EVALUATION OF RANGE-WIDE OCCUPANCY AND SURVEY METHODS FOR THE GIANT KANGAROO RAT (*DIPODOMYS INGENS*)

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ABSTRACT

EVALUATION OF RANGE-WIDE OCCUPANCY AND SURVEY METHODS FOR THE GIANT KANGAROO RAT (*DIPODOMYS INGENS*)

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Though habitat suitability and occupancy are often correlated, they cannot always be inferred from each other. Therefore, a solid understanding of both is essential to effectively manage species. Recent studies have assessed range-wide habitat suitability for the giant kangaroo rat (*Dipodomys ingens*; GKR), but data regarding occupancy is lacking in parts of its distribution. Satellite and aerial imagery were used to identify GKR burrows across their known range, producing a range-wide occupancy map and non-invasive survey methods including track plates, manned flight, unmanned aerial vehicle, and sign surveys were conducted to determine effective methods for monitoring GKR occupancy. The range-wide imagery survey detected well-studied GKR populations and revealed populations in the center of its range where GKR occupancy was previously unverified. Trapping results generally matched the range-wide imagery review findings where GKRs were present, and these areas typically had high estimates of habitat suitability. Manned flights accurately predicted GKR presence when compared to available trapping data though the method did not match well with the range-wide imagery survey. The sign surveys accurately predicted both GKR presence and absence

according to the trapping data. The track plates only recorded partial kangaroo rat prints, from which GKRs were indistinguishable from a sympatric species. Finally, the data collected with the UAV was too limited to statistically assess, though anecdotally the method shows promise as a GKR survey method. This study found that these techniques, though informative on their own, are most effective when combined with at least one other survey method to predict GKR presences. When used together, these non-invasive practices will be an asset for conservationists interested in preserving habitat for GKRs.

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INTRODUCTION

Effective conservation plans rely on a thorough understanding of habitat suitability and occupancy for target species. Habitat suitability, or the extent to which the elements necessary to promote the growth and stability of populations for a species are available in a given area (Kellner et al. 1992), and occupancy - whether or not a species is present at a location - are conceptually linked (Pulliam 2000). However, while the two are often positively correlated, occupancy and habitat suitability cannot always be neatly inferred from each other. Populations may occur in areas with low suitability. Fragmentation, modification, and abrupt changes in climate or other environmental conditions can leave remnant populations in habitat that lacks the resources to optimally sustain them (Clevenger et al. 1997, Schlaepfer et al. 2002), and sink populations can persist in unsuitable locations as long as they are replenished by a source population (Pulliam 1988). Conversely, the stochastic processes of population dynamics may result in suitable areas not being occupied continuously (Eriksson 1996).

Because the relationship between habitat suitability and occupancy is imperfect, it is important to assess both for species in need of protection (Pulliam 2000). Modeled estimates of habitat suitability are useful for identifying potential protected areas as well as connectivity corridors. However, the actions taken to protect areas highlighted by suitability models depend largely on whether species of concern are present. Areas that are occupied by sensitive species are often given the highest priority in conservation plans (USFWS 1998, Fox & Nino-Murcia 2005), especially if those areas have high

suitability estimates, as relatively little needs to be done to ensure that the place is valuable for the species. In contrast, unoccupied but suitable areas may be considered for reintroduction (e.g., D'Elia et al. 2015, Cui et al. 2017, Lentini et al. 2018). Additionally, in the case of land that is degraded but still climatically suitable, restoration can be used to expand the distribution of threatened species (e.g., Meineri et al. 2014, Questad et al. 2014, Butterfield et al. 2017). On the other hand, occupied areas that are not suitable and not restorable (i.e. sink populations) will not be able to sustain themselves if source populations are not preserved. Therefore, implementing protection plans for these populations may not be a good use of resources unless nearby source populations are protected as well (Crowder et al. 2000, Margules & Pressey 2000). Conservation is limited by space, resources and conflicts between the needs of human and wildlife (Balmford et al. 2001, Brooks et al. 2006, Naidoo et al. 2006). Setting aside one area for wildlife may mean that others will not be given the same protections. Conservation decisions therefore need to be made wisely and with all the information and tools available (Sutherland et al. 2004, Guisan et al. 2013, Johnston et al. 2015), including data on both habitat suitability and occupancy.

Habitat suitability models have become increasingly popular tools for conservation (Guisan & Thuiller 2005). Occurrence data and predictor variables (e.g., climate, topography, vegetation, soil) are used to estimate coverage of suitable habitat over varying spatial scales (Guisan & Thuiller 2005). These models are particularly useful for rare or elusive species as they require relatively few occurrence points and can be used to assess large regions without exhaustive data collection from all parts of the

study area (Stockwell & Peterson 2002). The models can also be projected using estimates of future or past climate conditions to extrapolate habitat suitability estimates in different time periods (Araújo et al. 2005). These projections are especially useful in a conservation context, as they can identify areas that may be suitable for sensitive species in the future, and therefore, with careful consideration, can be used to inform predictive management plans (Hijmans & Graham 2006).

Though habitat suitability models are informative, they are not without critics. There are a number of reasons why these models may not capture true underlying suitability. Models outputs are partly dependent on inputs chosen by a researcher and the results can be affected by the methods and predictors that are selected (Guisan & Zimmerman 2000, Wilson et al. 2005). Inaccurate models can result from a number of errors, including the use predictor data that is inaccurate, incomplete, or of unsuitable spatial resolution (Guisan & Zimmerman 2000, Araújo & Peterson 2012). In addition to issues with environmental predictors, species occurrence data can also negatively affect the accuracy of the model if they are spatially biased (Bean et al. 2012a). If the occurrence data that is used to build models does not include detections across the complete range of conditions that the species can tolerate then the resulting habitat suitability estimates will not include the entirety of the species' fundamental niche (Hutchinson 1957). Limited dispersal ability (Pearson & Dawson 2003), exclusion from otherwise suitable habitat by anthropogenic or other biotic means (Scheele et al. 2017), and short-term changes in occupancy (Bean et al. 2012a), for example, can affect the data used to build habitat suitability models, which can change the outcome of those

predictions. Even if these errors are avoided, a well-designed habitat suitability model will highlight areas with the right conditions to support healthy populations, but they do not necessarily reflect the reality of where the species actually occurs, especially if populations are not at equilibrium with the environment (Araújo & Peterson 2012). Because of these issues, managers should supplement habitat suitability estimates with up-to-date occupancy data before making decisions.

There are many ways to monitor species occupancy across a landscape. Live trapping is considered to be one of the most effective means of gathering information, including occupancy status, for many species, especially small mammals (Glennon et al. 2002). A benefit of live trapping is that a variety of data can be collected from each captured animal that can be used to answer a multitude of questions beyond occupancy. However, live trapping can be time intensive and expensive. It can also cause damage to habitat due to trampling from frequent site visits, and can stress captured animals while putting them at risk of injury or death (Glennon et al. 2002). Less invasive tactics such as camera trapping, hair snares, transect sign surveys, and track plates cause far less stress to the study animals, though they are often less informative (Van Horne et al. 1997). Under certain conditions, however, data collected from these methods can be used as indices to effectively monitor populations (Hubbs et al. 2000, Stanley & Royle 2005). Methods that collect or record sign (i.e. hair snares, track plates and camera trapping) can be expensive depending on the materials needed, and still require occasional site visits from technicians. However, equipment can usually be left unchecked for longer periods of time, resulting in less human disturbance and a wider temporal window for animal

detections (Gompper et al. 2006). Depending on the study design, transect sign surveys can require even fewer site visits. Some species can have a higher probability of detection over a shorter amount of time in sign surveys than cameras or track plates (Gompper et al. 2006).

Aerial surveys are another potential method for detecting species that are large (Smyser et al. 2016, Greene et al. 2017), live in dense colonies (Hodgson et al. 2015), or create especially visible sign (Puttock et al. 2015). Unmanned aerial vehicles (hereafter: UAVs) (Vermeulen et al. 2013, Weissensteiner et al. 2015), manned flight surveys (Smyser et al. 2016) and satellites (Rocchini et al. 2015) have all been used to assess species presence and abundance over large regions. Each of these techniques differs in costs and quality of information depending on the methods and type of equipment used. UAVs have the potential to provide data with high spatial accuracy and temporal precision (Hodgeson et al 2015), though they cannot survey as large an area as the other aerial methods in a given amount of time. Manned aircraft can be used to survey broader regions than UAVs in the same amount of time while providing temporally precise data. However, manned flight surveys can be expensive and impose some risk for the pilot and observers. Satellite and high altitude flight imagery can be used to survey very broad areas compared to the other two methods, though depending on the data source, the temporal precision and spatial accuracy could be much lower. Aerial surveys are limited not only by data quality, cost, and time, but also by the fact that they can only be used for species or sign that are visible from the air (Greene et al. 2017).

The giant kangaroo rat (*Dipodomys ingens*, hereafter, GKR) is an endangered rodent uniquely suited to aerial monitoring. The GKR is endemic to California's San Joaquin Valley where individuals defend territories within colonies. They build elaborate burrow structures, called precincts, which provide thermal refuges that are vital to their survival (Grinnell 1932, Kay & Whitford 1978). GKRs also use their precincts to store seeds, which they gather and place in shallow pit caches on the surface of their precincts and in deep caches within their burrows (Shaw 1934). Burrows and their associated food stores are fiercely defended against conspecific and heterospecific intruders by a single GKR, or by a mother and her offspring prior to their dispersal (Jones 1993, Cooper & Randall 2007). When a kangaroo rat dies or disperses its burrow is often taken over by another, resulting in continuous occupation (Grinnell 1932, Schooley & Wiens 2001).

Sustained burrowing activity over many generations leads to the accumulation of soil around burrows, forming precincts into mounds (Best 1972). GKR mounds are typically positioned about 20 meters apart from each other, center to center, creating a visible pattern on the landscape and signaling the amount of territory that GKRs are able to defend from encroaching neighbors (Grinnell 1932, Braun 1985, Cooper & Randall 2007). In addition to observable topographic patterns, the interaction between GKRs and vegetation make active precincts obvious landscape features (Grinnell 1932, Prugh et al. 2012). GKRs clip the vegetation so that by late spring there are clear bare patches covering their burrows, which contrast with the vegetated areas in between territories. Precincts are also distinctive during the rainy season and into early spring when the seeds gathered by GKRs germinate and grow in patches that are thicker than the surrounding

vegetation. Though these features are most obvious when precincts are active, GKRs produce lasting topographic and vegetation legacies (Grinath et al. 2017) that can be seen for up to a decade after GKR extirpation (J. Chestnut, personal communication, 30 August 2018).

Though conspicuous on the landscape, GKR occupancy throughout their range can be difficult to establish due to their historically patchy distribution (Grinnell 1932). This problem has been further exacerbated in the past century by habitat fragmentation primary driven by agricultural development (Williams 1992). Though habitat suitability estimates have been thoroughly assessed in recent years (Bean et al. 2014b, Widick 2018, Widick & Bean 2019, Rutrough et al. revised review) there are significant gaps in observed occupancy data. GKRs are limited by very specific habitat needs. They avoid thick vegetation and sloped terrain and tend to live in the wettest parts of the arid San Joaquin Valley (Bean et al. 2014b). Their small range combined with the visible sign they create provides a unique opportunity to conduct a range-wide occupancy survey.

Although an assortment of public and private agencies regularly survey for GKRs on their properties, there has not been a recent range-wide assessment of their distribution (USFWS 2010). A quick and reproducible method for assessing occupancy would help managers monitor GKR distribution and track changes from year to year, which is especially important because GKR populations fluctuate extensively with drought cycles (Prugh et al. 2018). In addition to the need for range-wide monitoring, there are currently no standardized field protocols for non-invasive methods to monitor GKRs. Tested,

standardized, non-invasive detection methods for GKRs would help different agencies charged with monitoring GKRs compare data, and could be used alone or in coordination with remote surveys.

This study sought to determine GKR occupancy throughout their range while testing the efficacy of non-invasive survey methods including 1) the review of high altitude imagery, 2) manned flight, 3) UAV, and 4) on-the-ground sign surveys, and 5) track plates. Each of these methods were tested against trapping data in order to calculate perceived proportions of correctly classified presence and absence determinations for each type of survey, and the high-altitude imagery survey was also compared to habitat suitability estimates.

I expected to easily detect GKR sign in areas where GKRs are already known to be located in the range-wide imagery survey, especially in the Carrizo Plain National Monument (hereafter: Carrizo), Ciervo-Panoche Natural Area (hereafter: Panoche) and Lokern (Figure 1). I also expected to detect them in less understood areas in the center of their range, particularly around the Kettleman Hills area (Figure 1). I expected a low rate of false absences from this survey method because GKR sign is distinct and easily recognizable, however, I expected there to be a higher rate of false presences because some sign, such as GKR mounds can persist on the landscape for years after extirpation and at very high altitudes the age of sign is indeterminable. When comparing the range-wide imagery survey to habitat suitability estimates, I expected most occupied areas to have high habitat suitability estimates, though I anticipated that there would be more land

that is estimated to climatically suitable than is occupied, primarily due to the amount of land converted for human use in the GKR historical range.

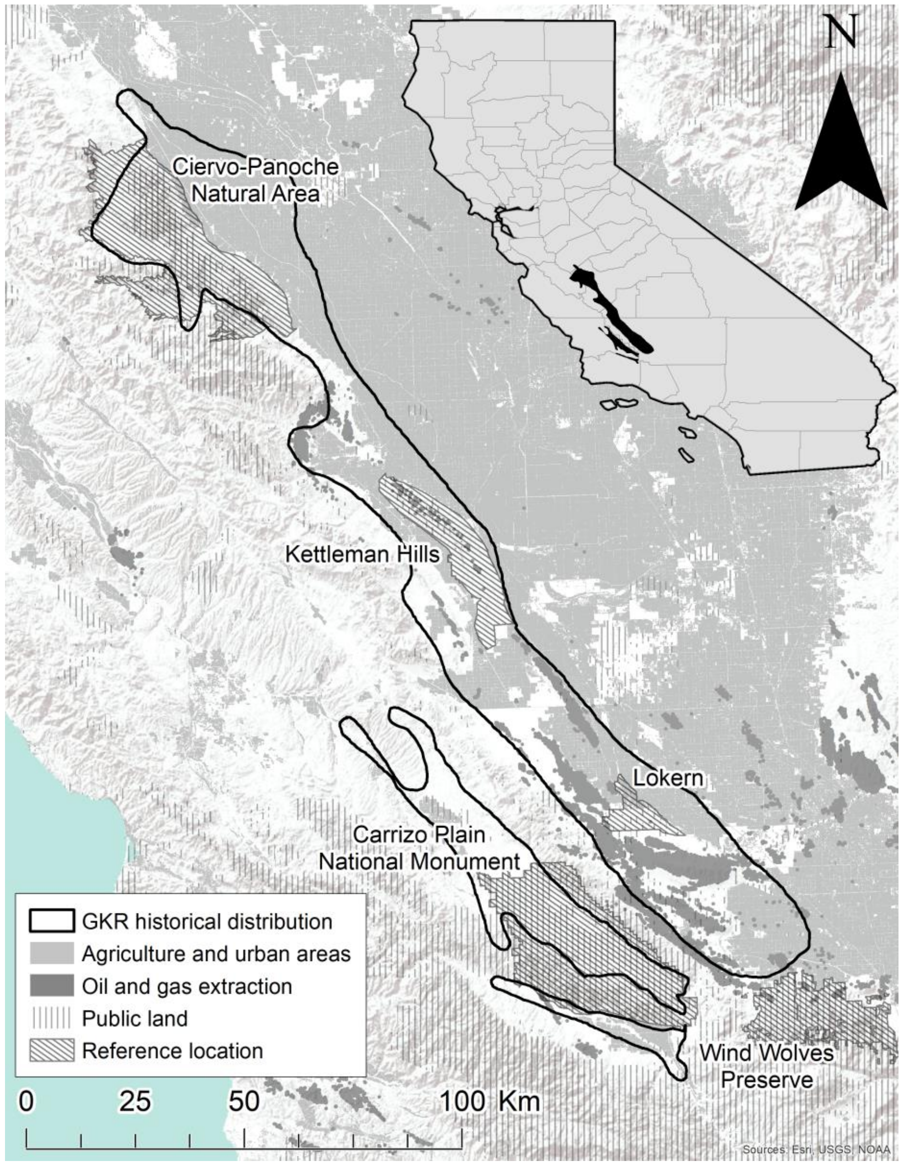

Figure 1: Historical GKR range outlined in black (Williams 1992), areas referenced frequently in this study are outlined with angled line fill and have corresponding labels. Public lands in shown with vertical lines (CPAD 2017). Agriculture and urban development as of 2011 is shown in light gray (Homer 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 dark gray (CDOGGR 2016).

The UAV and manned flight surveys both rely on recent GKR sign such as vegetation clipping to determine the location of active precinct, therefore I expected these methods to be more accurate than the range-wide imagery review. While I expected the results of the flight and UAV methods to be similar, I predicted that imprecision stemming from conducting surveys at a higher altitude, as well as the observer error introduced by collecting data in real time versus reviewing high quality images gathered from the field, would cause the manned flight results to differ more from trapping data then the UAV surveys (Bean et al. 2012b). GKRs create unique and plentiful sign on their precincts and are active and easily baited during the summer, so the transect sign surveys and track plates were expected to be closely correlated with occupancy at the site level.

By comparing the results of the range-wide imagery surveys to previous GKR habitat suitability models, this study aimed to provide insight into where GKRs are currently found and where they potentially could be. The range-wide imagery survey was also assessed as one of several non-invasive field methods for assessing occupancy throughout the GKR range. These findings will inform management decisions and provide standardized methods for collecting GKR data in the future.

METHODS

The overall goals of this project were to produce a map of range-wide occupancy for GKRs generated by a systematic review of aerial and satellite imagery, and to test a number of non-invasive techniques for estimating GKR occupancy at varying spatial levels. Live trapping is considered the ‘gold standard’ for monitoring GKRs (Bean et al. 2012b). Therefore, the results of the track plates, imagery review, manned flights, UAV, and sign surveys were tested against trapping data. The range-wide imagery review was also compared to a MaxEnt model from a recent study (Rutrough et al. revised review) to assess the relationship between habitat suitability estimates and occupancy throughout the GKR range.

Live Trapping

GKR live trapping was conducted between 2010 and 2017. The majority of trapping occurred in the Carrizo and the Panoche, though some trapping took place in the center of the range and in areas adjacent to the Carrizo in 2017 (Bean et al. 2014a, Alexander 2016, Widick 2018, Widick & Bean 2019). Sherman XL live traps were baited with millet-based birdseed and checked for 3 to 5 nights per session during summer months. Captured animals were identified to species and either given individually numbered ear tags or temporary marks with permanent markers. Trapping followed American Society of Mammalogists guidelines (Sikes et al. 2011) and was conducted under US Fish and Wildlife permits TE37418A-3. Scientific Collecting Permit SC-

11135, Humboldt State Animal Care Protocol 13-14.W.109-A and 16/17.W.96-A, and an MOU from California Department of Fish & Wildlife.

Plot designs were not consistent across year and location because the trapping occurred to meet the needs of several research objectives. In general, three trapping strategies were used. The majority of sites were set following a “target trapping” approach, with five to fifteen traps set near visibly active GKR burrows. The second plot design was a grid-based trapping approach, with 60 traps, each set 10 m apart, in a checkerboard grid. The grids were also set in areas with visually active GKR precincts to maximize the probability of detecting GKRs. Finally, in 2016 and 2017, sites in the southern part of the range included a mixture of target and grid traps. These plots contained fifteen trap locations, with the first ten arranged in a 2x5 grid with traps spaced 20 meters apart. The other five traps were placed at least 10 meters away from any other trap, targeting locations with apparent GKR activity. The first point of these grids was placed on apparent GKR precincts and from there the grid was cardinally oriented toward other precincts, if visible. In the event that there was no visible GKR activity in the area, other rodent sign was used for the starting location for the grid, and the targeted traps were added to the grid so that there was one 3 x 5 grid instead of a 2 x 5 grid with 5 additional traps scattered nearby. Site locations in the southern part of the range for 2017 were chosen based on range-wide imagery surveys. Six to nine plots were set during each session with plots evenly dispersed between areas with high confidence of GKR occupancy, low confidence of occupancy, low confidence of absence, and high confidence of absence. The majority of the trapping occurred on lands owned by the

Bureau of Land Management, though California Department of Fish and Wildlife, United States Fish and Wildlife Service, Wildlands Conservancy, and private lands were also accessed with permission.

Range-Wide Imagery Survey

Satellite and aerial imagery were used to identify areas with visible GKR sign to create a range-wide occupancy map. A set of 5 km^2 grids and 1 km^2 cells were superimposed over a 10 km buffer around the historical GKR range map (Williams 1992) (Figure 1) so that twenty-five 1 km^2 cells fit inside each 5 km^2 grid. Imagery within all 5 km cells contained in, or touching the buffer, was surveyed.

A team of 33 undergraduate volunteers and 3 project coordinators assisted in the survey. Each observer attended a training session where they were shown examples of aerial images of verified GKR burrows (Figure 2), as well as comparison images of other visually similar landscape features that might be confused with GKR precincts, such as other small mammal burrows, cattle sign, and dome-shaped topographic features called mima mounds (Figure 2). Project coordinators monitored observer performance until their findings consistently matched the coordinators, and then volunteers were able to work on their own.

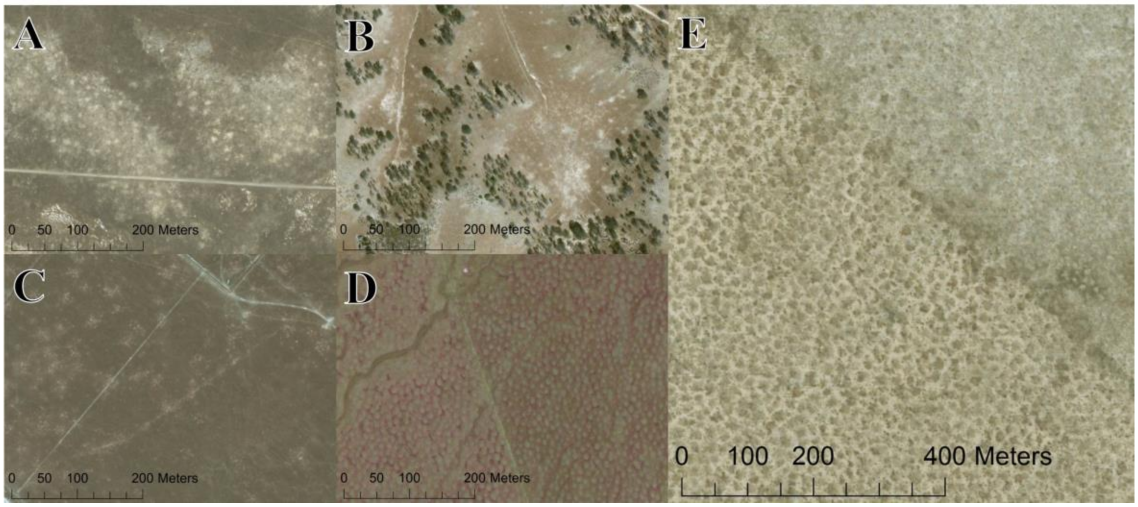

Figure 2: NAIP images of A) sparse GKR precincts, B) small mammal sign, not GKRs C) cattle sign, D) mima mounds E) Dense GKR colony

The survey utilized the default ArcMap basemap imagery which consisted of high-resolution National Agriculture Imagery Program (NAIP) images from 2014 and lower resolution *Satellite* Pour l'Observation de la Terre (SPOT) from 2008. Observers surveyed one 5 km^2 grid at a time. They zoomed to each 1 km^2 cell within the grid and searched using map ratios between 1:5,000 and 1:1,000. After scrolling through the entire 1 km^2 unit they noted whether GKRs were present in that cell and marked their confidence in their decision on a scale from 1 to 5. Presence designation and confidence in presence decisions were consolidated into a single score. Cells where observers indicated that GKRs were present were given positive values and cells where no GKRs were found were given negative value, so that a score of 5 indicated that the observer found GKRs in the cell and were very confident of their findings, a score of -5 indicated that the observer was very confident that there were no GKRs in the cell, and scores in between indicated GKR presence or absence with less certainty.

Two observers assessed each cell and the scores were averaged, except in the case of disagreement about GKR occupancy. In these instances, a project coordinator also surveyed the cell. The confidence scores for coordinator and the volunteer that agreed on GKR occupancy were averaged. Averaged scores were compiled to create a map indicating areas where GKRs were present or absent, and the confidence level of each observation. The results of the range-wide imagery review were tested against trapping data collected between 2010 and 2017. In several cases, there were multiple trapping sites within a single 1 km^2 range-wide imagery survey cell. GKRs only had to be captured at one site within a cell to consider GKRs 'captured' in that unit.

The range-wide imagery survey was tested against trapping data using different confidence scores to determine whether GKRs were 'present' or 'absent' in a cell. In separate tests, trapping data was compared to range-wide imagery cells with confidence scores greater than or equal to 1, 2, 3, or 4, or equal to 5. The proportion of cells that correctly identified GKR presence (sensitivity) and the number of cells correctly identified GKR absence (specificity) were calculated using trapping results and the presence-absence findings for each confidence category from the range-wide review.

The relationship between range-wide GKR occupancy and habitat suitability estimates was also assessed. A recent study reconstructed the historical distribution of GKRs using precincts detected in aerial imagery dating before 1960 as presence points to create a MaxEnt model for their historical range (Rutrough et al. revised review). Climatic water deficit, or the quantification of how local conditions supporting

evaporation exceed the amount of water available for actual evaporation (Stephenson 1998), slope, and soil qualities were the predictors in their top model. This model was projected using modern climatic values to estimate current suitability for GKRs across their range (Rutrough et al. revised review). Values from the modern projection of the MaxEnt model were extracted at the center of each 1 km^2 range-wide imagery survey cell. The model pixels were 0.810 km by 0.810 km. Because they were slightly smaller than the range-wide imagery survey cells, no single MaxEnt pixel was extracted from the center of a range-wide imagery review cell more than once. For the purpose of this analysis GKRs were considered ‘present’ when MaxEnt values were greater than or equal to the maximum sensitivity plus specificity threshold (Bean et al 2012a), and were considered ‘absent’ when the value was less. The maximum sensitivity plus specificity threshold, and resulting sensitivity and specificity for the habitat-range-wide imagery review test were calculated using the R package PresenceAbsence (R core team 2018, Freeman & Moisen 2008). Additionally, the trapping results for range-wide imagery review cells that contained trapping sites and had confidence values above three were summarized based on whether the cell was in suitable habitat and GKR were detected in the imagery, unsuitable habitat and GKR were detected in the imagery, suitable habitat with no GKR detections in the imagery, and unsuitable habitat with no GKR detected in the imagery.

Manned Flight Surveys

California Department of Fish and Wildlife conducted flight surveys for GKRs in the summer and fall of 2011, 2016 and 2017. A pilot followed pre-designed transects while two observers watched the landscape, one on each side of the plane, and recording GPS tracks when they saw GKR sign. Buffers were created post-hoc to fit in the space tracks signifying GKR sign to approximate observer line of site. In 2011 the buffers were 750m on each side of the flight lines and in 2016 and 2017 the buffers were 600m on each side. Positive predictive values for the flight data were calculated using trapping and, separately, range-wide imagery review results set to binary presence or absence values. Cells where GKR were present were those where sign was detected with a confidence score of three or higher. GKR were considered absent in cells where sign was not detected with a confidence of three or higher. Sensitivity, specificity and negative predictive values could not be calculated because the total area flown, and therefore places where GKRs were absent in the flights, was not available.

UAV Surveys

A DJI Phantom 3 Standard UAV equipped with a camera and GPS was used to help locate GKR precincts and determine trapping and survey locations during the summer of 2017. The UAV was controlled through either the DJI GO (SZ DJI Technology Co. Ltd 2018) or Litchi (VC Technology Ltd 2018) application on an iPhone 6s. Observers searched for GKR activity in video live-feed recorded between 30 to 400

feet above the ground around potential trapping sites. These flights were not systematic; rather they were intended to assist in fine-scale trapping site selection.

The UAV was also used to conduct standardized GKR surveys using pre-programmed missions and user defined waypoints in the Litchi app. Photos were taken every 100 meters with the camera angled straight down during the course of a 500-meter by 100-meter rectangular flight path. I assessed whether GKR sign was present in the photos using the same system as the range-wide imagery surveys.

Sign Surveys

This study sought to develop a standardized, non-invasive on-the-ground sign survey to determine GKR occupancy as a potential replacement for live trapping. Data were collected in the southern part of the GKR range in 2016 and 2017 and in the Panoche and surrounding area in 2017. Observers were trained by conducting surveys together on several plots and comparing results at the end of each survey until new observers consistently had results similar to more experienced data collectors. After training was completed, typically two observers started at opposite ends of a plot and worked toward each other until all survey locations had been visited.

The sign surveys were conducted once on each trapping plot during the session in which it was trapped. Survey points coincided with trap locations. The survey involved recording the presence of designated types of sign within a meter radius of each point. The sign categories included variables that were thought to correlate with GKR presence,

such as tracks and scats as well as variables that might indicate a lack of recent activity or burrow maintenance suggesting GKR absence, such as spider webs or debris in burrow openings (Appendix A). The survey was designed to be non-subjective by requiring only binary determinations of whether each sign category is present or absent, with no further quantifications. Additionally, the protocol was intended to be simple so that observers could collect data regardless of their level of prior GKR monitoring experience.

The proportion of trap locations where each sign category was observed was calculated for each plot. These proportions were used to test whether the surveys could predict GKR occupancy using boosted regression trees in the R package ‘gmb’ (Greenwell et al. 2018). Separate models were built using occupancy as determined by trapping data and the range-wide imagery review. The trapping models included data from 163 sites surveyed and trapped in 2016 and 2017. The range-wide imagery review models only used presence and absence data from survey cells with confidence scores greater than or equal to three. Cells with lower scores were removed from the analysis. The 85 sign survey sites that fell within cells with compatible range-wide imagery review scores were analyzed. Sensitivity and specificity for the models with the lowest deviance were calculated using five-fold cross validation.

Though trapping is considered an accurate method for determining GKR presence, it is possible that GKR were not caught at all sites where they were present. To test how sensitive the boosted regression tree analysis was to false negatives, datasets were created with known amounts of false negatives added in. In separate analyses

boosted regression trees were run on data with 5%, 10%, 25% and 50% of the sites where GKR were captured altered to falsely indicate that no GKR were caught there. Ten datasets with randomly selected false negatives were built for each percentage category. Top models for the forty datasets were chosen from the same candidate model set used to initially analyze the sign surveys (Appendix C). The top model for each data set was the one with the lowest deviance. Sensitivity, specificity, and true skill statistics were calculated for each top model using five-fold cross validation. Each top model was run again using unaltered, and specificity, sensitivity and true skill statistics were similarly calculated for each using five-fold cross validation.

The sensitivity, specificity and true skill statistics for the ten models built using data with each percentage of known false negatives were averaged, as were the corresponding values from the associated models run using unaltered data. The averaged sensitivities, specificities, and true skill statistics were compared to assess whether the results of boosted regression trees run with data with known false absences differ from models with no verified false absences.

Track Plates

Track plates were deployed as another non-invasive survey method in the southern part of the GKR range during the summer of 2017 (Appendix B, Figure 3. Track plates were placed alongside traps, alternating between targeted and grid traps. Five track plates were deployed at each site where they were used. The blotter paper would be

removed from the plastic backing upon collection. If there were tracks, the blotter paper would be sprayed with an art fixative and stored until the tracks could be identified. Tracks present on each card were identified to species, when possible, using the Peterson Field Guide to Animal Tracks (Murie & Elbroch 2005) with the aid of previous knowledge of the species found in the trapping areas. Sensitivity and specificity were calculated to test the track plates' ability to detect kangaroo rats against live trapping.

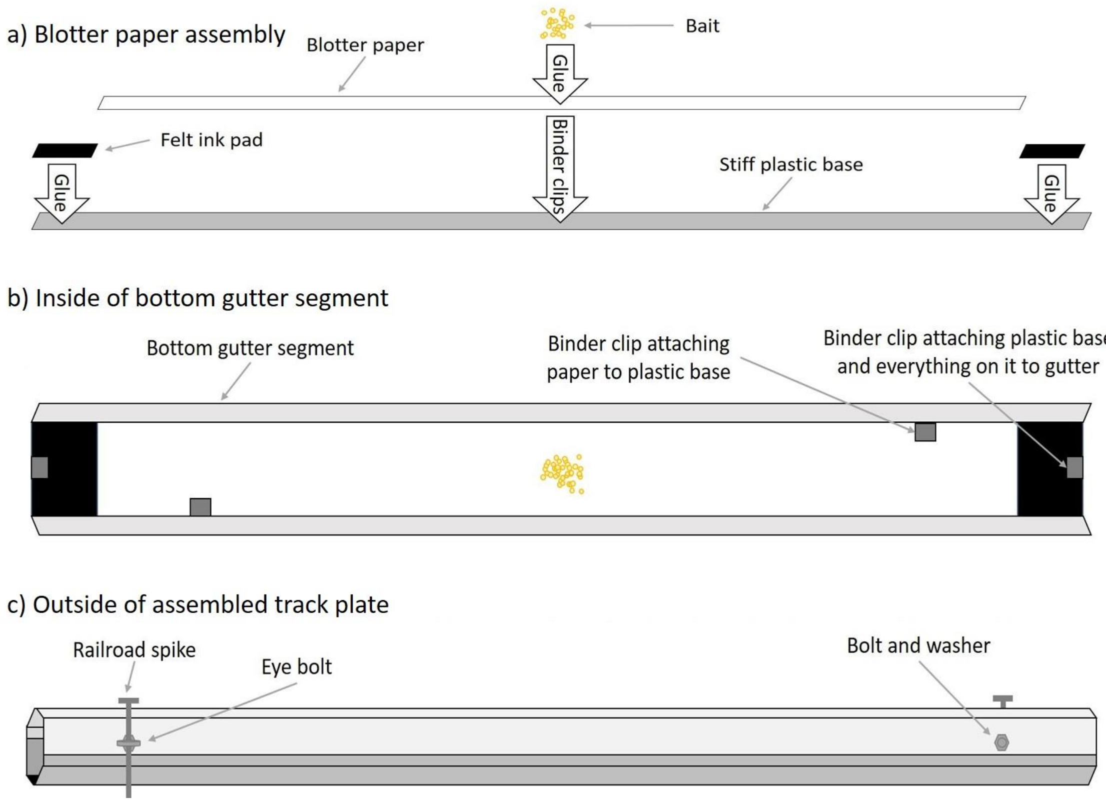

Figure 3: Track plate construction with: a) assembly of bait, blotter paper, and felt ink pads on the plastic base b) configuration of blotter paper and felt ink pads when attached to bottom gutter segment c) finished track tube with bolts and eye bolts attaching the top and bottom gutter segments.

RESULTS

Live Trapping

GKR were successfully captured at 289 of 436 trapping sites set across 5 counties in central California from 2010 to 2017 (Figure 4). GKRs were caught at 86 of the 148 plots trapped in and around the Carrizo in San Luis Obispo and Kern Counties, CA, 190 of the 279 plots in and around the Panoche in Fresno and San Benito Counties, CA and 3 of the 9 plots in the Kettleman Hills in Kings County, CA. During eight years that trapping occurred, 1,581 individual GKRs were captured and tagged. For plots where at least one GKR was caught, overall trap success was typically lowest on the first night of each session and highest on the fifth, though most plots were only trapped for three nights (Table 1). Conversely, the highest proportion of first GKR captures per site occurred on the first night of trapping, tapering considerably by the fifth night (Table 1).

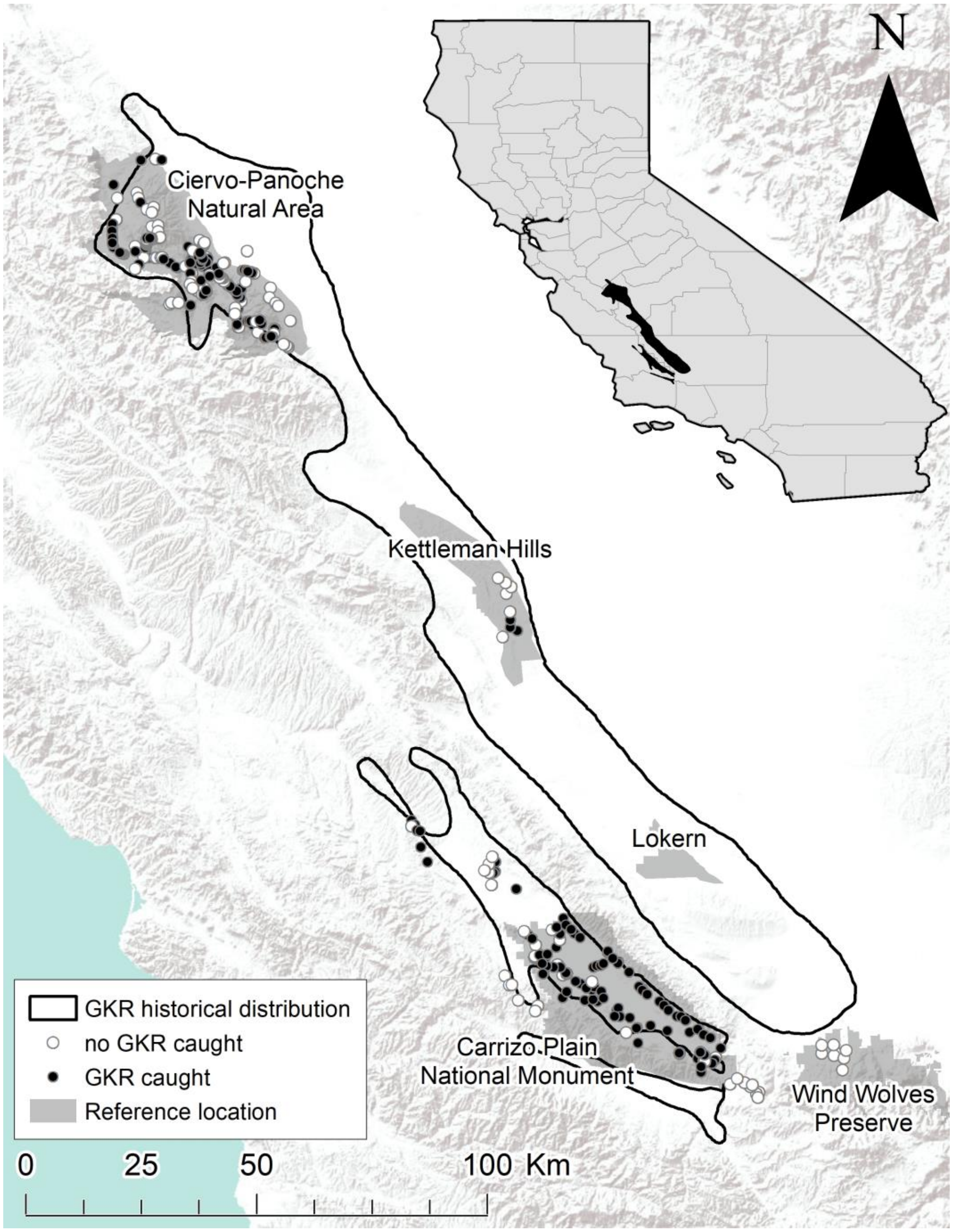

Figure 4: Sites trapped between 2010 and 2017. White dots symbolize sites where no GKRs were caught; black dots symbolize sites where they were captured. Gray shaded areas represent key GKR populations (Panoche, Carrizo, and Lokern) and other locations of particular interest for this study (Kettleman Hills and Wind Wolves Preserve).

Table 1: Outcomes for plots with 20 or fewer traps where at least 1 GKR was caught from 2016 to 2017.

Night of session (n = number of plots)	Proportion of traps that captured GKRs on the plot per session	Proportion of plots that caught their first GKR on a given night
Night 1 (n=138)	0.059	0.464
Night 2 (n=137)	0.139	0.341
Night 3 (n=129)	0.193	0.145
Night 4 (n=94)	0.184	0.044
Night 5 (n=43)	0.225	0.007

Range-Wide Imagery Survey

In total, observers reviewed imagery covering 17,375 km^2 of the San Joaquin Valley for GKR sign. Scores denoting observer confidence in GKR presence or for each 1 km^2 cell were compiled to create a range-wide map of GKR detections (Figure 5). GKRs were absent with a confidence score greater than or equal to 3 in 89.4% of the cells, GKR occupancy was uncertain in 4.5%, and GKRs were determined to be present with a confidence score of 3 or higher in 6.1% of the cells searched. Out of the 17,375 cells surveyed, 5,718 intersected or were contained within public or protected land. GKR

were observed with a confidence of 3 or higher in 9.8% of the cells intersecting public lands. Occupancy was uncertain in 5.5%, and GKRs were determined absent in 84.7% of those cells.

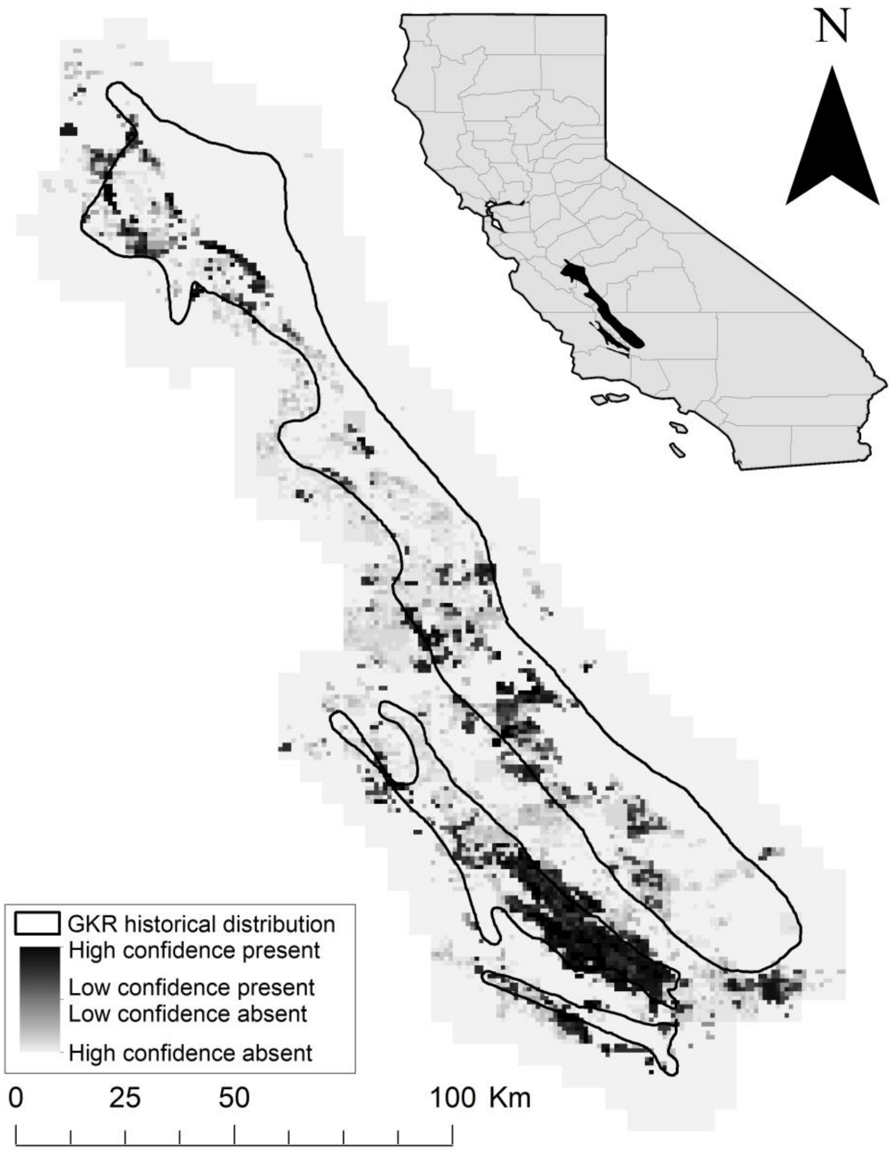

Figure 5: Historical GKR species distribution in black and average observer confidence on the presence or absence of GKRs. Black indicates high confidence that GKRs were present, light gray indicates high certainty that GKRs were absent, shades in between represent presence or absence with less certainty.

Trapping data collected between 2010 and 2017 were used to assess the accuracy of the range-wide imagery survey. There were 256 range-wide imagery review cells that contained trapping sites16 had a confidence score of one, 21 had a confidence score of two, 57 had a confidence score of three, 81 had a confidence score of four, and 81 had a confidence score of five. Sensitivity and specificity were lowest when all confidence values were included (Table 2). Both sensitivity and specificity increased as confidence scores increased, except that specificity dropped when only cells with confidence scores of five were used (Table 2).

Table 2: Sensitivity, specificity and true skill statistics for the range-wide imagery survey, using trapping data as the '**truth**'. Varying confidence scores were used as thresholds to determine which range-wide imagery review cells would be compared to trapping data. Confidence scores less than the threshold values were discarded for each test.

	# cells	Sensitivity	Sensitivity standard deviation	Specificity	Specificity standard deviation	True skill statistic
Confidence ≥ 1	256	0.768	0.040	0.465	0.0417	0.233
Confidence ≥ 2	240	0.784	0.041	0.457	0.0426	0.241
Confidence ≥ 3	219	0.809	0.0419	0.469	0.044	0.278
Confidence ≥ 4	162	0.841	0.0464	0.515	0.050	0.356
Confidence ≥ 5	81	0.880	0.066	0.393	0.066	0.273

Cells with a confidence level of three or higher were used for further analysis in this study. This confidence score was chosen because sensitivity and specificity were fairly high, and including some cells with confidence scores lower than 4 would include areas where observers were reasonably certain that GKR were present that may be of

interest to managers and should be subject to further investigation. There were 219 range-wide imagery survey cells that contained trapping sites and had confidence scores of three or higher and GKRs were caught in 141 of them. GKRs were caught in 64 of the 107 cells in and around the Panoche, 74 of the 103 cells in and around the Carrizo, and 3 of the 9 cells in Kettleman Hills. GKRs were successfully trapped at most of the sites that were located in cells where they were detected in the range-wide imagery review (sensitivity = 0.809, SD = 0.042), however, they were also captured in about half of the trapped cells where they were thought to be absent based the range-wide review (specificity = 0.479, SD = 0.044) (Table 3). The true skill statistic for this test was 0.278 (Allouche et al. 2006).

Table 3: Confusion matrix for live-trapping outcomes versus range-wide imagery review findings. Matrix includes results for the 219 range-wide imagery survey cells containing trapping sites and high confidence GKR presence-absence scores. GKRs were considered ‘observed present’ when they were caught at least once on a plot during trapping ‘observed absent’ when no GKRs were caught on a plot. GKRs were ‘predicted present’ when they were detected in the range-wide imagery review with a confidence score greater than or equal to 3 and ‘predicted absent’ when observers declared them absent with a confidence greater than or equal to 3.

	Present in range-wide imagery review	Absent in range-wide imagery review
GKR trapped	72	69
No GKR trapped	17	61

Range-wide imagery survey results were compared to MaxEnt values to determine whether occupancy could be predicted from habitat suitability estimates. The maximum sensitivity plus specificity threshold used for the MaxEnt values was 0.190. There were very few instances where GKRs were detected in the range-wide imagery review in areas with habitat suitability estimates below the threshold (specificity = 0.989), however, there were many areas where habitat suitability estimates exceeded the threshold but GKR sign was not detected in the range-wide imagery review (sensitivity = 0.114) (Table 4). The true skill statistic for this test was 0.103 (Allouche et al. 2006).

Table 4: Confusion matrix for habitat suitability estimates vs. range-wide imagery review findings. GKRs were considered 'observed present' when MaxEnt values were ≥ the maximum sensitivity plus specificity threshold and 'observed absent' when they were below the value. The maximum sensitivity plus specificity threshold was 0.19. GKRs were 'predicted present' when they were detected in the range-wide imagery review with a confidence score greater than or equal to 3 and 'predicted absent' when observers declared them absent with a confidence greater than or equal to 3.

	Habitat suitability estimate above threshold	Habitat suitability estimate below threshold
Present in range-wide imagery review	968	88
Absent in range-wide imagery review	7,528	7,914

Trapping results were summarized for range-wide imagery review cells with high habitat suitability estimates where GKR were detected in the imagery, low habitat suitability estimates where GKR were detected in the imagery, high habitat suitability estimates where GKR were not detected in the imagery, and low habitat suitability estimates where GKR were not detected in the imagery. Only 49 of the 219 cells had low habitat suitability estimates and GKR were detected in the range-wide imagery survey in 89 of the cells (Table 5). The category with the highest percentage of cells with GKR captures was the high suitability estimate-occupied in imagery category, with 81.93%. The percentages of cells with GKR captures in the high suitability estimate-not detected in imagery, low suitability-GKR present in imagery, and low suitability-GKR not detected in imagery categories were 56.32%, 66.67%, and 46.51%, respectively (Table 5).

Table 5: Summary of trapping results for range-wide imagery review cells where GKR were detected in the imagery and habitat suitability estimates were high, where they were not detected in the imagery and habitat suitability estimates were high, where they were detected in the imagery and habitat suitability estimates were low, and where they were not detected in the imagery and habitat suitability estimates were low.

	GKR caught	No GKR caught	Total
High suitability estimate, occupied in imagery survey	68	15	83
High suitability estimate, not occupied in imagery survey	49	38	87
low suitability estimate, occupied in imagery survey	4	2	6
Low suitability estimate, not occupied in imagery survey	20	23	43

Manned Flight Surveys

In 2011 surveyors spotted approximately 552 km^2 of GKR precincts, 812 km^2 in 2016, and 15 km^2 in 2017 (Figure 6). Altogether, with path overlap between surveys in 2011 and 2016 taken into account, the flights mapped 955 km^2 of GKR precincts. There were 90 trapping sites within the areas where GKRs were found during the manned flight surveys. GKRs were caught at 78 of the sites, resulting in a positive predictive value of 0.867 for the flight surveys. There were 1,471 range-wide cells that overlapped with areas

where GKRs were detected in the manned flights. GKRs were present in satellite-aerial image survey cells with scores ≥3 in 561 cells, resulting in a positive predictive value of 0.381 for flights when compared to the range-wide imagery review.

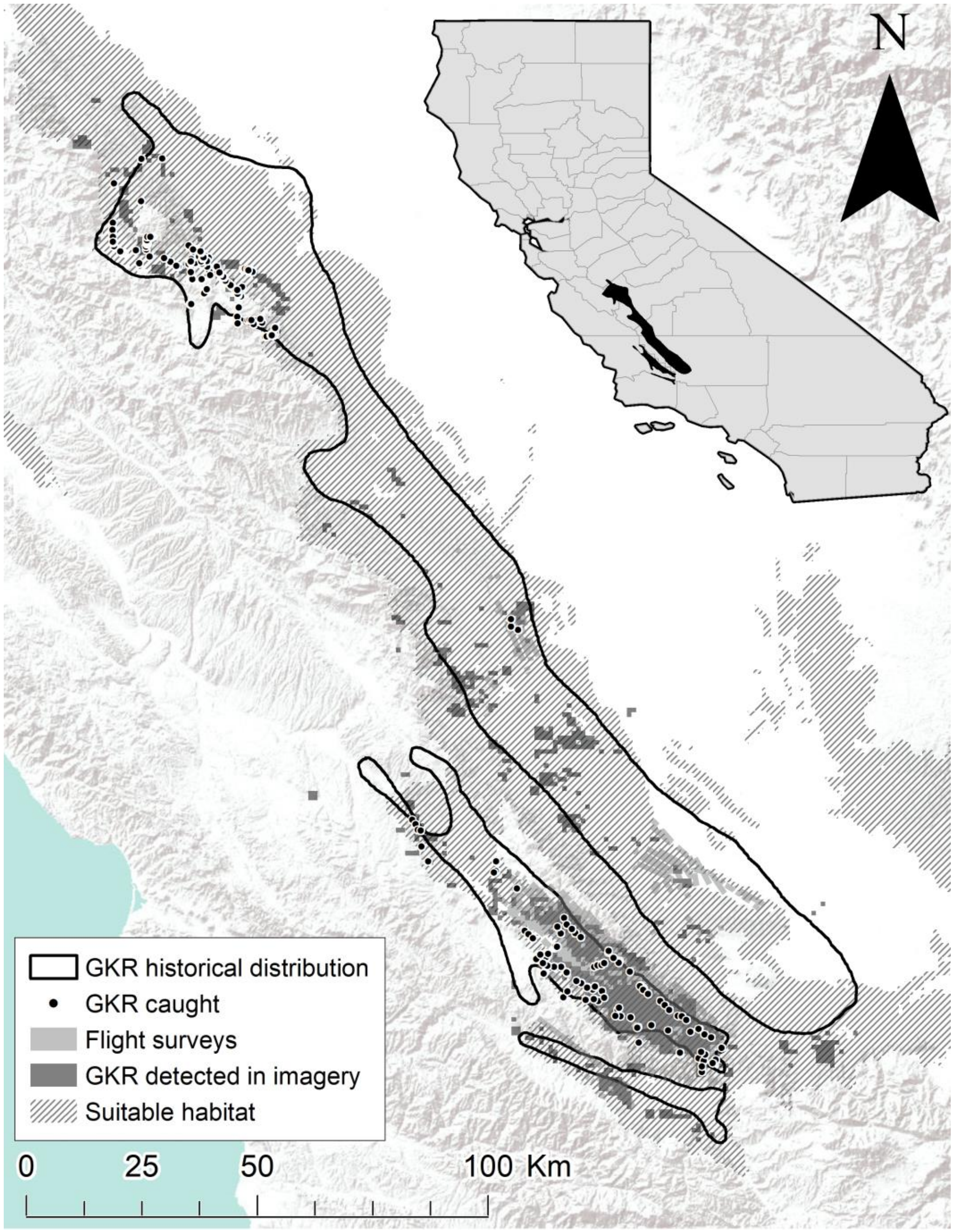

Figure 6: Historically suitable habitat as determined by a MaxEnt model thresholded to the maximum sensitivity plus specificity (Rutrough et al. revised review) in angled lines, locations where GKRs were observed during manned flight surveys in light gray, range-wide imagery review cells where GKRs were observed with a confidence of three or higher in dark gray, and sites where GKRs were trapped in black.

UAV Surveys

The UAV utilized by this study was primarily used to select trapping locations. During the summer of 2017, trapping locations were broadly influenced by the results of the range-wide imagery surveys, but finer-scale decisions were made in the field. Using the UAV to obtain an aerial view of general locations chosen for trapping proved to be a quick and effective way to narrow down specific trapping sites. By observing the live feed from the UAV, observers could note locations where there appeared to be GKR sign and set traps in those areas. This proved to be quicker than searching broad areas on foot.

This study also aimed to use the UAV to systematic survey for GKR sign. Unfortunately, there were some issues with the connection between the project's UAV and the controller, as well as some logistical difficulties that were not resolved until well into the short field season due to the prioritization of other tasks. Because of these issues there was not enough UAV data to conduct a formal analysis.

Sign Surveys

Seventeen variables from 163 sign surveys were used to build boosted regression tree models to predict GKR presence according to trapping data (Elith et al. 2008). Twenty-one models were built with learning rates between 0.0005 and 0.001 and complexities between 4 and 6 (Appendix C). All models had a bag rate of 0because of the

small sample size (Elith et al. 2008). Many of the models performed similarly, but the one with the lowest deviance was chosen for further assessment.

The best model had a complexity of 5 and a learning rate of 0.005. The model accurately predicted GKR presence and absence according to the trapping data with a cross validation AUC of 0.963 (SE = 0.014), sensitivity of 0.860 (SD = 0.073), specificity of 0.842 (SD = 0.111), and true skill statistic of 0.702. The variables that contributed the most to the model were tracks and tail drags, fresh aprons and non-vegetative debris in burrows (relative influence = 36.971, 15.603, 8.164, respectively) (Figure 7).

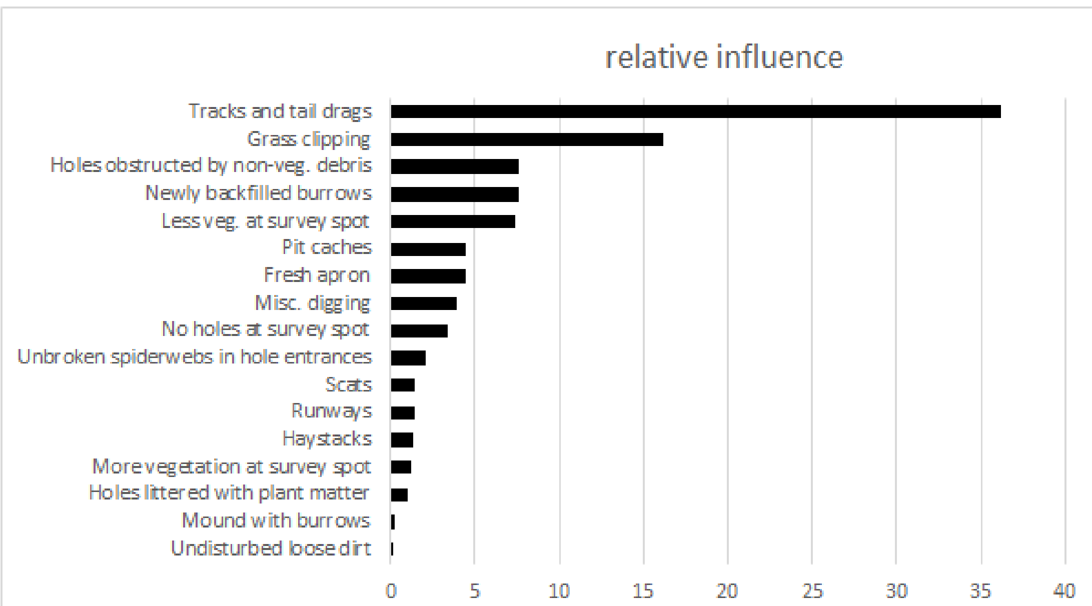

Figure 7: Relative influence for all variables used in boosted regression trees comparing sign surveys to live trapping.

Models using sign survey data to predict GKR occupancy at the 85 sites that fell within cells with confidence scores greater than or equal to 3 in the range-wide imagery review were built using the same method as those testing the relationship with the trapping data. The best model using range-wide imagery survey data had a complexity of 4 and a learning rate of 0.003. The model had a cross validation AUC of 0.780 (SE = 0.073), sensitivity of 0.883 (SD = 0.107), specificity of 0.962 (SD = 0.038), and true skill statistic of 0.795. The variables that contributed the most to the model were fresh aprons, tracks and tail drags, and mounds with burrows (relative influence = 18.378, 18.059, 10.216, respectively) (Figure 8).

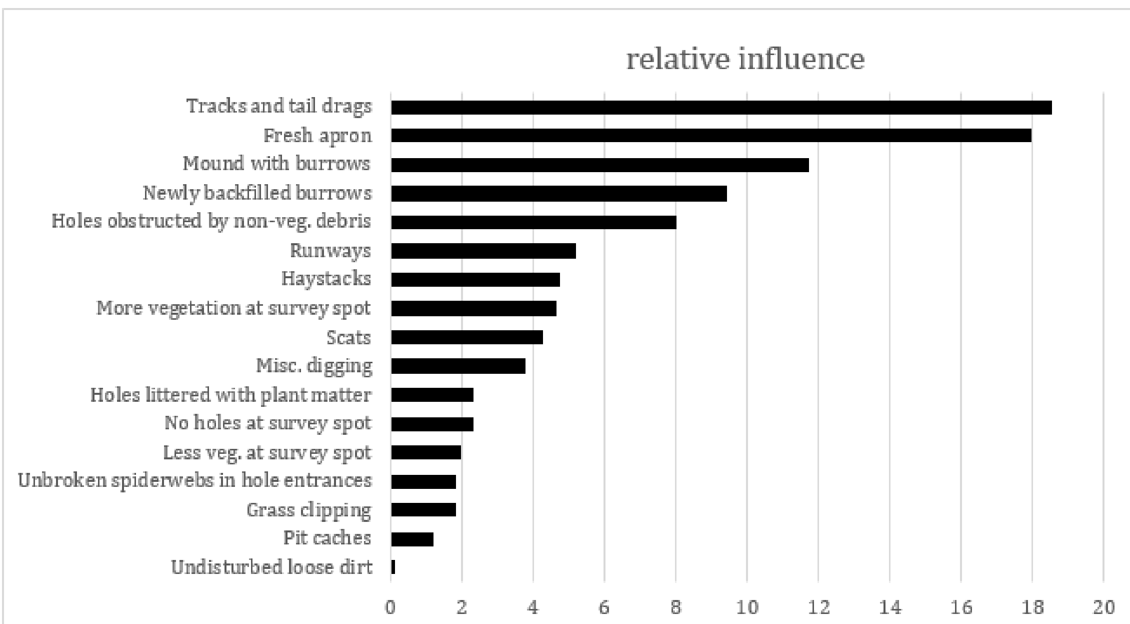

Figure 8: Relative influence for all variables used in boosted regression trees comparing sign surveys to range-wide imagery review results.

The sign survey data was augmented to create datasets were 5%, 10%, 25% and 50% of the sites where GKR were trapped were changed to indicate that no GKR were caught in order to assess how sensitive boosted regression trees were to false absences. Models run on the unaltered data had a higher average true skill statistic than those run on the data with added false absences, and the true skill statistics declined as the percentage of altered data increased (Table 6).

Table 6: Average sensitivity, specificity and true skill statistics for boosted regression trees built with data that was purposely altered to introduce false absences. The sensitivity and specificity of ‘observed’ results, achieved using altered data are compared to the sensitivity of the same models run using ‘actual’ or unaltered data.

% of captures changed to false negatives	Average ‘observed’ sensitivity	Average ‘actual’ sensitivity	Average ‘observed’ specificity	Average ‘actual’ specificity	Average ‘observed’ true skill statistic	Average ‘actual’ true skill statistic
0	NA	0.860	NA	0.842	NA	0.702
5	0.842	0.861	0.775	0.823	0.617	0.684
10	0.825	0.861	0.747	0.883	0.572	0.694
25	0.724	0.862	0.707	0.828	0.431	0.689
50	0.268	0.860	0.867	0.834	0.135	0.694

Track Plates

Track plates were set alongside 140 traps on 27 plots. Small mammals were

detected by 119 of the track plates. Of these, 35 had large kangaroo rat tracks while the remaining 84 had sign from other small mammals. Because kangaroo rats tend to walk on their toes while moving slowly (Bartholomew & Caswell 1951), kangaroo rat tracks left on the blotter paper were always incomplete. GKRs share their range with a similarly sized sympatric species, the Heermann's kangaroo rat (*Dipodomys heermanni*). While GKRs have a significantly larger hind foot than *D. heermanni* (mean = 49.043 mm and 43.425 mm, respectively; $t = 41.338$, $df = 677.64$, $p < 0.0001$; 95% confidence interval = (5.351, 5.885); A. Semerdjian, unpublished data), measurements for the two species were indistinguishable without a complete track including the heel. After combining GKR and Heermann's kangaroo rats into a single 'large kangaroo rat' category, the specificity of the track plates at both the site and trap scale were similar (specificity = 0.833 and 0.859, respectively) (Table 7) though the sensitivity at the site level was much higher (sensitivity = 0.952 and 0.458, respectively) (Table 8). The true skill statistics for these tests were 0.785 and 0.317, respectively.

Table 7: Sites with large kangaroo rat tracks registered on track plates and the GKR and Heermann's kangaroo rat capture rate at those sites.

	Large kangaroo rat caught	No large kangaroo rat caught
Large kangaroo rat tracks	20	1
No large kangaroo rat tracks	1	5

Table 8: Individual track plates with large kangaroo rat tracks and the capture rate of GKR and Heermann's kangaroo rats at the traps set next to each track plate.

	Large kangaroo rat caught	No large kangaroo rat caught
Large kangaroo rat tracks	22	13
No large kangaroo rat tracks	26	79

DISCUSSION

GKRs were live trapped throughout their range to collect occurrence data and to validate the findings of non-invasive methods. This study used aerial imagery to assess GKR occupancy across their distribution and tested non-invasive techniques for monitoring populations in the field. The range-wide imagery survey produced a coarse, but exhaustive occupancy map for GKRs that identified several known and understudied populations (Figures 5, 6). The high specificity and lower sensitivity indicate that GKRs are likely present in most of the areas where they were identified in the range-wide imagery review, but may also be present locations where they were not observed in the imagery. Other aerial methods were used to evaluate GKR occupancy as well. The manned flights outlined the boundaries of GKR populations in areas where surveys were conducted. These surveys mostly matched trapping data, but were less correlated with the results of the range-wide imagery review (Figure 6). The UAV surveys did not yield results, but with few modifications the method could prove valuable for land managers. Non-aerial, non-invasive methods included track plates and sign surveys. Track plates were deployed at sites where live-trapping and sign surveys occurred. Kangaroo rat tracks were collected on the plates at most locations, but these tracks could not be identified to species. The sign surveys' high sensitivity and specificity indicated that this method predicted GKR presences and absences accurately, according to the trapping data.

Live Trapping

Extensive live trapping occurred throughout the GKR range from 2010 to 2017. The data from this effort contributed toward studies investigating GKRs genetic connectivity (Alexander 2016, Statham et al. 2019), GKR habitat suitability (Bean et al. 2012a, Bean et al. 2014a, Bean et al. 2014b), and potential biotic and abiotic threats that GKRs might face in the future (Widick 2018, Widick & Bean 2019). Ideally, trapping sites would have been randomly distributed across areas with varying likelihoods of GKR presence, but the majority of trapping sites were chosen for other projects and targeted areas where GKRs were likely present. The only years where traps were set in areas with a lower probability of capture were 2016 and 2017, when data was being collected specifically for this study. This likely biases some of the comparative results. That being said, the size of the trapping plots and the specific time period in which a GKR can be detected in a location using traps makes this method the most spatially and temporally accurate survey method used here. By trapping, this study was able to definitively locate scattered GKR populations in the Panoche, monitor the edges of the population in the Carrizo, and confirm the existence of under-studied colonies near Kettleman Hills and north of the Carrizo.

Range-wide Imagery Survey

The ability to remotely survey a species' entire range is uncommon, making the range-wide imagery review a unique resource for managers interested in GKR conservation. Predicting where GKRs are located within their range is difficult, in part due to their historically patchy distribution, and in part because of the rapid development

and modification of their habitat (Grinnell 1932, Williams 1992). The range-wide imagery review map serves as a starting point for identifying GKR presence in order to make management decisions.

Habitat suitability models are another tool that managers use when deciding where to focus conservation efforts. However, suitability does not always correlate with occupancy, and vice versa (e.g. Pulliam 1988, Clevenger et al. 1997, Schlaepfer et al. 2002). Suitability models and occupancy maps for GKRs provide evidence of flaws in the relationship. GKRs were reliably absent in the range-wide imagery review in places with low habitat suitability estimates and the majority of the locations where GKRs were observed in the imagery review fell within areas with high habitat suitability estimates. However, much of the historical GKR range, though suitable in regards to abiotic variables, was unoccupied (Figure 6). This is likely due in part to anthropogenic habitat conversion and other abiotic interactions including conflicts with other rodent species (Widick 2018, Widick & Bean 2019) and the domination of historically sparse vegetation communities by non-native, thatch-producing grasses (Germano et al. 2001).

Mismatches between habitat suitability estimates and occupancy do not discount the value of either factor for species conservation. For example, large tracts of land with high habitat suitability estimates but no GKR detections are covered in invasive grasses that preclude GKR establishment. Cattle grazing and other management tactics may be used to restore these areas for use by GKR (Germano et al. 2012). Additionally, strategic fallowing plans cooperatively formed by land managers and farmers in the San Joaquin

Valley deal with land that is, for the most part, unoccupied by species of conservation concern (Butterfield et al. 2017). Occupancy in nearby areas should be a factor for these plans, as some species, including GKRs, can recolonize fields without human assistance (Blackhawk et al. 2016). However, habitat suitability models will ultimately determine which parcels are of the highest value for endangered species, with areas with low suitability estimates being ruled out for conservation purposes (Butterfield et al. 2017). Habitat suitability models have also been used to identify locations in the San Joaquin valley where development would substantially impact endangered species, including GKRs, and to suggest areas that would meet development needs while incurring less harm to sensitive species (Phillips & Cypher 2015).

Regardless of whether a location is considered good habitat, developers in the San Joaquin Valley must conduct surveys to determine whether endangered species are present on potential building sites (AEP 2018). In response to these surveys developers may have to modify or scale back their projects to protect endangered species (O'Farrell et al. 2016). Presence of endangered species is also a factor in deciding where mitigation lands should be established following development (Fox & Nino-Murcia 2005). Though habitat suitability models and species occupancy data are often used separately there is far more to be gained by using them together. Mitigation, for example, would be more impactful if long-term habitat suitability was taken into account as well as current species occupancy. There have been several studies assessing GKR habitat suitability at different temporal and spatial scales (Bean et al 2014b, Widick 2018, Widick & Bean 2019,

Rutrough et al. revised review), but this study is the first to assess occupancy throughout their entire range.

The regions where GKRs were identified in the range-wide imagery review with the highest levels of confidence include the well-studied populations in the Carrizo and Panoche, as well as potential populations in the center of the GKR range near the Kettleman Hills as well as in Wind Wolves Preserve and Cuyama Valley, which lies south of the Carrizo. GKR presence has been confirmed by trapping in many of the areas where they were detected remotely. During the course of this study they were live-trapped in many locations throughout the Carrizo and Panoche, and were caught near the Kettleman Hills. GKRs have been known to occur in the Cuyama Valley both historically (Grinnell 1932), and within the last 30 years (Williams 1992). I was not granted permission to conduct trapping or surveys in the region but, anecdotally, in the summer of 2017 researchers observed apparently active GKR precincts along Aliso Canyon Rd, a public road that transects the large patch where GKRs were detected in the range-wide imagery survey in Cuyama Valley.

There were no active GKR precincts found at Wind Wolves Preserve despite high confidence detections in the range-wide imagery review (figure 5, 6). During trapping observers noted that there were mounds on the landscape, but any burrow entrances that had been there were degraded beyond recognition. Reports from local managers suggest that it is very unlikely that there are currently GKRs in the area. It is possible that forces other than GKRs created the mounds, which were visible both on the ground and in aerial

imagery. However, Wind Wolves Preserve appears to be suitable habitat according to the MaxEnt model built from historical records, so it is also possible that they occupied the preserve in the past and have been extirpated (figure 6).

If a precinct is occupied over a long duration the burrow system will eventually develop a mound due to the continuous displacement of soil. In one example, banner-tailed kangaroo rats (*Dipodomys spectabilis*) in New Mexico developed mounds over 30 cm tall between 23 and 30 months after colonizing a new area (Best 1972). The mounds deteriorated after approximately a year following the removal of kangaroo rats (Best 1972) but in some cases kangaroo rat mounds can remain detectable for a decade or more after abandonment (J. Chestnut, personal communication 30 August 2018). The rate of deterioration likely depends on factors including the size of the mound, the length of occupation, and environmental variables including soil quality, vegetation, and amount of precipitation.

The results of the boosted regression trees predicting range-wide imagery survey results from on-the-ground sign survey transects distinguished mounds as one of the three most influential variables, suggesting that along with other signs of active use, the topographic features of precincts play heavily into observers' ability to see them in aerial imagery. An inherent limitation of the range-wide imagery review method is that some of the detected precincts, potentially including the mounds at Wind Wolves Preserve, may have been unoccupied when the imagery was gathered. However, because conditions would have to support GKRs for several years in order mounds to be visible in imagery

review, those areas likely are or were suitable for a long time. Therefore these detections offer information about GKR habitat needs, even if GKRs are not currently present. Depending on the reason for extirpation, these areas may be candidates for restoration or GKR reintroduction.

The influence of mounds for detecting GKRs in the range-wide imagery survey poses another limitation. Not all occupied precincts are mounded, and mounds are not the only sign that is visible in the imagery. A post-hoc review of 50 range-wide imagery review cells that contained trapping sites revealed that precincts that were not visible in the 2008 and 2014 imagery that we utilized, are clearly detectable in the imagery taken in 2017 (Maxar Technologies 2017). Out of the 50 cells that were revisited, GKRs were not detected in 2 of the cells where they had been called present in the initial survey, and GKRs were detected in 16 cells where they had previously been absent. On average the review differed from the initial assessment by 3.5 confidence points. GKR distributions have been known to fluctuate according to climatic conditions, and because the older imagery is from drier years (PRISM 2004), it is possible that GKR populations were simply not as widespread when the imagery was captured. It is also possible that GKR sign was simply more visible in the newer imagery. The effects that GKR have on vegetation would be more visible in years with higher rainfall because the rain would cause uneaten seeds in pit caches to germinate, resulting in thicker vegetation on precincts than in surrounding areas, and because there would be more vegetation surrounding precincts to contrast with the bare soil after GKR clip the vegetation around their burrows in late spring and early summer. Because of fluctuating population

boundaries and vegetation effects, it is likely that the results of the range-wide imagery survey would be different, and possibly more reflective of the trapping data, if it were conducted again using imagery from years with more precipitation.

Manned Flight Surveys

Another limitation of the range-wide imagery review is that precincts in shrubby areas may be harder to detect. The GKR population at Lokern is well documented (Germano & Saslaw 2017) but most of the GKR presences noted in the range-wide imagery review in that area had low confidence. A larger portion of the colony was identified in the manned flight surveys (figure 6). While the range-wide imagery review observations rely heavily on precinct topography, observers for the manned flight survey focus on spotting bare patches caused by GKR vegetation clipping on precincts. Because the flight surveys rely on sign created during the year of the survey they have a finer temporal scale than the range-wide imagery review, and because they occur at a lower altitude observers can spot precincts that are harder to find in lower resolution imagery.

The flight surveys corresponded to the trapping data better than they did to the range-wide imagery review. This may be in part due to similarities in temporal precision, as previously addressed, but bias in the placement of trapping sites is a likely factor as well. Most of trapping sites in the Carrizo, which is where the bulk of the sites used to analyze the flight surveys came from, were chosen to maximize the likelihood of catching

GKRs. Future research investigating whether flight surveys reflect trapping data for GKR should utilize trapping sites set in areas with varying likelihoods of GKR capture.

UAV Surveys

Manned flight surveys, though effective for monitoring GKR populations, may pose a risk to the pilots and biologists on board the small, low flying aircrafts and are limited by time and funding. UAV surveys may be a viable alternative. Unfortunately this study experienced technical difficulties resulting in insufficient data to analyze the effectiveness of UAV surveys. Anecdotally however, the UAV was useful for locating GKR precincts when they were active and densely clustered, but it was difficult to confidently identify them when they were sparse. While the UAV imagery could not be used to perfectly detect GKRs it was useful for detecting abundant activity, and identifying areas of interest for further investigation.

Advice for those interested in using UAVs to located GKRs in the future includes purchasing a UAV with the capability to connect with its controller over long distances. The UAV used for this project experienced issues moving more than 50 meters vertically or 500 meters horizontally from the controller before it lost connection and automatically returned to the start point. The problem did not affect pre-programmed surveys, but it limited the utility of exploratory flights. In addition, while the Litchi app was functional for creating pre-programmed flights, there are programs with more useful features for people surveying large parcels. DroneDeploy (Infatics, Inc. 2018), for example, has more

integrated functions for designing transects and splicing photographs to create a single image of the survey location. With protocol modifications, a UAV would be a useful tool for managers or researchers to identify possible GKR sign over areas too large to thoroughly survey on foot. Without further testing, however, any sign identified using UAVs should be verified using a secondary method.

Sign Surveys

Though trapping is considered the most reliable way to determine GKR occupancy, it is likely that occasionally GKR will not be trapped on sites where they are active. In order to test whether the sign survey analysis is sensitive to false negatives, datasets with artificial false absences were created. With the acknowledgement that trapping data used to build the original sign survey models likely already included some unidentified false absences, analysis showed that sensitivity and specificity generally declined as false negatives increased (Table 6). Additionally, the same models that were used to predict GKR presence using the altered data had higher sensitivity and specificity values that were similar to those calculated using the top model for the unaltered data. Sensitivity and specificity are a measure of false presences and absences, respectively. Values decreasing as data is artificially falsified tells us that the model is predicting GKR presences and absences even when the data disagrees. The decline in accuracy measures when the data is falsified coupled with the stable measures when unaltered data is used tells us that boosted regression trees are robust to false negatives in GKR trapping data, further proving the predictive power of this method.

The sign surveys performed well when compared to both trapping data and the range-wide imagery review. Fresh aprons and tracks and tail drags were among the top three influential variables in both tests. Dirt that was recently kicked out of a burrow opening and tracks are both signs of recent occupation, as wind and other disturbances can quickly degrade GKR sign. The third most influential variable for the test predicting trapping data from the sign surveys was non-vegetative debris in burrow openings. GKRs regularly maintain their precincts, including clearing clutter from burrow openings. Debris accumulation in burrows can indicate that they are absent, or less active at the site. GKRs spend considerable time underground (Braun 1985) and therefore may be present but not active above ground for extended periods. Because trapping only occurs at each site for a few days, GKR need to be active above ground in a relatively short time span in order to be caught. The sign surveys picked on details that can change over short timespans, matching nicely with the trapping data.

Fine-scale absences or occupancy turn over may not contribute significantly to the range-wide imagery review results. Mounding on burrow complexes occurs over a broad timespan. Mounds barely contributed to the results of the sign survey-trapping comparison, but they featured heavily when the sign surveys were compared to the range-wide imagery review. Mounds indicate that a colony persisted on the landscape for at least long enough for dirt to accumulate over burrows, but they do not necessarily signify current occupancy. By incorporating recent sign with long-term sign, the sign surveys offer insight into both long term and short-term occupancy, predicting both fairly accurately using slightly different models.

In addition to accurately predicting GKR occupancy, the sign survey protocol is based on binary determinations of sign presence with no quantification involved, making it less subjective. The survey was also designed to be easy to learn, regardless of whether observers have had past experience with GKR monitoring. They required fairly little effort and compared to live trapping, and were significantly faster. In addition, conducting sign surveys instead of trapping reduces stress on GKRs because animals are not caught or handled, and requires fewer site visits, therefore reducing trampling of habitat.

In most modeling situations sensitivities and specificities exceeding 0.80 would be considered accurate. However, it is important to note that in this case a sensitivity of 0.860 means that GKRs were not trapped at 14% of sites where the survey predicted that they would be and a specificity of 0.842 means that they were caught at 15.8% of sites where they survey predicted they were absent. This margin may be unacceptable depending on the context for which the surveys are being used. Conducting several surveys on the same parcel may help overcome the issue of false presences and absences. Additionally, those collecting data from many surveys over large areas may want to include some trapping sites to verify their results. Overall though, the sign surveys will be very useful for managers as a non-subjective, low impact, inexpensive and quick way to determine GKR presence.

Track Plates

Track plates were deployed with live-traps at sites in the south part of the GKR range during the 2017 trapping season. There was little concern of the track plates affecting trapping outcomes or vice-versa. The track plates did not restrain animal, so they could easily visit the track plate and then go into a trap. Conversely, the traps were ideally checked and closed several hours before dawn, so if a kangaroo rat was caught in a trap it is likely that it would be released and still have time to find its way back to a track plate that night.

The track-plate design (Figure 3; Appendix B) worked well in the field. The charcoal-mineral oil mixture did not evaporate off of the felt pads, even when exposed to extreme heat and served as effective ink that produced clear tracks. It is not uncommon to find sign from kit foxes, coyotes and ravens on or near traps, and occasionally traps are rolled over or moved. However, very few of the gutter constructions were moved or seriously disturbed due to the use of eyebolts and railroad spikes to secure the plates to the ground. The few times that the track plates were moved were likely the result of larger animals like cows investigating them.

The plates clearly picked up prints from kangaroo rats, but, because kangaroo rats walk on their toes when moving slowly, the tracks did not include the entire foot. Though Heermann's kangaroo rats, which co-occur with GKRs in many locations, have smaller feet, their tracks were indistinguishable when incomplete. The track plate results were

strongly related to capture success for these two large kangaroo rat species at a site level, and only two of the 27 plots with track plates had conflicting track plate-trapping results. Track plate and trapping were also related at the trap-location level, however the high specificity and low sensitivity suggests that this relationship is driven by locations where large kangaroo rats were not detected in either method, rather than locations where they were detected in both.

Though they can occupy similar habitat, Heermann's kangaroo rats do not build precinct complexes and their sign is not as conspicuous as GKR. Many of the sign surveys took place in locations where Heermann's kangaroo rats were caught, but no GKR were, and the accuracy of the results seem to reflect the difference in the sign they create. The track plates, though limited in application, could potentially be used along with sign surveys or non-invasive methods with less temporal certainty to determine current kangaroo rat occupancy.

CONCLUSIONS

The range-wide imagery survey provides an unprecedented complete census of the GKR range and despite some notable cases of sign not being detected in areas where GKRs are known to be present, as well as false presences, the survey provides a key foundation for assessing the distribution of GKRs. The range-wide imagery review is especially suitable for investigating GKR distribution at a broad-scale when paired with habitat suitability models. GKRs were trapped with roughly a 77% success rate in locations where GKRs were present in the imagery review and habitat suitability estimates were high. These results represent a starting point for prioritizing land acquisition for GKR conservation, potentially illustrating the importance of previously overlooked populations and saving time and energy for those considering large areas. Specifically, habitat suitability estimates, the range-wide imagery review, and the manned flight surveys all indicate that Cuyama Valley and Sunflower Valley, just west of the Kettleman Hills, are areas that managers may want investigate in the future.

The methods tested in this study varied widely in the temporal and spatial scale at which GKR were detected. Live trapping, sign surveys and track plates utilized the same plots, and therefore sampled the same amount of habitat, though the exact effective sampling area can be difficult to determine. These methods are the most limited in the extent to which results can be extrapolated into the surrounding area. It would be risky to assume that a GKR detection at a plot set in a heterogeneous environment indicates that they occupy the surrounding area. However, if GKRs are trapping in an area that appears

to have abundant GKR activity, the occupied area may potentially be projected to include the colony in which the trapping site was set. The effective area of a trapping site, and therefore the sign surveys, since they were conducted in the same locations, depends largely on where the plots are set. In principle the same risk of assuming GKR are present in areas that were not surveyed may apply to the UAV and flight surveys. However, because more data can be gathered over a large area using these aerial methods, extrapolations can be better informed. Finally, because the range-wide imagery review covers the GKRs entire range, though at a coarse scale, there is theoretically no habitat where likelihood of presence needs to be estimated.

In addition to operating at different spatial scales, the temporal coverage of these methods differs as well. From finest to coarsest, GKR detected during live trapping had to be active on the plot they were caught the night they were caught. The age of tracks left on track plates will depend on how long the track plates are left in the field, which is in this study was up to three nights. Observers were instructed to record fresh sign during sign surveys, though perception of freshness likely depends largely on how quickly the environment degrades it. Because GKR live in areas that are typically hot and often windy, most sign likely degrades in less than a week, which would reflect the maximum time since last activity that would be detected using the sign surveys. The data recorders for the UAV and manned flight surveys are instructed to look for fresh GKR sign, which from high altitude largely include grass clipping. Without clipping, vegetation would appear thicker, or the same as the areas surrounding precincts, so GKR sign would not be detected using these methods if GKRs were not actively maintaining burrows at least

through the spring before the surveys. Finally, the range-wide imagery surveys detect GKR sign over the longest time period because the topographic features of GKR precincts are highly visible in high altitude aerial imagery, and mounds can persist for a long time after GKR have been extirpated.

Which of these methods are used would likely depend on the management goal as well as the time and resources available. Agreement between two or more surveys, including the range-wide imagery review, would offer a fair degree of confidence in whether an area is occupied by GKRs, which could be estimated by multiplying the probability of occupancy as determined by each method. In the case of a very large area of interest, using aerial methods first and then conducting sign surveys in locations with contrasting results may be sufficient to ascertain occupancy. In the case of hopelessly unresolved disagreement between non-invasive methods, trapping may be necessary.

Comprehensive occupancy data for GKRs collected using comparable survey methods is limited. Perhaps the greatest potential of the non-invasive methods in this study lies in the ability to implement a standardized version of them. Standardizing data collection across the GKR range will result in a better understanding of their distribution and population dynamics across time. With these tools, entities tasked with conserving GKRs will be able to communicate more clearly to provide for the species into the future.

LITERATURE CITED

Alexander, N. 2016. Genetic structure and connectivity of the endangered giant kangaroo rat (*Dipodomys ingens*) in a heterogeneous environment. Thesis, Humboldt State University, California, USA.

Allouche, O., A. Tsoar & R. Kadmon. 2006. Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). Journal of Applied Ecology 43: 1223-1232.

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

Araújo, M.B., R.J. Whittaker, R.J. Ladle & M. Erhard. 2005. Reducing uncertainty in projections of extinction risk from climate change. Global Ecological Biogeography 14: 529-538.

Association of Environmental Professionals (AEP). 2018. 2018 California Environmental Quality Act (CEQA) Statute and Guidelines. Palm Desert, CA.

Balmford, A., J.L. Moore, T. Brooks, N. Burgess, L.A. Hansen, P. Williams, & C. Rahbek. 2001. Conservation conflicts across Africa. Science 291: 2616-2619.

Bartholomew, G.A., Jr & H.H. Caswell, Jr. 1951. Locomotion in kangaroo rats and its adaptive significance. Journal of Mammalogy 32: 155-169.

Bean. W.T., L.R. Prugh, R. Stafford, H.S. Butterfield, M. Westphal & J.S. Brashares 2014a. 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, & J.S. Brashares. 2012a. The effects of small sample size and sample bias on threshold selection and accuracy assessment of species distribution models. Ecography 35: 250-258.

Bean, W. T., R. Stafford, H. S. Butterfield & J. S. Brashares. 2014b. A multi-scale distribution model for non-equilibrium populations suggests resource limitation in an endangered rodent. PLoS ONE 9: 1-9.

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

Best, T.L. 1972. Mound development by a pioneer population of the banner-tailed kangaroo rat *Dipodomys spectabilis baileyi* Goldman, in Eastern New Mexico. The American Midland Naturalist 87: 201-206.

Blackhawk, N. C., D. J. Germano & P. T. Smith. 2016. Genetic variation among populations of the endangered giant kangaroo rat, Dipodomys ingens, in the southern San Joaquin Valley. American Midland Naturalist 175: 261-274.

Braun, S.E. 1985. Home range and activity patterns of the giant kangaroo rat, *Dipodomys ingens*. Journal of Mammalogy 66: 1-12.

Brehme, C.S., L.R. Albert, T.A. Matsuda, R.N. Booth & R.N. Fisher. 2010. Pacific pocket mouse sampling methodology study, Marine Corps Base, Camp Pendleton. Prepared for AC/S Environmental Security, Marine Corps Base, Camp Pendleton. 47p.

Brooks, T.M., R.A. Mittermeier, G.A.B. da Fonseca, J. Gerlach, M. Hoffmann, J.F. Lamoreux, C.G. Mittermeier, J.D. Pilgrim, & A.S.L. Rodrigues. 2006. Global biodiversity conservation priorities. Science 313: 58-61.

Butterfield, H.S., R. Kelsey, A. Hart, T. Biswas, M. Kramer, D. Cameron, L. Crane, and E. Brand. 2017. Identification of potentially suitable habitat for strategic land retirement and restoration in the San Joaquin Desert. Unpublished report. The Nature Conservancy, San Francisco, California. 25 pages.

California Division of Oil, Gas and Geothermal Resources (CDOGGR). 2016. AllWells. [Shapefile geospatial data]. http://www.conservation.ca.gov/dog/geothermal/maps

California Protected Area Database (CPAD). 2017. www.calands.org.

Cooper, L.D. & J.A. Randall. 2007. Seasonal changes in home ranges of the giant kangaroo rat (*Dipodomys ingens*): A study of flexible social structure. Journal of Mammalogy 88: 1000-1008.

Clevenger, A.P., F.J. Purroy & M.A. Campos. 1997. Habitat assessment of a relict brown bear *Ursus arctos* population in northern Spain. Biological Conservation 80:17-22.

Crowder, L.B., S.J. Lyman, W.F. Figueria & J. Priddy. 2000. Source-sink population dynamics and the problem of siting marine reserves. Bulletin of Marine Science 66: 799-820.

Cui, S., J. Milner-Gulland, N.J. Singh, H. Chu, C. Li, J. Chen & Z. Jiang. 2017. Historical range, extirpation and prospects for reintroduction of saigas in China. Scientific Reports 7: 44200.

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

Elith, J., J.R. Leathwick & T. Hastie. 2008. A working guide to boosted regression trees. Journal of Animal Ecology 77: 802-813.

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

Fox, J. & A. Nino-Murcia. 2005. Status of species conservation banking in the United States. Conservation Biology 19: 996-1007.

Freeman, E.A. & G. Moisen. 2008. PresenceAbsence: An R package for presence-absence model analysis. Journal of Statistical Software 23: 1-31. http://www.jstatsoft.org/v23/i11

Germano, D.J., G.B. Rathbun & L.R. Saslaw. 2001. Managing exotic grasses and conserving declining species. Wildlife Society Bulletin 29: 551-559.

Germano, D.J., G.B. Rathbun & L.R. Saslaw. 2012. Effects of grazing and invasive grasses on desert vertebrates in California. The Journal of Wildlife Management 76: 670-682.

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

Glennon, M.J., W.F. Porter & C.L. Demers. 2002. An alternative field technique for estimating diversity of small-mammal populations. Journal of Mammalogy 83: 734-742.

Gompper, M.E., R.W. Kays, J.C. Ray, S.D. Ladpoint, D.A. Bogan & J.R. Cryan. 2006. A comparison of non-invasive techniques to survey carnivore communities in northeastern North America. Wildlife Society Bulletin 34: 1142-1151.

Greene, K., D. Bell, J. Kioko & C. Kiffner. 2017. Performance of ground-based and aerial survey methods for monitoring wildlife assemblages in a conservation area of northern Tanzania. European Journal of Wildlife Research 63: 77.

Greenwell, B., B. Boehmke, J. Cunningham & GBM Developers. 2018. gbm: Generalized Boosted Regression Models. R package version 2.1.4. https://CRAN.R-project.org/package=gbm

Grinath, J.B., N. Deguines, J. W. Chestnut, L. R. Prugh, J. S. Brashares & K. N. Suding. 2018. Animals alter precipitation legacies: Trophic and ecosystem engineering effects on plant community temporal dynamics. Journal of Ecology 00: 1-16.

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

Guisan, A. & 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. Sutcliff, A.I.T. Tulloch, T.J. Regan, L. Brotons, E. McDonald-Madden, C. Mantyka-Pringle, T.G. Martin, J.R. Rhodes, R. Maggini, S.A. Setterfield, J. Elith, M.W. Schwartz, B.A. Wintle, O. Broennimann, M. Austin, S. Ferrier, M.R. Kearney, H.P. Possingham, Y.M. Buckley. 2013. Predicting species distributions for conservation decisions. Ecology Letters 16: 1424-1435.

Guisan A. & N.E. Zimmerman. 2000. Predictive habitat distribution models in ecology. Ecological Modelling 135: 147-186.

Hijmans, R.J. & C.H. Graham. 2006. The ability of climate envelope models to predict the effect of climate change on species distributions. Global Change Biology 12: 2272-2281.

Hodgeson, J.C., S.M. Baylis, R. Mott, A. Herrod & R.H. Clarke. 2015. Precision wildlife monitoring using unmanned aerial vehicles. Scientific Reports 6: 22574.

Homer, C.G., Dewitz, J.A., Yang, L., Jin, S., Danielson, P., Xian, G., Coulston, J., Herold, N.D., Wickham, J.D., and Megown, K., 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*, v. 81, no. 5, p. 345-354

Hubbs, A.H., T. Karels & R. Boonstra. 2000. Indices of population size for burrowing mammals. The Journal of Wildlife Management 64: 296-301.

Hutchinson, G.E. 1957. Concluding remarks. Cold Spring Harbor Symposia on Quantitative Biology 22: 145-159.

Infatics, Inc. 2018. DroneDeploy – Mapping for DJI (Version 2.80.0) [Mobile application software].

Johnston, A., D. Fink, M.D. Reynolds, W.M. Hochachka, B.L. Sullivan, N.E. Bruns, E. Hallstein, M.S. Merrifield, S. Matsumoto & S. Kelling. 2015. Abundance models improve spatial and temporal prioritization of conservation resources. Ecological Applications 25: 1749-1756.

Jones, W.T. 1993. The social systems of heteromyid rodents. Pp. 575–595 in Biology of the Heteromyidae (H. H. Genoways and J. H. Brown, eds.). Special Publication 10, The American Society Of Mammalogists.

Kay, F.R. & W.G. Whitford. 1978. The burrow environment of the banner-tailed kangaroo rat, *Dipodomys spectabilis*, in south central New Mexico. The American Midland Naturalist 99: 270-279.

Kellner, C.J., J.D. Brawn, & J.R. Karr. 1992. What is habitat suitability and how should it be measured? Pages 476-488 *in* Wildlife 2001: populations. Springer, Dordrecht.

Lentini, P.E., I.A. Stirnemann, D. Stojanovic, T.H. Worthy & J.A. Stein. 2018. Using fossil records to inform reintroduction of the kakapo as a refugee species. Biological Conservation 217: 157-165.

Margules C.R. & R.L. Pressey. 2000. Systematic conservation planning. Nature 405: 243-253.

Maxar Technologies. 2017. DigitalGlobe - https://www.digitalglobe.com/

Meineri, E., A.S. Deville, D. Grémillet, M. Gauthier-Clerc, & A. Béchet. 2014. Combining correlative and mechanistic habitat suitability models to improve ecological compensation. Biological Reviews 90: 314-329.

Murie, O.J. & M. Elbroch. 2005. Peterson field guide to animal tracks. 3rd ed. Houghton Mifflin Harcourt.

Naidoo, R., A. Balmford, P.J. Farraro, S. Polasky, T.H. Ricketts, & M. Rouget. 2006. Integrating economic costs into conservation planning. Trends in Ecology and Evolution 21: 681-687.

O'Farrell, T.P., N.E. Mathews, P.M. McCue & M.S. Kelly. 2016. Distributions of the endangered giant kangaroo rat, *Dipodomys ingens*, on the Naval Petroleum Reserves, California. (No. EGG-10282-2173). EG and G Energy Measurements, Inc., Goleta, CA (USA). Santa Barbara Operations.

Pearson, R.G. & T.P. Dawson. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? Global Ecology & Biogeography 12: 361-371.

Phillips, S.E. & B.L. Cypher. 2015. Solar energy development and endangered upland species of the San Joaquin Valley: Identifications of conflict zones. Prepared for: The California Department of Fish and Wildlife Agreement: P1440003 00.

PRISM Climate Group, Oregon State Univeristy, http://prism.oregonstate.edu, created 4 Feb 2004.

Prugh, L. R. & 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.

Prugh, L.R., N. Deguines, J.B. Grinath, K.N. Suding, W.T. Bean, R. Stafford & J.S. Brashares. 2018. Ecological winners and losers of extreme drought in California. Nature Climate Change 8: 819-824.

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

Pulliam, H. R. 2000. On the relationship between niche and distribution. Ecology Letters 3: 349-361.

Puttock, A.K., A.M. Cunliffe, K. Anderson & R.E. Brazier. 2015. Aerial photography collected with a multirotor drone reveals impact of Eurasian beaver reintroduction on ecosystem structure. Journal of Unmanned Vehicle Systems 3: 123-130.

Questad, E.J., J.R. Kellner, K. Kinney, S. Cordell, G.P. Asner, J. Thaxton, J. Diep, A. Uowolo, S. Brooks, N. Inman-Narahari, S.A. Evans & B. Tucker. 2014. Mapping habitat suitability for at-risk plant species and its implications for restoration and reintroduction. Ecological Applications 24: 385-395.

R Core Team. 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Rocchini, D., D.S. Boyd, J.B. Féret, G.M. Foody, K.S. He, A. Lausch, H. Nagendra, M. Wegmann & N. Pettorelli. 2015. Satellite remote sensing to monitor species diversity and potential pitfalls. Remote Sensing in Ecology and Conservation 2: 25-36.

Rutrough, A. I.V. Widick & W.T. Bean. revised review. Reconstruction of the historical range alters niche estimates for an endangered rodent.

Schooley, R.L. & J.A. Wiens. 2001. Dispersion of kangaroo rat mounds at multiple scales in New Mexico, USA. Landscape Ecology 16: 267-277.

Scheele, B.C., C.N. Foster, S.C. Banks & D.B. Lindenmayer. 2017. Niche contractions in declining species: mechanisms and consequences. Trends in Ecology and Evolution 32: 346-355.

Schlaepfer, M.A., M.C. Runge & P.W. Sherman. 2002. Ecological and evolutionary traps. Trends in Ecology and Evolution 17: 474-480.

Shaw, W.T. 1934. The ability of the giant kangaroo rat as a harvester and storer of seeds. Journal of Mammalogy 15: 275-286.

Sikes, R.S., W.L. Gannon & The Animal Care and Use Committee of the American Society of Mammalogists. 2011. Guidelines of the American Society of Mammalogists for the use of wild animals in research. Journal of Mammalogy 92: 235-253.

Smyser, T.J., R.J. Guenzel, C.N. Jaques & E.O. Garton. 2016. Double-observer evaluation of pronghorn aerial line-transect surveys. Wildlife Research 43: 474-481.

Statham, M.J., W.T. Bean, N. Alexander, M. F. Westphal, & B. Sacks. 2019. Historical population size change and differentiation of relict populations of the endangered giant kangaroo rat. Journal of Heredity, esz006, https://doi-org.ezproxy.humboldt.edu/10.1093/jhered/esz006

Stanley, T.R. & J.A. Royle. 2005. Estimating site occupancy and abundance using indirect detection indices. Journal of Wildlife Management 69: 874-883.

Stephenson, N. 1998. Actual evapotranspiration and deficit: biologically meaningful correlates of vegetation distribution across spatial scales. Journal of Biogeography 25: 855-870.

Stockwell, D.R.B. & A.T. Peterson. 2002. Effects of sampling size on accuracy of species distribution models. Ecological Modeling 148: 1-13.

Sutherland, W.J., A.S. Pullin, P.M. Dolman, & T.M. Knight. 2004. The need for evidence-based conservation. Trends in Ecology and Evolution 19: 305-308.

SZ DJI Technology Co., Ltd. 2018. DJI GO (Version 3.1.42) [Mobile application software]. Retrieved from http://itunes.apple.com.

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.

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.

Van Horne, B., R.L. Schooley, S.T. Knick, G.S. Olson & K.P. Burnham. 1997. Use of burrow entrances to indicate densities of Townsend's ground squirrels. The Journal of Wildlife Management 61: 92-101.

Vermeulen, C., P. Lejeune, J. Lisein, P. Sawadogo, P. Bouché. 2013. Unmanned aerial survey of elephants. PloS one: e54700.

VC Technology Ltd. 2018. Litchi for DJI Drones (Version 2.5.1) [Mobile application software]. Retrieved from http://itunes.apple.com.

Weissensteiner, M.H., J.W. Poelstra & J.B.W. Wolf. 2015. Low-budget ready-to-fly unmanned aerial vehicles: an effective tool for evaluation the nesting status of canopy-breeding bird species. Journal of Avian Biology 46: 425-430.

Widick, I., & W.T. Bean. 2019. Evaluating current and future range limits of an endangered, keystone rodent (Dipodomys ingens). Diversity and Distributions 00: 1-14.

Widick, I. 2018. Evaluating current and future range limits of an endangered, keystone rodent (Dipodomys ingens). Thesis, Humboldt State University, California, USA.

Williams, D. F. 1992. Geographic distribution and population status of the giant kangaroo rat, *Dipodomys ingens* (Rodentia, Heteromyidae). Endangered and Sensitive Species of the San Joaquin Valley, California: Their biology, management and conservation (D. F. Williams, S. Byrne & T. A. Rado, eds.). California Energy Commission, California State University, Bakersfield.

Wilson, K.A., M.I. Westphal, H.P. Possingham & J. Elith. 2005. Sensitivity of conservation planning to different approaches to using predicted species distribution data. Biological Conservation 22: 99-112.

APPENDICES

Appendix A: Sign categories recorded during non-invasive GKR surveys.

Sign type	Description
Grass clipping	Vegetation at survey point is clipped a couple of inches above the ground.
Haystacks	Pile of seeds and grass stalks on bare ground. Can be a couple of inches in diameter to a couple of meters.
Fresh apron	Pile of fresh dirt splayed out of a burrow entrance.
Tracks and tail drags	Kangaroo rat tracks include oblong parallel imprints from hind feet. May or may not include lines in the dirt from their tails dragging as they move slowly.
Pit caches	Tablespoon size imprints where GKRs stored seeds. There are often several in close proximity. Can cover the majority of the bare dirt around a precinct.
Scats	Smooth, slightly crescent shaped oblong scats measuring at least 1.5x5 mm, which is the size of the smallest scat collected from a GKRs during live trapping.
Runways	Narrow trails in the grass connecting burrows or precincts.
Miscellaneous signs of digging	Signs of digging that do not fall into the other categories listed here.
Large mound with burrows	Raised earth with one to several burrow entrances.
Newly backfilled burrows	Burrow with fresh (relatively dark and damp) loose dirt blocking the entrance.

Sign type	Description
Less vegetation on survey point then surrounding area	Survey area has more bare ground than surrounding area.
More vegetation on survey point than surrounding area	Vegetation is thicker at survey point than the area immediately surrounding it.
Holes obstructed by non-vegetation debris	Burrow has rocks or dirt that partially or fully obstruct entrance.
Hole entrances littered with plant matter	Burrow entrance has not been cleared of plant matter.
Unbroken spider webs in burrow entrances	Burrow has unbroken spider webs in entrance. Must fully obstruct entrance.
Undisturbed loose dirt	Soft loose dirt at survey point. No tracks or signs of recent digging.
No holes at survey point	Survey point lack holes or a precinct.

Appendix B: Track plate design protocol

The construction of the track plate housings followed a modified USGS protocol that was designed to detect pocket mice (Brehme et al. 2010). Each assemblage included two 2-foot segments of plastic rain gutters with 2 in wide flat bottoms, a 24 in x 2 in stiff plastic strip, two 2 in x 1.5 in felt pads, a 21 in x 2 in piece of blotter paper, millet based birdseed, glue, binder clips, bolts, eye bolts, washers, railroad spikes, a gallon milk jug, empty condiment bottles, food-grade mineral oil and powdered charcoal (Figure 3).

Felt pads were glued on the ends of the stiff plastic boards and holes for the bolts were drilled into the gutter segments 4 inches from the ends on all sides and the plate housings were assembled by attaching two pieces of gutter together with alternating bolts and eye bolts. Shortly before deploying the track plates about a tablespoon of birdseed was glued in the center of blotter paper using non-toxic glue sticks. The baited blotter paper was places on the stiff plastic backing between the felt pads and secured using binder clips with the handles removed after clipping. This assemblage was placed inside the gutter housing and secured to the bottom, also using binder clips with the handles removed. A 1:4 combination of mineral oil and charcoal were mixed in the gallon jug and then distributed into condiment bottles for easy pouring. The felt pads were saturated with the charcoal mixture, and track plate constructing secured to the ground by hammering railroad spikes through the eyebolt loops so that animals such as ravens, foxes, and coyotes could not move them (Figure 3).

Appendix C: Boosted regression tree model selection for models predicting trapping results from sign surveys, sorted by deviance.

Complexity	Learning rate	Number of trees	Deviance	Deviance standard error	Cross-validation correlation	Cross-validation correlation standard error
5	0.005	950	0.584	0.095	0.789	0.044
4	0.005	900	0.608	0.081	0.793	0.039
4	0.0005	9200	0.614	0.091	0.7787	0.041
6	0.002	1950	0.616	0.085	0.791	0.039
6	0.0007	6000	0.619	0.113	0.772	0.053
4	0.004	1050	0.619	0.106	0.787	0.051
5	0.001	4450	0.620	0.103	0.784	0.045
6	0.0005	7950	0.622	0.084	0.778	0.039
5	0.002	2350	0.625	0.093	0.788	0.040
6	0.001	4000	0.626	0.098	0.783	0.042

Complexity	Learning rate	Number of trees	Deviance	Deviance standard error	Cross-validation correlation	Cross-validation correlation standard error
6	0.005	1000	0.626	0.095	0.787	0.043
5	0.004	1000	0.632	0.116	0.785	0.051
5	0.0007	5700	0.633	0.073	0.769	0.035
4	0.002	1800	0.634	0.109	0.755	0.063
5	0.0005	8150	0.643	0.095	0.781	0.041
5	0.003	1350	0.650	0.115	0.769	0.049
4	0.003	1700	0.651	0.075	0.778	0.032
6	0.004	900	0.652	0.104	0.771	0.057
6	0.003	1250	0.654	0.085	0.761	0.041
4	0.0007	6200	0.657	0.137	0.784	0.045
4	0.001	4050	0.685	0.109	0.751	0.052