Wildlife Society Bulletin 36(3):587–593; 2012; DOI: 10.1002/wsb.171

Tools and Technology

An Evaluation of Monitoring Methods for the Endangered Giant Kangaroo Rat

WILLIAM T. BEAN,[1] *Environmental Science, Policy & Management and Museum of Vertebrate Zoology, University of California, 130 Mulford Hall, Berkeley, CA 94720, USA*

ROBERT STAFFORD, *California Department of Fish & Game, P.O. Box 6360, Los Osos, CA 93412, USA*

LAURA R. PRUGH, *Biology and Wildlife Department, University of Alaska Fairbanks, Fairbanks, AK 99775, USA*

H. SCOTT BUTTERFIELD, *The Nature Conservancy, 201 Mission Street 4th Floor, San Francisco, CA 94105, USA*

JUSTIN S. BRASHARES, *Environmental Science, Policy & Management, University of California, 130 Mulford Hall, Berkeley, CA 94720, USA*

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. We 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, we 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. We 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. © 2012 The Wildlife Society.

KEY WORDS aerial surveys, burrowing rodent, *Dipodomys ingens*, giant kangaroo rat, population indices.

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

Received: 13 February 2012; Accepted: 29 April 2012
Published: 10 August 2012

[1]*E-mail: bean@berkeley.edu*

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, we 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.

We assessed multiple methods of monitoring GKR range extent, abundance, and growth rate within the Carrizo Plain National Monument, California, USA (Fig. 1). Specifically, we 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. We then compare mark–recapture estimates of density with active burrow counts as measures of both GKR density and population growth rates.

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.

METHODS

Estimating Distribution Extent

We 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, we 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, we 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). We conducted 20-min estimates of activity at each site using these signs as characteristics of GKR presence. This estimation served as a rapid assessment of the site.

We then set 5 traps on burrows that appeared to be active. If we could not find active burrows, traps were place on apparently inactive burrows. If the site had no detectable GKR burrows, we placed traps near other rodent burrows. We trapped each site for 3 nights from June through August 2010, and again in June 2011. Sites were classified as occupied if $\geq$1 GKR was trapped, or if we 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).

We 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/hr 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.

We 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.

We 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, we estimated GKR abundance and growth using mark–recapture trapping at 30 sites (Krebs 1999). At each site, we 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. We trapped sites 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). We estimated density 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. We assumed that mark–recapture data provided the most accurate estimates of density and growth, against which we compared our burrow count estimates. Additional details of this trapping are provided in Prugh and Brashares (2010, 2011).

In 2007, we 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, we digitized burrows from an image acquired by the Quickbird-2 satellite (Fig. 1B), and we 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.

We 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. We 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, we 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), we compared burrow counts from each year to the 3-year mean mark–recapture estimates.

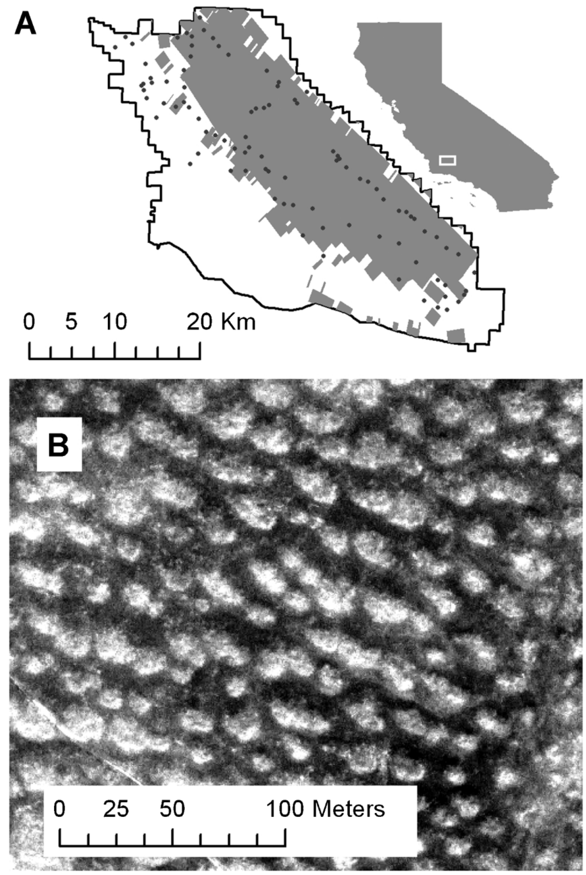

Figure 1. (A) Location of Carrizo Plain National Monument (black outline), eastern San Luis Obispo County, California, USA, with individual trapping locations used to determine range extent (shown as black dots). The gray polygon depicts the observed extent of giant kangaroo rats in 2011 from aerial 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.

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 1). Expert assessment had the highest agreement score of any method, with 91% total agreement with

Table 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 $\pm$ 0.5 km (2010)	0.925	0.679	0.824	0.604
Aerial survey $\pm$ 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."

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 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 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 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), 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, we 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). 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. 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. We 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 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). We 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, we 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 1). Specificity (the sites correctly classified as absent) was lower. That is, through expert assessment, we 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;

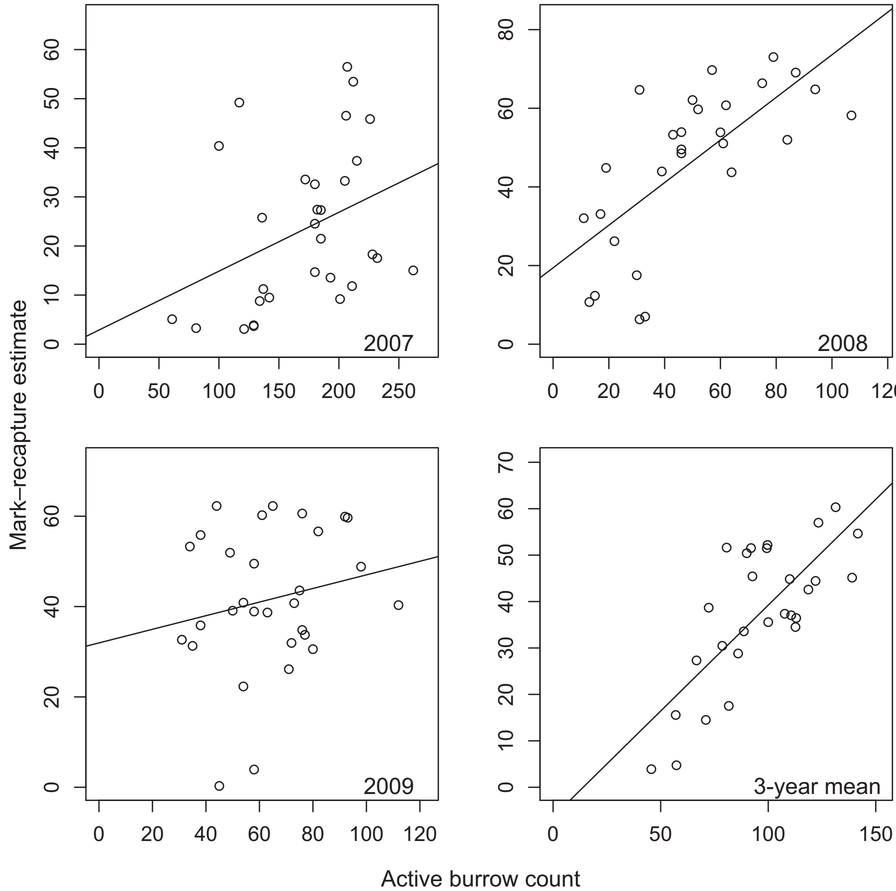

Figure 2. Correlations between mark–recapture estimates of giant kangaroo rat density and counts of active burrows in 2007, 2008, and 2009 in eastern San Luis Obispo County, California, USA. 2007 and 2008 showed significant, positive correlations between density estimates, but the relationship between 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.

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 we expected similar results between aerial surveys and photographs, we 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

Table 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

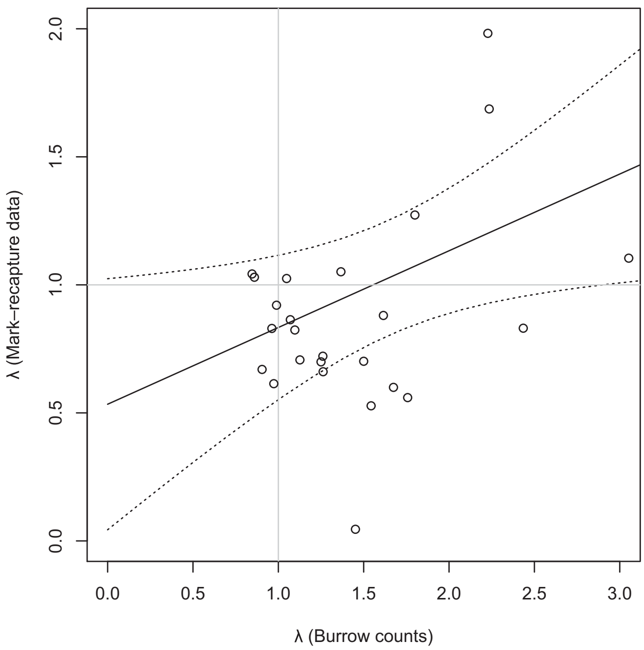

Figure 3. Relationship between site-specific population growth of the giant kangaroo rat estimated from mark–recapture data and estimates based on active burrow counts from 2008 to 2009 in eastern San Luis Obispo County, California, USA. Dashed lines show 95% confidence intervals of "true" growth calculated 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.

burrow counts, we found positive correlations in all 3 years of our study with a 3-year mean of GKR abundance. Unfortunately, we 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.

MANAGEMENT IMPLICATIONS

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, $\geq$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, we reiterate 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.

ACKNOWLEDGMENTS

We thank J. Hurl, K. Sharum, and L. Saslaw for logistical field support; and we thank the numerous field assistants who collected data for this study, in particular G. Pfau and A. Fedele. We thank 2 anonymous reviewers for incisive and helpful comments. Funding was provided by The Nature Conservancy, U.S. Department of Agriculture, Bureau of Land Management, California Department of Fish and Game, and the A. Starker Leopold Wildlife Graduate Student Fund.

LITERATURE CITED

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

Bean, W. T., R. Stafford, and J. S. Brashares. 2011. The effects of small sample size and sample bias on threshold selection and accuracy assessment of species distribution models. Ecography 35:250–258.

Caughley, G. 1977. Analysis of vertebrate populations. John Wiley & Sons, New York, New York, USA.

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

Crawley, M. J. 2005. Statistics: an introduction using R. John Wiley & Sons, Chichester, England, United Kingdom.

Forsyth, D. M., R. J. Barker, G. Morriss, and M. P. Scroggie. 2007. Modeling the relationship between fecal pellet indices and deer density. Journal of Wildlife Management 71:964–970.

Germano, D. J., G. B. Rathbun, L. R. Saslaw, B. L. Cypher, E. A. Cypher, and L. M. Vredenburgh. 2011. The San Joaquin Desert of California: ecologically misunderstood and overlooked. Natural Areas Journal 31: 138–147.

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

Krebs, C. J. 1999. Ecological methodology. Addison-Wesley, Menlo Park, California, USA.

Laake, J. L. 2009. RMark: R code for MARK analysis. R package version 1.9.0. http://www.phidot.org/software/mark/rmark/. Accessed 20 Nov 2009.

Lisicka, L., J. Losik, J. Zejda, M. Heroldova, J. Nesvadbova, and E. Tkadlec. 2007. Measurement error in a burrow index to monitor relative population size in the common vole. Folia Zoologica 56:169–176.

Odell, E. A., F. M. Pusateri, and G. C. White. 2008. Estimation of occupied and unoccupied black-tailed prairie dog colony acreage in Colorado. Journal of Wildlife Management 72:1311–1317.

Payne, N. F. 1981. Accuracy of aerial censusing for beaver colonies in Newfoundland. Journal of Wildlife Management 45:1014–1016.

Powell, K. L., R. J. Robel, K. E. Kemp, and M. D. Nellis. 1994. Aboveground counts of black-tailed prairie dogs—temporal nature and relationship to burrow entrance density. Journal of Wildlife Management 58:361–366.

Prugh, L. P., and J. S. Brashares. 2010. Basking in the moonlight? Illumination increases the capture success of the endangered giant kangaroo rat. Journal of Mammalogy 91:1205–1212.

Prugh, L. P., and J. S. Brashares. 2011. Partitioning the effects of an ecosystem engineer: kangaroo rats control community structure via multiple pathways. Journal of Animal Ecology 81:667–678.

Randall, J. A., E. R. Hekkala, L. D. Cooper, and J. Barfield. 2002. Familiarity and flexible mating strategies of a solitary rodent, *Dipodomys ingens*. Animal Behaviour 64:11–21.

Robel, R. J., and L. B. Fox. 1993. Comparison of aerial and ground survey techniques to determine beaver colony densities in Kansas. Southwestern Naturalist 38:357–361.

Rotella, J. J., and J. T. Ratti. 1986. Test of a critical density index assumption: a case study with gray partridge. Journal of Wildlife Management 50:532–539.

Rubidge, E. M., W. B. Monahan, J. L. Parra, S. E. Cameron, and J. S. Brashares. 2011. The role of climate, habitat, and species co-occurrence as drivers of change in small mammal distributions over the past century. Global Change Biology 17:696–708.

Sidle, J. G., D. H. Johnson, and B. R. Euliss. 2001. Estimated areal extent of colonies of black-tailed prairie dogs in the northern Great Plains. Journal of Mammalogy 82:928–936.

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

White, G. C., J. R. Dennis, and F. M. Pusateri. 2005. Area of black-tailed prairie dog colonies in eastern Colorado. Wildlife Society Bulletin 33:265–272.

Williams, D. F. 1992. Geographic distribution and population status of the giant kangaroo rat, *Dipodomys ingens* (Rodentia, Heteromyidae). Pages 301–329 *in* S. Byrne, T. A. Rado, and D. F. Williams, editors. Endangered and sensitive species of the San Joaquin Valley, California. California Energy Commission, Sacramento, USA.

Associate Editor: Applegate.