Title

Spatial Ecology of the Giant Kangaroo Rat (Dipodomys ingens): A Test of Species Distribution Models as Ecological Revealers

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Spatial Ecology of the Giant Kangaroo Rat (*Dipodomys ingens*): A Test of Species Distribution Models as Ecological Revealers

by

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Monitoring a species' distribution and abundance is a critical component in both applied and theoretical ecology. Wildlife managers demand effective and efficient methods for monitoring species of concern. Theoretical ecologists, as well, need accurate estimates of species' distributions and abundance, and measures of the quality of habitat that determines these parameters. Recent advances in species distribution models have suggested an inexpensive and robust way forward for estimating habitat suitability, but these models have rarely addressed species distributions at ecologically relevant spatial or temporal scales. Further, few studies have examined the relationship between habitat suitability, as estimated from species distribution models, and habitat quality, a better predictor of long-term population persistence. In this study, I (1) test current methods for monitoring giant kangaroo rat population extent and abundance; (2) create novel species distribution models that incorporate primary productivity as an ecological predictor for giant kangaroo rat distribution; and (3) test whether these models are actually related to independent measures of habitat quality. Aerial surveys are shown to be a reliable estimator for giant kangaroo rat population extent. Burrow counts may be a reliable index of long-term population size, but are inadequate to detecting short-term changes in size or growth. Distribution models that incorporate ecologically relevant variables on annual time scales are shown to better predict giant kangaroo rat distribution than static models that assume the species is at equilibrium. Finally, species distribution models perform well at measuring long-term giant kangaroo rat abundance, and temporally explicit models predict short-term abundance, but species distribution models are generally incapable of adequately distinguishing between high and low quality habitat as measured by survival or body condition.

Dedication

I am not certain why anybody would stick around while I counted rats from space, but Piper Bean, you did. Your support, care and understanding are the reason this study exists. I, and the giant kangaroo rats, thank you for your sanity and grace. I thank my parents, William and Barbara Bean, for giving me a curiosity in, and care for, the world around us. And finally, to my sisters, Meg Salgado and Amanda Bean, for leading the way down the trail.

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Chapter 1. Introduction

Ecology is fundamentally interested in the processes affecting the distribution and abundance of species (Krebs 2008). Humans have long been interested in where animals occur and why. In 1851, Lieutenant Matthew Maury produced a map of seasonal whale distributions and abundance on the world's oceans using whaling ship's logs (Maury 1851, Melville 1851). Of course, most early methods for estimating the extent of species' ranges were limited to a field biologist's knowledge and research.

Recent advances in data collection and collation, and novel modeling techniques, have made it easy and inexpensive to produce maps of "habitat suitability" (probability of species presence) for virtually any species on earth. These "species distribution models" take as input spatially explicit records of species presence and use environmental covariates to estimate a geographical distribution and, some would argue, a species' niche. Statistical methods for building and testing these distributions include generalized linear models (e.g. logistic regression); generalized additive models; non-parametric models (e.g. classification and regression trees); and machine-learning methods such as Maxent (Elith et al. 2006, Phillips et al. 2006). It is now easier than ever to make a simple map of a species' distribution with freely available satellite imagery, interpolated climate maps, and countless records of species locations downloaded from museums around the world.

Unfortunately, "cheap" and "easy" methods are not necessarily accurate or robust. Ecologists have frequently criticized species distribution models for failing to take into account a species' natural history, and ignoring ecological covariates at relevant scales (Guisan and Thuiller 2005). Global climate datasets may be useful for estimating a species' distribution at a continental scale, but they are unlikely to tease apart the complicated ecological interactions that determine a species' distribution and abundance at smaller geographic and temporal scales (Chapter 3). Further, a historical split between field biologists and ecological modelers suggests that those who produce maps of habitat suitability may be in a poor position to understand a species' natural history. The best species distribution models should incorporate both novel datasets and modeling techniques, but also a strong knowledge of the focal organism.

Accurate and reliable estimates of species distribution and abundance are essential for ecologists, theoretical or applied, so it is critical that current methods for monitoring wildlife be tested and, where possible, improved. Here, I use the giant kangaroo rat (GKR, *Dipodomys ingens*) as a model species to test a number of current wildlife monitoring techniques, specifically the use of aerial surveys and aerial photographs to map population extent, and the use of active burrow counts as an index for population size and growth (Chapter 2). Next, I examine the possibility of incorporating remotely sensed measures of primary productivity into species distribution models to improve their accuracy (Chapter 3). Finally, I test whether species distribution models can accurately predict habitat quality (Chapter 4). For each distribution model, I incorporate ecologically relevant environmental covariates in an attempt to bridge the gap between species distribution modeling and traditional field biology.

Species distribution models are currently used both as an ecological predictor (i.e., to estimate suitability or quality in unstudied habitats), and as an ecological revealer (i.e., to test hypotheses about a species' relationship to its biotic and abiotic environment). Many distribution models may be used as adequate predictors without necessarily revealing anything about the species' ecological niche. The use of an easily measured independent variable as a proxy for a different variable may be reliable in predicting habitat quality but may also omit the real driver behind the species' distribution. A model that used only latitude and longitude to predict suitable habitat for a species may be quite robust, but it would say little about the ecology of the species in question. Such a model would be essentially useless as a model for future shifts under different climate change scenarios. The best models, then, would serve as both predictors and revealers.

The GKR is a federally- and state-endangered burrowing rodent endemic to California. Once found throughout the western portion of the San Joaquin Valley, habitat alteration and rodenticide has reduced it to a handful of populations in and around the California Coast Range (Williams 1992). Giant kangaroo rats are ecosystem engineers, creating burrow mounds 3-4m in diameter that host a suite of threatened and endangered species including the blunt-nosed leopard lizard (*Gambelia sila*), San Joaquin antelope squirrel (*Ammospermophilus nelsoni*) and San Joaquin woolly-threads (*Lembertia congdonii*).

GKR appear to have a unique ecological niche within California grasslands. Grinnell (1932) was among the first to note its narrow habitat requirements, describing GKR occupying gentle slopes in areas with less than 5" (12.7 cm) annual precipitation with loamy or fine loamy soils. Of course, with more accurate and more widely-dispersed measurements, we now know the areas GKR occupy receive closer to 25 cm annual precipitation, although Grinnell's estimates of soil type and slope were quite good (Chapter 3). Regardless, the narrow range of conditions that limit GKR have had a direct impact on their conservation status, and limit managers' actions for recovery to a handful of remaining areas in the California Coast Range.

Understanding the ecological requirements of GKR is a critical component to their conservation. In this study, I incorporate ecologically meaningful covariates to create distribution models for GKR that may function not only as habitat predictors, but also ecological revealers (Chapter 3). In particular, the relationship between GKR and annual precipitation has been a matter of considerable concern. Managers have hypothesized a unimodal response to precipitation, with GKR populations suffering from too little or too much rain (Germano et al. 2001). In particular, GKR in the Carrizo Plain National Monument suffered drastic population declines in two consecutive years of higher-than-normal precipitation in the late 1990s (R. Stafford, pers. comm.). Hypotheses for the GKR's negative relationship with higher rainfall include the proliferation of non-native grasses (Germano et al. 2001), invasion and subsequent competition from larger rodents (e.g. California ground squirrel (*Otospermophilus beecheyi*) limited by too little rain, or flooding of burrows and/or seed cache spoiling (J. Brown, pers. comm.). Teasing apart this relationship between GKR and annual precipitation will be crucial currently, as managers seek to expand and protect GKR populations, and into the future, as precipitation may be higher or more variable under different climate change scenarios (e.g., Coquard et al. 2004).

Here, I attempt to incorporate ecologically meaningful variables at relevant scales into species distribution models for the GKR. In testing whether these models can serve as better estimates for habitat suitability and habitat quality, they also may serve as ecological revealers. In particular, the normalized difference vegetation index (NDVI) has been shown to function as an effective estimate of primary productivity in grassland systems (Butterfield and Malmström 2009). Incorporating primary productivity into these distribution models appears to provide better estimates of habitat suitability (Chapter 3) and, by some measures, quality (Chapter 4). These models may therefore provide managers better estimates of habitat that ought to be prioritized for protection. In addition, incorporating climate variables directly tied to GKR persistence may provide a way forward in estimating the effects of climate change on GKR.

In most of my study area, I found GKR to be competitively dominant, to the near total exclusion of other small nocturnal mammals. I trapped at 100 sites in the Carrizo Plain National Monument and 50 sites in the Ciervo-Panoche Natural Area, and where GKRs were present I rarely caught any other species. Species trapped where GKR were absent included deer mouse (*Peromyscus maniculatus*), brush mouse (*Peromyscus boylii*), San Joaquin pocket mouse (*Perognathus inornatus*), southern grasshopper mouse (*Onychomys torridus*), desert woodrat (*Neotoma lepida*), as well as Heermann's kangaroo rat (*D. heermanni*), and short-nosed kangaroo rat (*D. nitratoides brevinasus*).

This work was conducted in the Carrizo Plain National Monument and Ciervo-Panoche Natural Area, both lying in the Coast Range of California. Both areas are dominated by non-native grasses, including red brome (*Bromus madritensis rubens*) and filaree (*Erodium cicutarium*), and native bunchgrass (*Poa secunda*), as well as ephedra (*Ephedra californica*) and saltbush (*Atriplex* spp.). Average precipitation is low and variable (Germano et al. 2011). Both areas were generally spared the agricultural development of the Central Valley due to their slightly higher elevation in the Coast Range and subsequent lack of irrigation. Both are now experiencing land-use change due to solar developments either proposed (Ciervo-Panoche) or under construction (Carrizo). Ongoing monitoring of the GKR will be a crucial aspect to their recovery and delisting.

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Chapter 2. An Evaluation of Monitoring Methods for the Endangered Giant Kangaroo Rat

Abstract

Accurate, reliable and efficient monitoring methods for detecting changes in the distribution and abundance of wildlife populations are the cornerstone of effective management. Aerial surveys of active burrow sites and ground counts of open burrows have been used to estimate distribution and abundance, respectively, of a number of rodent species. I compared the efficacy of these and other methods for estimating distribution, abundance, and population growth of the endangered giant kangaroo rat (*Dipodomys ingens*) to determine the best practices for monitoring. Specifically, I compared aerial surveys, rapid expert assessments, and live-trapping for estimating giant kangaroo rat range, and burrow counts and live-trapping for estimating abundance and growth. I carried out the study in the Carrizo Plain National Monument, California, USA, from 2007 to 2011. Expert rapid assessment of sites performed nearly as well as trapping in determining range extent, while aerial surveys provided estimates of total range extent but with less precision. Active burrow counts were adequate to determine relative abundance averaged over multiple years, but were not reliable as an estimate of annual population size or growth.

Introduction

Reliable indices for monitoring changes in a species' range extent and abundance are a fundamental component of wildlife management. Burrow monitoring is a commonly used method for estimating range extent and abundance for a variety of mammal species (Powell et al. 1994, Van Horne et al. 1997, Lisicka et al. 2007). Burrow monitoring potentially replaces more expensive, and often invasive, methods for estimating range extent (e.g., occupancy trapping) and population size (e.g., mark–recapture). However, estimates based on burrow monitoring are seldom rigorously evaluated, particularly insofar as to their accuracy in reliably assessing 3 critical questions: 1) Where is the species of interest present? 2) At what density? and 3) How is the abundance of the population changing?

Efforts to monitor small mammal populations indirectly by quantifying the number and distribution of active burrows take several forms. These include aerial surveys, expert assessment of aerial imagery and ground counts. Aerial survey of rodent distribution has the potential to be a cheap and accurate method for determining population status (Sidle et al. 2001, White et al. 2005, Odell et al. 2008), but only a small number of assessments of survey applicability have been reported. Although ground surveys may be more reliable in determining precise location data, aerial surveys can provide important information on the areal (i.e., complete) range extent at low cost per unit area. Aerial surveys have proven effective in some, but not all, contexts. For example, a series of studies of black-tailed prairie dog (*Cynomys ludovicianus*) colonies in eastern Colorado, USA, suggested that aerial surveys are an effective tool to estimate distribution of active colonies of burrowing rodents (Sidle et al. 2001, White et al. 2005, Odell et al. 2008). In contrast, aerial surveys of North American beaver (*Castor canadensis*) distribution have not been as successful. Payne (1981) and Robel and Fox (1993) found that ground surveys were better able to identify active beaver sites.

Just as aerial surveys may be useful in determining range extent, estimating population abundance and growth from ground-based counts of active burrows may also be a more cost-effective tool for management than are mark–recapture techniques. However, the effectiveness of burrowing activity as a measure of population size has been inconsistent among different studies. Most studies have found burrowing activity to be reliable for estimating occupancy, but less accurate at estimating density or, importantly, changes in density. Evaluating counts of burrow entrances for the Townsend's ground squirrel (*Urocitellus townsendii*), Van Horne et al. (1997) found that a) burrow counts did not correlate with density estimates from trapping data, b) repeated counts varied through time in a single season, and c) individual observers were inconsistent in their burrow counting. Similarly, Powell et al. (1994) found little correlation between burrow entrance densities and aboveground counts of black-tailed prairie dogs. Further complicating the issue, Lisicka et al. (2007) found a nonlinear relationship between burrow indices for common voles (*Microtus arvalis*), with estimates 'quite reliable' at high densities, but with errors >400% in low-density populations.

Useful population indices ought to closely resemble absolute population numbers. However, because indices (e.g., burrow openings, scat, tracks) may not directly correlate with abundance, they may need first to be calibrated with absolute abundance. In these cases, simple regression techniques may be applied in order to adjust counts of sign to fit population estimates; more complicated models might also incorporate external factors (e.g., disease, weather). In order to be useful, however, the regression model must not change over time. If the models do change over time, the index may not be used without measured abundance data (Caughley 1977). Further, although population indices may be useful in contrasting habitats of 'high' and 'low' abundance, their use in estimating population change over time is more problematic. Many studies of population indices are compared only with a single, fixed population abundance, rather than change in abundance over time (Rotella and Ratti 1986, Forsyth et al. 2007). If the variance between population indices and actual population size is large enough, managers may find a situation where the correlation in abundance is significant but the correlation in growth rates is not.

Here, I assess and compare 5 monitoring techniques frequently employed in monitoring the giant kangaroo rat (GKR; *Dipodomys ingens*). The GKR is a California-listed and federally listed endangered, fossorial rodent. Giant kangaroo rats spend the summer months clearing vegetation from a circle of approximately 2–4 m in diameter surrounding their main burrow entrance. This clearing results in characteristic and highly visible circles of bare soil. These circles are a species-specific sign of GKR occupancy and allow for semi-annual aerial surveys of their distribution (Bean et al. 2011). In addition, GKRs are believed to be solitary (Randall et al. 2002), and therefore counts of active burrows are thought to provide a direct estimate of density.

I assessed multiple methods of monitoring GKR range extent, abundance, and growth rate within the Carrizo Plain National Monument, California, USA. Specifically, I compare trapping across the Monument with aerial surveys, expert assessment of aerial photography, and in situ rapid assessment of occupancy as measures of range extent. I then compare mark–recapture estimates of density with active burrow counts as measures of both GKR density and population growth rates.

Methods

Study Area

The Carrizo Plain National Monument (35.19°N, 119.73°W) was the largest, relatively intact portion of San Joaquin Valley desert grassland (Germano et al. 2011). The Plain, in eastern San Luis Obispo County, California, lay approximately 700 m above sea level and was 1,012 km^2 in extent. The majority of the Monument consisted of the Carrizo and Elkhorn Plains, both key areas for GKR recovery. Annual precipitation in Carrizo averaged 230 mm, with the majority of rain falling from October through April. Precipitation was variable (SD = 102 mm). Vegetation was characterized by nonnative annual grasses (e.g., *Bromus madritensis rubens*), with some areas dominated by native bunchgrass (e.g., *Poa secunda*) and *Ephedra* scrubland. During the spring, cattle grazing was permitted most years on portions of the Monument.

Estimating Distribution Extent

I estimated extent of GKR distribution in the Monument using 4 methods: live-trapping, rapid expert assessment, aerial photographs, and aerial surveys. Trapping was considered to be the ‘best’ method in that it was assumed to provide results that most closely represent the actual presence or absence of GKRs in areas trapped. Aerial surveys and aerial photographs were considered less reliable due to the potential difficulty in distinguishing occupied from unoccupied burrows. Results of the aerial surveys and photographs, and of rapid assessment, were compared against the trapping data to evaluate their performance.

Using Hawth’s Tools and ArcGIS 9.3, I randomly selected 85 sites throughout the Monument for live-trapping. Each trapping site was located between 50 m and 250 m from an accessible road. At each site, before setting traps on the first night, I estimated GKR activity in the area by searching in a 100-m radius for areas of bare, recently disturbed soil. Giant kangaroo rats leave characteristic tail drags in soil, and create circular burrow openings approximately 60 mm in diameter (Williams 1992). I conducted 20-minute estimates of activity at each site using these signs as characteristics of GKR presence. This estimation served as a rapid assessment of the site.

I then set 5 traps on burrows that appeared to be active. If I could not find active burrows, traps were place on apparently inactive burrows. If the site had no detectable GKR burrows, I placed traps near other rodent burrows. I trapped each site for 3 nights from June through August 2010, and again in June 2011. Sites were classified as occupied if ≥ 1 GKR was trapped, or if I heard foot-drumming at the site or saw GKRs while setting or closing traps. The GKR is the only species of rodent that performs foot-drumming displays in our study area. Trapping was conducted under authorization from University of California Animal Care and Use Committee (R304), U.S. Fish and Wildlife Service (TE1572210), and California Department of Fish and Game (SC 9452).

California Fish and Game personnel conducted aerial surveys of the study area on 27 October 2010 and 14 and 15 August 2011. Two observers flew straight-line transects in a small plane across the Monument at approximately 145 km/hour at approximately 250-m altitude, recording flight path and location points whenever the plane entered or exited an area of GKR activity. Each transect was separated by 800 m, global positioning system points were connected along the flight paths using ArcGIS 9.3, and buffered by 400 m on each side to represent the estimated range extent from the surveys.

I obtained a 100-km^2 aerial photograph of the central portion (10%) of the Monument, taken in early November 2010. The photograph coincided with 30 trapping sites. Two independent observers (L. Prugh and C. Gurney) with experience working with GKRs, though not at the sites in question, viewed the area of the image that showed each trapping site, and they estimated GKR presence or absence.

I compared each method of distribution mapping with the distribution extent estimated from trapping using multiple metrics of agreement: percent correctly classified; sensitivity (the percent of correctly identified presences); specificity (the percent of correctly identified absences); and the true skill statistic (TSS), a commonly used metric for estimating observer agreement. True skill statistic scores >0.5 are considered strong, while scores <0.4 represent unreliable agreement (Allouche et al. 2006); TSS scores that differed by >0.05 were considered significantly different (Rubidge et al. 2011).

Estimating Animal Density

In April and August of 2007, 2008, and 2009, colleagues (L. Prugh, pers. comm..) estimated GKR abundance and growth using mark–recapture trapping at 30 sites (Krebs 1999). At each site, they placed 60 traps on a 11 × 11 grid in a checkerboard fashion (i.e., at every other point on the grid) with traps spaced at 20 m. Sites were trapped for 3 nights/session. Giant kangaroo rats were tagged with a Passive Integrated Transponder tag and a National Band and Tag ear tag (Newport, KY). Density was estimated using the RDHet model (robust design with heterogeneity) in the RMark package (Laake 2009). Growth was then calculated from estimates of abundance using the standard equation for discrete growth (λ): N_{t+1}/N_t. I assumed that mark–recapture data provided the most accurate estimates of density and growth, against which I compared burrow count estimates. Additional details of this trapping are provided in Prugh and Brashares (2010, 2011).

In 2007, colleagues conducted ground-based mapping of active and inactive GKR burrows using a map of the trapping grid to record precise locations. In 2008 and 2009, I digitized burrows from an image acquired by the Quickbird-2 satellite (Fig 2-1B), and I then classified each burrow as active or inactive based on visual inspection on the ground, with the digitized burrows stored in a Trimble GeoXH (Trimble Navigation, Ltd., Sunnyvale, CA). Burrows were classified as active if there were signs of fresh digging, vegetation clipping, and evidence of tail dragging, a characteristic that distinguished GKRs from the co-occurring San Joaquin antelope squirrel (*Ammospermophilus nelsoni*). Researchers who mapped burrows had experience with trapping GKRs, as well as expertise in distinguishing between active and inactive burrows.

I compared population size (in 2007, 2008, and 2009) and growth (2008–2009) estimates between methods using Spearman rank correlations, because estimate values were nonnormally distributed. I did not compare growth for 2007–2008 due to the slightly different methodologies in burrow counting. In order to assess inter-annual changes in the relationship between burrow counts and mark–recapture estimates, I conducted an analysis of variance with year as a factor (Crawley 2005). Finally, to test the capability of active burrow counts as indices of relative abundance over time (i.e., as a relative metric of habitat quality or potential carrying capacity), I compared burrow counts from each year to the 3-year mean mark–recapture estimates.

Results

Estimating Distribution Extent

Giant kangaroo rats were trapped, seen, or heard at 55% of occupancy trap sites in 2010 and at 64% of sites in 2011. Only 4 sites in 2010 and 2 sites in 2011 were occupied by GKRs but not trapped (i.e., seen or heard only). Both aerial surveys and expert rapid assessment methods were reasonably accurate when compared against spatial results of trapping, while accuracy of estimation from aerial photographs was less reliable (Table 2-1). Expert assessment had the highest agreement score of any method, with 91% total agreement with trapping results in both years, and a high mean TSS of 0.795. Mean sensitivity from expert assessment, the percent correctly classified as active, was 96%. Mean specificity, the percent correctly classified as inactive, was 83% (7 sites incorrectly classified as absent; Table 2-1).

Aerial surveys correctly classified a relatively high percent of sites ($\bar{x}$ = 79%), and the TSS ($\bar{x}$ = 0.55), while still ‘strong,’ was not as high as with on-the-ground rapid assessment (Table 2-1). However, nearly all disagreements occurred within 500 m of the edge of GKR range extent, which suggests high accuracy but low precision of aerial surveys. Removing trapping locations situated within 0.5 km of the edge of the aerial surveys improved the mean TSS by 20% ($\bar{x}$ = 0.65).

Expert assessment of burrow activity from aerial photographs proved to be an inaccurate method for mapping GKR range extent, with one observer correctly classifying 70% of sites, and the other only 60%. True skill statistic scores were also much lower, with one observer scoring 0.40 and the other 0.20 (Table 2-1).

Estimating Animal Density

Estimates of GKR density based on burrow counts were positively correlated with mark–recapture estimates of GKR abundance both in 2007 ($\rho = 0.42$, $P = 0.02$, $n = 30$) and 2008 ($\rho = 0.72$, $P < 0.001$, $n = 30$; Fig. 2-2), but not in 2009 ($\rho = 0.17$, $P = 0.37$, $n = 30$). Burrow count estimates in 2008 were closest to a 1:1 relationship with measured GKR abundance (intercept = 7.75, slope = 0.89, $n = 30$), while burrow counts in 2007 and 2009 did not appear to have a 1:1 relationship (i.e., would have to be corrected to serve as a direct estimate of abundance). Further, I found both an effect of year and an interaction between year and burrow counts, which suggests an inconsistent relationship between active burrow counts and GKR density (Table 2-2). However, all 3 years of active burrow counts were significantly and positively correlated with the 3-year average GKR density estimated from mark–recapture data (2007: $\rho = 0.56$, $P < 0.01$, $n = 30$; 2008: $\rho = 0.70$, $P < 0.01$, $n = 30$; 2009: $\rho = 0.48$, $P < 0.01$, $n = 30$).

Giant kangaroo rat population growth rates calculated from burrow counts in 2008 and 2009 were weakly positively correlated with growth rates calculated from mark–recapture estimates ($\rho = 0.35$, $P = 0.07$, $n = 30$; Fig. 2-3). Generally, trapping sites identified as having a growing GKR population based on mark–recapture analysis were correctly assessed as growing by burrow counts (concurrence = 82%, $n = 11$). However, burrow counts performed poorly in detecting population declines; 76% of sites that showed a decline in GKR abundance from 2008 to 2009 using mark–recapture estimation ($n = 17$) were deemed to be increasing based only on burrow counts. In total, agreement was very weak (TSS = 0.06).

Discussion

Monitoring the range extent, abundance, and growth of wildlife populations can be an expensive, time-consuming process, but it is essential to effective management. Mark–recapture estimates of density and in situ estimates of occupancy are considered the gold standard for monitoring, but developing less expensive and less time-consuming methods is of great value to wildlife managers. I found aerial surveys and in situ rapid assessment to be adequate tools for monitoring the range extent (i.e., distribution) of GKRs. Counts of active burrows may be useful in determining relative abundance, but a comparison with intensive mark–recapture data suggested these methods were not adequate for assessing population change in GKRs over time (Table 2-1).

Wildlife managers in the Carrizo Plain National Monument have been using aerial surveys sporadically over the past decade to detect changes in GKR occupancy across the Monument (Bean et al. 2011). I found that, compared with in situ trapping, these methods were adequate to assess GKR distribution. However, although aerial surveys were accurate, they were not as precise as on-the-ground methods. For most management purposes, I suggest the small loss of precision is more than made up for by the increased information provided from the areal range, and the lower cost of aerial surveys.

Our comparison of indirect assessments of GKR activity and live-trapping revealed that estimating GKR site occupancy on the ground from burrows and activity was almost as accurate as trapping. Sensitivity (i.e., sites correctly classified as active) was particularly high (Table 2-1). Specificity (the sites correctly classified as absent) was lower. That is, through expert assessment, I categorized a number of sites as active, but trapping (and the associated listening and/or observing) did not detect any GKRs present. Errors of specificity are generally less desirable for wildlife managers; as a precautionary principle, it is better to under-estimate population size or extent than to over-estimate. For ongoing monitoring of GKR range extent, either aerial surveys or on-the-ground assessment may be considered reliable. Aerial surveys will provide areal maps of distribution, while on-the-ground assessment will be more precise but will provide less coverage. Aerial photographs are more expensive than aerial surveys and, from our results, do not appear to be a reliable method for mapping GKR extent. While I expected similar results between aerial surveys and photographs, I believe the loss of visual information in aerial photographs makes it difficult to distinguish occupied burrows from unoccupied burrows.

On-the-ground rapid assessment of GKR occupancy is not always reliable. In Carrizo Plain National Monument, GKRs tend to be a dominant nocturnal mammal, to the point of exclusion of other species. Based on our experience with a similar trapping design in the Ciervo–Panoche Natural Area of central California, GKR dominance is not always the case. In a more heterogeneous habitat, GKRs are much more likely to be found in areas with *Dipodomys heermanni* and *D. venustus.* In environments with higher *Dipodomys* diversity, it may be difficult to distinguish between the burrows of each species, because recent shifts in community structure appear to have resulted in *D. heermanni* and *D. venustus* occupying GKR burrows. In mixed communities, rapid assessment is much less reliable than trapping methods (W. T. Bean, unpublished data).

Active burrow counts appear to be a reliable method for determining long-term, relative abundance. Using active burrow counts, I found positive correlations in all 3 years of our study with a 3-year mean of GKR abundance. Unfortunately, I did not find the same reliability estimating single-year abundance or estimating population growth. Burrows tend to be very stable from year-to-year, and thus may be considered an indicator of long-term carrying capacity for a particular site. Because of this, it stands to reason that a site with a higher density of burrows will have a higher density of GKRs. However, while each burrow is occupied by a single GKR, this behavior can change depending on population density and season (Cooper and Randall 2007). In years of high density, GKRs have been known to share burrows, and in years of low density, GKRs may expand their home range to encompass multiple burrows (Cooper and Randall 2007). It is therefore not surprising that burrow counts do not provide a reliable measure of growth or decline.

Hubbs et al. (2000) tested infrared cameras as a way to count occupied burrows by detecting higher temperatures in tunnels with Arctic ground squirrels (*Urocitellus parryii*). Their approach was an accurate and less invasive method than trapping, and the authors found it a more reliable method than simple burrow counts for estimating density. However, the same problems that made burrow counts an unreliable estimator of abundance and growth for GKRs may plague an infrared monitoring project: a burrow shared by multiple GKRs would likely be indistinguishable from a burrow occupied by just one. Further, burrows occupied by other species (e.g., San Joaquin antelope squirrel) would also appear to be occupied by GKRs. On the other hand, burrows unoccupied but within the home range of a GKR would be more likely to be correctly classified. For this reason, infrared monitoring may be better at detecting population declines than would counts of active burrows. Until further tests can confirm the reliability of infrared monitoring in estimating growth, mark–recapture estimates remain the only appropriate approach to detecting changes in GKR abundance.

Monitoring GKR populations is a key component for their management. Stability of GKR populations is critical to their recovery, and efficient monitoring will be a cornerstone of their potential down-listing. In particular, ≥3 large-scale solar projects are in various stages of development within GKR habitat. Monitoring on these lands before and after installation, and on mitigation lands, will be a critical element in the projects' success. To this end, I re-iterate that mark–recapture estimates are currently the only dependable method for detecting changes in GKR population abundance, while aerial surveys and in situ rapid assessment are adequate tools for estimating range extent or occupancy, respectively.

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Tables

Table 2-1. Performance of methods used to monitor the giant kangaroo rat relative to estimates derived from extensive live-trapping in 2010 and 2011 in eastern San Luis Obispo County, California, USA.

Test	Sensitivity[a]	Specificity[b]	% correctly classified	True skill statistic (TSS)[c]
Rapid assessment (2010)	0.979	0.816	0.906	0.795
Rapid assessment (2011)	0.944	0.839	0.906	0.783
Aerial survey (2010)	0.851	0.658	0.765	0.509
Aerial survey (2011)	0.870	0.710	0.812	0.580
Aerial survey ± 0.5 km (2010)	0.925	0.679	0.824	0.604
Aerial survey ± 0.5 km (2011)	0.935	0.765	0.889	0.699
Aerial photograph (mean)	0.647	0.654	0.650	0.301

[a] Sensitivity was calculated as the ratio of sites correctly classified as active divided by total active sites (from the trapping data).

[b] Specificity was calculated as the ratio of sites correctly classified as inactive divided by total inactive sites.

[c] TSS is a frequently used measure of agreement; values >0.5 are considered 'strong,' while values <0.4 are considered 'poor.'

Table 2-2. Analysis of variance for active burrow counts and mark–recapture estimates of giant kangaroo rat density from 2007 to 2009 in eastern San Luis Obispo County, California, USA, with year as an interacting factor. Because year was a significant factor, both independently and as an interacting term, active burrow counts cannot serve as an estimate for inter-annual changes in GKR density without a correction factor (i.e., without mark–recapture estimates as a baseline).

Variable	df	Sum square	Mean square	*F*-value	Probability (> *F*)
Year	2	8,393.8	4,196.9	17.8	<0.001
Count	1	4,028.8	4,028.8	17.1	<0.001
Count:Year	2	2,608.2	1,304.1	5.5	<0.010

Figures

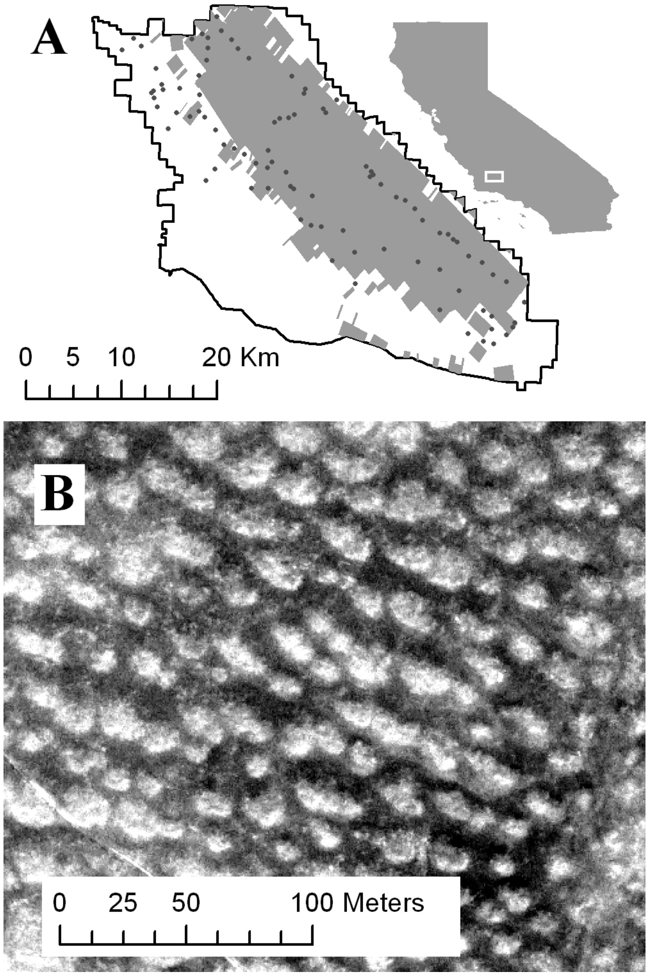

Figure 2-1. (A) Location of Carrizo Plain National Monument (black outline), eastern San Luis Obispo County, California, USA, with individual trapping locations used to determine range extent (shown as black dots). The grey polygon depicts the observed extent of giant kangaroo rats in 2011 from aerial surveys. (B) A sample from Quickbird imagery of active giant kangaroo rat burrows (shown in white). Individual burrows were digitized in 2008 and 2009 and then surveyed on the ground for activity.

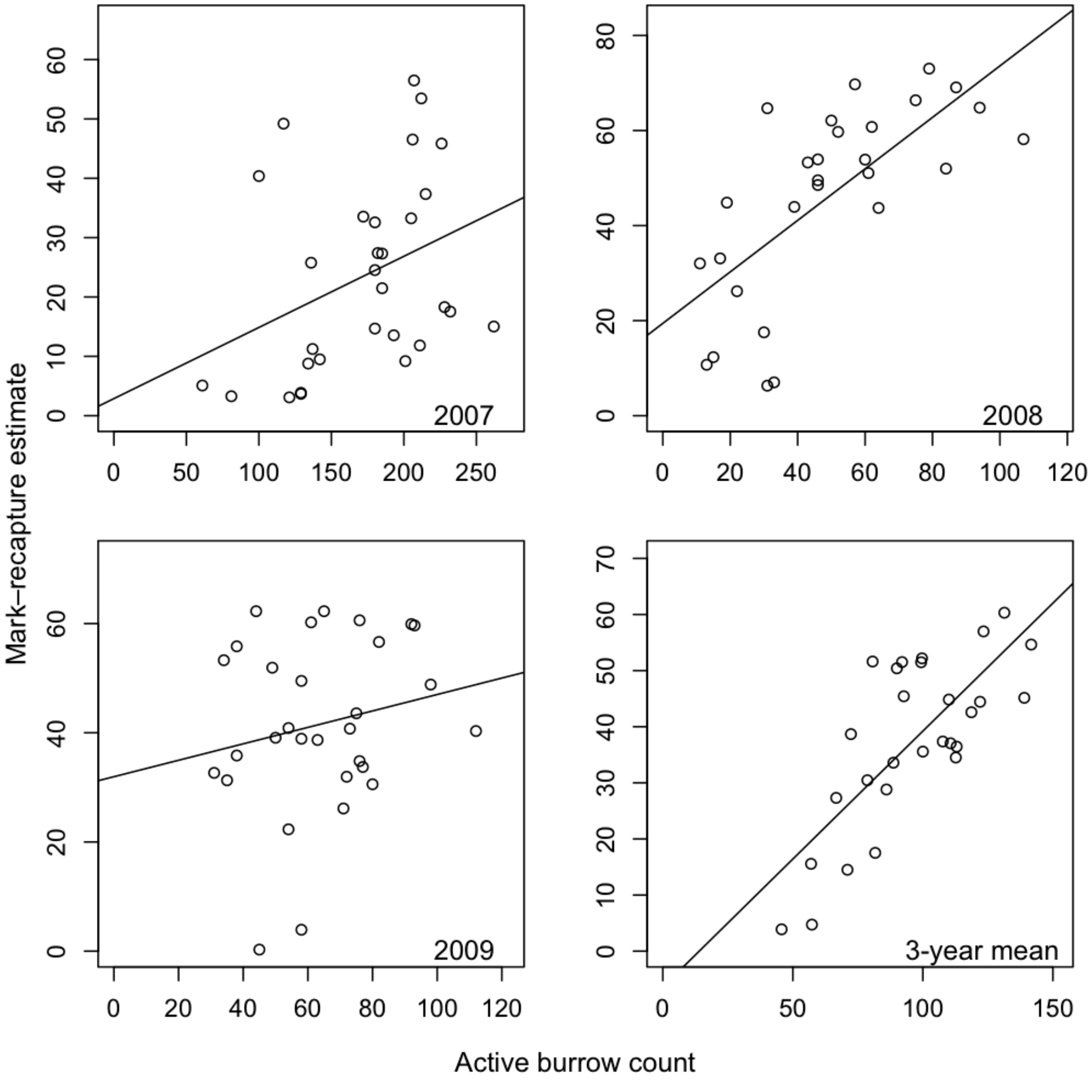

Figure 2-1. Relations between mark–recapture estimates of giant kangaroo rat density and counts of active burrows in 2007, 2008, and 2009 in eastern San Luis Obispo County, California, USA. 2007 and 2008 showed significant, positive correlations between density estimates, but the relationship between years was not consistent. While active burrow counts failed to detect inter-annual variability in giant kangaroo rat density, counts from each year and the mean counts across the 3 years were significantly, positively correlated with the 3-year average mark–recapture estimates of density.

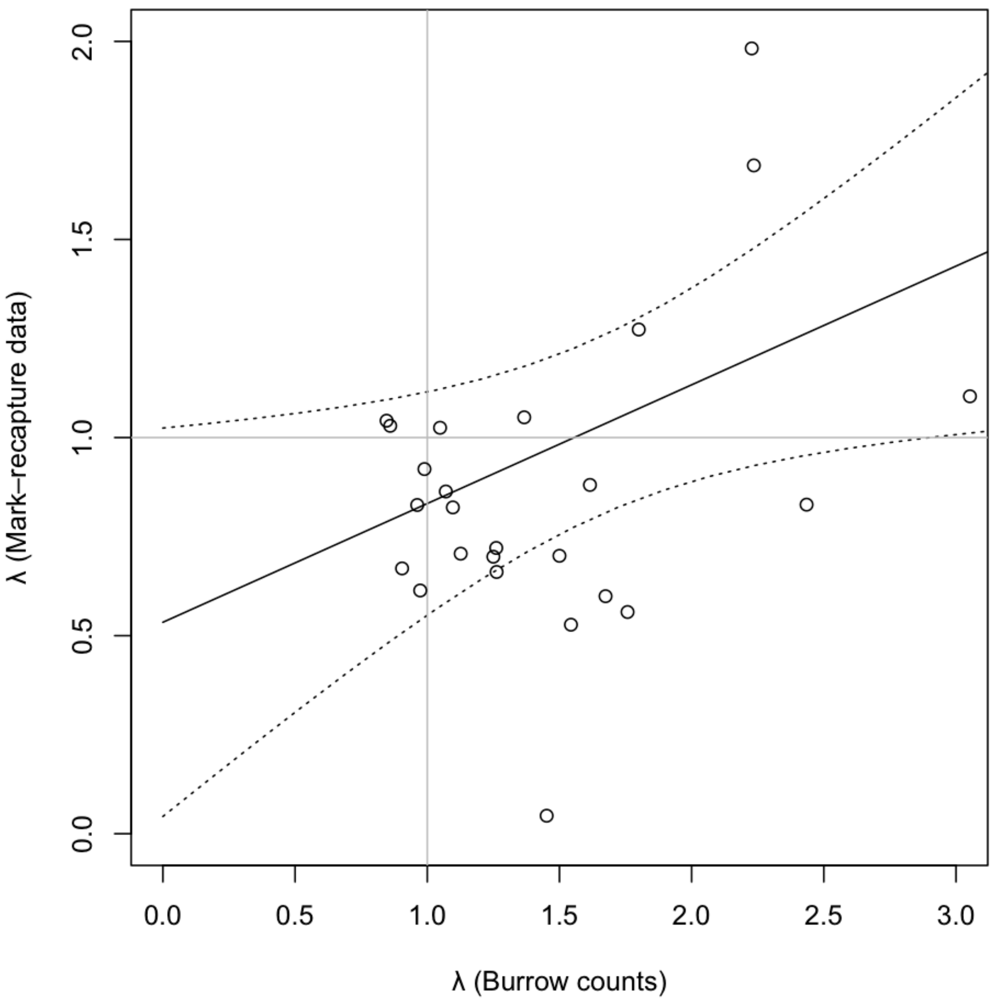

Figure 2-2. Relationship between site-specific population growth of the giant kangaroo rat estimated from mark–recapture data and estimates based on active burrow counts from 2008 to 2009 in eastern San Luis Obispo County, California, USA. Dashed lines show 95% confidence intervals of 'true' growth calculated from burrow counts. Detecting changes in growth (i.e., 'growing' or 'declining') would only be possible at the 95% confidence level at extreme values. At normal rates, population growth and decline were indistinguishable based on burrow counts.

Chapter 3. Multi-step realized distribution models suggest bottom-up control of population extent in an endangered rodent

Abstract

Species distributions are believed to be determined at two levels: the broad and relatively static association between physiological traits and environmental attributes (potential distribution), and the finer-scale, more dynamic response of individuals to variable ecological conditions (realized distribution). However, few species distribution models address these levels simultaneously. In this study, I created a multi-step distribution model for the giant kangaroo rat (*Dipodymys ingens*), first modeling its landscape-level, fixed environmental constraints, then within this theoretical potential distribution, estimating the limits on its realized distribution due to temporally-variable resource abundance. At the potential distribution level, the best model indicates *D. ingens* was limited to areas of low annual precipitation. In contrast, the best model of realized distribution showed a positive correlation between species presence and resource abundance in the current and previous year (*i.e.,* wetter areas). These results suggest that the distribution of the giant kangaroo rat was limited within its potential and realized distributions by resource abundance, but in opposite directions. This multi-step approach reinforces the differing relationship species may have with environmental variables at different scales, and suggests a way to create distribution models at spatial and temporal scales relevant to theoretical and applied ecologists.

Introduction

Species distribution models (a.k.a. habitat suitability, environmental niche, and bioclimatic envelope models) have become indispensable to practitioners from an array of fields (Guisan and Theurillat 2000). Such models have been used to ask questions relating to evolution (Graham et al. 2004, Kozak et al. 2008), ecology (Anderson et al. 2002), and conservation (Kremen et al. 2008). In these models, spatially explicit species occurrence data and environmental correlates are used to define the limits of a species' distribution (Guisan and Theurillat 2000). Most research in this area has focused on developing modeling techniques and assessing their accuracy using more traditional approaches (*e.g.,* generalized linear and generalized additive models) as well as more advanced techniques (*e.g.,* artificial neural networks, maximum entropy; for a review of modeling approaches see Elith et al. 2006). Less work has attempted to link distribution models to basic ecological niche theory. Indeed, at its root, the question of why a species occurs where it does is one of the defining questions of ecology. Yet, literature on distribution models often relies too heavily on ever-improving statistical modeling algorithms and not enough on the mechanisms that actually limit species in space and time (Austin 2007, Franklin 2010).

In 1917, Joseph Grinnell proposed (Grinnell 1917 and later formalized by Hutchinson 1957) the theory that a species' distribution is defined by its environmental (or “Grinnellian”) niche, the complete set of environmental variables and conditions where a species can exist indefinitely. It has long been assumed in species distribution modeling that this model represents, or is analogous to, a species’ Grinnellian niche. Specifically, the statistical model relates a species’ occurrence records (the response variable) to some collection of environmental correlates (the independent variables) to define the Grinnellian niche. However, a species’ distribution is limited not just by physiological constraints, but also by competition (Anderson et al. 2002), dispersal (Lidicker 2002, Guisan and Thuiller 2005), and source-sink dynamics (Hanski 1998). Hutchinson therefore divided a species’ distribution into two parts: its “fundamental” niche – the climate space that represents a species’ Grinnellian niche – and its “realized” niche – the restricted areas within the environmental space where a species can occur, taking into account competition, dispersal and source-sink dynamics (Pulliam 2000). Nevertheless, there is some controversy over the relation between a species’ niche and its distribution (Austin 2002, Soberon 2007), so I hereafter refer only to a species’ potential and realized distribution, with the caveat that the two concepts are fundamentally linked, and that the concept of a species’ distribution owes much to the field of niche theory.

Species distribution models address potential and realized distributions separately. Models developed from presence and confirmed absence data may directly estimate the probability of species presence (Johnson et al. 2006). However, models that use only presence data, or presence and pseudo-absence data may provide an estimate of use versus availability, but the interpretation of the models is debated. Because presence-pseudo-absence models offer no direct restrictions on where a species can occur, they may represent a hypothesis of the species’ potential distribution. The potential distribution can never be fully tested, although physiological (Kearney and Porter 2009) or translocation experiments (Cunningham et al. 2009) may provide supporting evidence. Including confirmed absences in a model allows for restrictions on a species distribution, and therefore more closely represents the realized distribution and habitat suitability. Jimenez-Valverde et al. (2008) provide a conceptual framework for the difference in these two approaches. Guisan and Thuiller (2005) conceive of modeling the potential and realized distributions along a spectrum: at large scales (e.g. continental), species distributions tend to approach their potential distribution, whereas locally, species are more limited by local community factors such as dispersal, predation and competition. Their work, echoing Hutchinson (1957), suggests a multi-step approach to modeling. That is, they encourage practitioners to first define a species’ potential distribution, and then model limiting factors within that area to define its realized distribution. This multi-step approach has been used to model realized distribution limited by dispersal (Pulliam 2000) and habitat type (Pearson et al. 2004), but resource availability has rarely been tested as a local control on potential distribution.

Resource availability has long been shown to limit population dynamics. In a spatial context, resource availability has been hypothesized as a limit on a species’ distribution (Grinnell 1917), and recent work has supported this (e.g. Pettorelli et al. 2005, Ito et al. 2006, Mueller et al. 2008). In particular, the temporal dynamics of resource availability can be critical to fine-scale distribution modeling. While species at large spatial and temporal scales may be considered at equilibrium, managers are frequently tasked with understanding shifts in distribution at much finer time intervals, such as between years or even seasons (Bissonette and Storch 2007). At such scales, variability of resources can greatly impact species distributions, particularly where the presence of a species is positively or negatively related with resource availability (Falcucci et al. 2009). A further complication is that species often vary in their local distribution seasonally or mult-annually.

Our ability to consider fine-scale variability in the availability of key resources is limited by the challenges inherant to quantifying resources continuously and regularly over large spatial and temporal scales. However,recent advances in remote sensing techniques have allowed for wide-scale estimates of resource abundance (Pettorelli et al. 2005). In particular, the use of the Normalized Difference Vegetation Index (hereafter “NDVI”) has been used as a reliable estimate of biomass in grassland systems (Kawamura et al. 2003), and population dynamics in herbivores have been shown to be correlated with NDVI, although most studies have focused on population-level demographics rather than distribution (e.g. Andreo et al. 2009, Hamel et al. 2009, Cao et al. 2011, Jiang et al. 2011). Fortunately, many contemporary satellites offer spectral bands that allow the user to compute spatially explicit NDVI values from an image.

In this study, I created a multi-step species distribution model for the giant kangaroo rat (*Dipodomys ingens*, hereafter “GKR”). First, I estimated the potential distribution of GKR using distribution data from four years of spatial monitoring collected over the past decade (2001, 2006, 2010 and 2011) and static environmental response variables using the software package Maxent (Phillips et al. 2006). Next, within the boundaries of the potential distribution, I created temporal models of realized distribution using a suite of primary productivity estimates. In particular, I predicted, based on ecological theory and previous work, that GKR presence would show a positive correlation with resource abundance, possibly with a time lag reflecting a delayed demographic response of GKR to resource availability. Other factors that may also limit population extent (*e.g.*, predation and competition) were not considered in these models.

Methods

Study Site and Focal Species

The giant kangaroo rat (GKR) is a state and federally endangered, burrowing, granivorous rodent endemic to California, USA. Once widespread in the western San Joaquin Valley, agriculture and other development have severely restricted its range to a half-dozen populations in and around the California Coast Range (Williams 1992). The GKR is considered both a keystone species and an ecosystem engineer (Goldingay et al. 1997, Prugh and Brashares 2012). GKRs’ extensive burrowing provides habitat for the federally endangered blunt-nosed leopard lizard (*Gambelia sila*) and state threatened San Joaquin antelope squirrel (*Ammospermophilus nelsoni*). In addition, GKR serve as the primary prey item of the endangered San Joaquin kit fox (*Vulpes macroitis mutica*; U.S. Fish and Wildlife Service 1998).

This study is based in the Carrizo Plain National Monument (hereafter "Carrizo"), an area that contains the largest remaining population of GKRs. While not situated directly within the San Joaquin Valley, Carrizo Plain represents the largest representative landscape of valley annual grassland (Germano et al. 2011). Carrizo experiences variable precipitation (mean = 20cm, sd = 10 cm) that contributes directly to variability in primary productivity, which in turn may drive dramatic annual changes in GKR distribution (Williams and Kilburn 1991). Understanding the role of primary productivity in driving these changes is crucial to biodiversity management in Carrizo. Both the size of the GKR population and its management and monitoring history make Carrizo an ideal study site for examining the role of resource availability on species distributions.

At a range-wide scale, GKR are thought to be limited to areas of low annual precipitation, gentle slopes, and coarse soils suitable for digging burrow systems (Williams and Kilburn 1991, Williams 1992). Within this fundamental distribution in Carrizo, primary productivity may be the main constraint on GKR. I therefore expected a multi-scale response to precipitation for GKR: at a large scale, I predicted GKR would be limited to dry areas. Within these dry areas, however, I predicted GKR distribution would be positively correlated with primary productivity. In other words, I expected the finer-scale analyses would show that GKR are limited to the wettest parts of the driest areas within their potential distribution.

Potential Distribution Modeling

I created a multi-step model to distribution, first estimating the potential GKR distribution within Carrizo using aerial surveys and Maxent, and then estimating limits to the potential distribution using resource abundance and logistic regression (Fig. 3-1).

As grasses around their burrows begin to senesce, GKR remove all vegetation from above their burrow (Grinnell 1932, Shaw 1934). This clipping activity creates a pockmarked landscape, with active burrows appearing as 3-4 m in diameter circles of bare soil in a matrix of dried grass. Such clipping has made it possible to map the annual distribution of GKR with aerial flight surveys (Bean et al. 2012, Chapter 2).

In 2001, 2006, 2010 and 2011, California Fish & Game personnel (B. Stafford) conducted monument-wide aerial flight surveys to estimate GKR extent (Bean et al. 2012, Chapter 2). Using 800 m wide transects (*i.e.*, monitoring 400 m on each side) and a GPS, they mapped the total extent of active burrows. Although it would be theoretically impossible to measure the potential distribution of GKR, historical maps and expert opinion suggest these four years, distributed throughout the past decade, represented a realistic sample of the potential distribution for GKR within Carrizo. In 2011 in particular, GKR population abundance and extent seemed to be at a recent maximum. However, because it may never be possible to observe the complete potential distribution (due to limits on their distribution from resource availability, predation, dispersal, *etc.*), I modeled the potential distribution using occurrence points from these four years. This model, extrapolated from the areas GKR were observed, served as an estimate of all the areas GKR could occur in Carrizo based on relatively fixed environmental constraints.

I used the software package Maxent to estimate GKR potential distribution (Phillips et al. 2006). Maxent uses a maximum entropy approach to estimate the most uniform distribution of a species' occurrence across the study area, constrained by the provided environmental correlates. Maxent is a presence-only model, and therefore may be expected to model the species' potential distribution. In fact, Maxent's creators explicitly state that the model created represents the species' potential distribution (Phillips et al. 2006). I combined the four years of observed GKR distributions into a single polygon using the *Merge* tool in ArcGIS 9.2 (Environmental Systems Research Institute 2011). I then randomly selected 250 points from within the areas of observed GKR extent using the *spsample* command in the R package *sp* (Bivand et al. 2008). Because I had an accurate approximation of the total GKR distribution within Carrizo for all four years, I could have selected a much higher number of sample points for the model. However, additional points may have over-constrained the model, resulting in a modeled distribution smaller than the potential distribution. Including too many samples from a limited area can result in a model that underestimates the total potential distribution (Bean et al. 2011). That is, if too many points are included from the known distribution, the model may be restricted to known areas and not include areas of potential distribution. 250 points has been shown to be a large enough sample to estimate a distribution without over-constraining the model (Hernandez et al. 2006).

To estimate the potential distribution for GKR in Carrizo, I selected a suite of fixed environmental variables believed to limit GKR distribution at a scale appropriate to this study. I used elevation and slope (United States Geological Survey 2006), soil texture derived from the SSURGO database (Soil Survey Staff), vegetation type (USDA Forest Service 2008), and mean annual precipitation (PRISM Climate Group 2006) as predictor variables. Soil, vegetation and mean annual precipitation layers were converted to raster format using ArcGIS 9.2 (Environmental Systems Research Institute 2011), and all inputs were analyzed at 30m resolution. I ran the model using the *dismo* package for R (Hijmans et al. 2012). Soil texture and vegetation type were considered categorical variables, with slope, elevation and precipitation considered continuous. All parameters in Maxent were set to their default. Spearman rank correlations were calculated for the independent variables and ranged from r=-0.46 to 0.75 (Table 3-1).

The output of the initial Maxent distribution model was a map of habitat suitability, with each 30m x 30m cell representing a probability of species presence. To convert the map from a continuous probability distribution to a binary map of potential distribution, I selected a probability threshold, above which cells were classified as potential GKR distribution and below which cells were classified as outside the potential distribution. A number of methods have been proposed for selecting thresholds (Liu et al. 2005, Bean et al. 2012). In order to err on the side of inclusiveness (*i.e.*, in order to best estimate the maximum potential distribution within Carrizo), I selected a threshold (0.185) in order to include 99% of presence points from the observed distributions as within the potential distribution.

This model of potential distribution was created within the boundaries of the Carrizo Plain National Monument. While models are typically created for an entire distribution (*e.g.*, Beaumont et al. 2009), I used a finer scale analysis to more accurately assess the potential distribution of GKR in Carrizo. However, to validate my approach and also facilitate comparison with other studies, I completed a second analysis using a more traditional approach of potential distribution modeling, using bioclimatic variables and GKR presence records from across their historical distribution. Results of that analysis are presented in Appendix 1. The variables limiting GKR distribution were different in the traditional model, but the modeled potential distribution within Carrizo was broadly similar, as were results of the realized distribution models.

Realized Distribution Modeling

Having produced an estimate of the potential distribution for GKR, I then examined the effects of biomass on GKR realized distribution for each year (2001, 2006, 2010 and 2011). Because of GKR reliance on grass seeds as a food resource, I expected a positive correlation between primary productivity and GKR presence. GKR dry and cache most of the seeds they collect (Shaw 1934), so GKR presence in a given area may lag primary productivity for a year or more.

To create a spatially explicit measure of primary productivity in Carrizo I acquired 16-day composites (250 m x 250 m) of NDVI measured by the Moderate Resolution Imaging Spectroradiometer (“MODIS”) satellite (Carroll et al. 2006). NDVI is calculated as

$$(NIR - R) / (NIR + R) \qquad \text{(Equation 1)}$$

where NIR represents the near infrared band (841 – 876nm), and R represents the red band (620 – 670nm). Values approaching -1.0 tend to represent areas with water, while areas greater than 0 and approaching 1.0 tend to represent areas of photosynthetic activity (Huete et al. 2002). Pre-processed 16-day composites of NDVI have been shown to accurately measure NDVI, and correlate well with biomass in grassland systems (Kawamura et al. 2003). For each year of analysis, I analyzed NDVI between early February of the previous year, to late August of the year in question. This period comprises the full growing season for vegetation in Carrizo as well as coverage of pre- and post-growing stages.

NDVI can be inflated by soil moisture if the soil is visible (Huete et al. 2002) and NDVI appeared to peak approximately 1-2 weeks before the typical peak growth in Carrizo, suggesting that soil moisture was influencing the measurement. However, precipitation and aboveground biomass are correlated and, despite the lag in measurements, peak NDVI has been shown to correlate with peak aboveground grassland biomass (Butterfield and Malmstrom 2009).

Although individual GKR burrows (~27m^2) represent a small fraction of a single MODIS pixel (250m^2), the heterogeneity of the landscape supports analyses at this scale.

The density and heterogeneity of the GKR burrows suggest that a mixed pixel with GKR activity will have a significantly different signal than one without GKR activity.

I created a suite of generalized linear models (GLM) to predict GKR presence using NDVI for each year. I examined two drivers of GKR presence: first, and of primary interest, I tested the effect of primary productivity (i.e., resource abundance) on GKR presence. Second, I tested if GKR presence in the previous year would also be a significant predictor of GKR presence in the current year. The independent variables included in the model to evaluate these predictions represented resource abundance in the current or previous year, or were proxies of GKR presence in the previous year (Table 3-2). I tested each hypothesis independently using 500 randomly sampled points from the aerial surveys in 2011 (Fig. 3-2). To estimate resource abundance, I used the highest recorded NDVI value for a given year as an estimate of primary productivity for that 250m x 250m cell. Primary productivity was measured for the current year, as well as the previous year.

For three of the four years of surveys, no estimate was available for GKR presence in the previous year. Instead of a direct estimate from aerial surveys, it was therefore necessary to create proxies of GKR presence in the previous year. Because GKR clear their burrow mounds of vegetation, I assumed that GKR would have a direct effect on NDVI after peak green up. First, I assumed that later in the summer, the areas with GKR would have lower plant biomass than areas without GKR. I therefore included the lowest measured NDVI value from later in the year (April to December) as a proxy for GKR presence, assuming a negative correlation between the two (*i.e.,* areas with GKR would have lower minimum NDVI). Second, I assumed that GKR removed vegetation from around their burrows faster than vegetation naturally senesced. To estimate vegetation removal by GKR, I measured the slope of NDVI decline from its peak. I subtracted the NDVI value from one time step after peak from the peak NDVI value, and again hypothesized that a larger difference would suggest GKR activity. These two measurements (minimum NDVI and NDVI slope) were used as proxies for GKR presence in an area, and in effect represent a null model of GKR distribution: if current GKR distribution could be predicted solely from the prior year's presence, plant biomass would not be considered a factor limiting the realized GKR distribution.

GKR distribution models were ranked using Maximum Likelihood Estimation and Akaike Information Criteria (AIC) (Burnham and Anderson 2002). Models were created for all of the presence points, with year included as a fixed effect. For each year of the model, I used 1,000 random points from the potential distribution, 500 within GKR realized distribution and 500 outside active areas. The accuracy of the best model (as identified using AIC) was assessed with the PresenceAbsence package in R (Freeman and Moisen 2008). For each model, I calculated the area under the curve (AUC), a common threshold-independent method for assessing accuracy (Hanley and McNeil 1982). Values greater than 0.5 are considered better than random, while values higher than 0.7 are considered "useful" (Pearce and Ferrier 2000). I also calculated a threshold to map predicted presence and absence points for each model. Each threshold was calculated using the mean probability of presence technique (Cramer 2003). I then calculated the percent correctly classified (PCC), Cohen's kappa, sensitivity, specificity, and the true skill statistic (TSS, sensitivity + specificity - 1), a prevalence-independent measure of accuracy (Allouche et al. 2006).

Results

Potential Distribution Modeling

The area classified in the Maxent model as the potential distribution of giant kangaroo rats (GKR) closely resembled the combined distribution from 2001, 2006, 2010 and 2011 (Fig 3-2). However, there were portions of Carrizo in the northwest and southeast classified as suitable that were not part of the realized distribution in any of the years monitored. AUC for the potential distribution model was 0.729.

Mean annual precipitation contributed 55.9% of the "training value" (a Maxent-specific term equivalent to the amount of variance explained by a particular variable) to the model. GKR was negatively related with mean annual precipitation, with a threshold at about 28 cm annual precipitation. Vegetation type (17.3%) and slope (13.7%) were present in the Maxent potential distribution model but contributed less information to the model than annual precipitation. As expected, GKR presence was negatively related with slope, positively related with annual grassland and negatively related with all other vegetation types.

Realized Distribution Modeling

In the best model of GKR realized distribution, the distribution was positively related with primary productivity in both the previous and current year, suggesting a strong influence of bottom-up regulation on GKR distribution (Table 3-3). GKR presence in the previous year also was an important predictor of GKR presence in the current year. Both proxies of prior GKR presence performed as expected: GKR distribution was negatively correlated with both minimum NDVI and the slope from the peak NDVI from the previous year. Realized distribution model accuracy was "useful" (AUC = 0.77). The threshold was set at 0.50 (as expected, due to the prevalence of the model data (Liu et al. 2005)). Model sensitivity was 0.68 and specificity 0.69. The model Kappa score was 3.1 and the true skill statistic (TSS) was 0.38. The best model correctly classified 68.8% of all test points as inside or outside the GKR's estimated realized distribution.

Discussion

Species distribution modeling has been a rapidly developing area of research, focused more on the modeling (*i.e.,* mathematical and statistical approaches) and less on integration with ecological theory. This study joins a growing body of literature that attempts to use ecological theory to inform and interpret species distribution models (e.g. Pearson et al. 2004, Rushton et al. 2004, Austin 2007, Anderson et al. 2009). Specifically, I presented a technique of multi-step modeling to define a species' potential and realized distribution, and in doing so explored the relationship between primary productivity and animal distribution.

Consistent with ecological theory, my results showed that the potential distribution of giant kangaroo rats (GKR) was larger than any of the distributions observed in the four years I sampled. In other words, there were areas within Carrizo that should have been suitable for GKR, but monitoring documented them as uninhabited. This result supports conclusions of Guisan and Thuiller (2005), and Grinnell (1917) and Hutchinson (1957) before them, who suggested that species' distributions are limited by more than fixed environmental conditions, a fundamentally important concept for distribution modelers and ecologists. The fact that distribution models built only on static bioclimatic factors may poorly estimate realized distributions has several important implications for how these models are applied to questions in biodiversity conservation. For example, distribution models are often relied upon to project the impact of climate change on species' distributions. Without incorporating mechanisms that limit the focal species' realized distribution, these models are likely over-estimating the range of conditions within which the species will survive and reproduce under different climate change scenarios (Pearson and Dawson 2003, Franklin 2010). At the same time, we may be ignoring important local ecological processes by examining patterns of distribution at range-wide spatial scales (Morin and Thuiller 2009). In this study, GKR potential distribution was limited by annual rainfall; therefore, any future increase in average annual precipitation would be expected to reduce GKR distribution. However, I found that within the area of potential distribution, GKR were positively correlated with primary productivity (driven by annual precipitation). It is possible, then, that an increase in mean annual precipitation would decrease the potential distribution range-wide (where agriculture has already rendered suitable habitat uninhabitable), but increase the realized distribution within a core conservation area.

Within the potential distribution, I found that the best model of factors limiting the realized distribution of GKR showed a clear, positive correlation between primary productivity (measured as peak NDVI) and the presence of GKR in the previous year. This result conforms to recent findings from studies of other species that show rapid changes in distribution in response to temporal and spatial variability of NDVI (*e.g.,* Mongolian gazelles (*Procapra gutturosa*; Ito et al. 2006, Mueller et al. 2008); African buffalo (*Syncerus caffer*; Ryan et al. 2006); Viña et al. 2008).

This study of GKR distribution in Carrizo, while conducted at a relatively small spatial scale, focused on the temporal dynamics of species' distributions. Niche and distribution theory tend to assume a species is at equilibrium, but this study and others (e.g., Suarez-Seoane et al. 2008, Bissonette and Storch 2007) show that for many applications, considering the temporal dynamics of a species' distribution is essential. Although the importance of non-static suitability models in grassland systems has been recognized (Fryxell et al. 2004), the difficulties in addressing such variability have thus far limited research in this area (Fernandez-Gimenez and Allen-Diaz 1999).

This study focused specifically on resource abundance as a limiting factor for GKR. Other factors that often limit a species' realized distribution – predation, parasitism, competition and dispersal – were not believed to be limiting factors for GKR in Carrizo. Within the study area, the open and flat topography, coupled with GKR reproductive habits allow for rapid dispersal. Within Carrizo, GKR appear to be competitively dominant (Grinnell 1932, Prugh and Brashares 2012). Because of these features of their ecology, GKR distribution was less likely to be affected by dispersal or competition and, thus, the GKR was a good species for testing models of realized distribution based solely on resource abundance.

While the approach presented here combining distribution models at different scales allows new insights, it is not without its shortcomings. One particular problem is our inability to identify the "true" potential distribution. By its very nature, it may be impossible to know a species' potential distribution; in fact the potential distribution may only be a theoretical construct. We can only measure the realized distribution and estimate the potential distribution from those measurements. This issue is highlighted regularly in the invasive species modeling literature. Species that appear to have a limited distribution in their native range often show a spectacular ability to live in "unsuitable" conditions when introduced to new areas (e.g. Steiner et al. 2008, Beaumont et al. 2009). In these cases, the species' realized distribution in its native range is so limited by competition, dispersal, and other ecological factors that any estimate of its potential distribution will be woefully inadequate for predicting the spread of a species. Oftentimes, ecological limits to the realized distribution may be correlated with environmental conditions, thereby preventing true knowledge of the species' limits of its potential distribution. In this case, additional steps (e.g. physiological tests) may be required to estimate its potential distribution.

As for GKR's competitive dominance, the relationship between precipitation limitation and competition may be impossible to untangle. The *Heteromyidae* in general appear to have evolved to claim a desert-grassland niche unfilled by other small mammals. The observed boundary of 28 cm mean annual precipitation may be as much related to the *lower* limit for larger rodents (e.g. the California ground squirrel, *Otospermophilus beecheyi*) than an upper limit for GKR. Again, this illustrates the conceptual difficulty surrounding niche theory, but the temporal mechanisms outlined in this study ought to remain relevant. Assuming the average annual precipitation remains unchanged in Carrizo, there will be a hard limit on GKR distribution at about 28 cm. Of course, the potential for a changing climate may have great impacts on what appear to be relatively stable environmental conditions. GKR display different responses to precipitation at range-wide and local scales. This fact is a crucial finding for those interested in modeling ecologically relevant species' distributions.

Incorporating detailed mechanisms into species distribution models, at ecologically relevant scales and informed by ecological theory is an important next step in the field of spatial ecology. I have presented an approach to estimating a species' potential distribution and address questions about the ecological limits to its realized distribution. I presented further evidence that a species is often limited not just by fixed, environmental conditions, but also other ecological conditions that vary spatially and temporally. Such research will be important as species distribution modeling moves from the “how” to the “why.”

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Tables

Table 3-1. Spearman rank correlations between independent variables used in modeling the potential distribution of giant kangaroo rat in Carrizo, CA. All variables are represented by 500 points randomly selected from within the study area. Vegetation type was obtained from the CALVEG project, and classified into categories by cover type. Soil texture was obtained from the SSURGO project and classified into categories (loam, clay, silt, sand, and combinations therein). All correlations were significant ($p<0.05$).

	Elevation	**Mean Annual Precipitation**	**Slope**	**Soil Texture**	**Vegetation Type**
Elevation	1				
Mean Annual Precipitation	0.69	1			
Slope	0.75	0.05	1		
Soil texture	-0.16	-0.26	-0.15	1	
Vegetation Type	-0.44	-0.46	-0.40	-0.17	1

Table 3-2. Hypothesized relationships between estimates of primary productivity (NDVI) and the local presence of the giant kangaroo rat. T1 represents the Normalized Differential Vegetation Index data from the same year as the rat distribution was estimated; T0 is data from the previous year.

Candidate Predictors	**Hypothesized Mechanism**
Maximum $\text{NDVI}_{T1,T0}$	Estimate of primary productivity, a bottom-up limitation on GKR presence (with potential one year lag)
Minimum NDVI_{T0}	Proxy for GKR presence in previous year
NDVI slope during plant senescence_{T0}	Proxy for GKR presence in previous year (GKR remove vegetation more quickly than it senesces)

Table 3-3. Logistic regression of GKR presence in relation to NDVI. The full model performed the strongest. In this model, GKR presence is positively correlated with peak primary productivity in the current year and previous year, and negatively correlated with minimum NDVI and NDVI slope in the previous year. This suggests that the best predictor of GKR presence in a given year is a positive correlation with resource abundance over two years, and presence in the area the previous year.

Model	**AIC**	**ΔAIC**	**w_i**
-1.40 + 7.66*$\mathrm{MaxNDVI}_{T1}$ + 4.57*$\mathrm{MaxNDVI}_{T0}$ – 28.2*$\mathrm{MinNDVI}_{T0}$ - 3.09*$\mathrm{SlopeNDVI}_{T0}$	**4,563.3**	**0**	**1**
$\mathrm{MaxNDVI}_{T1}$ + $\mathrm{MaxNDVI}_{T0}$ + $\mathrm{MinNDVI}_{T0}$	4,584.5	21.2	0
MaxDVI_{T1} + $\mathrm{MinNDVI}_{T0}$ + $\mathrm{SlopeNDVI}_{T0}$	4,618.5	55.2	0
$\mathrm{MaxNDVI}_{T1}$ + $\mathrm{MinNDVI}_{T0}$	4,636.9	73.5	0
$\mathrm{MaxNDVI}_{T0}$ + $\mathrm{MinNDVI}_{T0}$ + $\mathrm{SlopeNDVI}_{T0}$	4,766.1	202.8	0
$\mathrm{MaxNDVI}_{T0}$ + $\mathrm{MinNDVI}_{T0}$	4,775.1	211.8	0
$\mathrm{MaxNDVI}_{T1}$ + $\mathrm{MaxNDVI}_{T0}$	5,079.4	516.1	0
$\mathrm{MaxNDVI}_{T1}$ + $\mathrm{MaxNDVI}_{T0}$ + $\mathrm{SlopeNDVI}_{T0}$	5,080.5	517.2	0
$\mathrm{MaxNDVI}_{T1}$	5,085.6	522.3	0
$\mathrm{MaxNDVI}_{T1}$ + $\mathrm{SlopeNDVI}_{T0}$	5,086.9	523.6	0
$\mathrm{MaxNDVI}_{T0}$	5,312.3	749.0	0
$\mathrm{MaxNDVI}_{T0}$ + $\mathrm{SlopeNDVI}_{T0}$	5,313.5	750.2	0

Figures

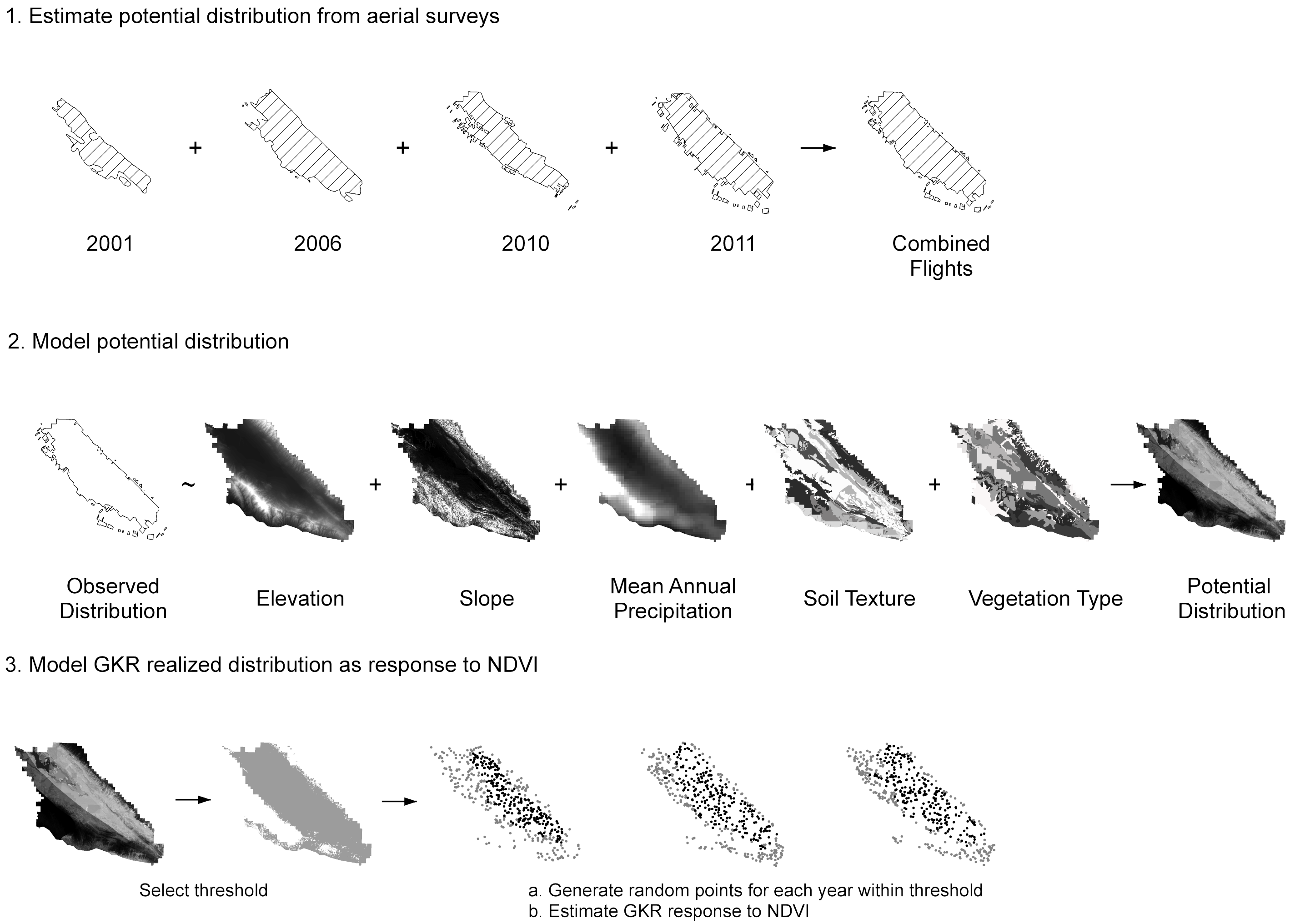

Figure 3-1. Flow chart of multi-step modeling approach. In 2001, 2006, 2010 and 2011, aerial surveys were used to document GKR distribution in the Carrizo Plain National Monument (Step 1). GKR potential distribution was estimated by combining all areas of observed GKR presence from these four years, then inputting these observed presences into the distribution model Maxent, with predictor variables elevation, slope, mean annual precipitation, soil texture and vegetation type (Step 2). Finally, a potential distribution was estimated by selecting a minimum threshold from the Maxent model; within the potential distribution, GKR realized distribution was modeled using estimates of primary productivity (Step 3).

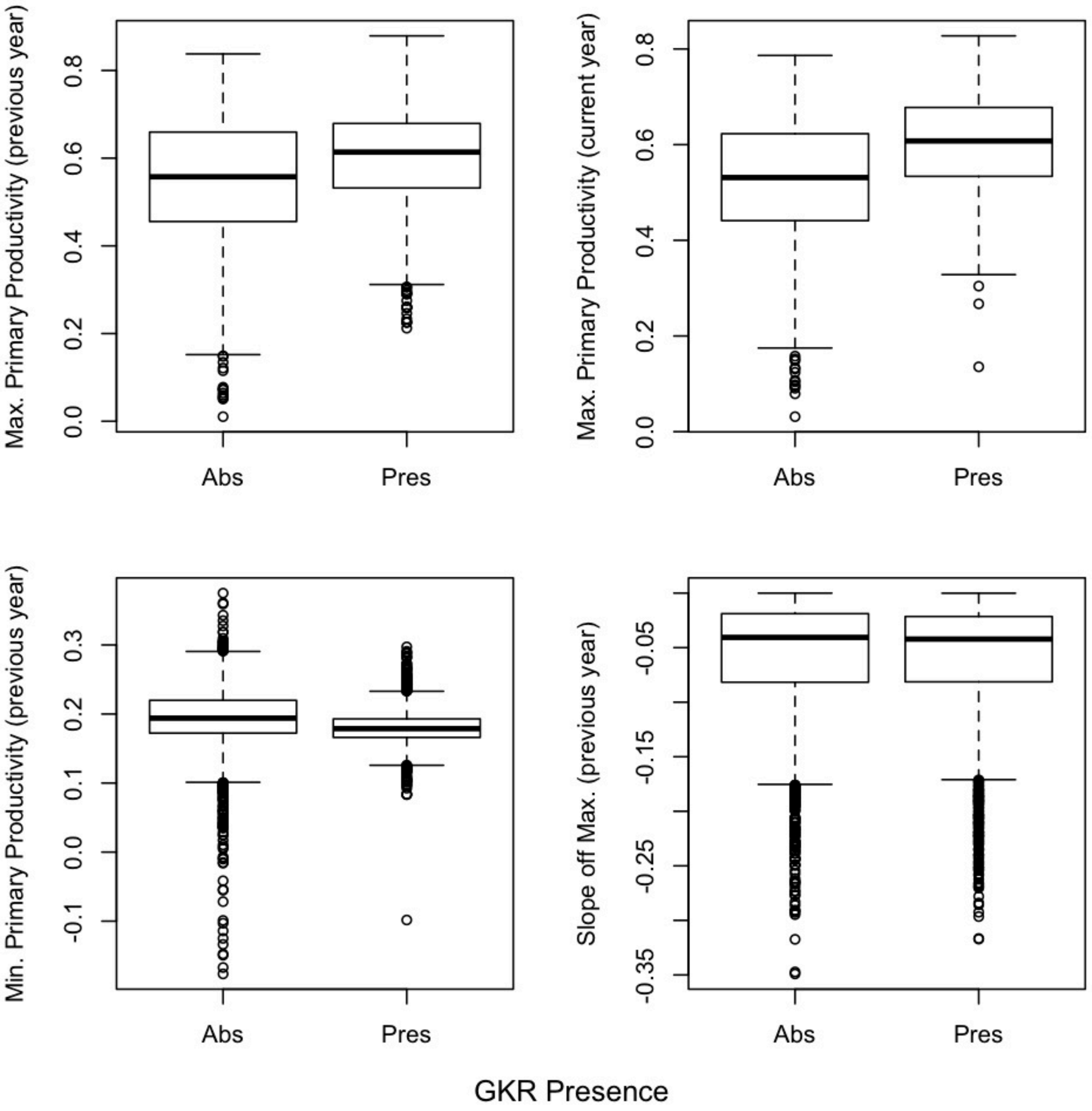

Figure 3-2. Relationships between primary productivity (measured from NDVI) and GKR presence. GKR were expected to have a positive relation with maximum primary productivity in the previous and current year; a negative relationship with the minimum primary productivity measured in the previous year; and a negative relationship with the rate of decrease of primary productivity in the previous year. Relationships are shown from 500 random points estimated from aerial surveys in 2011.

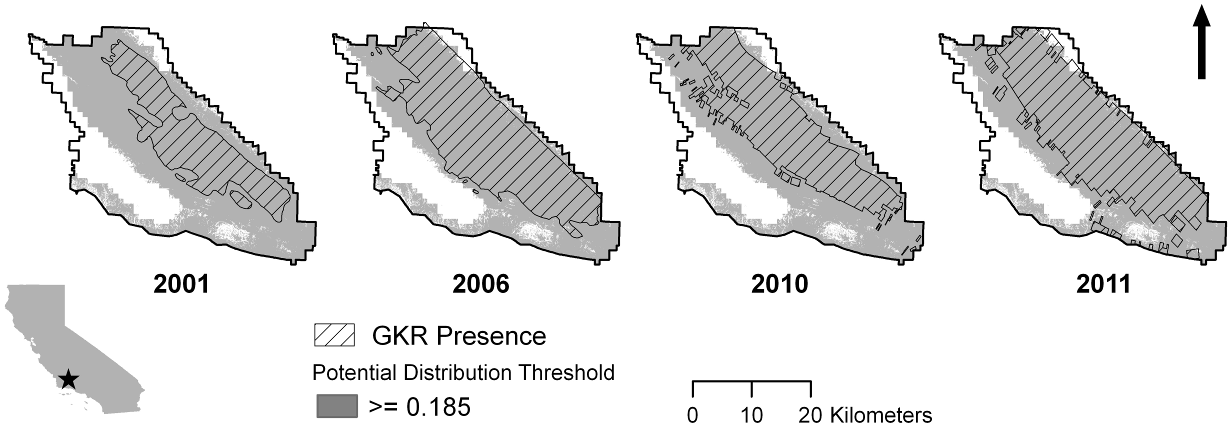

Figure 3-3. Results of GKR distribution mapping and potential distribution modeling. Hatched polygons show areas of GKR activity in 2001, 2006, 2010 and 2011. Dark grey areas indicate the thresholded potential distribution for GKR from a Maxent model using presence points from all four years of GKR distribution.

Chapter 4. Species distribution models predict abundance but not survival at multiple scales

Abstract

The high cost of directly measuring habitat quality has led ecologists to test alternate methods for estimating and predicting this critically important ecological variable. In particular, it is frequently assumed but rarely tested that models of habitat suitability ("species distribution models") may provide useful indices of habitat quality. Recent tests of this relationship have provided mixed results, suggesting species distribution models may predict abundance but not other, more realistic, measures of high quality habitat (*e.g.*, survival, reproductive success). In this study, I created a suite of distribution models with the machine-learning method Maxent for the endangered giant kangaroo rat (*Dipodomys ingens*) at three distinct spatial and temporal scales, and compared these models with a suite of measures of habitat quality: survival, population abundance, and body condition. Most Maxent models were not correlated with survival, while models at all scales were positively correlated with abundance. Finer-scale models were more closely correlated with abundance than the largest scale. Body condition (measured as body mass and parasite load) was not correlated with habitat suitability at any scale. The inability of models to consistently predict survival may be due to a lack of information in the environmental covariates; unpredictable stochastic events or unmeasured community processes; or simply the inadequacy of using models predicting species presence to also predict demography. While distribution models, especially fine scale ones, may be useful for longer-term management goals, such as for defining high quality habitat, they should not be used for short-term management decisions.

Introduction

Identifying habitat quality is a key component of both theoretical and applied ecology (Rodenhouse et al. 1997, Johnson 2007), and is a critical element in developing ecological indicators (Niemi and McDonald 2004). Wildlife managers and policymakers require estimates of habitat quality in order to make decisions related to adaptive management (Boyd and Svejcar 2009), to design reserves for conservation (Pressey et al. 1993) or to designate critical habitat under the Endangered Species Act (Hagen and Hodges 2006). Theoretical ecologists have developed a suite of predictions relating species to distribution (Brown 1995), but often times success in testing these predictions has been stymied by a lack of a good estimate of habitat quality. Boyce and McDonald (1999) placed habitat ecology at "the very core" of ecology.

"Habitat quality" has been both inconsistently defined and inconsistently measured (Hall et al. 1997, Salomon et al. 2006, Gaillard et al. 2010). Van Horne (1983) defined habitat quality as "the product of density, mean individual survival probability, and mean expectation of future offspring." Johnson (2007) defined habitat quality as "the per capita contribution to population growth expected from a given habitat." Most definitions incorporate some measure of "fitness," although this is generally taken to mean something akin to an individual's contribution to population persistence rather than an evolutionary measure.

The multiple scales at which habitat quality may be measured further complicates the creation of a single definition. Habitat measurements within a single individual's home range will focus on the variable contribution of habitat to individual performance, whereas measurements of habitat across populations may focus at the population level. In this study, I focus on habitat quality at the population level and therefore will rely on a definition focused on probability of population persistence.

Habitat quality has not only been difficult to define, but it has been just as inconsistently measured. Johnson (2007) showed that, mostly due to the difficulty of directly measuring quality, ecologists have used a suite of proxies for estimating habitat quality. He divided metrics into two broad categories, specifically measures of habitat believed to contribute directly to population persistence (*e.g.*, resource availability or other environmental constraints) and measures of individual well-being to reveal quality (*e.g.*, demographic, distributional, or physiological measures).

Understanding the contribution of habitat to population persistence has been exceedingly difficult due to the research resources required (although see Coulson et al. (2006)) and ecologists have instead turned to a range of proxies to estimate habitat quality (e.g., Resource Selection Functions (Boyce and McDonald 1999)). Species distribution models, in particular the machine-learning method Maxent (Phillips et al. 2006), have increasingly been used to develop habitat quality indices. Maxent and other species distribution models have become a cornerstone of applied ecological research, consistently providing relatively accurate estimates of probability of species presence (Elith et al. 2006). Maxent requires only records of species presence to train the model, making it an attractive method for estimating habitat quality: the data requirements are considerably smaller than direct measurements of habitat quality.

It is unclear, however, to what extent the probability of a species' presence in a given area is related to habitat quality. Perhaps the biggest, and often cited, problem with equating habitat suitability (i.e., probability of species presence) with habitat quality is the mismatch in scale (Gaillard et al. 2010). Habitat suitability is often modeled range-wide, with environmental variables fixed at multi-decadal time scales, while habitat quality and associated population processes likely occur at much finer spatial and temporal scales (Guisan and Thuiller 2005). Further, the probability of presence may be more closely related to population density, season, or cyclic phase than individual condition or welfare, a problem long recognized in measuring habitat quality (Van Horne 1983). That is, occurrence records uncorrected for detection may be biased to high-density sites (Rondinini et al. 2006), but density may not be directly related to habitat quality due to a number of factors (e.g., source-sink dynamics). It is therefore critical that species distribution models be tested as indices of habitat quality.

Research into the relationship between habitat quality and species distribution models has generally found positive correlations between distribution model values and population abundance (e.g., Pearce and Ferrier 2001, VanDerWal et al. 2009), but few studies have gone beyond investigating abundance. Recent work on birds and butterflies in the UK found that while abundance was positively correlated with probability of presence (measured from a suite of different species distribution models), a derived metric of population stability was not (Oliver et al. 2012).

In this study, I examine multiple models of habitat suitability, created with Maxent, at different spatial and temporal scales to examine how well each correlates with *in situ* measures of habitat quality for an endangered rodent, the giant kangaroo rat (GKR, *Dipodomys ingens*). I use estimates of survival, population density, and body condition as proxies for habitat quality. First, I compare range-wide species distribution models with estimates of habitat quality. Next, I create a more spatially restricted model to test whether models of smaller extent better estimate average habitat quality over time. Finally, I create local species distribution models that incorporate annual changes in resource availability to test whether small-scale distribution models are capable of predicting inter-annual changes in habitat quality.

Methods

Study Sites

Trapping was conducted at two sites in the California Coast Range: the Carrizo Plain National Monument, located in eastern San Luis Obispo County, and the Ciervo-Panoche Natural Area, on the border of San Benito and Fresno counties. Two types of trapping occurred. At 28 sites in the Carrizo Plain, 61 traps were set in a 100m x 100m grid to estimate density and survival, which we translate to an effective trapping area of 110m x 110m. Twenty of these sites were established in 2007 in core GKR habitat as part of a larger ecological research project (Prugh and Brashares 2012). Eight additional sites were established in the Carrizo Plain in August 2010, stratified across a wider range of habitat suitability. At an additional 85 sites in Carrizo Plain and 72 sites in the Ciervo-Panoche, I set five traps for three nights. These sites were also spread across a wider range of habitat suitability, and provided both records of occupancy and measures of body condition and average habitat quality, but not mark-recapture estimates of abundance or survival.

Measures of Habitat Quality

I considered a suite of metrics of individual and population persistence associated with habitat quality that fall into three categories: (1) survival, (2) abundance, and (3) body condition. These three metrics are commonly used as measures of habitat quality (Johnson 2007).

Survival and abundance were estimated using robust design mark-recapture estimates (Kendall 2012). Primary trapping occasions occurred twice annually, once in the spring (April-May) and once in the late summer (August). Twenty-eight sites were trapped for three to five nights on each primary occasion, and individuals were ear-tagged with National Band and Tag ear tags in both ears. At 20 of the sites, individuals were injected with a Passive Integrated Transponder tag and just one ear tag.

Population parameters were estimated using the robust design with heterogeneity models (Kendall 2012) in the “RMark” package for R (Laake 2009). The robust design allows for direct estimates of survival (S) by partitioning survival into emigration rates (*i.e.*, animals that left the study area) and true survival (those that died). I used a model selection framework using Maximum Likelihood Estimation and Akaike’s Information Criteria (AIC) (Burnham and Anderson 2002). Parameters estimated with the robust design with heterogeneity were p (probability of capture), $1-\gamma'$ (probability of immigration), γ'' (probability of emigration), S (survival), N (abundance), and π (a partitioning factor that allows for within-population heterogeneity among the other parameters). N and S were estimated to vary by time and plot. I tested three variants of p, varying by primary and secondary session, and by plot. I also tested three models for GKR movement: “random flow,” where the probability of immigrating and emigrating are equal; “Markov movement,” where the probability of immigrating or emigrating are dependent on the previous state of the individual (in or out of the population); and a movement model where GKR that had emigrated would not immigrate back into the population (i.e. $1-\gamma' = 0$). Estimates of N and S for each site at each time were then derived through model averaging based on the relative weight of each model calculated from the AICc score.

Trapping on 20 of the plots had occurred since the summer of 2007, while the trapping on the remaining eight plots began in August 2010. Program Mark does not allow for missing primary capture sessions, so I tested two model designs: first, I combined all trapping data but removed any trapping data from before August 2010. I also separated the trapping data, grouped by sites with identical primary and secondary sessions and conducted separate model selections on each set of data.

In addition to abundance estimated from the mark-recapture data, I used counts of burrow mounds at 157 sites to estimate longer-term mean abundance. Burrow mounds counted on the ground have been shown to be positively correlated with carrying capacity, or long-term mean population abundance (Chapter 2, Bean et al. 2012). This method of estimating carrying capacity allowed for the inclusion of additional sites from across the study area and across a wider range of habitat suitability values. At each of the 157 sites that had been trapped across Carrizo Plain and Ciervo-Panoche with only 5 traps, I walked a 50m x 10m transect and counted every active and inactive burrow mound.

In order to measure body condition, captured GKR were weighed, the length of the skull was measured, and most individuals were examined for parasites (fleas and an unidentified orange mite). On the 20 sites established in 2007, GKR were not systematically checked for fleas, and were therefore removed from this analysis. Individuals with seeds in their cheek pouches were also removed from body mass analyses. Only adults were included in analysis of body mass. Individuals were assigned an age class (“Adult”, “Yearling” and “Juvenile”) based on body mass as well as condition of the fur and ears. Juveniles were identified as having softer fur and intact ears, whereas individuals with tears or notches in their ears were assigned the adult class. Due to the qualitative nature of this age assignment, kangaroo rats may also be assigned an age class based on mass (Prugh, pers. comm.). However, we found quite a few individuals lighter than the typical lower cut-off for adult mass that were clearly adults (based on reproductive status, condition of the ears or record of previous capture). Selecting a mass threshold would have biased the results by ignoring lighter individuals. I therefore also conducted body mass analyses only for individuals re-captured in more than one primary trapping session (*i.e,* individuals that were guaranteed to be older than 6 months). In addition, body condition is often defined as a ratio of body mass to a measure of skeletal size, such as body length, hind foot length, or skull size. We measured skull length and I used body mass to skull length ratio as an additional measure of body condition.

Range-wide Distribution Model

I created a distribution model for GKR using Maxent, a commonly used presence-only modeling method (Phillips and Dudik 2008). In addition to the 102 GKR presence points acquired from our trapping data, I used the *gbif* function in the *dismo* package in R (Hijmans et al. 2012) to obtain 189 spatially-referenced records for GKR from museum collections. I then obtained 19 climate layers (Hijmans et al. 2005) frequently used in distribution modeling as the independent variables in the distribution model (Graham and Hijmans 2006). In addition to climatic layers, I included soil particle size, elevation and slope as predictor variables. Details on model creation are provided in (Chapter 3). Maxent produces, as an output, an estimate of habitat suitability, represented by a raster at the same extent and grain as input layers. Model values may be output in three formats: raw, logistic and cumulative (Phillips et al. 2006). The logistic output may range from 0 to 1 and, if prevalence is well estimated in the model, may represent a probability of presence. Estimating prevalence with presence-only data may be difficult, and so the Maxent output is typically treated as a more general measure of habitat suitability, with suitability likely correlated with probability of presence.

Next, I examined to what extent the range-wide distribution model (i.e. habitat suitability) correlated with measures of habitat quality. I calculated Spearman rank correlation coefficients for the distribution model with mean survival and mean density across the four trapping sessions. Spearman correlations were calculated rather than Pearson due to heteroscedasticity (unequal variance) in one or both of the variables. Three sampling sites had no GKR at any time during the study, and were therefore removed from analyses of survival. I also calculated correlations for the distribution model with counts of burrow density across Carrizo Plain and Ciervo-Panoche. Finally, I compared body condition from all individuals captured in Carrizo Plain and the Ciervo-Panoche with the distribution model values. Specifically, I examined whether adult body mass or the presence of parasites was correlated with distribution model values at each site.

Local Distribution Model

To further examine the effect of study extent, I then created a GKR distribution model, with the same bioclimatic layers, limited to the area of the Carrizo Plain. This model allowed for greater variation of habitat suitability for the Carrizo GKR population. All relationships tested for the range-wide model were tested for the local distribution model: mean survival and density, body mass, and presence of parasites.

Local Temporal Distribution Models

I created finer-scale models specific to the Carrizo Plain to consider the temporally dynamics of habitat suitability. Using aerial surveys flown over Carrizo Plain in 2010 and 2011 as presence points, I used Maxent to model habitat suitability for each year. Rather than using broad-scale climatic factors, I incorporated local measures of soil particle size (Soil Survey Staff); vegetation type (USDA Forest Service 2008); slope and elevation (United States Geological Survey 2006); and mean annual precipitation isohyets (United States Geological Survey 2004). In Chapter 3, I report that resource availability in the current and previous year were contributing factors to GKR presence in a given year, where resource availability was estimated as the peak measurement in a time series of Normalized Difference Vegetation Index (NDVI) from the Moderate Resolution Imaging Spectroradiometer (MODIS). Therefore, in addition to the local fixed environmental layers, I also included measures of maximum NDVI from the current and previous year in the yearly models of habitat suitability. Environmental layers had a 250 m^2 cell size.

Using similar analyses to the range-wide models, I then examined how well these finer scale models correlated with measures of habitat quality. I calculated Spearman correlation coefficients for survival and abundance for each trapping session of the study (Summer 2010, Spring and Summer 2011, and Spring 2012) with distribution model values. I also examined how well the local distribution models predicted parasite load and body mass in each given year.

Results

Estimates of Survival and Abundance

Models estimated from the combined data but limited time frame were generally unreliable and frequently failed to converge. I therefore relied on separate candidate models for (1) the longer trapping data from twenty sites and (2) the more recent trapping data from the other eight (Table 4-1). While analyses were conducted separately, the same suite of models had the best support for both sets of data. Only models that incorporated probability of capture as a function of time or time and plot were supported. In addition, the "random flow" and Markov movement models were the only movement types supported; none of the models that hypothesized GKR, having emigrated, would not return to the population received any weight.

Abundance and survival on the eight new sites were generally lower than the twenty long-term sites, but otherwise comparable (Table 4-2, Prugh and Brashares 2012). Only four of the eight sites had GKR during all trapping sessions. GKR appeared to move onto a fifth site during the summer of 2011. The other three sites had a higher diversity of small mammals in general, but no GKR trapped and no apparent burrow mounds.

Distribution Models

Distribution models at all scales were generally similar, but variation was high at specific points in Carrizo (Fig. 4-1). All models had "useful" Area Under Curve (AUC) scores, a commonly used metric for model accuracy (Hanley and McNeil 1982), although AUC score declined with increasing model resolution (0.981 range-wide to 0.752 for the 2011 model).

Variables ranked as important by Maxent differed by scale, but in general the climatic and environmental variables that define GKR distribution followed patterns described by Grinnell (1932) and Williams (1992). Specifically, GKR preferred flat areas or gently-sloping hills dominated by California grassland, in areas with hot, dry summers and average annual precipitation of ~30 cm or less.

In the 2010 and 2011 models, long-term annual rainfall was the most important variable (50.8% and 47.9% contribution). In 2011, GKR also had a positive correlation with resource availability (measured from peak NDVI), whereas in 2010, NDVI measures were not an important variable in GKR distribution.

Variability of habitat suitability values at trapped sites increased in models with smaller extent and finer resolution. Trapped site suitability ranged from 0.70 to 0.82 in the range-wide model; 0.39 to 0.82 in the Carrizo-only model; and 0.09 to 0.69 in the temporal models.

Abundance

Population abundance, estimated from 28 mark-recapture plots, was positively correlated with distribution models at local scales, but not significantly correlated at the range-wide scale (Fig. 4-2). However, long-term mean abundance, estimated from counts of burrow mounds at 93 sites in Carrizo Plain and 51 sites in Ciervo-Panoche, were positively correlated at all scales. I found no relation between standard deviation of population abundance, a potential measure of habitat quality, and distribution model value at any scale.

Survival

Models with no temporal component (*i.e.*, range wide and Carrizo only) were not correlated with survival at any of the 28 sites (Fig. 4-3). Models created for GKR distribution in 2010 and 2011 that incorporated measures of resource abundance were generally not significantly correlated with survival for the majority of time periods tested. However, the 2011 model was significantly correlated with survival between August 2011 and April 2012.

Body Condition

Body mass was not significantly correlated with distribution model values at any scale. Results were similar examining only re-captured individuals or skull length to body mass ratios. In general, the presence of orange mites was negatively correlated with distribution model values. Presence of fleas was not correlated with distribution model value at the range-wide or fixed Carrizo model; however in the 2011 model, presence of fleas was positively correlated with distribution model value.

Discussion

In this study, I examined to what extent species distribution models, using presence and pseudo-absence records and relevant environmental layers, correlated with proxies of habitat quality. While models at all scales were correlated with long-term average abundance and body mass, the largest-scale model did not correlate with abundance estimated from mark-recapture trapping. Correlation between abundance and species distribution model value also increased at finer temporal and spatial scales. In addition, only one model (2011) of the four was positively correlated with survival (from summer 2011 to spring 2012).

Correlation between estimated abundance and distribution model value conform to previous findings (Oliver et al. 2012), but the use of abundance as a measure of habitat quality has been questioned (Van Horne 1983). However, in addition to measuring population abundance from mark-recapture estimates, I also used counts of burrow mounds as a proxy for long-term population size. Studies on GKR population (Chapter 2, Bean et al. 2012) and behavioral ecology (Randall et al. 2002) support the use of burrow mounds as, in essence, a measure of the habitat carrying capacity: GKR are solitary and, in times of higher-than-average density, will share burrows, and in times of lower-than-average density, will increase home range to incorporate multiple burrows. At the largest scales, then, it is unsurprising, but reassuring, that species distribution models predict longer-term habitat quality.

At the same time, two findings of this study raise some concern about the use of species distribution models as indices of habitat quality. First, scale matters. By decreasing the study extent and increasing resolution of the environmental layers, the models produced greater variability in species distribution model value within GKR population extent. The distribution model for the entirety of GKR range produced a homogenous suitability value for most of the Carrizo Plain, whereas the distribution model using the same environmental layers but with smaller total extent created greater variability in suitability scores. As always, the management question will dictate the appropriate scale for model building. Large-scale studies may be appropriate for designing protected areas or designating critical habitat: the two largest known GKR populations (Carrizo and Ciervo-Panoche) had the highest suitability values. However, local management (*e.g.,* restoration or other active management strategies) would best be focused on high quality habitat, which is better defined by more local distribution models.

Further, while longer-term management may be conducted with coarse-scaled models, only the finest temporal and spatial models ought to be used when conducting management on population-level processes. The models created using single year estimates of GKR population extent and temporal environmental layers (*e.g.*, NDVI) were best at predicting population abundance, and the model from 2011 was the only model to be correlated with survival. In fact, correlation was strong enough from these yearly models that it may be possible to estimate GKR population size in Carrizo from the distribution model (ρ=0.62 in 2011). A linear regression of the 2011 model against abundance in August 2011 gives a y-intercept (β_0) of -19.90 and a relationship to Maxent value (β_1) of 122.93. Incidentally, this places the x-intercept at 0.162 – that is, assuming a linear relationship between GKR abundance and Maxent, there should be 0 GKR at or below Maxent values of 0.162. Indeed, of the 105 sites trapped across Carrizo in 2011, only one site had GKR present below a Maxent value of 0.162 (at 0.139). In other words, GKR abundance is predicted to be 0 at approximately the same value Maxent predicted a probability of presence of 0. Each Maxent cell is 30m x 30m (900m^2), whereas abundance of GKR is calculated for 120m x 120m cells (12,100m^2). So, total abundance in 2011 for Carrizo Plain should be the sum of all Maxent cells, adjusted by the regression

$$(-19.90 + 122.93 * \text{maxent value}) * (900/12{,}100) = 1{,}898{,}728 \qquad \text{Equation 1}$$

which equates to a population density of about 18/ha.

Although local models do a better job of estimating mean abundance over time, I was unable to generate a model that consistently predicted survival, even though mean survival in time is positively correlated with mean abundance in time at each site. At this scale, local community level factors likely play a larger role in survival than habitat quality, processes (*e.g.*, interspecific competition and especially predation) that cannot be defined with single-species distribution models. Two sites could have similar habitat quality, support the same number of GKR over time, but if one is located close to a kit fox (*Vulpes macrotis mutica*) natal den (as was observed in this study), survival will be substantially lower. It should be noted, then, that distribution models ought not be used for management decisions that will require high survival in a short time scale (*e.g.*, relocation efforts).

The weak relationship found between the species distribution models and survival at each site may also be due to poor estimates of survival from the mark-recapture models. The robust design theoretically is able to estimate “true” survival by partitioning emigration rates (or “excursions”) separately from survival (Kendall 2012). Although giant kangaroo rats are believed to have high site fidelity, the best-supported models suggested some background level of emigration and immigration, suggesting some bias in the “excursion” rate. While these estimates of survival are believed to be the least biased of any population estimate without direct measures of survival, the variability in the estimates may have contributed to the poor relationship between distribution model values and survival. Further investigation into populations where survival rates are better known (e.g., through recovery of collared individuals) is necessary.

A second remaining question is to what extent we can actually model population-level processes given the available spatial data. If we were to create a spatially explicit model of habitat quality with survival as the response variable, how much better would that model fare than the species distribution models used in this study? Unfortunately, I did not have enough samples to conduct a robust GAM to test this, but Pierce and Ferrier (2001) found that models using abundance data did no better than models using occupancy data at predicting abundance. Whether this failure is due to the quality and scale of the spatial data available or due to community-level interactions deserves further attention.

In conclusion, I found that species distribution models can be effective proxies for habitat quality, but that the nature of the question addressed and the temporal and spatial scales used can considerably alter their efficacy. For long time scales and broad, range-wide questions, range-wide distribution models can effectively target areas of high habitat quality, but at finer scales, more local models are necessary. While distribution model values are correlated with long-term trends in abundance, most models are incapable of predicting survival. Additional research is required to understand how much this failure is due to the data or models used, and how much is simply due to stochastic or un-detected community-level processes.

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Tables

Table 4-1. Model selection results for mark-recapture estimates for giant kangaroo rats under a robust design with heterogeneity, with four primary sessions of three secondary sessions each from August 2010 to May 2012. Additional models incorporating a fixed movement with no immigration failed to converge.

p	Movement	π	Param.	AICc	ΔAICc	Weight
~session	Random	~1	21	215.30	0	0.59
~session	Markov	~1	22	217.45	2.157	0.20
~session + Plot	Random	~1	24	217.68	2.389	0.18
~session + Plot	Markov	~1	26	222.05	6.756	0.02
~session	Markov	~1	21	224.79	9.489	0.01
~session + Plot	Markov	~1	25	229.06	13.765	0.00
~1	No immigration	~1	8	230.47	15.177	0.00

Table 4-2. Model-averaged parameter estimates for abundance (N) and survival (S) on eight sites trapped for three nights on four primary occasions from August 2010 to May 2012. N was estimated August 2010 (T_1), April 2011 (T_2), August 2011 (T_3) and May 2012 (T_4). S was estimated for periods between trapping sessions, winter 2010 (T_1), summer 2011 (T_2) and winter 2011 (T_3). Parameters were estimated from a suite of robust design with heterogeneity models, with varying predictors for probability of capture (p) and movement (γ' and γ'').

Parameter	Site	Lat/Lon	T_1	T_2	T_3	T_4
N	G1	35.2121, -119.8974	0	0	0	0
N	G2	35.2070, -119.8834	0	0	2	4
N	G3	35.1722, -119.8433	0	0	0	0
N	G4	35.1744, -119.8339	0	0	0	0
N	G5	35.1184, -119.7624	10.73	27.17	37.46	40.62
N	G6	35.0998, -119.7170	23.70	32.14	14.43	37.58
N	G7	35.1037, -119.7140	31.08	38.32	33.71	32.92
N	G8	35.0648, -119.6707	4.12	12.95	16.04	11.09
S	G1	35.2121, -119.8974	0	0	0	-
S	G2	35.2070, -119.8834	0	0	0	-
S	G3	35.1722, -119.8433	0	0	0	-
S	G4	35.1744, -119.8339	0	0	0	-
S	G5	35.1184, -119.7624	0.84	0.56	0.52	-
S	G6	35.0998, -119.7170	0.78	0.46	0.42	-
S	G7	35.1037, -119.7140	0.85	0.58	0.54	-
S	G8	35.0648, -119.6707	0.81	0.51	0.47	-

Figures

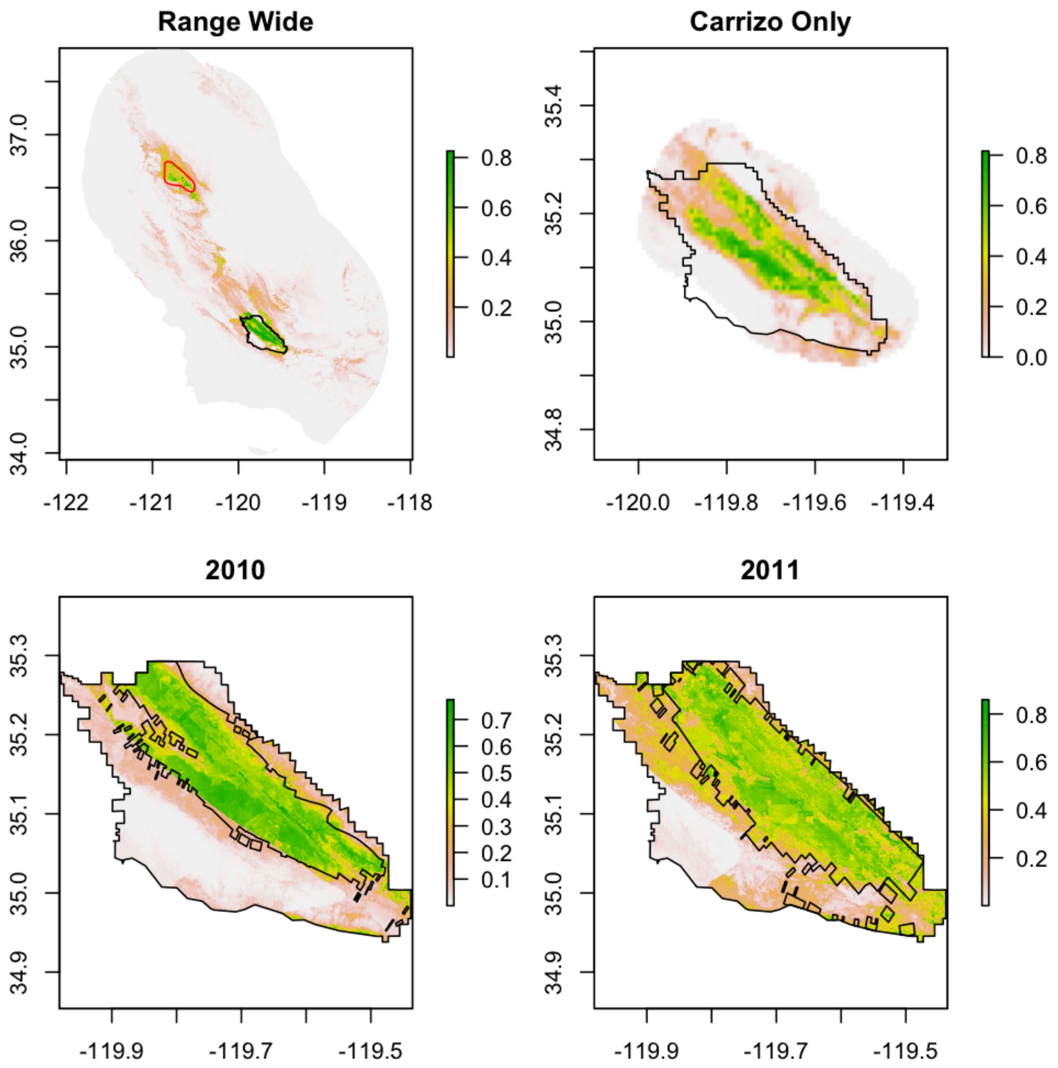

Figure 4-1. Giant kangaroo rat distribution models created with Maxent at three scales. Longitude and latitude are given on the x and y axes; color depicts habitat suitability value, with white corresponding to low suitability, green with high suitability. The range-wide and Carrizo only models were created using low resolution climate data (BIOCLIM), slope, elevation and soil particle size, while the 2010 and 2011 models were created with higher resolution data for mean annual precipitation, elevation, slope, soil particle size and vegetation type. Suitability values are represented from low (orange) to high (green). Carrizo Plain National Monument is outlined in black and the Ciervo-Panoche Natural Area in red. GKR distribution in Carrizo, based on aerial flight surveys, is also outlined in black for 2010 and 2011. While the models described the same broad pattern – GKR prefer dry, flat, grassland habitat- variation within Carrizo differed substantially at each scale of analysis. AUC scores for each model were "useful" (Range Wide: 0.981; Carrizo Only: 0.908; 2010: 0.832; 2011: 0.752).

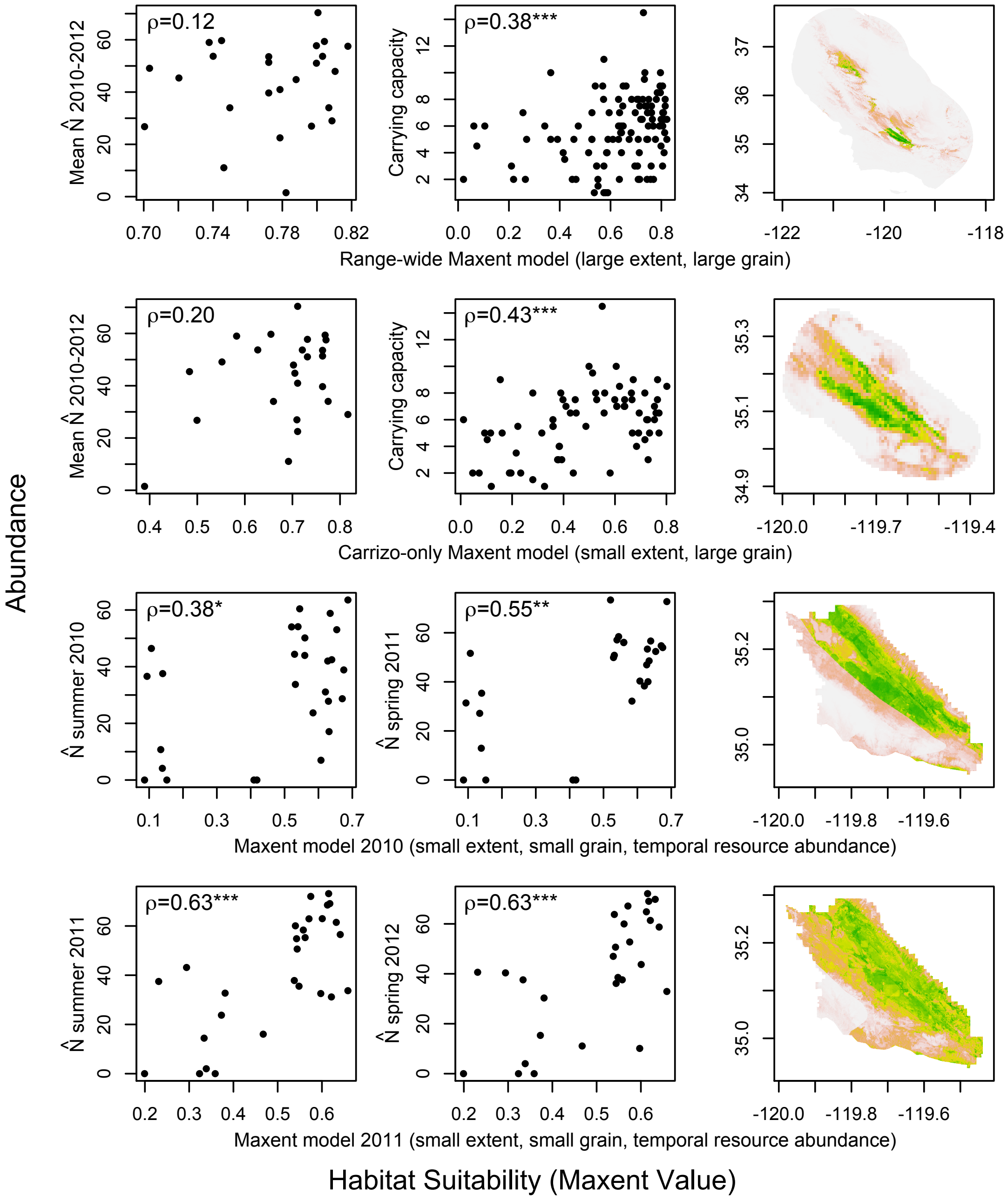

Figure 4-2. Relation of abundance to habitat suitability at three scales and two time periods. N was estimated using robust design mark-recapture models for four trapping occasions from August 2010 to May 2012. Carrying capacity was estimated as number of burrow counts in a 50m x 10m transect at sites in Carrizo Plain National Monument and Ciervo-Panoche Natural Area. Habitat suitability was estimated with four species distribution models created in Maxent: a range-wide model, a Carrizo-only model, and two models for Carrizo that incorporated giant kangaroo rat resource availability (measured as primary productivity in a given year). Large-scale models were significantly correlated with carrying capacity, but showed little variability in suitability among trapped sites. Local models that incorporated resource availability better distinguished between high and low quality sites.

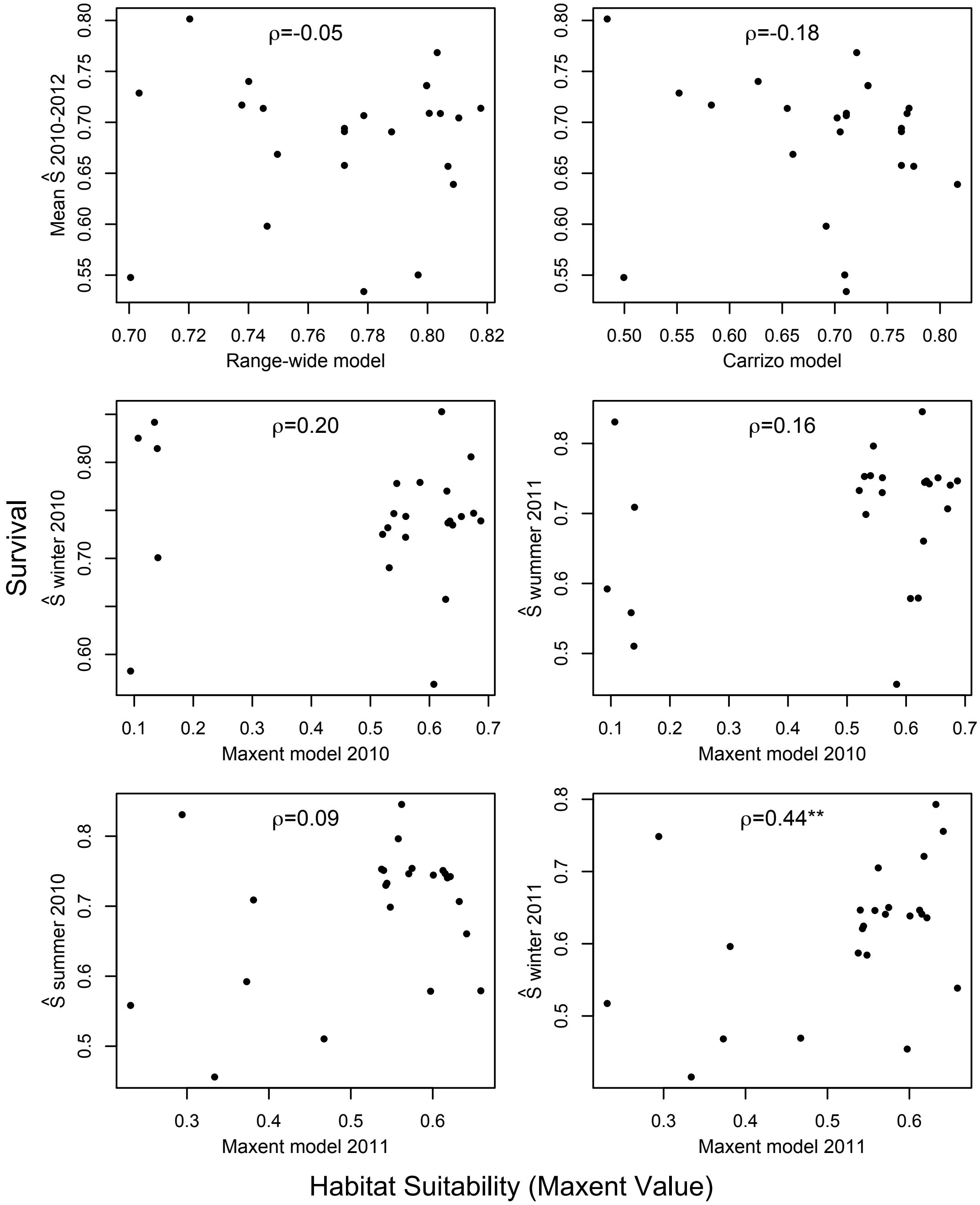

Figure 4-3. Relation of habitat suitability to giant kangaroo rat survival estimated with mark-recapture models at twenty-eight sites in Carrizo Plain National Monument. Species distribution models were unable to predict survival at all but one time period. One model ("Maxent model 2011") that incorporated resource availability was positively correlated with over-winter survival in 2011 (**p < 0.01).

Appendix 1

The most common approach for modeling species distributions with Maxent is to use species occurrence records across the distribution, and to use derived climatic variables from the Bioclim dataset (Hijmans et al. 2005). Although I believe the scale and environmental variables used in the main text were more appropriate to understand the potential distribution of GKR in Carrizo, I also conducted the same analyses with a range-wide estimate of GKR potential distribution using BIOCLIM variables and occurrence records from the Global Biodiversity Information Facility (2012). Having modeled the potential distribution with these data in Maxent, I conducted the same analyses for estimating potential distribution.

As can be seen in Figure A-1, potential distribution within Carrizo was essentially identical between the range-wide and Carrizo-specific models. The main contradiction consisted of a band of the western portion of the monument modeled as unsuitable at a local scale, but suitable at a range-wide scale.

BIOCLIM consists of a series of more descriptive climatic variables than simply mean annual precipitation. The main predictors of GKR presence included the minimum temperature of the coldest month (~0.8° C), high seasonality of temperature, mean precipitation of the wettest month (maximum of ~7.5cm), and mean precipitation of the driest month (0 cm). Low slope was also a strong predictor of GKR presence.

The realized distribution models had the same outcome as in the main text: the best, and only, model selected by AIC included all of the variables, including a positive correlation between GKR presence and resource abundance in both the present and previous years, as well as the two proxies for GKR presence in the previous year.

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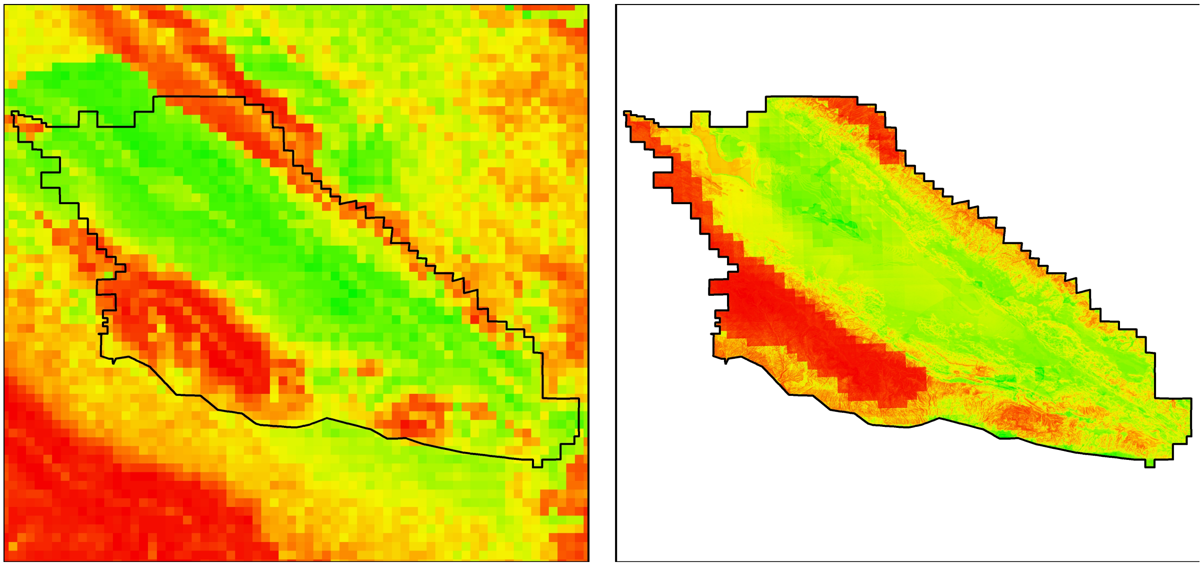

Figure A-1 Comparison of potential distribution models for giant kangaroo rats. On the left, a model was created range-wide with 225 historical records, with 20 BIOCLIM variables, as well as slope, elevation, vegetation type and soil texture. On the right, a model was created specifically for Carrizo using 250 points from four years of aerial surveys.