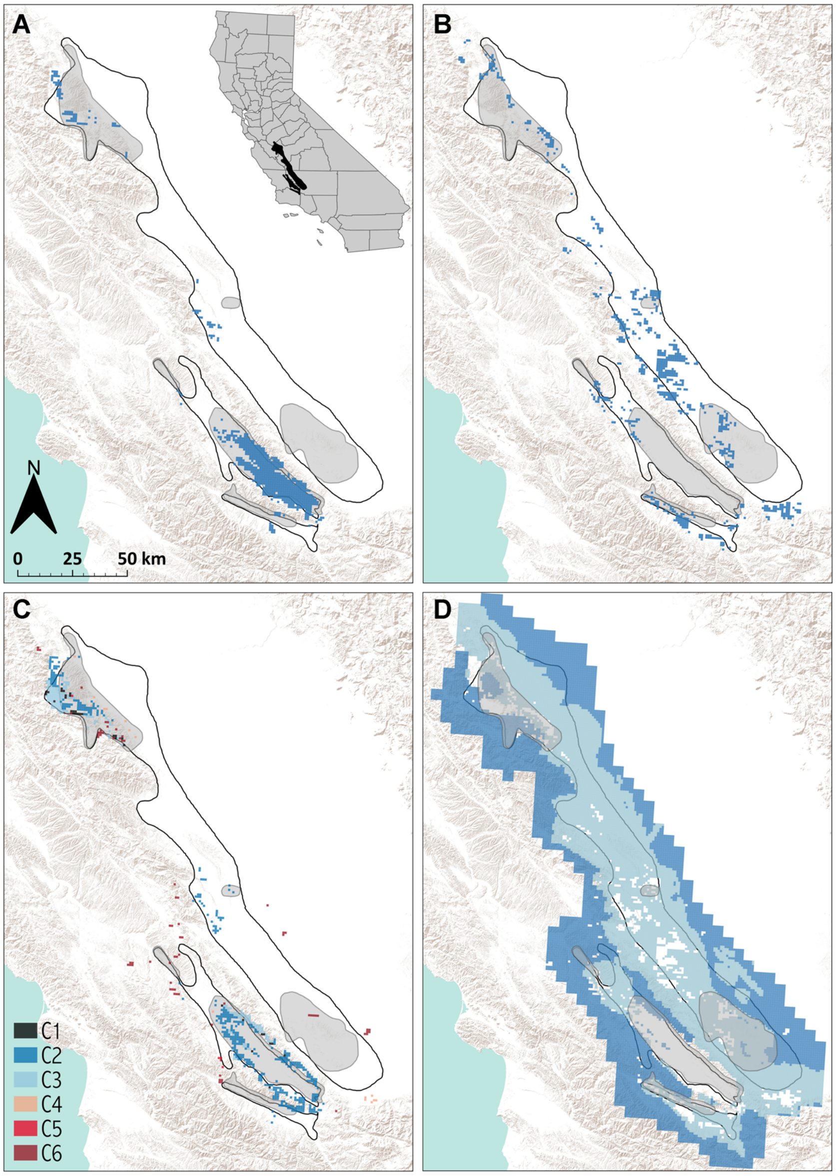

Figure 4. Areas of agreement and disagreement among occurrence data, which consists of manned flight surveys (2001, 2006, 2010, 2011, 2016, and 2017) and live trapping (2010–2017), burrow mound distribution determined through satellite imagery survey using imagery from 2008 and 2014, and a habitat suitability model representing the giant kangaroo rat's fundamental niche in San Joaquin Valley, California, USA. Areas referenced in the species recovery plan (USFWS 2010) are shaded in gray. A) Sites with giant kangaroo rats present in manned flight surveys or trapping with burrow mounds visible in aerial imagery and predicted high quality. B) Sites with burrow mounds visible and predicted high quality, where no trapping or manned flight surveys occurred. C) Areas of disagreement. C1 = sites with giant kangaroo rats present and burrow mounds visible but predicted low quality. C2 = sites with giant kangaroo rats present and predicted high quality but no burrow mounds visible. C3 = giant kangaroo rats present but no burrow mounds visible and predicted low quality. C4 = giant kangaroo rats absent during trapping and no flight survey data available but burrow mounds visible and predicted high quality. C5 = Predicted low quality, burrow mounds visible but giant kangaroo rats not present during trapping and no flight survey data available. C6 = Predicted low quality, burrow mounds visible, no trapping or flight survey data available. D) Light blue areas were predicted high quality but no burrow mounds visible and giant kangaroo rats not surveyed; dark blue areas represent areas predicted low quality and no burrow mounds visible. Basemap sources: Esri, United States Geological Survey, National Oceanic and Atmospheric Administration.

Ciervo-Panoche natural area. These represent locations where either the model or imagery survey was wrong, but further surveys would be needed to confirm which is the case (Table 1).

DISCUSSION

We used a habitat suitability model based on historical distribution and abiotic predictors (i.e., climate, soil, slope), imagery surveys conveying stable occurrence and therefore long-term persistence, and contemporary occurrence data from trapping and manned aerial surveys to make management suggestions for the giant kangaroo rat throughout its entire range. Rather than elevate 1 set of these typically competing data above the other, we treated each as equally likely to be right (i.e., represent areas of habitat). In doing so, we identified areas of high priority for conservation and further surveys for occurrence, areas that can be ignored for present conservation efforts, and, perhaps most importantly, areas of disagreement that with additional studies of the species' demographics should lead to a much greater understanding of demographics and habitat needs for the species.

In general, our 3 data sets demonstrated agreement about the distribution of giant kangaroo rat habitat and occurrence in most of the places we would expect them to be based on the species' natural history and land use in the San Joaquin Desert. Chi-square tests confirmed that the relationships between each data set were not due to random chance. Just over 4% of sites evaluated had meaningful disagreement among the data (e.g., areas predicted high quality with burrow mounds visible but no giant kangaroo rats present, or areas with giant kangaroo rats present but predicted to be low quality or no sign of visible burrow mounds). Burrow mounds were almost exclusively within areas predicted to be high quality by the model—just 7% of visible burrow mounds were in areas predicted low quality, and nearly 99% of the sites predicted low quality had no sign of burrow mounds. There were many sites predicted to be high quality where no burrow mounds were found, but these were almost all developed land. We therefore conclude that giant kangaroo rats are very unlikely to persist in areas predicted low quality by the model.

Areas of disagreement between the habitat suitability model and imagery survey, representing just 754 km^2 out of the 17,385-km^2 study area, were generally consistent with current understanding of the species. Most disagreements occurred on the edges of the 2 largest populations, where population dynamics likely influence the patterns. Areas with model error (i.e., areas predicted low quality but with giant kangaroo rats recently present and burrow mounds visible), for example, were mostly on the periphery of these populations where climate change may be changing habitat quality in places where giant kangaroo rats historically thrived (Widick and Bean 2019). A similar phenomenon has been documented in other San Joaquin Desert endemics, including the blunt-nosed leopard lizard (*Gambelia sila*; Stewart et al. 2019). Alternately, these areas may represent false positives in the manned flight surveys; follow-up studies *in situ* would further our understanding of habitat relationships at the peripheries of the species' distribution.

We found areas that were predicted suitable with giant kangaroo rats present but no signs of burrow mounds throughout the giant kangaroo rat range. In 1 of the 2 well-studied, large populations, this pattern may be due to a recent (<20 yr) documented expansion in that population; that is, the expansion was recent enough that burrow mounds will likely start to appear in the near future. In the other population, the presence of kangaroo rats in predicted high-quality habitat with no burrow mounds is likely influenced by a more unstable set of sub-populations that have historically displayed a pattern of source-sink dynamics (Loew et al. 2005, Statham et al. 2019). Further investigation is recommended in these areas to determine whether a lack of burrow mounds is due to recent expansion, edaphic conditions, or demographic fluctuations.

Similarly, areas predicted low-quality habitat with giant kangaroo rats recently present and with no signs of burrow mounds were exclusively on the periphery of the 2 main populations; these areas were most likely temporary populations that may serve an important function in source-sink dynamics but, again, require additional demographic studies to resolve. Most areas predicted to be low quality with burrow mounds visible and no giant kangaroo rats present were at the edge, or outside of, the historical range and likely represent observer error. A few scattered sites with these conditions can be seen east of the Ciervo-Panoche population and just north of the Carrizo Plain National Monument. Another cluster of these sites can be found southeast of the Carrizo Plain National Monument. These areas predicted to be low quality with observed burrow mounds but no giant kangaroo rats detected in other surveys are adjacent to predicted high-quality habitat and deserve additional surveys to clarify whether this represents model error (Fig. 4).

The majority of sites where burrow mounds were detected in imagery and where additional surveys did not occur or giant kangaroo rats were recently present were within predicted high-quality habitat. This includes some important giant kangaroo rat habitat outside of the 2 largest known populations. One such area is part of a long-term study of the species, which confirms species persistence (Germano and Saslaw 2017). Surprisingly, we also found strong, consistent evidence for a large population and wide-spread predicted high-quality habitat outside of the currently identified recovery areas. These populations deserve greater management attention. Giant kangaroo rats are an ideal species for testing remote survey methods because they produce highly visible, distinct sign that indicates long-term habitat quality, and they have a relatively small distribution. Though it may be difficult to survey entire ranges for species with larger distributions, this method is feasible for species that are visible in imagery (e.g., manatees [*Trichechus manatus*], Miller et al. 1998; elephants [*Loxodonta africana*], Vermeulen et al. 2013) or create conspicuous sign (e.g., beavers [*Castor canadensis*], Martin et al. 2015; prairie dogs [*Cynomys ludovicianus*], Sidle et al. 2012) over portions of their ranges. Projects can be scaled depending on need. Additionally, occurrence for species that are not observable in aerial imagery can be determined using other methods such as motion-sensitive cameras or track plates set over systematic grids. Using non-aerial methods would spatially limit assessment, but comparisons of suitability and occurrence over smaller areas could still be useful depending on the conservation needs of target species.

To our knowledge, there has been relatively little other work attempting to use disagreements between suitability models and independently collected occurrence data to identify areas of conflict. Most efforts have relied on data more directly related to fitness. For example, researchers have created integrated occupancy models for grizzly bears (*Ursus arctos*) based on occurrence data and human-caused mortality events to distinguish source from sink habitat in Alberta, Canada (Nielsen et al. 2006) and Spain

(Falcucci et al. 2009). Aldridge and Boyce (2007) used occurrence and survival data to model greater sage-grouse (*Centrocercus urophasianus*) habitat. A study of Ord's kangaroo rats (*Dipodomys ordii*) revealed that a large proportion of habitat with predicted high suitability actually represented sinks (Heinrichs et al. 2010). In the cases where data on demographics is available across a species' distribution, incorporating such information should improve conservation outcomes. When demographic data are not available, however, our approach allows researchers to prioritize future research into areas of high uncertainty, where demographic data will assist with management actions.

Our categorization of land into different management priorities fits with what is known about the status of giant kangaroo rat populations. In particular, the importance of the Carrizo Plain and Ciervo-Panoche highlighted in our study matches current recovery priorities (USFWS 2010). Nevertheless, our approach has a few limitations. First, we are using multiple lines of evidence to speculate about habitat quality through the species' range. Although the presence and density of burrow mounds in aerial and satellite imagery does correlate with long-term habitat quality (Bean et al. 2014), we do not have demographic data from across the range with which to truly test our findings. Further work will be needed to survey lands predicted high quality with visible burrow mounds to test how well our approach works outside of the recovery areas. Second, it is possible that some burrow mounds were incorrectly classified—either non-target land features were classified as giant kangaroo rat burrows, or some giant kangaroo rat burrows were not found in the survey. Given the high overall agreement among independent observers (>95%) and the distinct sign that giant kangaroo rat burrows were present, we suspect this source of error is low. Sites that had visible burrow mounds but no giant kangaroo rats present and predicted low quality were most likely to be a result of observer error—pending further surveys in some areas, only a maximum of 74 out of 17,385 total cells fit this category. Sites with giant kangaroo rats present and predicted high quality but no visible burrow mounds may also have been incorrectly classified in the imagery surveys. We believe these more likely represent areas of recent giant kangaroo rat expansion. A *post hoc* review of more recent aerial imagery showed that many of these areas now contain signs of burrow mounds made by giant kangaroo rats, consistent with the idea that these sites were recently colonized. This finding particularly highlights the problem of using absences in a recovering species to determine model accuracy. Third, manned aerial surveys for active giant kangaroo rat sign are accurate but somewhat imprecise; almost all error in an earlier study occurred within 500 m of the surveyed edge (Bean et al. 2012). We categorized areas with giant kangaroo rats present but no visible burrow mounds and predicted low quality as probable sink, trap, dispersal, or temporary habitat. These areas, particularly in the northern portion of the Carrizo Plain, may have been a result of spatial imprecision in the manned aerial surveys.

Nevertheless, the value of our approach is to identify areas of disagreement among multiple methods, which all have low but unknown sources of error. Although we cannot yet resolve cases where our data sets disagree, this study emphasized such disagreements to prioritize monitoring actions. From an area of 17,385 km^2, managers can now focus efforts on land protection (668 km^2), surveys (744 km^2), and additional demographic studies (754 km^2). Scientific advances, small and large, often come as a result of conflicting data (Kuhn 1962). We suggest that traditional approaches to occurrence data and habitat suitability models, particularly for species in decline, give too much weight to the truth of the occurrence data and fault the models when predictions do not match observations. We suggest that additional research into these disagreements offers the best opportunity for gaining new insight into wildlife-habitat relations because they both can be correct.

MANAGEMENT IMPLICATIONS

By fusing multiple data sources, we categorized land into multiple management actions. Sites with giant kangaroo rats present, visible burrow mounds, and predicted high quality ought to be prioritized for conservation. Sites not surveyed with visible burrow mounds and predicted high quality should be prioritized for new surveys and, if giant kangaroo rats are found, conserved. If giant kangaroo rats are not found, these sites would be ideal candidates for translocation after the reason for their absence is investigated. Particular priority should be placed on the central portions of the species' range in northwestern Kings and southwestern Fresno counties, and on the Cuyama Valley. These populations occur almost exclusively on private land and likely represent important genetic lineages. Finally, sites predicted high quality but with no visible burrow mounds may be candidates for restoration, especially if they occur close to extant populations.

ACKNOWLEDGMENTS

Thanks A. Rutrough for providing invaluable assistance during the imagery survey. We appreciate the funding and logistical support provided by the Bureau of Land Management, CDFW, Humboldt State University, The Nature Conservancy, and the many participants in fieldwork and imagery review.

LITERATURE CITED

Alagona, P. S. 2013. After the grizzly: endangered species and the politics of place in California. University of California Press, Berkeley, USA.

Alexander, N. B., M. J. Statham, B. N. Sacks, and W. T. Bean. 2019. Generalist dispersal and gene flow of an endangered keystone specialist (*Dipodomys ingens*). Journal of Mammalogy 100:1533–1545.

Aldridge, C. L., and M. S. Boyce. 2007. Linking occurrence and fitness to persistence: habitat-based approach for endangered greater sage-grouse. Ecological Applications 17:508–526.

Araújo, M. B., and A. T. Peterson. 2012. Uses and misuses of bioclimatic envelope modeling. Ecology 93:1527–1539.

Battin, J. 2004. When good animals love bad habitats: ecological traps and the conservation of animal populations. Conservation Biology 18:1482–1491.

Bean, W. T., L. R. Prugh, R. Stafford, H. S. Butterfield, M. Westphal, and J. S. Brashares. 2014. Species distribution models of an endangered rodent offer conflicting measures of habitat quality at multiple scales. Journal of Applied Ecology 51:1116–1125.

Bean, W. T., R. Stafford, L. R. Prugh, H. S. Butterfield, and J. S. Brashares. 2012. An evaluation of monitoring methods for the endangered giant kangaroo rat. Wildlife Society Bulletin 36:587–593.

Bissonette, J. A., and I. Storch. 2007. Temporal dimensions of landscape ecology: wildlife responses to variable resources. Springer, New York, New York, USA.

Boone, R. B., and W. B. Krohn. 2002. Modeling tools and accuracy assessment. Pages 265–270 *in* J. M. Scott, P. J. Heglun, M. L. Morrison, J. B. Haufler, M. G. Raphael, W. A. Wall, and F. B. Samson, editors. Predicting species occurrences: issues of accuracy and scale. Island Press, Washington, D.C., USA.

Bryant, B. P., T. R. Kelsey, A. L. Vogl, S. A. Wolny, D. MacEwan, P. C. Selmants, T. Biswas, and H. S. Butterfield. 2020. Shaping land use change and ecosystem restoration in a water–stressed agricultural landscape to achieve multiple benefits. Frontiers in Sustainable Food Systems 4(138):1–15.

California Department of Fish and Wildlife [CDFW]. 2016. State and federally listed endangered and threatened animals of California. CDFW, Sacramento, California, USA.

California Division of Oil, Gas and Geothermal Resources. 2016. https://maps.conservation.ca.gov/oilgas. Accessed 1 Mar 2019.

California Protected Area Database. 2017. www.calands.org. Accessed 1 Mar 2019.

Dallas, T. A., and A. Hastings. 2018. Habitat suitability estimated by niche models is largely unrelated to species abundance. Global Ecology and Biogeography 27:1448–1456.

D'Elia, J., S. M. Haig, M. Johnson, B. G. Marcot, and R. Young. 2015. Activity-specific ecological niche models for planning reintroductions of California condors (*Gymnogyps californianus*). Biological Conservation 184:90–99.

Eriksson, O. 1996. Regional dynamics of plants: a review of evidence for remnant, source-sink and metapopulations. Oikos 77:248–258.

Falcucci, A., P. Ciucci, L. Maiorano, L. Gentile, and L. Boitani. 2009. Assessing habitat quality for conservation using an integrated occurrence-mortality model. Journal of Applied Ecology 46:600–609.

Freeman, E. A., and G. Moisen. 2008. PresenceAbsence: an R package for presence-absence model analysis. Journal of Statistical Software 23:1–31.

Garshelis, D. 2000. Delusions in habitat evaluation: measuring use, selection, and importance. Pages 111–164 *in* L. Boitani and T. K. Fuller, editors. Research techniques in animal ecology: controversies and consequences. Columbia University Press, New York, New York, USA.

Gaston, K. J. 2003. The structure and dynamics of geographic ranges. Oxford University Press, Oxford, England.

Germano, D. J., G. B. Rathbun, L. R. Saslaw, B. L. Cypher, E. A. Cypher, and L. M. Vredenburgh. 2011. The San Joaquin Desert of California: ecologically misunderstood and overlooked. Natural Areas Journal 3:138–147.

Germano, D. J., and L. R. Saslaw. 2017. Rodent community dynamics as mediated by environment and competition in the San Joaquin Desert. Journal of Mammalogy 98:1615–1626.

Griggs, F. T., J. M. Zaninovich, and G. D. Werschkull. 1992. Historic native vegetation map of the Tulare Basin, California. Pages 111–118 *in* D. F. Williams, S. Byrne, and T. A. Rado, editors. Endangered and sensitive species of the San Joaquin Valley, California: their biology, management and conservation. California Energy Commission, California State University, Bakersfield, USA.

Grinnell, J. 1932. Habitat relations of the giant kangaroo rat. Journal of Mammalogy 13:305–320.

Guisan, A., and W. Thuiller. 2005. Predicting species distribution: offering more than simple habitat models. Ecology Letters 8:993–1009.

Guisan, A., R. Tingley, J. B. Baumgartner, I. Naujokaitis-Lewis, P. R. Sutcliffe, A. I. T. Tullock, T. J. Regan, L. Brotons, E. McDonald-Madden, C. Mantyka-Pringle, et al. 2013. Predicting species distributions for conservation decisions. Ecology Letters 16:1424–1435.

Guisan, A., and N. E. Zimmerman. 2000. Predictive habitat distribution models in ecology. Ecological Modelling 135:147–186.

Heinrichs, J. A., D. J. Bender, D. L. Gummer, and N. H. Schumaker. 2010. Assessing critical habitat: evaluating the relative contribution of habitats to population persistence. Biological Conservation 143:2229–2237.

Homer, C. G., J. A. Dewitz, L. Yang, S. Jin, P. Danielson, G. Xian, J. Coulston, N. D. Herold, J. D. Wickham, and K. Megown. 2015. Completion of the 2011 National Land Cover Database for the conterminous United States-representing a decade of land cover change information. Photogrammetric Engineering and Remote Sensing 81:345–354.

Johnson, C. J., S. E. Nielsen, E. H. Merrill, T. L. McDonald, and M. S. Boyce. 2006. Resource selection functions based on use-availability data: theoretical motivation and evaluation methods. Journal of Wildlife Management 70:347–357.

Krausman, P. R., and M. L. Morrison. 2016. Another plea for standard terminology. Journal of Wildlife Management 80:1143–1144.

Kuhn, T. 1962. The structure of scientific revolutions. University of Chicago Press, Chicago, Illinois, USA.

Loew, S. S., D. F. Williams, K. Ralls, K. Pilgrim, and R. C. Fleischer. 2005. Population structure and genetic variation in the endangered giant kangaroo rat (*Dipodomys ingens*). Conservation Genetics 6:495–510.

MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, J. A. Royle, and C. A. Langtimm. 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology 83:2248–2255.

Martin, S. L., B. L. Jasinski, A. D. Kendall, T. A. Dahl, and D. W. Hyndman. 2015. Quantifying beaver dam dynamics and sediment retention using aerial imagery, habitat characteristics, and economic drivers. Landscape Ecology 30:1129–1144.

Miller, K. E., B. B. Ackerman, L. Y. Lefebvre, and K. B. Clifton. 1998. An evaluation of strip-transect aerial survey methods for monitoring manatee populations in Florida. Wildlife Society Bulletin 26:561–570.

Morrison, M. L., B. G. Marcot, and R. W. Mannan. 2006. Wildlife-habitat relationships: concepts and applications. Island Press, Washington, D.C., USA.

Murphy, D. D., and B. R. Noon. 1992. Integrating scientific methods with habitat conservation planning: reserve design for northern spotted owls. Ecological Adaptations 2:3–17.

Nielsen, S. E., G. B. Stenhouse, and M. S. Boyce. 2006. A habitat-based framework for grizzly bear conservation in Alberta. Biological Conservation 130:217–229.

Phillips, S. J., and J. Elith. 2013. On estimating probability of presence from use-availability or presence-background data. Ecology 94:1409–1419.

PRISM Climate Group. 2004. Oregon State University. http://prism.oregonstate.edu. Accessed 15 Jan 2020.

Prugh, L. R., and J. S. Brashares. 2012. Partitioning the effects of an ecosystem engineer: kangaroo rats control community structure via multiple pathways. Journal of Animal Ecology 81:667–678.

Pulliam, H. R. 1988. Sources, sinks, and population regulation. American Naturalist 132:652–661.

R Core Team. 2018. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Reed, S., and R. Amundson. 2007. Sediment, gophers, and time: a model for the origin and persistence of Mima mound—vernal pool topography in the Great Central Valley. Vernal Pool Landscapes 14:1527–1555.

Rutrough, A., I. V. Widick, and W. T. Bean. 2019. Reconstruction of the historical range alters niche estimates in an endangered rodent. Ecography 42:1742–1751.

Semerdjian, A. E. 2019. Evaluation of range-wide occupancy and survey methods for the giant kangaroo rat (*Dipodomys* ingens). Thesis, Humboldt State University, Arcata, California, USA.

Sidle, J. G., D. J. Augustine, D. H. Johnson, S. D. Miller, J. F. Cully, Jr., and R. P. Reading. 2012. Aerial surveys adjusted by ground surveys to estimate area occupied by black-tailed prairie dog colonies. Wildlife Society Bulletin 36:248–256.

Statham, M. J., W. T. Bean, N. Alexander, M. F. Westphal, and B. N. Sacks. 2019. Historical population size change and differentiation of relict populations of the endangered giant kangaroo rat. Journal of Heredity 110:548–558.

Stewart, J. A. E., H. S. Butterfield, J. Q. Richmond, D. J. Germano, M. F. Westphal, E. N. Tennant, and B. Sinervo. 2019. Climatic niche contraction, habitat restoration opportunities, and conservation biogeography in California's San Joaquin Desert. PLoS ONE 14(1): e0210766.

U.S. Fish and Wildlife Service [USFWS]. 1998. Recovery plan for the upland species of the San Joaquin Valley, California. U.S. Fish and Wildlife Service, Portland, Oregon, USA.

U.S. Fish and Wildlife Service [USFWS]. 2010. Giant kangaroo rat (*Dipodomys ingens*) 5-year review: summary and evaluation. U.S. Fish and Wildlife Service, Sacramento, California, USA.

Vermeulen, C., P. Lejeune, J. Lisein, P. Sawadogo, and P. Bouché. 2013. Unmanned aerial survey of elephants. PLoS ONE 8(2):e54700.

Weber, M. M., R. D. Stevens, J. A. F. Diniz-Filho, and C. E. V. Grelle. 2017. Is there a correlation between abundance and environmental suitability derived from ecological niche modeling? A meta-analysis. Ecogeography 40:817–828.

Widick, I., and W. T. Bean. 2019. Evaluating current and future range limits of an endangered, keystone rodent (*Dipodomys ingens*). Diversity and Distributions 25:1074–1087.

Wiens, J. A. 2002. Predicting species occurrences: progress, problems, and prospects. Pages 739–750 *in* J. M. Scott, P. J. Heglund, M. L. Morrison, J. B. Haufler, M. G. Raphael, W. A. Wall, and F. B. Samson, editors. Predicting species occurrences: issues of accuracy and scale. Island Press, Washington, D.C., USA.

Williams, D. F. 1992. Geographic distribution and population status of the giant kangaroo rat, *Dipodomys ingens* (Rodentia, Heteromyidae). Pages 301–327 *in* D. F. Williams, S. Byrne, and T. A. Rado, editors. Endangered and sensitive species of the San Joaquin Valley, California: their biology, management and conservation. California Energy Commission, California State University, Bakersfield, USA.

Williams, D. F., and K. S. Kilburn. 1991. Dipodomys ingens. Mammalian Species 377:1–7.

Associate Editor: Amy Kuenzi.