

Species distribution models of an endangered rodent offer conflicting measures of habitat quality at multiple scales

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Summary

1. 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', SDMs) may provide useful indices of habitat quality, either from an individual animal or manager's perspective. Critically, SDMs are increasingly used to estimate species' ranges, with an implicit assumption that areas of high suitability will result in higher probability of persistence. This assumption underlies efforts to use SDMs to design protected areas, assess the status of cryptic species or manage responses to climate change. Recent tests of this relationship have provided mixed results, suggesting SDMs may predict abundance but not other measures of high-quality habitat (e.g. survival, persistence).

2. In this study, we created a suite of SDMs for the endangered giant kangaroo rat *Dipodomys ingens* at three distinct scales using the machine-learning method Maxent. We compared these models with three measures of habitat quality: survival, abundance and body condition.

3. Species distribution 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 was not correlated with habitat suitability at any scale. The inability of models to predict survival may be due to a lack of information in environmental covariates; unmeasured community processes or stochastic events; or the inadequacy of using models that predict species presence to also predict demography.

4. *Synthesis and applications.* Species distribution models (SDMs), especially fine scale ones, may be useful for longer-term management goals, such as identifying high-quality habitat for protection. However, short-term management decisions should be based only on models that use covariates appropriate for the necessary temporal and spatial scales. Assumptions about the relationship between habitat suitability and habitat quality must be made explicit. Even then, care should be taken in inferring multiple types of habitat quality from SDMs.

Key-words: *Dipodomys ingens*, giant kangaroo rat, habitat suitability, mark–recapture, Maxent, survival

Introduction

Measuring habitat quality is a key component of theoretical and applied ecology (Rodenhouse, Sherry & Holmes 1997; Johnson 2007), and a critical element in developing

ecological indicators of disturbances (Niemi & McDonald 2004). Managers require estimates of habitat quality to adaptively manage populations (Boyd & Svejcar 2009), design reserves for conservation (Pressey *et al.* 1993) and designate critical habitat (Hagen & Hodges 2006). Theoretical ecologists have developed a suite of predictions relating species' abundances to their distributions (Brown 1995),

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but testing these predictions has been stymied by the challenges of operationalizing and quantifying habitat quality.

'Habitat quality' has been inconsistently defined and measured (Hall, Krausman & Morrison 1997; Salomon, Ruesink & DeWreede 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.' While most definitions incorporate some measure of 'fitness,' this is generally taken to mean something akin to an individual's contribution to population persistence rather than an evolutionary measure.

Of even greater importance is the notion that habitat quality from an individual animal's perspective may not always align with habitat quality from a manager's perspective (Johnson 2005). A population at carrying capacity will likely have a lower survival rate than a nearby population at half carrying capacity. From a management perspective, conservation actions should be focused on the population with the highest probability of long-term persistence. Short-term estimates of survival, density or body condition may or may not lead to reliable estimates of habitat quality from a manager's perspective due to basic issues of population regulation or behavioural interactions [i.e. ideal despotic distributions, Fretwell (1972)].

Understanding habitat quality's contribution to population persistence has been difficult due to the resources required to monitor the necessary demographic rates. Ecologists have instead turned to a range of proxies to estimate habitat quality. Species distribution models (SDMs), in particular the machine-learning method Maxent (Phillips, Anderson & Schapire 2006), have increasingly been used to develop habitat quality indices (e.g. Brambilla & Ficetola 2012; Cimino *et al.* 2013). SDMs have become a cornerstone of applied ecological research, consistently providing accurate estimates of the relative 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 models that require absence data, or direct measurements of habitat quality. In fact, McDonald (2013) suggests that presence-only (or use-available) data may be *more* appropriate for estimating habitat suitability. However, Maxent and similar models are designed to predict probabilities or indices of species' occurrence or habitat suitability, and it is unclear to what extent habitat suitability in a given area relates to habitat quality.

Species distribution models rely heavily on environmental niche theory to explain both range limits and relative habitat suitability (Peterson *et al.* 2011). Species are expected to have higher probability of occupancy in geographic areas with environmental conditions at the centre of a species' niche than at the edges. It is frequently assumed that the same should be expected for habitat

quality: quality should be highest in areas with environments that most closely match the centre of a species' niche and decline towards the edges. Researchers have used both evolutionary (e.g. Kawecki 1995) and ecological (Pearson & Fraterrigo 2011) explanations to relate habitat quality and fitness to the environmental niche.

Unfortunately, due to issues of data collection, it is rarely possible to directly estimate a species' environmental niche from existing data sets. Perhaps the biggest, and often cited, problem with equating habitat suitability with habitat quality is the mismatch in scale (Gaillard *et al.* 2010). Habitat suitability is often modelled range-wide, with environmental variables fixed at multidecadal time-scales, while habitat quality and associated population processes likely occur at much finer spatial and temporal scales (Guisan & Thuiller 2005). Further, the probability of presence may be more closely related to density, season or cyclic phase than individual condition, 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). Most SDMs rely on museum records for occurrence data. It is likely impossible to distinguish species locations that were drawn from a sink or trap population, thus adding potential bias to estimates of habitat suitability and, thereby, habitat quality, however recent efforts to relate intensity of use may be more useful in determining a species' distribution (Nielson & Sawyer 2013).

Nevertheless, despite the potential problems with estimating a species' environmental niche from location records that may be biased in time, space or that are not always drawn from a species' source populations, these models continue to be used to measure both habitat suitability and, by extension, habitat quality. It is therefore critical that SDMs, as they are currently practiced, be tested as indices of habitat quality before they are applied to that task.

Research into the relationship between habitat quality and SDMs has generally found positive correlations between SDM values and population abundance (Pearce & Ferrier 2001; VanDerWal *et al.* 2009), but few studies have gone beyond investigations of abundance. Recent work on birds and butterflies in the UK found that while abundance was positively correlated with suitability (measured from a suite of different SDMs), a derived metric of population stability was not (Oliver *et al.* 2012).

In this study, we 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 the giant kangaroo rat (*Dipodomys ingens*; hereafter GKR). The GKR is an ideal species to test the relationship between SDMs and habitat quality: their distribution is easily mapped; long-term population abundance is measurable without intensive trapping;

and the main hypothesized driver of population dynamics can be estimated using freely available satellite imagery. We use estimates of survival, population density and body condition as proxies for habitat quality. First, we compare range-wide SDMs with estimates of habitat quality. Next, we create a more spatially restricted model to test whether models of smaller extent better estimate mean habitat quality over time. Finally, we create local SDMs that incorporate annual changes in resource availability to test whether small-scale SDMs are capable of predicting interannual changes in habitat quality.

Materials and methods

STUDY SPECIES

The GKR is a federally endangered fossorial rodent and California-endangered fossorial rodent. GKRs construct large burrow mounds, 2–7 m in diameter (Williams & Kilburn 1980). After grasses begin to senesce, GKRs clip vegetation from atop their burrow leaving a circle of bare soil amidst standing dry vegetation. GKR home range size is typically 60–350 m² (Braun 1985). The pattern of burrows on the landscape offer a reasonable estimate of long-term mean abundance, while the bare circles created by their active clipping provides an easy way of mapping population extent with aerial surveys (Bean *et al.* 2012). GKRs are, throughout much of their range, competitively dominant (Grinnell 1932). Their populations are believed to be bottom-up limited by primary productivity (Bean 2012).

STUDY SITES

Trapping of GKRs was conducted at two sites in the California Coast Range: the Carrizo Plain National Monument (35°19'N, 119°73'W), located in eastern San Luis Obispo County, and the Ciervo-Panoche Natural Area (36°58'N, 120°69'W), on the border of San Benito and Fresno counties. Both areas represented relatively intact habitat of the San Joaquin desert grassland system (Germano *et al.* 2011). Climate was similar in both areas (mean annual precipitation = 230 mm, SD = 102 mm), with the majority of rain falling from October through April (Horel *et al.* 2002). Both areas were influenced by a north-south gradient in precipitation, with the more southern and eastern areas experiencing drier conditions. Both sites were dominated by non-native annual grasses, primarily red brome (*Bromus madritensis rubens*). The Carrizo Plain and the Ciervo-Panoche represent the two largest remaining populations of GKRs.

Two types of trapping occurred. At 28 sites in the Carrizo Plain, 61 traps were set in a 100 m × 100 m grid to estimate density, survival and body condition, which we translate to an effective trapping area of 110 m × 110 m. Twenty of these sites were randomly selected in 2007 in high-quality GKR habitat as part of a long-term ecological research project (Prugh & Brashares 2012). Eight additional sites were established in the Carrizo Plain in August 2010, stratified across a wider range of habitat suitability, with two sites each randomly placed within quartiles of habitat suitability from a preliminary SDM. At an additional 85 sites in Carrizo Plain (in 2010 and 2011) and 72 sites in the Ciervo-Panoche (in 2011), we set five traps for three nights. These sites were selected randomly between 100 and 250 m from roads and provided both records of

occupancy and measures of body condition and long-term mean abundance, but not mark–recapture estimates of abundance or survival.

MEASURES OF HABITAT QUALITY

We considered a suite of commonly used metrics of individual and population persistence associated with habitat quality that fall into three categories: (i) survival, (ii) abundance and (iii) body condition (Johnson 2007).

Survival and abundance were estimated using robust design mark–recapture estimates at the 28 density sites in Carrizo (Kendall 2012). Primary trapping occasions occurred twice annually, once in the spring (April–May) and once in late summer (August). Twenty-eight sites were trapped for three 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 program MARK (White & Burnham 1999) implemented via the 'RMark' package in program R (Laake 2009). The robust design consists of primary and secondary trapping sessions, with survival estimated between primary sessions and abundance estimated within secondary sessions. Secondary sessions are assumed to be closed to births, deaths, immigration and emigration. 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 did not die). We used a model selection framework with Maximum Likelihood Estimation and corrected Akaike Information Criterion (AICc) (Burnham & 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) (Kendall 2012). N and S were estimated to vary by time and plot. We tested three variants of p , varying by primary and secondary session, and by plot. We 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. $1-\gamma' = 0$) (Kendall 2012). 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 sites had occurred since the summer of 2007, while the trapping on the remaining eight sites began in August 2010. Because MARK does not allow for missing primary capture sessions, we tested two model designs: first, we combined all trapping data but removed any trapping data from before August 2010. We 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, we used counts of burrow mounds at an additional 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 (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 SDM values. At each of the 157 sites that had been trapped across the Carrizo Plain and Ciervo-Panoche with only five traps, we walked a 50 m × 10 m transect and counted every active and inactive burrow mound. Burrow mounds were identified as topographical features, 2–4 m in diameter, with greater vegetation and composition distinct from the surrounding habitat. Burrows were attributed to GKR based on tunnel size opening (height: 78–81 mm; width: 88–89 mm; Williams & Kilburn 1980).

In order to measure body condition, captured GKR were weighed, length of the skull was measured, and most individuals were examined for ectoparasites (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. Due to variability of juvenile body size, 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 downy fur with less distinct colour patterning and undamaged ears. Assigning age class to GKRs can be problematic; we therefore also conducted body mass analyses only for individuals recaptured in more than one primary trapping session (i.e. individuals that were guaranteed to be older than 6 months). We used body mass to skull length ratio as an additional measure of body condition.

RANGE-WIDE DISTRIBUTION MODEL

We created a distribution model for GKR using Maxent (Phillips & Dudik 2008). In addition to the 120 GKR presence points acquired from our trapping data, we used the *gbif* function in the *dismo* package in R (Hijmans *et al.* 2012) to obtain 38 spatially referenced records for GKR from museum collections. Records were restricted to those obtained after 1950, in order to match the temporal range of environmental variables. We then obtained 19 climate layers (Hijmans *et al.* 2005) frequently used in distribution modelling as independent variables (Graham & Hijmans 2006). Bioclim layers are estimated as mean conditions from 1950 to 2000. From the initial 19 layers, we limited our models to six that we believed to be most important in describing GKR distribution and that were only partially correlated with each other. These layers were annual mean temperature (BIO1); annual precipitation (BIO12); minimum temperature of the coldest month (BIO6); precipitation of the driest month (BIO14); and precipitation of the driest quarter (BIO17). In addition to climatic layers, we included soil particle size and slope as predictor variables. Giant kangaroo rats require medium-sized soil particles in order to construct their burrow systems and are generally restricted to areas of less than 10° slope (Grinnell 1932; Williams 1992). Study extent was limited to a buffer of 100 km from all occurrence records. The climate layers were the coarsest resolution layer (30 s), and thus soil particle size and slope were aggregated to match this resolution.

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, Anderson & Schapire 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. Performance was measured using the Area Under the Curve (AUC, Hanley & McNeil 1982).

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

LOCAL DISTRIBUTION MODEL

To further examine the effect of study extent (i.e. the geographic limit of environmental variables included in the model), we then created an SDM, with the same bioclimatic layers as the range-wide model at 30-s resolution, but limited to the area of the Carrizo Plain. This model produced 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 the presence of parasites.

LOCAL TEMPORAL DISTRIBUTION MODELS

We created finer-scale models specific to the Carrizo Plain to consider the temporal dynamics of habitat suitability. Using random points selected from estimates of population extent based on aerial surveys flown over Carrizo Plain in 2010 and 2011 as presences, we used Maxent to model habitat suitability for each year. GKR distribution was mapped using 0.5-km-wide aerial transects, with observers recording the beginning and end of active GKR burrows along each transect. This produced an areal estimate of population extent in our study area (Bean *et al.* 2012). From this total extent, points were randomly selected to be used as occurrence locations for the SDMs. Rather than using broad-scale climatic factors, we 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 1994) at 30-m resolution. We have found 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) (Bean 2012). Therefore, in addition to the local fixed environmental layers, we also included measures of maximum NDVI from the current and

previous year in the yearly models of habitat suitability. All environmental layers for these local models had a 250-m resolution.

Using similar analyses to the range-wide models, we then examined how well these finer-scale models correlated with measures of habitat quality. We 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 SDM values. We also examined how well the local SDMs predicted parasite load and body mass in each given year.

Results

ESTIMATES OF SURVIVAL AND ABUNDANCE

Mark–recapture models estimated from the combined data representing a limited time frame of sampling were generally unreliable and frequently failed to converge. We therefore relied on separate candidate models for (i) the longer trapping data from 20 sites and (ii) the more recent trapping data from the other eight sites (Table 1). While analyses were conducted separately, the same suite of models had the best support for both data sets. 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.

Abundance and survival on the eight new sites were generally lower than the 20 long-term sites, but were otherwise comparable (Table 2, Prugh & Brashares 2012). Only four of the eight more recently established sites had GKR present 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 were trapped and no burrow mounds were apparent.

DISTRIBUTION MODELS

Species distribution models at all scales were generally similar, but variation was high at specific locations in

Table 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	Latitude, Longitude	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	–

Carrizo Plain (Fig. 1). All models had ‘useful’ AUC scores (Hanley & McNeil 1982), although AUC score declined with finer model resolution (0.96 range-wide to 0.75 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 *c.* 30 cm or less.

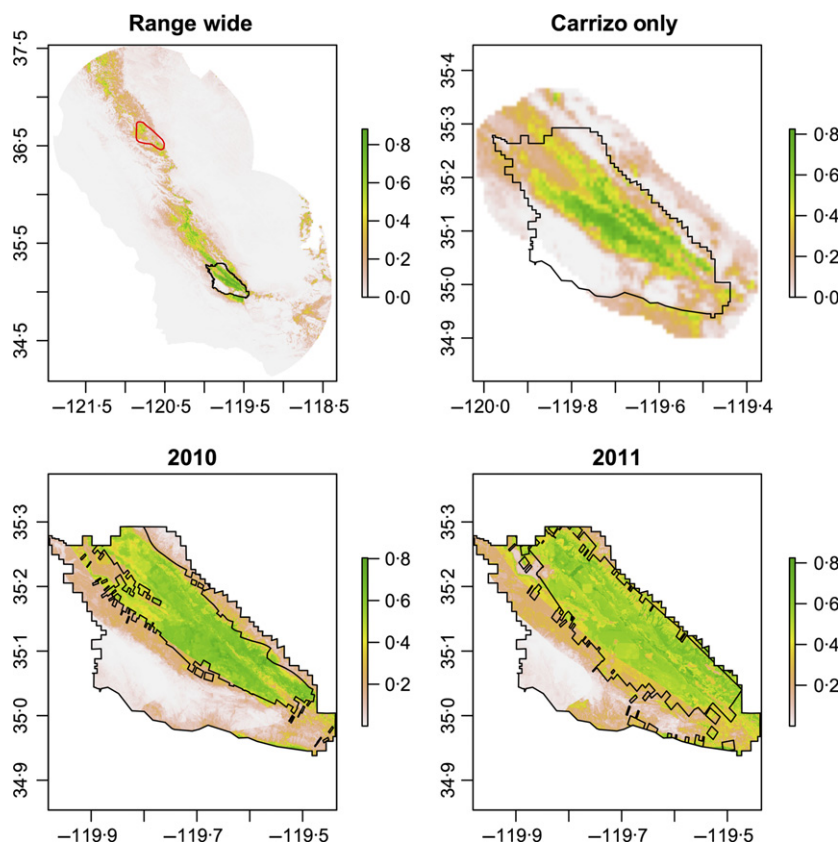
In the 2010 and 2011 models, long-term annual rainfall was the most important variable (50.8% and 47.9% contribution). In 2011, GKR also had a positive correlation

Table 1. Model selection results for mark–recapture estimates of survival and abundance for giant kangaroo rats under a robust design with heterogeneity, with four primary sessions and three secondary sessions each from August 2010 to May 2012. Additional models incorporating a fixed movement with no re-immigration failed to converge. Parameters estimated were survival (ϕ), probability of capture (p) and abundance (N). Two types of movement were tested. Random movement (R) allowed for equal probability of immigration or emigration, while Markov movement (M) estimated different immigration and emigration rates. Models were estimated from 91 unique capture histories

Model	Movement	k	AIC _c	Δ AIC _c	Weight
$\phi(\text{time+Plot})p(\text{session})N(\text{session+Plot})$	R	21	215.30	0	0.59
$\phi(\text{time+Plot})p(\text{session})N(\text{session+Plot})$	M	22	217.45	2.157	0.20
$\phi(\text{time+Plot})p(\text{session+Plot})N(\text{session+Plot})$	R	24	217.68	2.389	0.18
$\phi(\text{time+Plot})p(\text{session+Plot})N(\text{session+Plot})$	M	26	222.05	6.756	0.02
$\phi(\text{time+Plot})p(\text{session})N(\text{session+Plot})$	M	21	224.79	9.489	0.01
$\phi(\text{time+Plot})p(\text{session+Plot})N(\text{session+Plot})$	M	25	229.06	13.765	0.00
$\phi(\cdot)p(\cdot)N(\text{session})$	–	8	230.47	15.177	0.00

AIC_c, Akaike Information Criterion.

Fig. 1. Giant kangaroo rat (GKR) distribution models created with Maxent at three spatial scales. Longitude and latitude are given on the x and y axes; colour 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 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. Area Under the Curve scores for each model were ‘useful’ (range-wide: 0.981; Carrizo-only: 0.937; 2010: 0.832; 2011: 0.752).



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. Suitability values for all trapping sites ranged from 0.62 to 0.86 in the range-wide model; 0.60 to 0.87 in the Carrizo-only model; and 0.04 to 0.73 in the finest scale models that incorporated changes in population extent and resource availability.

HABITAT SUITABILITY VS. HABITAT QUALITY

Long-term mean abundance, estimated from counts of burrow mounds at 93 sites in Carrizo Plain and 51 sites in Ciervo-Panoche, was positively correlated with habitat suitability at all scales. Population abundance, estimated from 28 mark–recapture plots, was positively correlated with habitat suitability at local scales. Three-year mean abundance was positively correlated at the range-wide scale, but not the Carrizo-only scale (Fig. 2). We found no relationship between standard deviation of population abundance (i.e. stability), a potential measure of habitat quality, and SDM value at any scale. SDMs were not correlated with survival at any of the 28 sites (Fig. 3).

Body mass was not significantly correlated with SDM values at any scale. Results were similar examining only recaptured individuals or skull length to body mass ratios. In general, the presence of orange mites was negatively

correlated with habitat suitability. The presence of fleas was not correlated with distribution model value at the range-wide or fixed Carrizo Plain model; however, in the 2011 model, the presence of fleas was positively correlated with SDM value.

Discussion

In this study, we examined the extent to which SDMs correlated with proxies of habitat quality for the GKR. While models at all scales were correlated with long-term mean abundance estimated from burrow density, the model built from data collected at a local spatial scale did not correlate with abundance estimated from mark–recapture trapping. Correlation between abundance and SDM value also increased at finer temporal and spatial scales. None of the SDMs were significantly correlated with survival.

Correlations between estimated abundances and SDM values conformed 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, we also used counts of burrow mounds as a proxy for long-term population size. Studies of GKR population (Bean *et al.* 2012) and behavioural ecology (Randall *et al.* 2002) support the use of burrow mounds as a measure of carrying capacity: GKR are solitary and in times of higher-than-average density will share

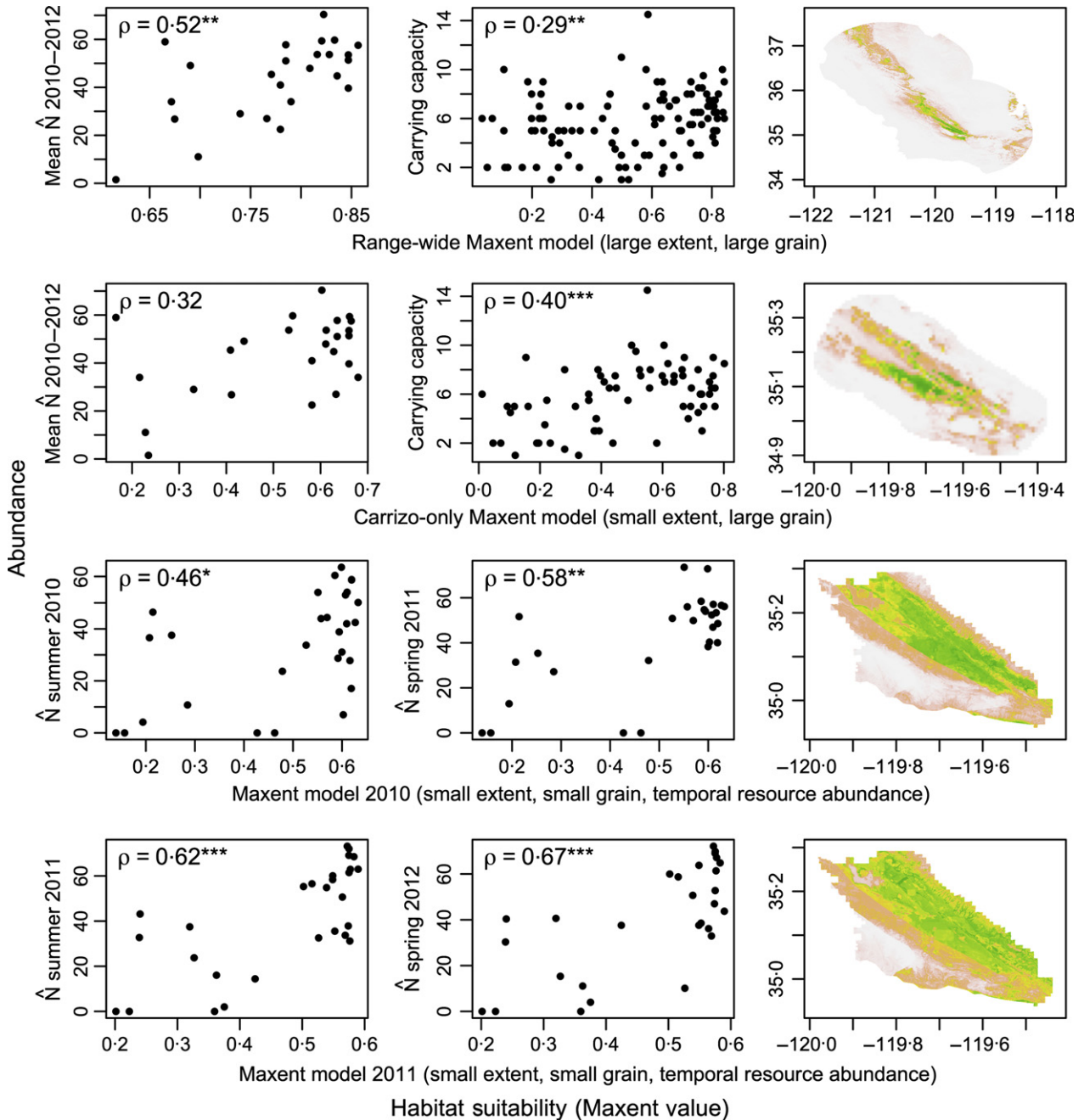


Fig. 2. Relation of abundance to habitat suitability at three spatial scales and two time periods. N was estimated using robust design mark–recapture models for four trapping occasions from August 2010 to May 2012. Carrying capacity was estimated as number of burrow counts in a 50 m \times 10 m transect 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 estimated from Normalized Difference Vegetation Index in a given year). Broad-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. * $P < 0.5$; ** $P < 0.1$; *** $P < 0.01$.

burrows, while in times of lower-than-average density will increase home range to incorporate multiple burrows. At the broadest scales, then, it is unsurprising, but reassuring, that SDMs predict habitat quality as measured by long-term abundance.

At the same time, two findings of this study raise some concern about the use of SDMs 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 SDM values within GKR population extent. The range-wide SDM produced a homogenous suitability value for most of the Carrizo Plain, whereas the SDM using the same environmental layers but with smaller total extent created greater

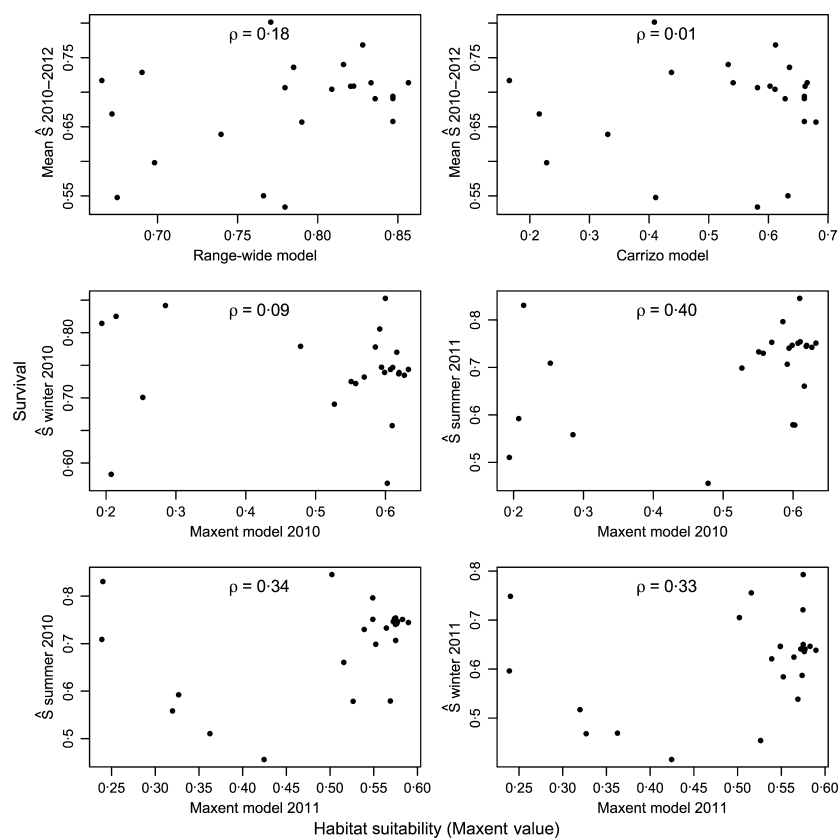


Fig. 3. Relation of habitat suitability to giant kangaroo rat survival estimated with mark–recapture models at 28 sites in Carrizo Plain National Monument. Species distribution models were unable to predict survival at any spatial scale or time period.

variability in suitability scores. As always, the management question will dictate the appropriate scale for model building. Broad-scale studies may be appropriate for designing protected areas or designating critical habitat: the two largest known GKR populations (Carrizo Plain 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. Environmental variables differed between each spatial and temporal scale, and additional years of data are always recommended in order to understand determinants of a species' niche.

Further, while longer-term management may be conducted with coarse-scaled models, our results suggest only the finest temporal and spatial models should be used to inform management of 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 no models were correlated with survival.

Although most models adequately estimated mean abundance over time, we were unable to generate a model that consistently predicted survival, even though mean survival is positively correlated with mean abundance over time at each site. At the individual site scale, local community-level factors likely play a larger role in determining survival than habitat quality. Processes such as interspecific competition and predation cannot be defined

with single-species distribution models. Two sites could have similar habitat quality and support the same number of GKR over time, but if one site is located close to a kit fox (*Vulpes macrotis mutica*) natal den (as was observed in this study), for example, survival will be substantially lower. Further, for many species, survival is likely to be negatively related to density. For some applications, abundance may be a more appropriate measure of habitat quality. It should be noted, then, that SDMs may be problematic for management decisions that seek high animal survival over short time frames (e.g. relocation efforts).

In fact, correlations were strong enough from these yearly models that it may be possible to estimate GKR population size in Carrizo from the SDM ($\rho = 0.62$ in 2011). A linear regression of abundance predicted by SDM value in August 2011 gives a y-intercept (β_0) of -19.90 and a slope (β_1) of 122.93 . Incidentally, this places the x-intercept at 0.162 – that is, assuming a linear relationship between GKR abundance and habitat suitability value, there should be 0 GKR at or below suitability values of 0.162 . Indeed, of the 105 sites trapped across Carrizo in 2011, only one site had GKR present below a model value of 0.162 (at 0.08). In other words, GKR abundance based on trapping is predicted to be 0 at approximately the same value Maxent predicted a probability of presence of 0. Each Maxent cell is $30\text{ m} \times 30\text{ m}$ (900 m^2), whereas abundance of GKR is calculated for $120\text{ m} \times 120\text{ m}$ cells ($12\,100\text{ m}^2$). So, total abundance in 2011 for Carrizo

Plain should be the sum of all Maxent cells, adjusted by the equation

$$(-19 \cdot 90 + 122 \cdot 93 \cdot \text{maxent value}) \cdot (900/12100) = 1898728 \quad \text{eqn 1}$$

which equates to a population density of *c.* 18 per ha. This estimate matches well with our observed estimates at trapping grids, where estimated density ranged from *c.* 1 to 50 individuals per hectare.

The weak relationship found between SDMs 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 separately from survival (Kendall 2012). Although GKR 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 SDM values and survival. However, a pilot telemetry project on a subset of five of our study plots estimated similar survival rates using data from radio-collared adults (S. Etter, unpublished data).

In conclusion, we found that species SDMs can be effective proxies for some measures of 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 SDMs may effectively target areas of high habitat quality, but at finer scales, more local models were necessary. Resource selection functions may be better at predicting these finer-scale measures of habitat quality, and on-going research to unite the literature on SDMs with resource selection functions is likely to lead to greater synthesis in spatial ecology (Warton & Aarts 2013). While SDM values were correlated with long-term trends in abundance, most models were incapable of predicting survival. Additional research is required to understand how much this failure was due to the data or models used and how much was simply due to stochastic or undetected community-level processes.

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Data accessibility

Recapture histories for mark–recapture analysis: dx.doi.org/10.5061/dryad.3c5r8.

Environmental predictors used in Maxent models: <http://dx.doi.org/10.5061/dryad.3c5r8>

Additional environmental predictors (BIOCLIM): www.worldclim.org/bioclim.

Additional giant kangaroo locations: www.gbif.org.

Giant kangaroo rat burrow density: doi: dx.doi.org/10.5061/dryad.3c5r8 (Bean *et al.* 2014).

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