RANGE-WIDE MONITORING OF THE MOJAVE DESERT TORTOISE (*GOPHERUS AGASSIZII*):

2013 AND 2014 ANNUAL REPORTING

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JUNE 2015

Recommended Citation: U.S. Fish and Wildlife Service. 2015. Range-wide Monitoring of the Mojave Desert Tortoise (*Gopherus agassizii*): 2013 and 2014 Annual Reports. Report by the Desert Tortoise Recovery Office, U.S. Fish and Wildlife Service, Reno, Nevada.

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Acknowledgements

Funding or support-in-kind was provided by the Marine Corps Air Station, Yuma; Arizona Strip Office, Bureau of Land Management (2013); Southern Nevada Office, Bureau of Land Management (2013); and National Training Center, Ft. Irwin (2014).

The original design for this project and considerations for optimizing it based on new information and experience were first set out in Anderson and Burnham (1996) and Anderson et al. (2001). Estimation methods were further refined during a 2008 workshop for distance sampling held by S. Buckland, L. Thomas, T. Marques, E. Rexstad, and D. Harris in Marshall, California.

The analysis of adult trends benefited greatly from reviews by R. Steidl, K. Ralls, J. M. Reed, R. Averill-Murray, C. Darst, K. Field, and 2 anonymous reviewers of a larger manuscript prepared and submitted for publication.

Personnel from Joshua Tree National Park led by M. Vamstad, from Kiva Biological Consulting (California) led by I. Daly, and from the Great Basin Institute (Nevada, Arizona, and the Beaver Dam Slope of Utah) led by T. Christopher and K. Dutcher conducted the field surveys. The field monitors from these teams who did the hard work of collecting and verifying the data were:

2013: M. Bassett, I. Daly, A. d'Epremesnil, K. Foley, B. Hanley, A. Johnson, S. Johnson, G. Keyes, T. Kreofsky, D. Leach, J. MacNaughton, C. McClurg, C. Michaud, L. Mjos, B. O'Brien, T. Rode, D. Sanderson, W. Schultz, B. Sparks, A. Sturgill, S. Vaghini.

2014: M. Bassett, R. Crawford, I. Daly, A. Eberly, A. d'Epremesnil, K. Foley, B. Hanley, G. Keyes, K. Lalumiere, J. MacNaughton, C. McClurg, L. Mjos, B. O'Brien, D. Sanderson, F. Smith, L. Smith, R. Vorhoorst, A. Wiley, N. Wiley.

R. Patil (University of Nevada, Reno), M. Brenneman (Topoworks), and B. Sparks (GBI) provided specialized training instruction for field crews. D. Zeliff, D. Wiersma, and C. Grasteit (Mojave Desert Ecosystem Program) provided independent review and post-processing of data submitted by both field groups. In 2013, R. Patil (University of Nevada, Reno) updated the electronic data-collection forms and procedures used in both 2013 and 2014. K. Dutcher ran first-level quality assurance/quality control for both 2013 and 2014. M. Brenneman developed GIS tools for correctly reflecting transect paths and tracking completion of assigned transects and developed the final databases.

EXECUTIVE SUMMARY

The recovery program for desert tortoises in the Mojave and Colorado deserts (USFWS, 2011) requires range-wide, long-term monitoring to determine whether recovery goals are met. Specifically, will population trends within recovery units increase for a period of 25 years? In 1999, the Desert Tortoise Management Oversight Group endorsed the use of line distance sampling (Buckland et al., 2001) for estimating range-wide desert tortoise density. From 2001 to 2005 and 2007 to 2014, the USFWS has coordinated the distance sampling monitoring program for desert tortoises in 4 of the 5 recovery units. (The Upper Virgin River Recovery Unit is monitored by Utah Division of Wildlife Resources (UDWR; McLuckie et al., 2014).)

This report describes quality assurance steps and final results for the 2013 and 2014 monitoring efforts. Although in the past effort was directed annually at 16 long-term monitoring strata, in 2012 and especially 2013, agency funding was severely curtailed. In 2013, the decision was made to survey only in well-funded strata to generate robust estimates rather than attempting to cover more strata in a less satisfactory manner, and this approach continued in 2014. Data were collected on transects and at telemetry sites by field personnel working with three different groups, Kiva Biological (11 and 15 personnel in 2013 and 2014, respectively), Great Basin Institute (10 personnel in 2013), and Joshua Tree National Park (4 personnel in 2014). Only personnel with prior training and experience were utilized for distance sampling, so training was trimmed from an intensive, 12-day training session, to only 2 days preseason training and testing provided by the USFWS in 2013 and crew-led training in 2014. In 2013, crews completed 173 transects (2019 km) between 7 March and 24 May. In the course of these surveys, they reported 83 live tortoises, 71 of which were at least 180 mm midline carapace length (MCL). In 2014, crews completed 230 transects (2649 km) between 13 March and 5 May. In the course of these surveys, they reported 134 live tortoises, 119 of which were at least 180 mm MCL.

Annual detection curves were developed to describe the decreasing ability of each team to see tortoises farther from the walked transect line. In 2013, crews detected 44.5% (CV = 19.7%) of tortoises within 16 m of the transect centerline. The proportion of tortoises that were visible to be counted varied in different parts of the range, surveyed during different periods in the spring. Visibility was as high as 84.1% in the Chuckwalla telemetry site during 8 days in early March. Visibility in Gold Butte-Pakoon during the last 3 weeks of April and first 3 days of May was 67.8% and was very similar (67.7%) during the next 3 weeks at the Halfway Wash telemetry site near Mormon Mesa. On average, crews walked 29.7 km for each tortoise that was observed, but this number varied considerably between monitoring strata. Estimated densities in the Northeastern Mojave Recovery Unit were lower (Gold Butte-Pakoon 1.7 tortoises/km^2, CV=40.3%; Beaver Dam Slope 2.6 tortoises/km^2, CV=41.3%) than in the Chocolate Mountain portion of the Colorado Desert (7.3 tortoises/km^2, CV=26.9%), a pattern similar to past years.

In 2014, estimated densities in Chocolate Mountain stratum were 8.4 tortoises/km^2 (CV = 25.0%). The three strata of the Western Mojave Recovery Unit were also surveyed and had an adult densities ranging from 2.5 tortoises/km^2 (SC; CV = 24.4%) to 4.7 tortoises/km^2 (FK; CV = 22.1%). The transect width was set narrower at 10 m, within which 60.8% (CV = 6.1%) of visible tortoises were detected. The encounter rate averaged 22.5 km for each tortoise that was observed. Visibility was as low as 58.5% in the Chuckwalla telemetry site during 8 days in mid-March. Visibility in Ord-Rodman was 98.8% during the first 8 days of April and averaged only slightly lower (91.3%) over the following 28 days in Superior-Cronese.

Fourteen years after this project was initiated range-wide (18 years after it was piloted in the Upper Virgin River Recovery Unit), the USFWS and UDWR took the opportunity to evaluate whether interim population trajectories were on track to meet the specific recovery plan criterion of increasing densities in each recovery unit after 25 years (Allison and McLuckie, in review). Methods for collecting these data were comparable between years since 1999 in Upper Virgin River and since 2004 where monitoring has been coordinated by USFWS. Using annual density estimates for each stratum (strata correspond to tortoise conservation areas [TCAs] in the recovery plan), we applied a log-linear mixed-effects regression model to estimate annual percent change in densities through 2014 for each of 17 TCAs in the 5 recovery units. There were increases in density of adults in the 4 TCAs in the Northeastern Mojave Recovery Unit, but declines in all but 2 TCAs in the other 4 recovery units. We estimate that in 2004 there were 126,346 adult tortoises (SE = 41,291) in the 17 TCAs, with an overall loss of 40,660 adult tortoises (SE = 13,288) by 2014.

Estimated adult Mojave desert tortoise densities and abundance in each recovery unit in 2014 and change in abundance in each recovery unit between 2004 and 2014 based on multi-year trends in density/km^2. See Table 10 for information by TCA.

Recovery unit	Surveyed area (km^2)	Density (SE)	2004 Abundance (SE)	2014 Abundance (SE)	Δ Abundance (SE)
Western Mojave	6294	2.8 (1.0)	35777 (9703)	17644 (4785)	-18133 (4918)
Colorado Desert	11,663	3.7 (1.3)	67087 (23312)	42770 (14862)	-24317 (8450)
NE Mojave	4160	4.4 (1.8)	4920 (2190)	18220 (8109)	13300 (5919)
Eastern Mojave	3446	1.5 (0.6)	16165 (4515)	5292 (1478)	-10873 (2949)
Upper Virgin R.	115	15.3 (1.6)	2397 (783)	1760 (575)	-637 (208)
Overall	25,678		126,346 (41,292)	85,686 (28,004)	-40,660 (13,288)

This monitoring program provides an integrated measure of the effectiveness of past recovery activities and informs adaptive management in the future. Prevailing declines in the abundance of adults overall and in four of the five recovery units indicate the need for more aggressive implementation of recovery actions and more critical evaluation of the suite of future activities and projects in tortoise habitat that may exacerbate ongoing population declines.

RANGE-WIDE MONITORING OF THE MOJAVE DESERT TORTOISE 2013 & 2014

INTRODUCTION

The Mojave Desert population of the desert tortoise (*Gopherus agassizii*) was listed as threatened under the Endangered Species Act in 1990. This group of desert tortoises north and west of the Colorado River are now recognized as the species *G. agassizii*, separate from *G. morafkai* south and east of the Colorado River (Murphy et al., 2011). The revised recovery plan (USFWS, 2011) designates five recovery units to which decisions about continued listing status should be applied. The recovery plan specifies that consideration of delisting should only proceed when populations in each recovery unit have increased for at least one tortoise generation (25 years), as determined through a rigorous program of long-term monitoring. Before the tortoise was listed, populations were monitored either using strip transects (Luckenbach, 1982), where indications of tortoise presence (live or dead tortoises, scats, burrows, or tracks) were converted to tortoise abundance categories based on calibration transects conducted in areas of better-known tortoise density, or by using capture-recapture population estimates on a limited number of (usually) 1-mi^2 study plots (Berry and Nicholson, 1984). Although data have continued to be collected on transects and study plots in recent years for various purposes, these methods suffer design limitations and/or logistical constraints that render them unsuited for monitoring trends in abundance applicable to entire recovery units (Corn, 1994; Anderson et al., 2001; Tracy et al., 2004). In 1999 the Desert Tortoise Management Oversight Group endorsed the use of line distance sampling (Buckland et al., 2001) for estimating range-wide desert tortoise density.

Distance sampling methods use measurements taken from the center of the transect lines to tortoises to model detection as a function of distance from the walked path; tortoises farther from the travelled path have a lower probability of detection. To estimate the true (not relative) proportion of tortoises detected within a given distance from the center of the transect, all tortoises must be detected on the transect centerline (Anderson et al., 2001; Buckland et al., 2001). There are additional assumptions in distance analysis – that distance is measured to the point where the animal was first detected and that distance is measured accurately – but these are easily satisfied in line distance sampling of desert tortoises. Because they are so cryptic, however, the assumption that detection at the centerline of the transect is perfect, can be violated during line distance sampling of tortoises. The use of two observers therefore minimizes the probability that tortoises are missed on the centerline and if needed provides a correction factor in the form of an estimate of the number of tortoises on the line that were missed (USFWS, 2009). Another correction factor is needed to account for tortoises that were not visible because they were deep in burrows. This proportion is estimated by observing transmittered tortoises that can be located whether they are visible or not.

Distance methods were first applied to estimate abundance of Sonoran Desert Tortoises (*G. morafkai*) in 2000 (Swann et al., 2002; Averill-Murray and Averill-Murray, 2005) and for *G. agassizii* in the Upper Virgin River Recovery Unit in Utah since a pilot study by Utah Division of Wildlife Resources (UDWR) in 1997 (McLuckie et al., 2002). The USFWS used line distance sampling to estimate abundance of tortoises in the remaining five recovery units for *G. agassizii* in Utah, Arizona, Nevada, and California starting in 2001 (USFWS 2006, 2009, 2012a, 2012b, 2013, 2014). This report describes implementation of monitoring and presents the analysis of desert tortoise density in 2013 and 2014. Because these protocols have been maintained since the original pilot years in each TCA, the report also uses annual density estimates since 1999 in the Upper Virgin River Recovery Unit and since 2004 in the remaining recovery units to describe ongoing trends in adult densities.

METHODS

Study areas and transect locations

Long-term monitoring strata (Figure 1) will be used over the life of the project to describe population trends in areas where tortoise recovery will be evaluated. These areas are called "tortoise conservation areas" (TCAs) in the recovery plan to describe designated critical habitat as well as contiguous areas with potential tortoise habitat and compatible management. The area associated with each critical habitat unit (CHU) is generally treated as one monitoring stratum, although the portion of Mormon Mesa CHU that is associated with Coyote Springs Valley is treated as a separate stratum. Chuckwalla CHU is also treated as dual monitoring strata, with potentially unequal sampling effort in the areas managed by the Department of Defense (Chocolate Mountain Aerial Gunnery Range, CMAGR) and by the Bureau of Land Management (BLM). New recovery units were established under the revised recovery plan (USFWS, 2011), so while making the corresponding changes to our databases we also separated the Piute and Eldorado Valleys into 2 distinct strata since they are in different recovery units. Fenner Valley is a distinct stratum from Piute Valley to simplify reporting by state. The Joshua Tree stratum does not encompass all suitable habitat for desert tortoises in Joshua Tree National Park (JTNP). The national park designation and current boundaries just post-date the designation of CHUs, so some of the Pinto Mountains and Chuckwalla CHUs (and monitoring strata) are in the current JTNP. Where annual density estimation is described, we use "strata" to describe the same areas that are called "TCAs" when describing population trends that apply to recovery criteria.

In 2013, we surveyed the AG stratum in California and the BD and GB strata in Nevada, Arizona, and Utah. In 2014, surveys were conducted exclusively in California in the AG, FK, OR, and SC strata. The optimal number of transects in a monitoring stratum was determined by evaluating how these samples would contribute to the precision of the annual density estimate for a given stratum (Anderson and Burnham, 1996; Buckland et al., 2001). Power to detect an increasing population size is a function of 1) the magnitude of the increasing trend, 2) the "background noise" against which the trend operates, and 3) the length of time the trend is followed (even a small annual population increase will result in a noticeably larger population size if the increase continues for many years).

The magnitude of the population trend is a function of recovery activities and the population dynamics of the tortoise, which are unaffected by monitoring design and sample size. The second contributor to the power to detect a trend is the level of background variability in the density estimates, which is directly affected by the number, length, and placement of transects in the monitoring strata. Anderson and Burnham (1996) recommended that transect number and length be chosen to target precision reflected in a coefficient of variation (CV) of 10-15% for the estimate of density in each recovery unit. The CV describes the standard deviation (a measure of variability) as a proportion of the mean and is often converted to a percentage. The target CV is achieved based on the number of tortoises that might be encountered there (some strata have higher densities than others), as well as the area of the stratum – its proportional contribution to the recovery unit density estimate (Buckland et al., 2001).

The actual number of transects assigned in each stratum was a function of the optimal numbers described above, as well as on available funding. Transects were selected from among a set of potential transects laid out systematically across strata, with a random origin that was established in 2007 for the lattice of transects. Systematic placement provides more even coverage of the entire stratum, something that may not occur when strictly random placement of transects is used. Once the number of transects in a stratum was determined, these were selected using randomization procedures; in 2013 and 2014 I used R software to implement the Generalized Random Tesselated Stratified (GRTS) spatially balanced survey design procedure (R Core Team, 2014; Kincaid and Olsen, 2013). The US Environmental Protection Agency developed GRTS as a means to generate a spatially balanced, random sample (Stevens and Olsen, 2004). I used it to select planned transects with these qualities as well as a set of alternative transects that would contribute to the final sample having the same spatially representative and random properties if any planned transects were replaced due to field logistics. Because the same set of potential transects has been used since 2007, some transects are repeated between years but others may not have been selected in the past.

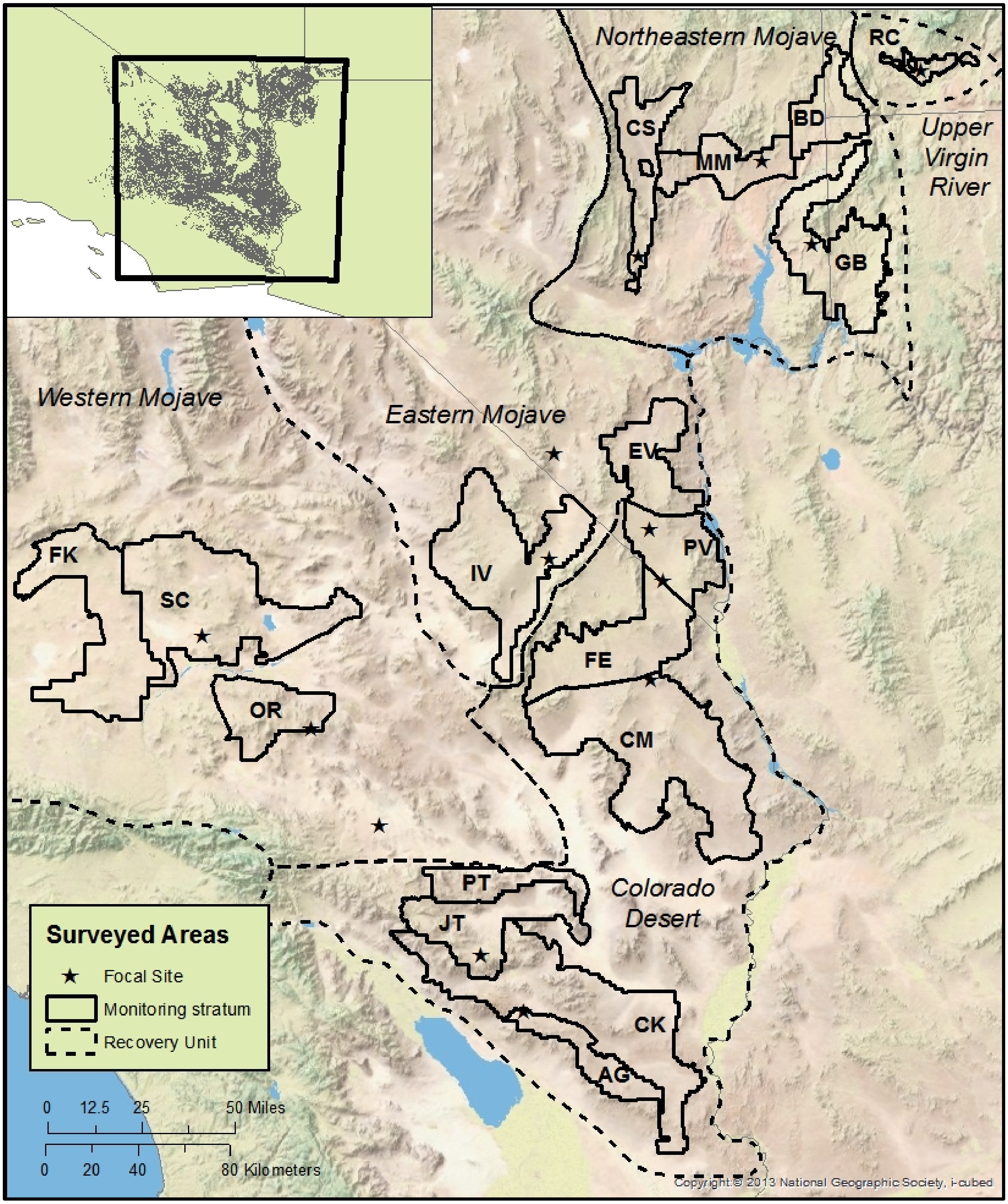

Figure 1. Long-term monitoring strata (n=17) corresponding to tortoise conservation areas (TCAs) in each recovery unit. TCA codes are given in Table 1. Potential habitat is overlain on the southwestern United States in the extent indicator.

Distance sampling transect completion

One adaptation that tortoises have for living in the desert is to restrict surface activity to fairly narrow windows of time during the year. In general, tortoises emerge from deep within shelters (burrows) from mid-March through mid-May and then again (less predictably) in the fall. These periods coincide with flowering of their preferred food plants (in spring) and with annual mating cycles (in fall). The annual range-wide monitoring effort is scheduled to match the spring activity period for tortoises.

During this season, not all tortoises are above ground or visible in burrows. To encounter as many tortoises as possible, monitoring is scheduled for early in the day and to be completed before the hottest time of day. Because tortoises are located visually, monitoring is restricted to daylight hours. Based on past experience, we expect tortoises to become most active after 8am during March (it is usually too cool before this time), but to emerge earlier and earlier until their optimal activity period includes sunrise by the beginning of May. In May, we also expect daytime temperatures to limit tortoise above-ground activity as the morning progresses to afternoon.

Field crews completed transects during this optimal period each day. Start times were decided a week in advance, so crews arrived at transects at similar times on a given morning. However, completion times will be more variable, as a consequence of terrain, number of tortoises encountered, etc. Under normal conditions, each team walked one 12-km square transect each day. Teams were comprised of two field personnel who switched lead and follow positions at each corner of each transect, so they each spent an equal amount of time in the leader and follower positions. The leader walked on the designated compass bearing while pulling a 25 m length of durable cord; the walked path is also the transect centerline and was indicated by the location of the cord. The length of cord also spaced the two observers, guiding the path of the follower; when the cord was placed on the ground after a tortoise or carcass was detected, it facilitated measurement of the local transect bearing. The walked length of each transect was calculated as the straight-line distance between GPS point coordinates that were recorded at 500 m intervals (waypoints) along the transect and/or whenever the transect bearing changed. Leader and follower each scanned for tortoises independently without leaving the centerline, and the role of the crew member finding each tortoise was recorded in the data. Although the leader saw most of the tortoises, the role of the follower was to see any remaining tortoises near the centerline, crucial to unbiased estimation of tortoise densities.

Distance sampling requires that distance from the transect centerline to tortoises is measured accurately. When a tortoise was observed, crews 1) used a compass to determine the local transect bearing based on the orientation of the 25 m centerline, 2) used a compass to determine the bearing from the point of observation to the tortoise, and 3) used a measuring tape to determine the distance from the observer to the tortoise. These data are sufficient to calculate the perpendicular distance from the observed tortoise to the local transect line. If the tortoise was outside of a burrow, was handled enough to measure midline carapace length (MCL), to determine its sex, assess its body condition (USFWS 2012c), and to apply a small numbered tag to one scute. If a tortoise could not be measured because it was in a burrow, because temperatures precluded handling, or for any other reason, crews attempted to establish by other means whether the animal was larger than 180 mm MCL, the criterion for including animals in density estimates.

Because transects are 3 km on one side, it is not unusual for that path to cross through varied terrain or even be blocked by an obstacle such as an interstate highway. In the first years of this program, smaller transects in inconvenient locations were shifted or replaced, but this compromised the representative nature of the sample. Since 2007, the basic rules for modifying transects involve 1) reflecting or elongating transects to avoid obstacles associated with human infrastructure or jurisdictions (large roads, private inholdings, administrative boundaries, etc.), or 2) shortening transects in rugged terrain (USFWS 2012a). Substrate and access to transects can also make it difficult to complete transects during the optimal period of times, so 3) transects could be shortened to enable completion before 4pm each day.

If it was anticipated that fewer than 4 km could be walked, the transect was replaced with a transect from the alternate list. I assumed that the proportion of the area that is unwalkable is the same as the proportion of total planned kilometers (12 X number of planned transects) that were unwalkable. As in previous years, unwalked transects were replaced from the list of alternates that were also prioritized using the GRTS procedure. Specifics of how transect paths were to be modified for rugged terrain (shortened) or for administrative boundaries (reflected) can be found online in the current version of the handbook, the *2015 Desert Tortoise Monitoring Handbook* (USFWS, 2015).

Proportion of tortoises available for detection by line distance sampling, G_0

Basing density estimates only on the tortoises that are visible will result in density estimates that are consistently underestimated (biased low). Instead, we use telemetry to estimate the proportion of tortoises available for sampling, G_0 (“gee-sub-zero”), which was incorporated in estimate of adult tortoise density to correct this bias.

We used telemetry to locate radio-equipped tortoises that were visible as well as those that were otherwise undetectable in deep burrows or well hidden in dense vegetation. To quantify the proportion that were available for detection (visible), telemetry technicians used a VHF radio receiver and directional antenna to locate 9-14 radio-equipped G_0 tortoises in each of 3 (2013) or 4 (2014) focal sites throughout the Mojave and Colorado deserts (Fig. 1).

Each time a transmittered tortoise was located, the observer determined whether the tortoise was visible (*yes* or *no*). Through careful coordination, observers at telemetry sites monitored visibility during the same daily time period when field crews were walking transects in the same region of the desert. Observers completed a survey circuit of all focal animals as many times as possible during the allotted time, recording visibility each time. Bootstrapped estimates of G_0 started by selecting one visibility record at random for each tortoise on each day it was located. The average visibility of all tortoise observations at a site on a given day was calculated and used to estimate the mean and variance of G_0 at that site. One thousand bootstrap samples were generated in PASW Statistics (release 18.0.2; SPSS, Inc., 2 April 2010) to estimate G_0 and its standard error.

Field observer training

Training for careful data collection and consistency between crews is a fundamental part of quality assurance for this project. This training includes instruction as well as required practice time on skills such as tortoise handling, walking practice transects, and developing detection and distance-measuring techniques. The latter skills include practice on a training course with tortoise models, where standards for detection on the centerline and pattern of detections with distance are evaluated. The monitoring handbook first developed in 2008 was comprehensive and serves as a training manual and documentation of training that is provided. Chapters are updated each year as needed and printed for training. They are also posted to the Desert Tortoise Recovery Office website with the full handbook (USFWS 2015).

Kiva Biological (Kiva) supplied crews for monitoring in the Chocolate Mountain portion of the Colorado Desert Recovery Unit in 2013 and added the Western Mojave TCAs in 2014. Great Basin Institute (GBI) supplied field crews for monitoring 2 TCAs in the Northeastern Mojave Recovery Unit in 2013 only. Due to the limited scope of monitoring in 2013 and 2014, it was possible to require that all surveyors for Kiva (11 in 2013, 15 in 2014) had previous experience with this monitoring program, as did the 10 personnel for GBI. The two teams went through refresher training on 2 separate occasions, right before each team left for the field in 2013. In 2014, the day before field surveys, the team leader for Kiva held a review session for her crews during which they walked a transect and reviewed handling procedures specific to this project. She also reviewed data collection specific to telemetry collection with personnel from Joshua Tree National Park. For a description of the full training program and evaluations, see USFWS (2014).

Data management, quality assurance, and quality control

Two sets of data tables were maintained through the field season, organizing data collected on transects and at the G_0 focal sites. Collection data forms, sheets, applications, and databases were designed to minimize data entry errors and facilitate data verification and validation. Data were collected in both electronic and paper formats by the separate survey organizations, then combined and processed in a series of phases to create final database products. Data quality assurance and quality control (data QA/QC, also known as verification and validation) was performed during the data collection, data integration, and data finalization phases. During the data integration phase, after combining data from separate groups, some attribute fields were added and all fields were formatted for final processing. The third phase, data finalization, involved consolidation, resolution of data inconsistencies, and generation of final spatial and non-spatial data products used for analysis. Figure 2 describes the overall data flow.

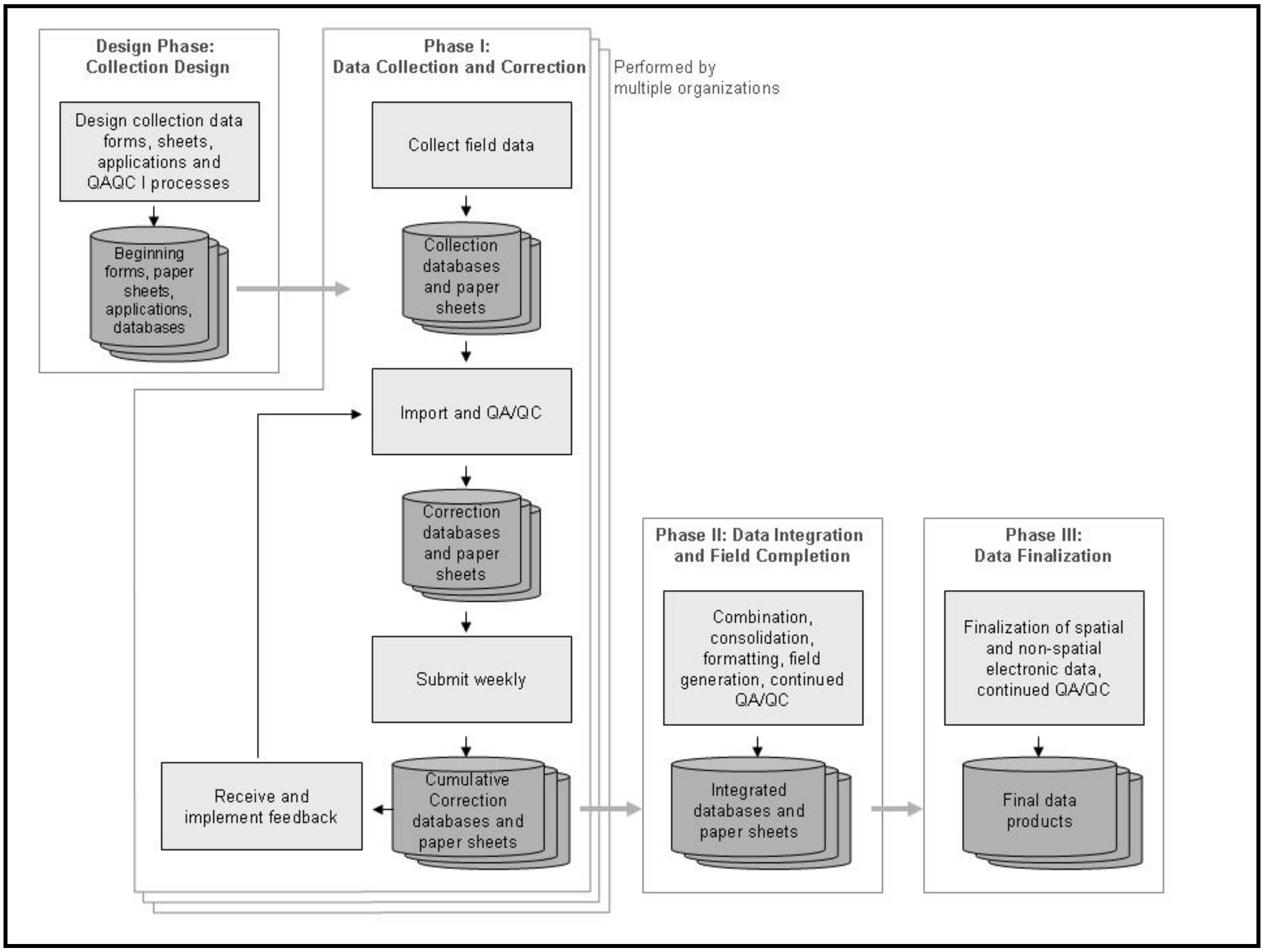

Figure 2. Data flow from collection through final products.

Tortoise encounter rate and development of detection functions

The number of tortoises seen in each stratum and their distances from the line are used to estimate the encounter rate (tortoises seen per kilometer walked) and the detection rate (proportion of available tortoises that are detected out to a certain distance from the transect centerline). Detection function estimation is "pooling robust" under most conditions (Buckland et al., 2001). This property holds as long as factors that cause variability in the curve shape are represented proportionately (Marques et al., 2007). Factors that can affect curve shape include vegetation that differentially obscures vision with distance and different detection protocols used by individual crews (pairs). The low overall number of detections led me to develop one overall detection curve each year. The encounter rate is less sensitive to small sample sizes, so it was estimated for each stratum separately.

I used Program DISTANCE, Version 6, Release 2 (Thomas et al., 2010) to fit appropriate detection functions, to estimate the encounter rate of tortoises in each stratum, and to calculate the associated variances. Analysis was applied to all live tortoises larger than 180 mm MCL. Transects were packaged into monitoring strata ("regions" in Program DISTANCE).

I truncated observations to improve model fit as judged by the simplicity (reasonableness) of the resulting detection function estimate (Buckland et al., 2001:15-16). Any observations that were not used to estimate detection functions were also not used to estimate the encounter rate (tortoises detected per kilometer walked). In distance sampling applications for many other species, encounter rate can be estimated with relatively high precision, but tortoise encounter rates are low enough that truncation was applied conservatively to maximize the number of observations per stratum. Using truncated data, I used the Akaike Information Criterion (AIC) to compare detection-function models (uniform, half normal, and hazard-rate) and key function/series expansions (none, cosine, simple polynomial, hermite polynomial) recommended in Buckland et al. (2001). I also used AIC to compare models with and without the factor for field team modifying the shape of the curve.

Proportion of available tortoises detected on the transect centerline, *g(0)*

Transects were conducted by two-person crews using the method adopted beginning in 2004 (USFWS, 2006). Transects were walked in a continuous fashion, with the lead crew member walking a straight line on a specified compass bearing, trailing about 25 m of line, and the second crew member following at the end of the line. This technique involves little lateral movement off the transect centerline, where attention is focused. Use of two observers allows estimation of the proportion of tortoises detected on the line; and thereby provides a test of the assumption that all tortoises on the transect centerline are recorded ($g(0) = 1$). The capture probability (p) for tortoises within increasing distances from the transect centerline was estimated as for a two-pass removal or double-observer estimator (White et al., 1982): p = (lead–follow)/lead, where lead = the number of tortoises first seen by the observer in the leading position and follow = the number of tortoises seen by the observer in the follower position. The corresponding proportion detected near the line by two observers was estimated by $g = 1 - q^2$, where $q = 1 - p$. Figure 4 graphs the relationship between the single-observer detection rate (p) and the corresponding dual-observer detection rate (*g(0); "gee at zero"*). The actual proportion detected can be estimated, but to avoid the necessity of compensating for imperfect detection, during training field crews (pairs) are expected to detect 96% of all models within 1 m of the transect centerline. This corresponds to the leader being responsible for at least 80% of the team's detections near on the centerline in order to meet this standard and is the basis for one of the training metrics.

Few or no tortoises are located exactly on the line, and even examining a small interval (such as 1 m on each side of the transect line) results in few observations to precisely estimate *g(0)*. Instead, my test of the assumption involves examination of the lead and follow proportions starting with counts of tortoises in larger intervals from the line, moving to smaller intervals centered on the transect centerline. As the intervals get smaller the sample sizes also get smaller, but the estimates are more relevant to the area right at the transect centerline. The expectation is that the estimates should converge on *g(0)* = 1.0.

If the test does not indicate that all tortoises were seen on the transect centerline, the variance of p can be estimated as the binomial variance = $q(1 + q)/np$ (White et al., 1982), where n = the estimated number of tortoises within 1 m of the transect centerline, and the variance of *g(0)* is estimated as twice the variance of p.

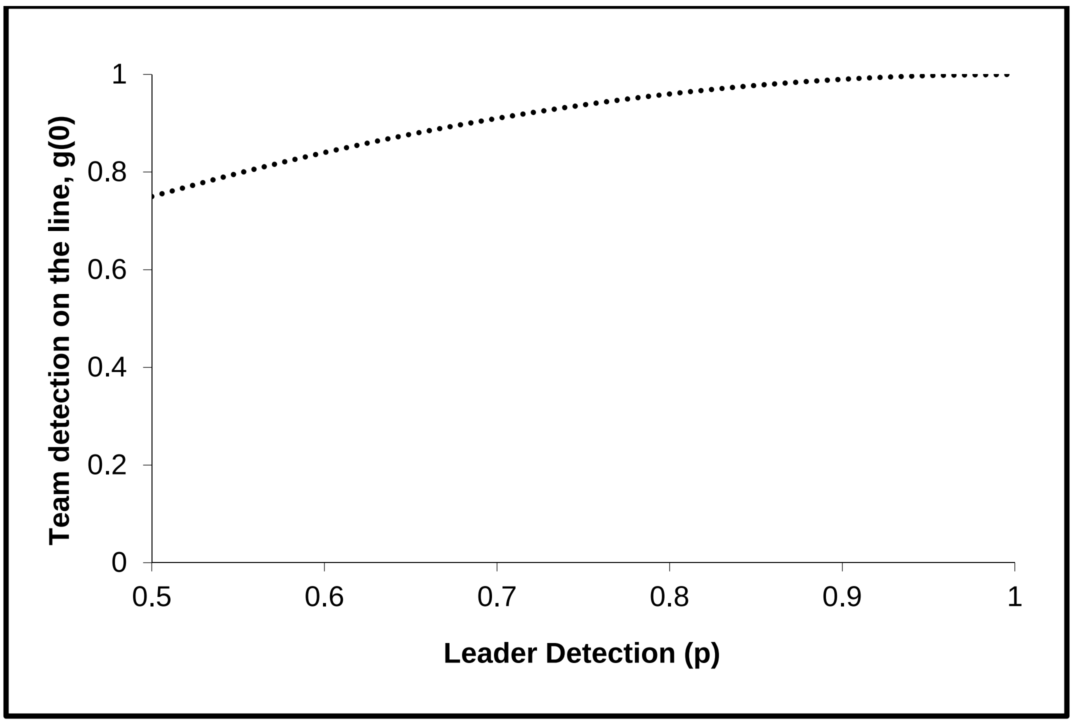

Figure 3. Relationship between single-observer detections (by the leader, p) and dual-observer (team) detections, *g(0)*.

Estimates of tortoise density

Each year, the density of tortoises is estimated at the level of the stratum (TCA). The calculation of these densities starts with estimates of the density of tortoises in each stratum from Program DISTANCE, as well as their variance estimates:

$$D = \frac{n}{2wLP_a G_0 g(0)},$$

where L is the total length of kilometers walked in each stratum and w is the distance to which observations are truncated, so $2wL$ is the area searched in each stratum. This is a known quantity (not estimated). P_a is the proportion of desert tortoises detected within w meters of the transect centerline and was estimated using detection curves in Program DISTANCE. The encounter rate (n/L) and its variance were estimated in Program DISTANCE for each stratum. Calculation of D requires estimation of n/L, P_a, G_0, and $g(0)$, so the variance of D depends on the variance of these quantities as well.

For desert tortoise densities, the encounter rate (n/L) is estimated independently for each stratum, whereas proportion of available tortoises and proportion of available tortoises detected on the transect centerline are estimated jointly for all strata ($g(0)$) or for all strata in the recovery unit (G_0). The detection function, which comes into the above equation as P_a, may be estimated jointly or separately for each team, depending on the number and quality of observations. In 2013, a single detection curve was created by pooling observations across all 3 strata for all crews on both teams (GBI and Kiva). A schematic of the process leading to density estimates is given in Figure 4. Contributing estimates in the four left-hand columns are listed with the subsets of the data on which they are based. These estimates combined from left to right to generate stratum and recovery unit density estimates.

Tortoise encounter rate	Proportion that are visible, G_0	Detection rate, P_a	Proportion seen on the line, $g(0)$	Density	Density
Stratum	*Neighboring G_0 sites*	*Data collection group*	*Overall*	*Stratum*	*Recovery unit*
2013					
AG	Chuckwalla	Kiva & GBI	All data	AG	Colorado Desert
GB	Gold Butte			GB	Northeastern Mojave
BD	Halfway Wash			BD	
2014					
AG	Chuckwalla	Kiva	All data	AG	Colorado Desert
FK	Superior-Cronese			FK	Western Mojave
SC				SC	
OR	Ord-Rodman			OR	

Figure 4. Process for developing density estimates in 2013 (top) and 2014 (bottom). For each type of estimate, the full set of data was subdivided appropriately, as indicated by columns.

Estimating the area of each stratum sampled and the number of tortoises in that area
Based on past experience and visual examination of DEM overlays, all assigned transects were classified as possible for completion as 12 km, shortened, or as unwalkable (USFWS 2014). These classifications before the field season are advisory only, because exact ground conditions, weather, substrate, and crew condition all affect the ability to complete a transect. If a non-standard transect (not 12 km square) is walked, crews indicate the obstacles they encountered that forced the change in protocol.

At the end of each field season, transects that were not completed as expected are evaluated, and might be reclassified. The classification is used to advise future transect completion, but also to estimate the proportion of each monitoring stratum that is actually represented by the walked transects. Proportions used in this report reflect all years of experience with this set of transects through the 2014 field season.

Crews completed all transects using the 12-km square path, completing as much of that path as possible. The calculation of unwalkable area in these strata is based on the proportion of unwalkable kilometers. The total area of the stratum that is walkable is estimated as:

$$Proportion\ walkable = \frac{transect\ kilometers\ walked}{12\ X\ transects\ completed}.$$

If a given stratum covers 5000 km^2, but only 90% was walkable, the density estimate applies to 4500 km^2, and can be used to estimate for the number of tortoises in those 4500 km^2. These area estimates add another source of imprecision, so abundance estimates are slightly less precise than the density estimates they derive from. The error of this estimate is calculated as the error for a binomial proportion.

Population trend estimation
To test whether we could discern patterns including trends in adult tortoise density, I used the above estimates of tortoises/km^2 in each TCA in conjunction with earlier published density estimates (USFWS 2009, 2012a, 2012b, 2013, 2014; McLuckie et al., 2014). Although only a limited number of TCAs were surveyed in 2013 and 2014, I evaluated patterns in all long-term monitoring areas and their associated G_0 focal sites (Table 1, Figure 1). I used R (Version 3.1.1, R Core Team 2014) to develop and compare linear mixed-models (Pinheiro et al., 2014) that described the natural log of tortoise density as a function of input variables representing year and TCA. As fixed effects, models included TCA, Year, and Year^2. "Year" was centered before modeling (Scheilzeth, 2010). The full model also included interactions between TCAs and each of the linear and quadratic time factors.

I used the model with all fixed effects to develop the random structure of the model set, then adjust the fixed structure of the final model (Zuur et al., 2009). I used model selection procedures based on AIC_c (Anderson and Burnham, 2002; Mazerolle, 2014) to decide whether to weight the analysis by the variance or CV of the annual density estimates, and whether to model correlations among residuals for density estimates from the same Year, or due to use of pooled G_0 and P_a estimates for multiple TCA density estimates (see above description of how density estimates are developed).

With the final random structure in place, I used AIC_c for selecting among models with alternative fixed structures and examined the fit of the best model using marginal and conditional R^2 (Nakagawa and Schielzeth, 2013). I used ANCOVA tests to examine whether slopes and intercepts of TCAs in each recovery unit described the same pattern (Zar, 1996).

Table 1. Tortoise Conservation Areas including total area (km^2) and total effort (km) by year. Tortoise Conservation Areas are grouped under corresponding recovery units, identified in bold. Red Cliffs Desert Reserve was also surveyed in 1999 (307 km), 2000 (302 km), 2001 (314 km) and 2003 (309 km). Transects were selected from the area reported; a certain proportion of this area was too rugged to survey, so the actual surveyed area is less (see previous section for estimation of sampled area).

Tortoise Conservation Area		Area (km^2)	2004	2005	2007	2008	2009	2010	2011	2012	2013	2014
Colorado Desert		**13530**	**3319**	**3984**	**2007**	**1348**	**1375**	**2383**	**1316**	**1403**		
Chocolate Mtn Aerial Gunnery Range	AG	755	331	228	404	158	378	378		363	413	554
Chuckwalla	CK	3509	1083	866	747	112		613	280	213		
Chemehuevi	CM	4038	836	1129	180	84	119	458	354	176		
Fenner	FE	1841	410	288	178	108	121	246	179	168		
Joshua Tree	JT	1567	278	601	135	102	240	227	147	183		
Pinto Mountains	PT	751	56	155	131	72	162	213	118	140		
Piute Valley	PV	1070	325	717	231	713	355	249	239	159		
Eastern Mojave		**3720**	**876**	**620**	**368**	**714**	**548**	**578**	**746**	**639**		
Eldorado Valley	EV	1153	361	452	188	594	427	212	331	320		
Ivanpah	IV	2567	515	168	180	120	120	365	416	318		
Northeastern Mojave		**4889**	**1037**	**1489**	**2304**	**1485**	**4154**	**4265**	**3984**	**4184**		
Beaver Dam Slope	BD	828		421	478	2578	631	662	751	819	683	
Coyote Springs Valley	CS	1117	365	237	906	1592	1504	1046	967	996		
Gold Butte-Pakoon	GB	1977	361	432	300		733	1258	1039	1116	923	
Mormon Mesa	MM	968	311	398	621	691	1286	1298	1227	1253		
Western Mojave		**6873**	**1534**	**1979**	**896**	**599**	**1351**	**2144**	**1257**	**876**		**2095**
Fremont-Kramer	FK	2417	463	661	300	216	361	566	264	193		815
Ord-Rodman	OR	1124	381	310	141	102	197	270	174	158		472
Superior-Cronese	SC	3332	690	1009	456	281	793	1307	820	525		808
Upper Virgin River		**115**		**305**	308		**310**		**310**			
Red Cliffs Desert Reserve	RC	115		305	308		310		310			

RESULTS

Quality assurance and quality control

There were 4772 (6275) transect records and 1788 (1190) G_0 records associated with the monitoring effort in 2013 (2014). After data specialists with the field teams had finished verifying and validating the information in these databases, there were 195 (232) cases where the data were inconsistent with constraints and expectations. Note that many more issues are addressed each year by data specialists for field crews before the field data are submitted. Most of these (186/178) were errors created by the field crews (sometimes faulty equipment, other times data entry error), of which all but 28 (35) were corrected by later phases of QA/QC with recourse to paper datasheets. Another 1 (58) errors were "processing" errors that were identified and corrected before the final database products were created. Processing steps were associated with correcting other errors (perhaps the correct entry is misentered), with adding new fields, or any other manipulation that occurs after the data have been collected. For these 2 years, no entries that violated QA/QC rules were attributable to extreme or explicable entries.

These years of data had relatively few errors, comparable to the previous 2 years of improved QA/QC. Data for these and previous years are available at http://psw.databasin.org/galleries/af8e55a0197a4c95a3120b278075a2b1.

Transect completion

Tables 2 and 3 report the number of assigned and completed transects in each stratum in 2013 and 2014. In 2014, all assigned transects were completed or alternates were walked in their stead. In 2013, Kiva was assigned 33 transects and walked two additional transects. Two other unwalkable transects were replaced. The Great Basin Institute completed 138 transects, replacing 17 assigned but unwalkable transects with alternates in the same strata. Two assigned transects were not walked or replaced because surveyor injury limited the number of transects that could be completed during the field season. This eventuality (incomplete transect completion) was an accepted risk when USFWS considered alternative team sizes within the scope of the budget.

Tables 2 and 3 also indicate the number of assigned transects that could be completed as standard square 12-km transects or by reflecting around property boundaries and infrastructure (column 4). An additional number (column 5) were shortened and represent more rugged terrain. Finally, some transects were considered unwalkable (column 6). Figures 6 to 9 show locations of transects and observations of live tortoises.

Table 2. Number and completion of transects in each stratum in 2013.

Stratum	Assigned transects	Assigned and alternate transects completed*	Assigned, completed 12k	Assigned, completed shortened	Assigned, judged unwalkable
AG	33	35	30	1	2
BD	60	58	51	5	4
GB	80	80	59	8	13
Total	173	173	140	14	19
GBI	140	138	110	13	17
Kiva	33	35	30	1	2

*Assigned transects that were not walked were to be replaced by alternates. Cost savings allowed the survey team to complete 2 additional transects than planned in the AG stratum.

Table 3. Number and completion of transects in each stratum in 2014.

Stratum	Assigned transects	Assigned and alternate transects completed*	Assigned, completed 12k	Assigned, completed shortened	Assigned, judged unwalkable
AG	48	48	36	5	7
FK	68	68	66	2	0
OR	42	42	25	11	6
SC	72	72	53	18	1
Total/Kiva	230	230	180	36	14

*Assigned transects that were not walked were to be replaced by alternates.

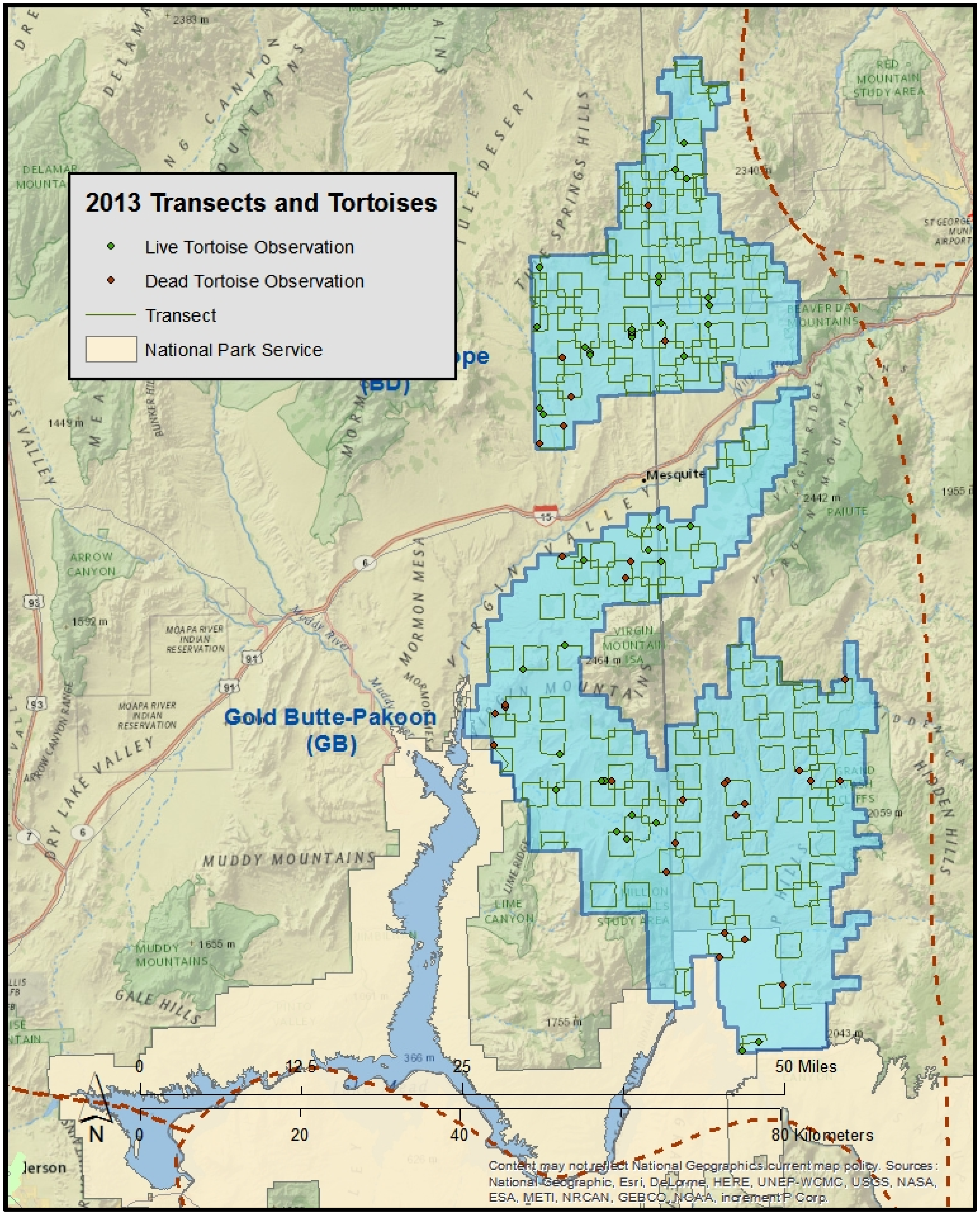

Figure 5. Distribution of distance sampling transects and live tortoise observations in 2013 in the Northeastern Mojave Recovery Unit (only Beaver Dam Slope and Gold Butte-Pakoon monitoring strata were surveyed).

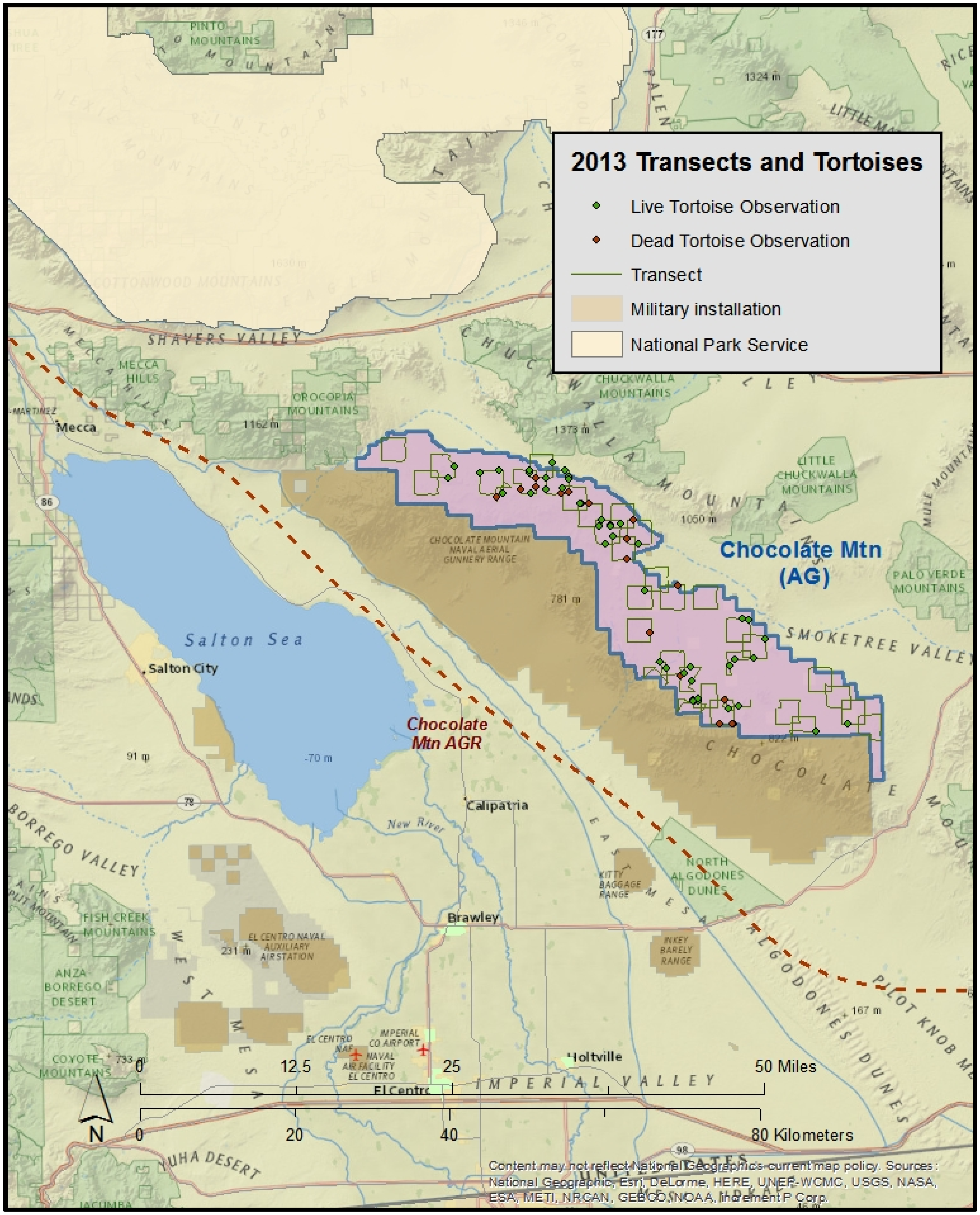

Figure 6. Distribution of distance sampling transects and live tortoise observations in 2013 in the Chocolate Mountain Aerial Gunnery Range stratum in the Colorado Desert Recovery Unit.

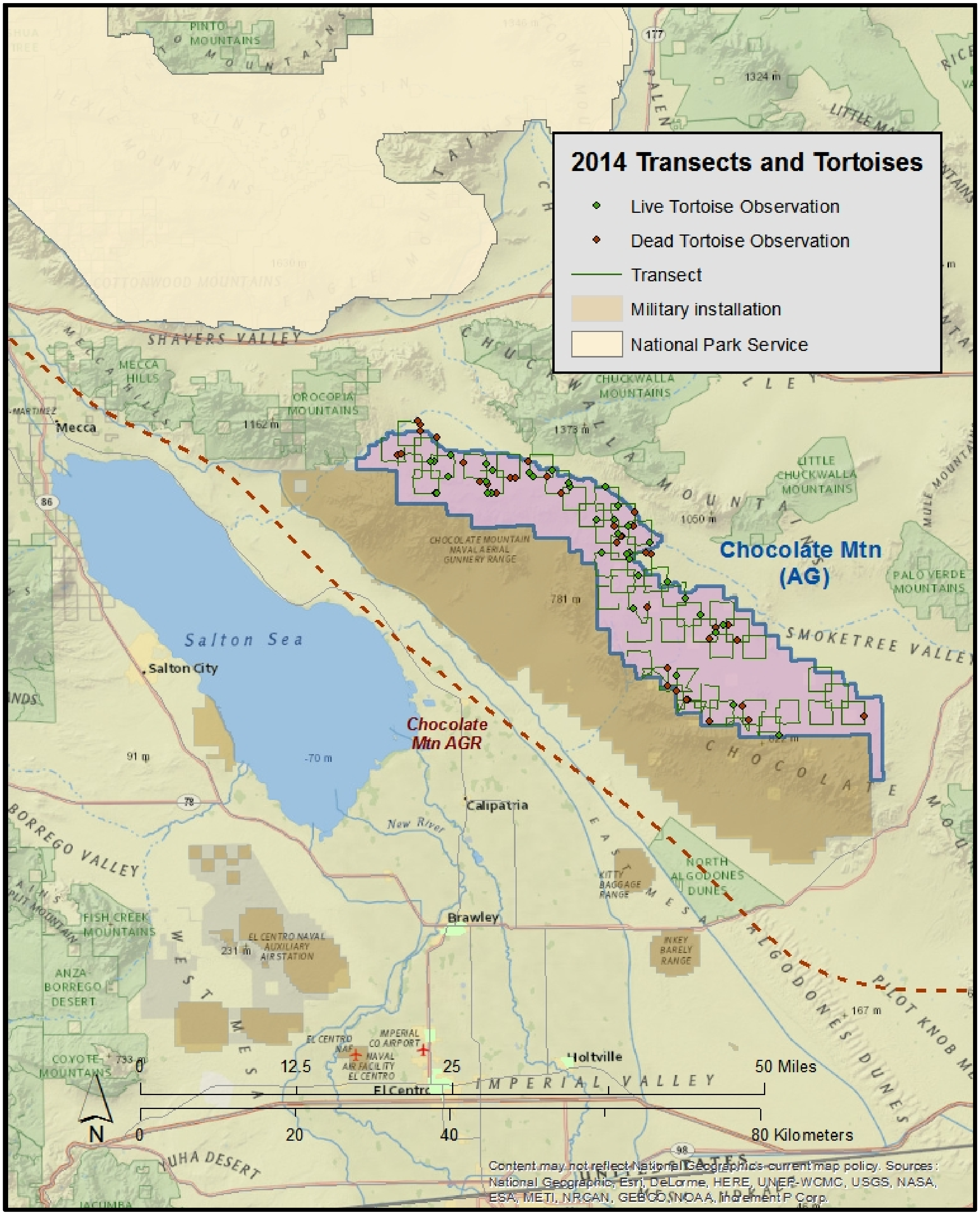

Figure 7. Distribution of distance sampling transects and live tortoise observations in 2014 in the Chocolate Mountain Aerial Gunnery Range stratum in the Colorado Desert Recovery Unit.

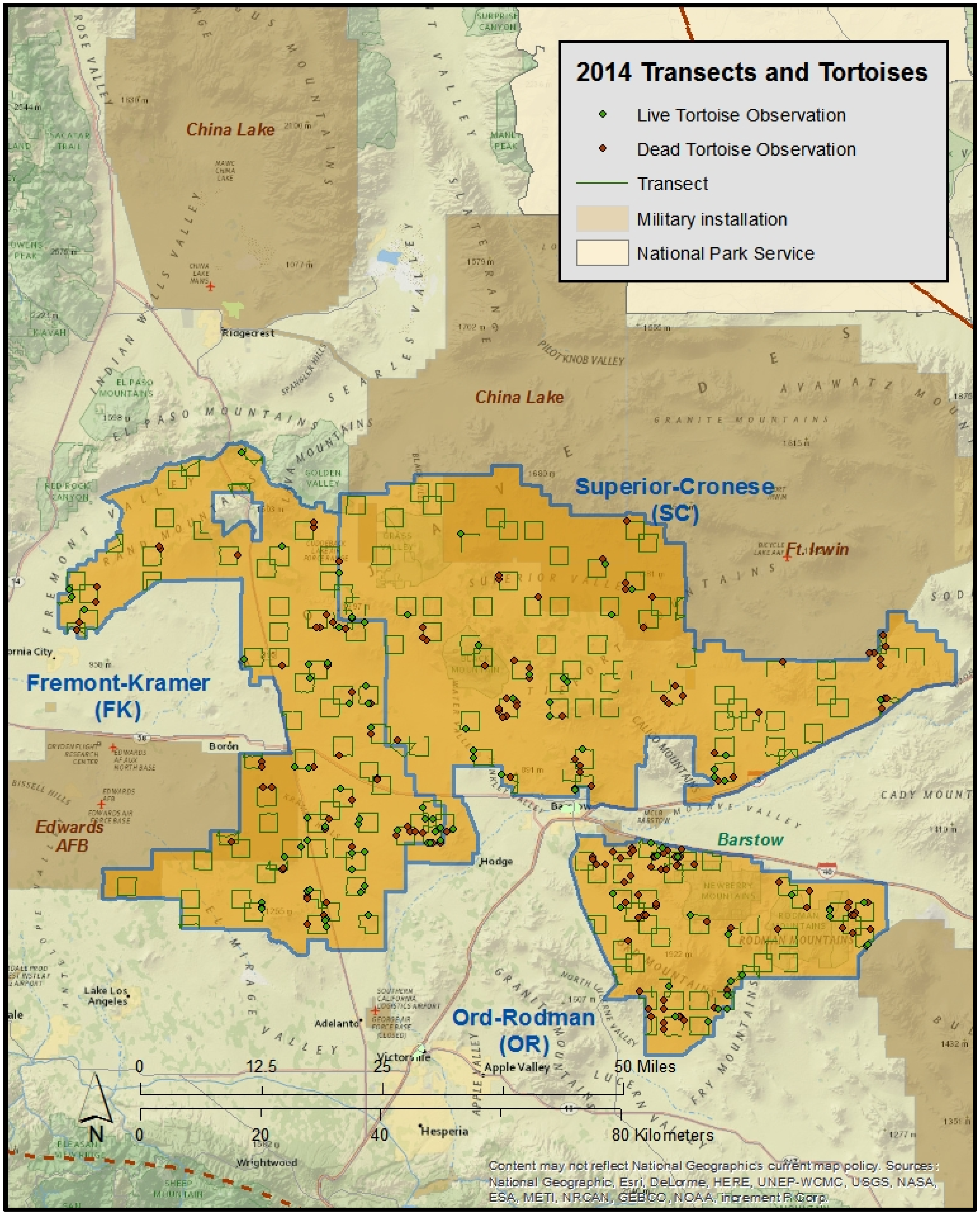

Figure 8. Distribution of distance sampling transects and live tortoise observations in 2014 in all 3 strata in the Western Mojave Recovery Unit.

Proportion of tortoises available for detection by line distance sampling, G_0

In general, telemetry sites and associated strata were completed sequentially, from south to north. This pattern corresponds to the expected timing of tortoise activity; peaking first in the south, later in the north. Visibility from the Chuckwalla telemetry site was high during the 8 days of surveys in 2013 (Table 4). This is not completely unexpected although the timing of emergence from burrows in early March in this area is not reliable (M. Vamstad, pers. comm.). Note the extremely low visibility during roughly the same period in 2014. During the latter year, low activity presumably reflected the continuing drought conditions rather than later emergence conditions. Tortoise activity in the eastern part of the range is generally lower than in the west, but G_0 estimates for Gold Butte and Halfway Wash in 2013 were average-to-high compared to previous years..

Table 4. Availability of tortoises (G_0) during the periods in 2013 and 2014 when transects were walked in each group of neighboring strata.

G_0 sites	Strata	Dates	Days	G_0 (Std Error)
Chuckwalla	Chocolate Mountain AGR	10 – 17 Mar 2013	8	0.84 (0.058)
Gold-Butte	Gold Butte-Pakoon	8 Apr – 3 May 2013	26	0.68 (0.124)
Halfway Wash	Beaver Dam Slope	6 – 24 May 2013	19	0.68 (0.136)
Chuckwalla	Chocolate Mountain AGR	13 – 20 Mar 2014	8	0.59 (0.087)
Joshua Tree NP	Not applied to transects	13 – 20 Mar 2014	8	0.94 (0.065)
Ord-Rodman	Ord-Rodman	1 – 7 Apr 2014	8	0.99 (0.030)
Superior-Cronese	Fremont-Kramer, Superior-Cronese	8 Apr – 5 May 2014	28	0.91 (0.101)

Tortoise encounter rates and detection functions

In 2013, all pairs worked together from the beginning to the end of the season. Each Kiva crew walked on 7 transects and overall they detected 37 tortoises larger than 180 mm MCL; GBI crews walked a median of 35 transects each and detected 34 tortoises overall.

Figure 9 is a histogram of the observed number of tortoises seen at increasing distance from the transect centerline in 2013. Truncation was conservative to maximize the number of observations per stratum. Use of only observations within 16 m allowed a model with no extra inflections and with all but 4% of the observations. At this distance, the half-normal model with no adjustments had the lowest AICc, but the hazard-rate model with no adjustments fit better near the centerline and ΔAICc = 2.50 so it was selected. The same hazard-rate model but with a factor added to model shape differences between Kiva and GBI performed worse (ΔAIC=3.30). The area below the curve is the proportion of tortoises that were detected, P_a; the teams detected 44.5% (CV=0.197) of the visible tortoises within 16 m of the centerline in 2013.

In 2014, delayed funding precluded planning for the size or duration of surveys, so crew availability during the field season resulted in changing crew composition. Most surveyors completed 30-43 transects during the season, although one person was only present on 8 and another on 20. Figure 10 is a histogram of the observed number of tortoises seen at increasing distance from the transect centerline. Truncation was conservative to maximize the number of observations per stratum. Use of only observations within 10 m allowed a model with no extra inflections and using all but one of the observations. At this distance, the negative-exponential model performed best, but the uniform model with first-order cosine adjustment had ΔAIC = 1.3 and a better fit near the centerline so it was adopted instead. The detection rate for crews within 10 m of the transect centerline was 44.5% (CV=0.197).

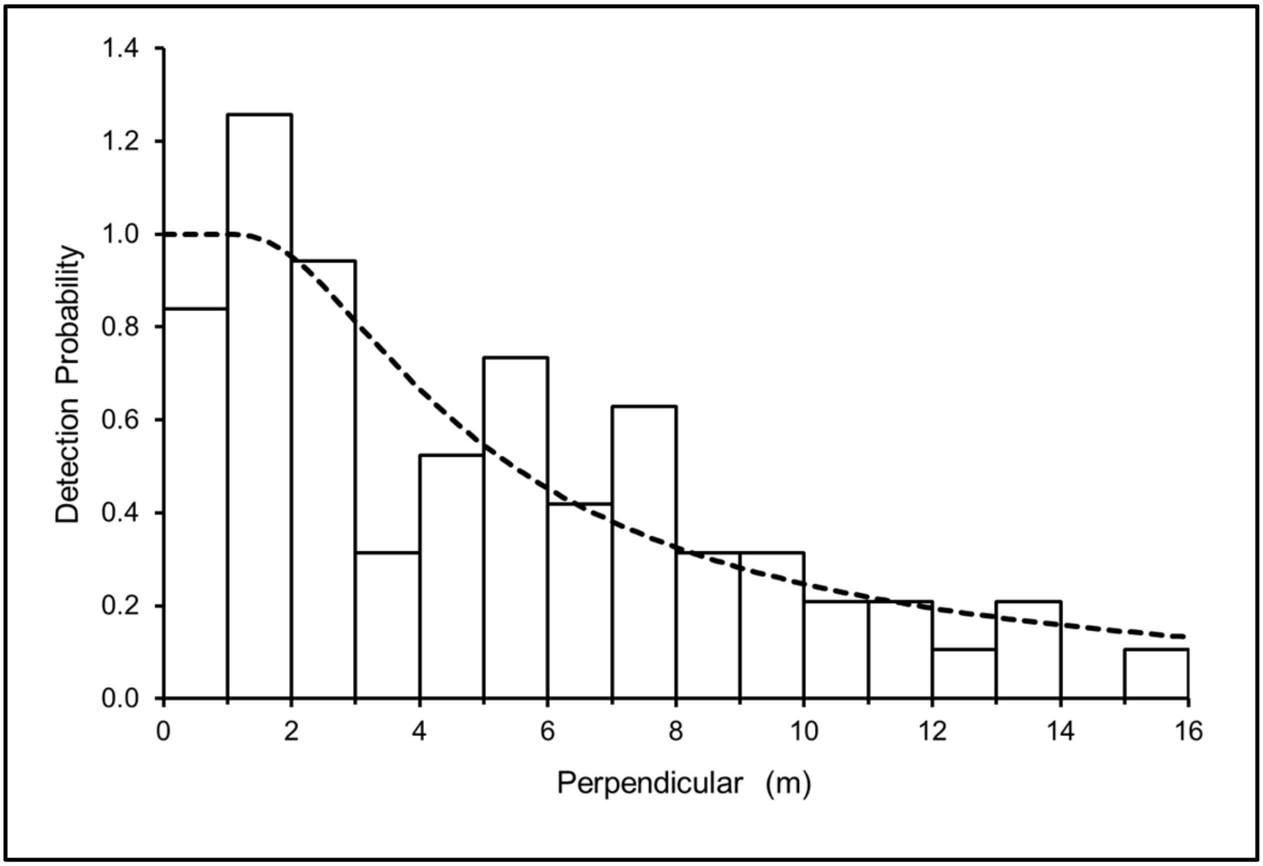

Figure 9. Observed detections (histogram) and the resulting detection function (smooth curve) for live tortoises with MCL ≥ 180mm found in 2013 by GBI (n=31) and Kiva (n=37). This curve uses only observations found within 16 m of the line.

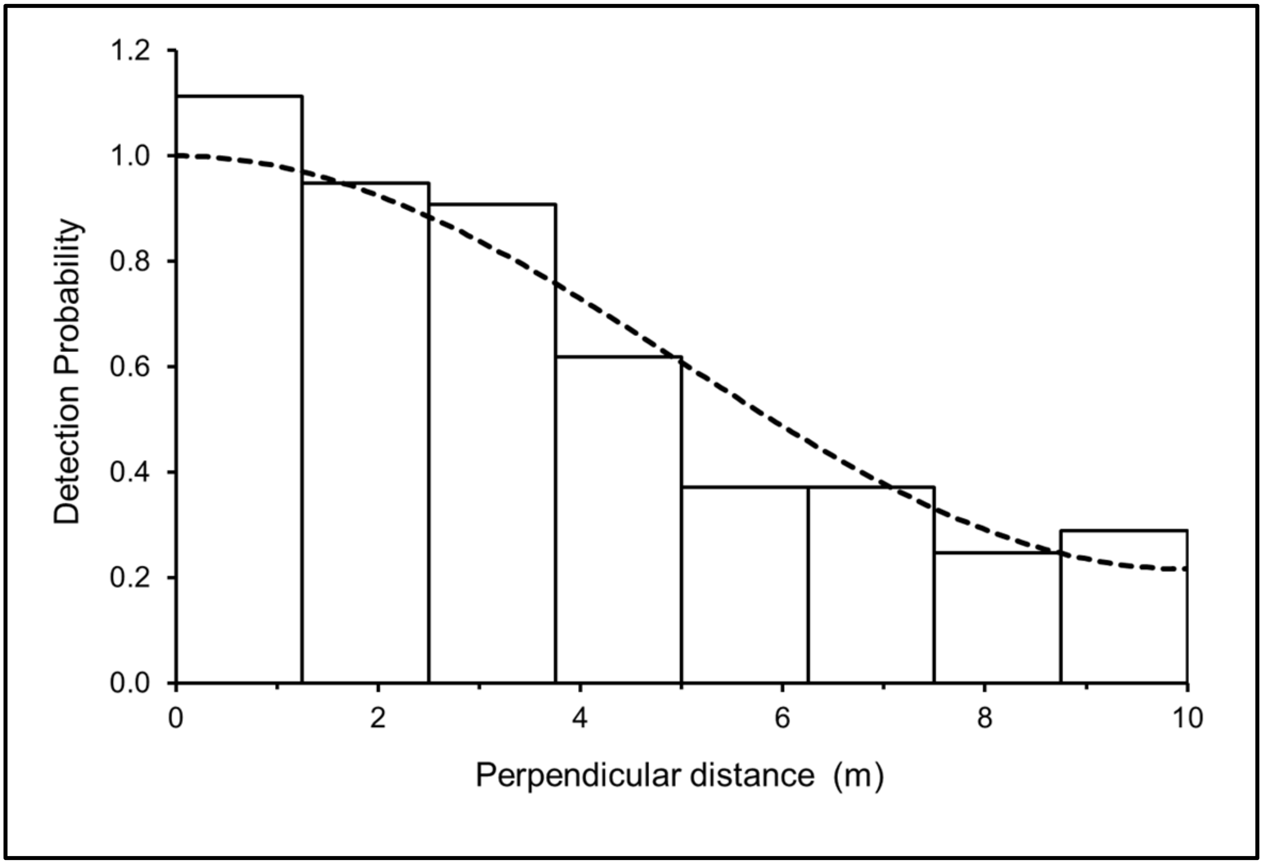

Figure 10. Observed detections (histogram) and the resulting detection function (smooth curve) for live tortoises with MCL ≥ 180mm found by Kiva in 2014 (n=118).
This curve uses only observations found within 10 m of the line.

Proportion of available tortoises detected on the transect centerline, *g(0)*

Because they are cryptic, even tortoises that are visible (not covered by dense vegetation or out of sight in a burrow) and close to the surveyor may not be detected. In 2013, for 37 detections of tortoises within 5 m of the transect centerline, 33 were found by the observer in the lead position and 4 by the follower, so that the probability of detection by single observer, $p = 0.879$, and the proportion detected using the dual observer method, *g(0 to 5 m)* = 0.985 (SE = 0.091). In 2014, 14 of 86 observations within 5 m of the centerline were found by the follower, and $p = 0.806$ with *g(0 to 5m)* = 0.962. Figure 11 shows that *g(0)* was converging on 1.0 in both 2013 and 2014, indicating the assumption of perfect detection on the centerline was met; consequently, no adjustment was made to the final density estimate. The curves since dual observers were first used in 2004 have all supported the premise that complete detection on the transect line was achieved for years in which the dual-observer method was used (USFWS 2009, 2012a, 2012b, 2013, 2014).

Estimates of tortoise density

Density estimates were generated separately for each monitoring stratum (Table 5).

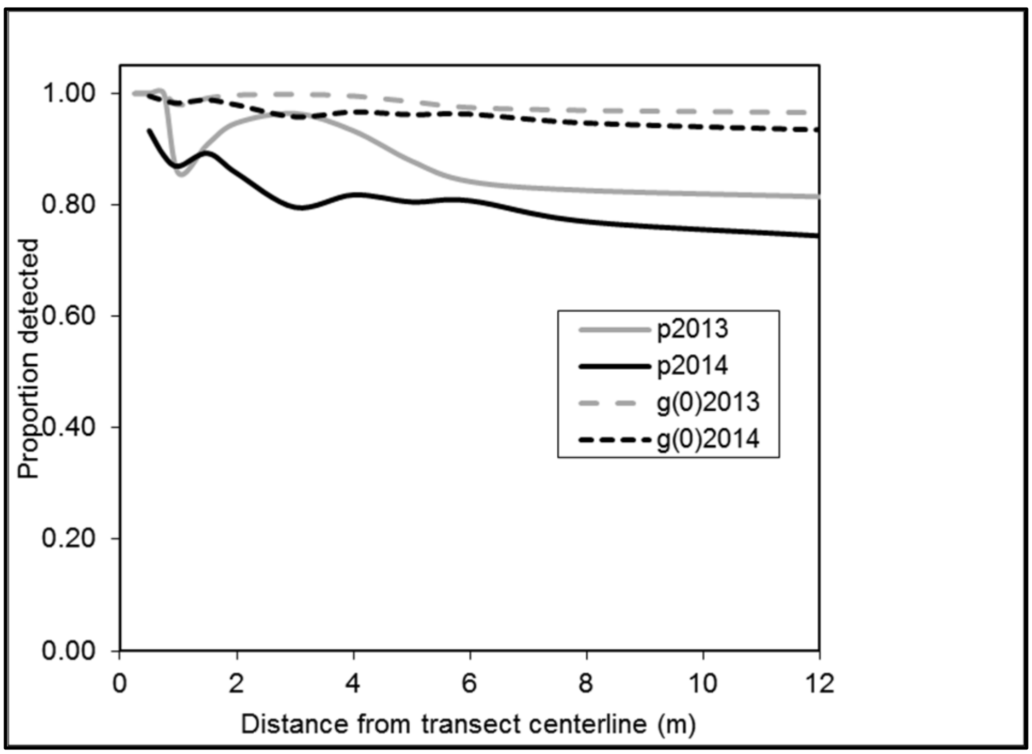

Figure 11. Detection pattern for the leader (*p*) and by the team (*g(0)*) based on all observations out to a given distance (*x*) from the centerline in 2013 and 2014. Note convergence of *g(0)* on 1.0 as *x* goes to 0.

Table 5. Stratum-level encounters and densities in 2013 and 2014 for tortoises with MCL ≥ 180mm within 16 m (2013) or 10 m (2014) of the centerline. Coefficients of variation expressed as a percentage.

Recovery Unit & Year	Stratum	Area (km2)	Number of Transects	Total transect length (km)	Sampling Dates		Field Observers	*n* (tortoises observed)	CV(*n*)	Density (/km2)	CV(Density)
					Begin	End					
Colorado Desert - 2013		**755**									
Chocolate Mountain	AG	755	35	413	10-Mar	17-Mar	Kiva	36	17.0	7.3	26.9
Northeastern Mojave - 2013		**2805**									
Beaver Dam Slope	BD	828	58	683	6-May	24-May	GBI	17	30.2	2.6	41.3
Gold Butte-Pakoon	GB	1977	80	923	8-Apr	3-May	GBI	15	30.2	1.7	40.3
Colorado Desert - 2014		**755**									
Chocolate Mountain	AG	755	48	554	13-Mar	20-Mar	Kiva	33	19.2	8.4	25.0
Western Mojave - 2014		**6873**									
Fremont-Kramer	FK	2417	68	815	8-Apr	5-May	Kiva	43	18.2	4.7	22.1
Ord-Rodman	OR	1124	42	472	1-Apr	7-Apr	Kiva	20	24.0	3.5	24.9
Superior-Cronese	SC	3332	72	808	8-Apr	5-May	Kiva	22	20.9	2.5	24.4

Area of each stratum sampled and tortoise abundance

Evaluating transect classification

In 2013 and 2014, 76 of the 403 walked and 33 unwalked transects were not completed or addressed as predicted. Table 6 summarizes conclusions after examining these transects. Nineteen were reclassified based on crew experience. In some cases, this reflects a discrepancy between on-the-ground conditions and interpretation of terrain from imagery; in others, classification is ambiguous because over the course of a 12-km transect, terrain is so variable that it was not a simple matter to evaluate the ability of a typical crew to complete it. The remaining 57 anomalous transects were not reclassified, because earlier experience indicated that most crews would use the original completion strategy. The 19 transects that were reclassified represent only 0.6% of the 3218 potential transects in the long-term monitoring strata, having very little impact on our estimate of the proportion of each stratum that is walkable.

Table 6. Transects completed other than as planned and any resulting reclassification

Previous substratum	Situation	New substratum	# transects 2013	# transects 2014
12k	Shortened on military base due to operations	No change	2	4
12k	First field experience differs from imagery.	No change	2	5
12k	Shortened; in past years usually 12k	No change	18	5
12k	Attempted but completed < 6km	Unwalkable	1	0
12k	Unwalked on military base due to operations	No change	0	3
Shortened	12k more often than not in past	12k	3	5
Shortened	Crews walked 12k on first field attempt.	No change	0	12
Shortened	Crews walked 12k, but usually shortened in past	No change	0	1
Shortened	Unwalked on military base due to operations	No change	0	3
Shortened	Unwalked based on first field attempt	No change	0	2
Shortened	Unwalked now and more often in past	Unwalkable	4	0
Unwalkable	First field experience contradicted imagery	12k	0	3
Unwalkable	First field experience contradicted imagery	Shortened	0	3

Number of tortoises based on single-year density and area sampled

The proportion of each stratum represented by distance sampling is estimated as the proportion of planned kilometers that can be walked (Column 4 in Table 7). Table 7 reports the area of each stratum, the proportion covered by our density estimates, and the associated single-year estimate of tortoise abundance. Because the density trend estimates (next section) are based on multiple-years of data, they provide more robust estimates of the density in any year.

Table 7. Estimated tortoise abundance in sampled areas of each stratum based on single-year density estimates from 2013 or 2014.

Year	Stratum	Area (km^2)	Proportion walkable	SE(Prop. walkable)	Sampled area (km^2)	N (number of tortoises)	95% Confidence Interval Lower Limit	Upper Limit
2013	AG	755	0.9451	0.0252	714	5192	3083.6	8741.9
2013	BD	828	0.9053	0.0301	750	1934	886.9	4216.6
2013	GB	1977	0.8128	0.0266	1607	2701	1259.0	5796.0
2014	AG	755	0.9451	0.0252	714	5966	3671.9	9694.8
2014	FK	2417	0.9711	0.0102	2347	11147	7260.4	17115.3
2014	OR	1124	0.7581	0.0385	852	3002	1837.9	4904.5
2014	SC	3332	0.9288	0.0133	3095	7590	4731.1	12175.9

Population trend estimation

For describing variation in adult tortoise densities between TCAs and years, based on ΔAICc among models that differed only in random effects we added covariance structure to the random portion of our models to account for residuals correlated within Year. The best random effects structure also weighted optimization procedures as a function of the CV of annual density estimates. Using this random effects structure, the fixed effects in the best model supported the hypothesis that densities changed proportionally over time, with different linear trends in each TCA (Table 8). Models based on linear trends had strong support (cumulative model weights = $\sum w = 0.9999$), whereas those including quadratic effects of time had essentially no support ($\sum w < 0.0001$). Table 9 reports trend estimates based on the best-performing model which had $w > 0.999$ and described a large amount of the variation in $\log_e$(Density) (marginal $R^2 = 0.77$, conditional $R^2 = 0.81$). Taken together, these estimates of R^2 indicated that there is a considerable amount of variation that can be attributed to the fixed and random effects in the final model, and the fixed effects explained a much larger part of the variance. Covariance between TCA density estimates from the same year accounted for 18.3% of the total variance in the final model. Visual inspection of residual plots did not reveal any obvious deviations from homoscedasticity or normality.

Table 8. Model selection table for all mixed effects models fit to log-transformed annual densities of Mojave desert tortoises through 2014 for all Tortoise Conservation Areas (TCAs), starting in 1999 for Red Cliffs Desert Reserve and in 2004 for remaining 16 TCAs.
Model weights (*w*) express the relative support for each model given the data and are based on relative scores for the second order Akaike's Information Criterion (AICc). Random effects included weighting by a power function of the coefficient of variation of each annual density estimate as well as covariance structure accounting for correlation of residuals within Year.

Model	Log likelihood	AICc	ΔAICc	*w*
TCA + Year + TCA×Year	-42.4	186.4	0.0	0.9996
TCA + Year	-76.4	203.9	17.5	0.0002
TCA	-78.7	204.4	18.0	0.0001
TCA + Year + Year^2	-76.4	205.4	19.0	0.0001
TCA + Year + Year^2 + TCA×Year + TCA×Year^2	-25.6	229.1	42.7	0.0000
Year + Year^2	-150.5	313.6	127.3	0.0000
Year	-155.9	322.2	135.8	0.0000
Random effects only	-160.8	329.8	143.4	0.0000

Densities of adult Mojave desert tortoises were declining, on average, in every recovery unit except the Northeastern Mojave (Table 9, Figure 12). Average density of adult tortoises increased in the Northeastern Mojave Recovery Unit at 13.1%/y (SE = 4.3%) since 2004, with especially large rates of increase (>13%/y) estimated in BD and GB. Adult densities in the other four recovery units have declined at different annual rates: Colorado Desert (-4.5%, SE = 2.8%), Upper Virgin River (-3.1%, SE = 2.0%), Eastern Mojave (-11.2%, SE = 5.0%), and Western Mojave (-7.1%, SE = 3.3%). Based on analysis of covariance, three of the four recovery units with more than one TCA could be characterized by common regression slopes (Eastern Mojave: $F_{1,12} = 0.305$, $P = 0.591$; Western Mojave: $F_{2,21} = 0.094$, $P = 0.910$; Northeastern Mojave: $F_{3,24} = 1.206$, $P = 0.317$; Colorado Desert: $F_{6,43} = 2.391$, $P = 0.044$), but intercepts indicate different initial densities of TCAs in two of the recovery units (Eastern Mojave: $F_{1,13} = 2.560$, $P = 0.134$; Western Mojave: $F_{2,23} = 3.326$, $P = 0.054$; Northeastern Mojave: $F_{3,27} = 11.073$, $P < 0.001$; Colorado Desert: $F_{6,49} = 5.090$, $P < 0.001$). The parameter estimates reported above and in Table 9 are therefore total regression results for the Colorado Desert and Northeastern Mojave recovery units to characterize this greater within-recovery unit variation in slopes and/or intercepts, but common regression results for the other recovery units. Slopes differed between recovery units ($F_{4,119} = 9.422$, $P < 0.001$). Although this project generates annual (single-year) density estimates where surveys are conducted, better density estimates rely on all of the years of data and the resulting density trends reported here (Table 10).

Table 9. Parameter estimates and standard errors (SEs) from the best-fitting model describing $\log_e$-transformed Mojave desert tortoise density/km^2.
The model applies for the period through 2014 for all recovery units, starting in 1999 in Upper Virgin River and in 2004 for the remaining four recovery units.

Recovery unit	Tortoise Conservation Area	Intercept (SE)	Slope (SE)
Western Mojave		-3.174(0.102)	-0.071(0.033)
	Fremont-Kramer (FK)	-3.248(0.097)	-0.068(0.028)
	Ord-Rodman (OR)	-2.855(0.099)	-0.083(0.029)
	Superior-Cronese (SC)	-3.193(0.086)	-0.095(0.027)
Colorado Desert		-3.051(0.078)	-0.045(0.028)
	Chocolate Mtn Aerial Gunnery Range (AG)	-2.429(0.116)	-0.035(0.033)
	Chuckwalla (CK)	-3.145(0.114)	-0.047(0.041)
	Chemehuevi (CM)	-2.992(0.129)	-0.104(0.046)
	Fenner (FE)	-2.615(0.123)	-0.075(0.046)
	Joshua Tree (JT)	-3.612(0.130)	0.058(0.043)
	Pinto Mountains (PT)	-3.188(0.148)	-0.092(0.058)
	Piute Valley (PV)	-3.220(0.117)	0.048(0.048)
Northeastern Mojave		-3.870(0.119)	0.131(0.043)
	Beaver Dam Slope (BD)	-4.003(0.142)	0.216(0.052)
	Coyote Springs Valley (CS)	-3.782(0.096)	0.097(0.040)
	Gold Butte-Pakoon (GB)	-4.388(0.143)	0.135(0.047)
	Mormon Mesa (MM)	-3.184(0.096)	0.078(0.039)
Eastern Mojave		-3.544(0.132)	-0.112(0.050)
	Eldorado Valley (EV)	-3.635(0.128)	-0.095(0.050)
	Ivanpah (IV)	-3.316(0.123)	-0.082(0.047)
Upper Virgin River		-1.702(0.107)	-0.031(0.020)
	Red Cliffs Desert Reserve (RC)	-1.702(0.107)	-0.031(0.020)

I applied estimated TCA densities in 2004 and 2014 in each TCA to the area of the TCA that was surveyed (see above) (Table 10). I estimate that within TCAs, there has been a loss of 40,660 adult tortoises (SE = 13,288) compared to the 126,346 tortoises (SE = 41,292) present in 2004. Potential habitat for the Mojave desert tortoise (Nussear et al., 2009) includes approximately 68,502 km^2 that has a probability of occupancy $\geq$ 0.5 (Liu et al., 2005) and has not been converted to an impervious surface (Fry et al., 2011). The area of potential habitat meeting these criteria within TCAs comprises 30.6% of this area (C. Darst, pers. comm.). This is probably an underestimate of the proportion of current tortoise habitat that is within TCAs, because much more of the area outside is likely to be impervious but undocumented. Because potential habitat outside TCAs is also more likely to be degraded without management to conserve tortoise habitat, the magnitude of population declines range-wide is probably greater than that within TCAs

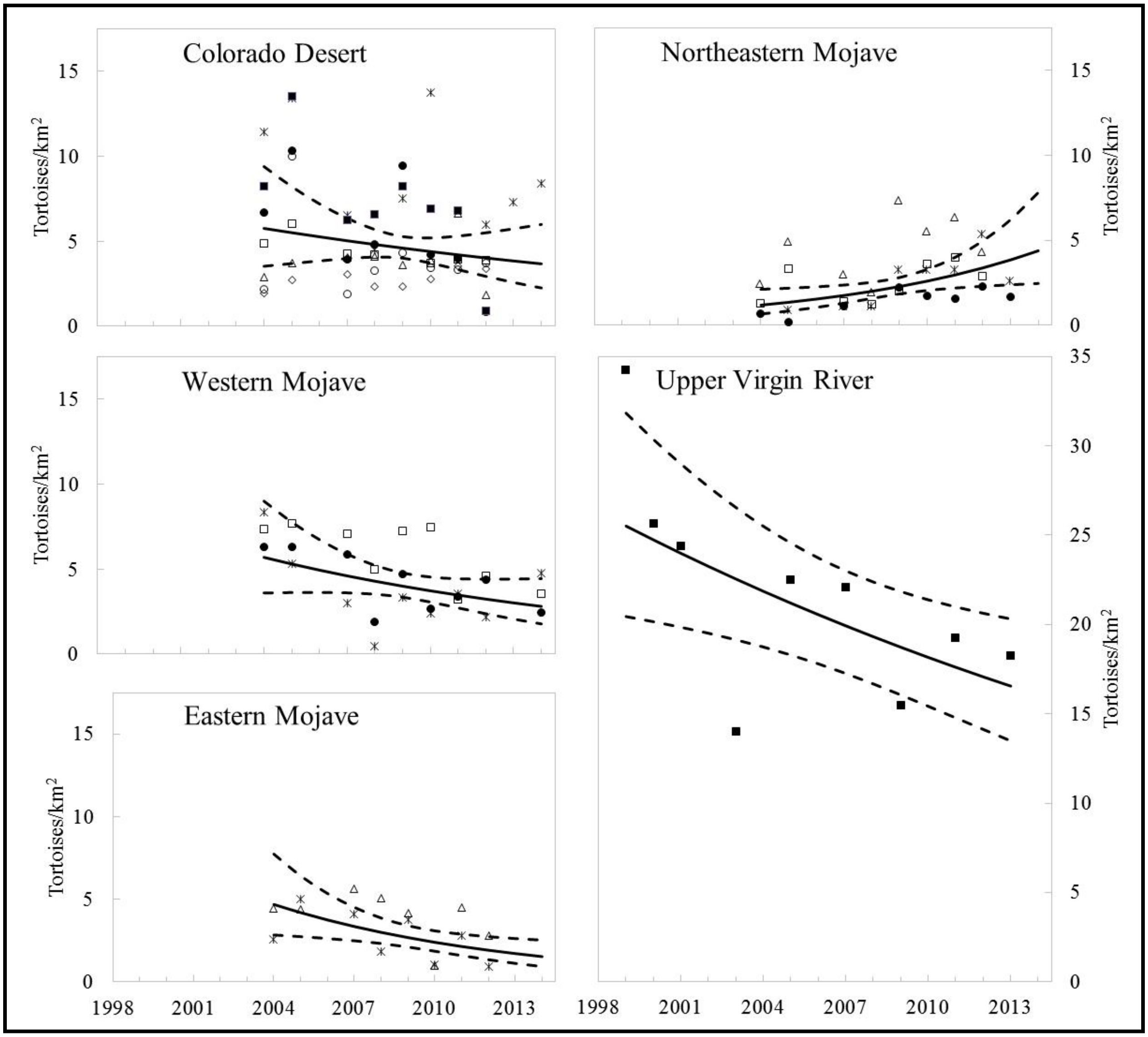

Figure 12. Trends in density (tortoises/km^2) of adult Mojave desert tortoises in each recovery unit through 2014, since 1999 for Upper Virgin River Recovery Unit and for others since 2004. Separate markers are used for annual density estimates for each tortoise conservation area within the recovery unit. The modeled change in density is the bold line and its 90% CI is shown with the dashed line, reflecting the Type I error specified in U.S. Fish and Wildlife Service (2011).

Table 10. Estimated adult densities in each TCA in 2014 and change in abundance within TCAs in each recovery unit between 2004 and 2014 based on multi-year trends from the best-fitting model describing log_e-transformed Mojave desert tortoise density/km^2. Because the model is log-linear, standard errors are multiples of the density estimates. The multiplier for the TCA estimates was 0.3268. Because recovery unit estimates are based on the ANCOVA parameter estimates (Table 9) and are affected by missing years of data, they may differ from simple sums of abundance for TCAs. Tortoise Conservation Area abbreviations in Table 1.

Recovery unit	TCA	Surveyed area (km^2)	2014 Density (SE)	2004 Abundance (SE)	2014 Abundance (SE)	Δ Abundance (SE)
Western Mojave		6294	2.8 (1.0)	35777 (9703)	17644 (4785)	-18133 (4918)
	FK	2347	2.6 (0.3)	12251 (4004)	6196 (2025)	-6055 (1979)
	OR	852	3.6 (0.4)	7036 (2299)	3064 (1001)	-3972 (1298)
	SC	3094	2.4 (0.3)	19216 (6280)	7398 (2418)	-11818 (3862)
Colorado Desert		11663	3.7 (1.3)	67087 (23312)	42770 (14862)	-24317 (8450)
	AG	713	7.2 (0.8)	7327 (2395)	5146 (1682)	-2181 (713)
	CK	2818	3.3 (0.4)	14869 (4859)	9304 (3041)	-5565 (1819)
	CM	3763	2.8 (0.3)	29660 (9693)	10469 (3421)	-19191 (6272)
	FE	1782	4.8 (0.5)	18067 (5905)	8517 (2784)	-9550 (3121)
	JT	1152	3.7 (0.4)	2418 (790)	4319 (1412)	1901 (621)
	PT	508	2.4 (0.3)	3126 (1022)	1241 (406)	-1885 (616)
	PV	927	5.3 (0.6)	3002 (981)	4874 (1593)	1872 (612)
Northeastern Mojave		4160	4.4 (1.8)	4920 (2190)	18220 (8109)	13300 (5919)
	BD	750	6.2 (0.7)	537 (176)	4652 (1520)	4115 (1345)
	CS	960	4.0 (0.4)	1434 (469)	3801 (1242)	2367 (774)
	GB	1607	2.7 (0.3)	1113 (364)	4278 (1398)	3165 (1034)
	MM	844	6.4 (0.7)	2494 (815)	5432 (1775)	2938 (960)
Eastern Mojave		3446	1.5 (0.6)	16165 (4515)	5292 (1478)	-10873 (2949)
	EV	999	1.5 (0.2)	3971 (1298)	1543 (504)	-2428 (794)
	IV	2447	2.3 (0.2)	12693 (4148)	5578 (1823)	-7115 (2325)
Upper Virgin River		115	15.3 (1.6)	2397 (783)	1760 (575)	-637 (208)
	RC	115	15.3 (1.6)	2397 (783)	1760 (575)	-637 (208)
Overall		25678		126346 (41292)	85686 (28004)	-40660 (13288)

DISCUSSION

Improving ability to detect trends in desert tortoise abundance

The primary goal of the monitoring program is to provide population trend estimates that are the basis for evaluating recovery plan criteria (USFWS, 2011). The priority for this and every field season is therefore to improve ability to detect trends in desert tortoise abundance at the recovery unit level. The approach in the past was to generate annual recovery unit density estimates to estimate trends within recovery units; to accomplish this, all TCAs in each recovery unit must be surveyed in the same year. Funding commitments in 2013 and 2014 would only have allowed us to survey all strata at a very minimal level, so instead we surveyed fewer strata but at levels planned to detect enough tortoises for adequate TCA density estimates (Buckland et al., 2001). Reflecting the fact that we can no longer estimate recovery unit densities each year, the approach has changed to estimating recovery unit trends based on composite TCA trends rather than on recovery unit densities.

Although our results demonstrate the power of this monitoring program to detect large positive and negative trends over a 10–15 year period, large SEs for density trends in Table 9 reflect two important sources of imprecision in the population growth estimates. First, long-term monitoring programs spread over a large area are describing multiple underlying local phenomena. This can be seen in the difference in trends between TCAs within the same recovery unit (Table 9). The same phenomenon is expected within TCAs, where for example each end of a valley may be experiencing different population dynamics, or where lowland habitat may offer different population growth potential from upland habitat. It is also to be expected that there is some variation in the degree of population growth supported by year-to-year environmental conditions. These sources of variability in TCA- or recovery-unit-level population dynamics are reflected in the SE of our population trend estimates. By modeling Year as a random factor leading to covariation between density estimates, we accounted for some of the process variation due to annual conditions.

Another source of variance in annual density estimates is sampling error from estimating each of the correction factors to adjust our raw encounter rates each year in each TCA. Estimation of P_a consistently contributes about 10% to the variance in the annual density estimates (e.g., McLuckie et al., 2002). This estimate is based on curve-fitting to a set of detections, and many more detections are needed to develop a detection curve than to estimate encounter rate. Detection curves based on 60 observations might be minimally acceptable (Buckland et al., 2001), whereas encounter rate estimates based on the same number of detections would be robust. This issue underlies the simulations by Freilich et al. (2005), which led them to reject distance sampling as a viable method for such sparsely distributed animals. The current monitoring program always applied much greater survey effort to estimate TCA-specific encounter rates than modeled by Freilich et al. (2005); also, to avoid poor detection estimates, we pooled detection distances across all TCAs completed by a given team of surveyors. A certain amount of precision is also lost to the annual density estimates by correcting for G_0. However, this quantity can vary considerably between years, so failure to correct population estimates adequately would add bias to annual density estimates (Freilich et al., 2000).

Encounter rate estimation is consistently the largest variance component in all TCA density estimates (e.g., McLuckie et al., 2002). Most encounter rate variance is inherent to the distribution of tortoises on the landscape (Krzysik, 2002), with additional sampling variance reflecting relative survey effort. The planned and sustained effort in RC has resulted in much larger sample sizes than in other TCAs and more precision for annual population density estimates (CV = SE/density consistently between 0.12 and 0.15, McLuckie et al., 2014), contributing to lower between-year sampling error. The declining trend in abundance was therefore discernible even though RC was only monitored every other year, an approach that has not been pursued in the rest of the range where survey effort has fluctuated at a generally suboptimal level based on inconsistent available funding. The survey effort outside of RC in some years was insufficient to locate even five animals within a TCA.

Prevailing population trends in Mojave desert tortoises

The regional and range-wide trends in adult Mojave desert tortoise densities described here indicate that overall this threatened species is experiencing large, ongoing population declines, and some recovery units experienced over 50% decline of adult tortoises since 2004. Although TCAs within the same recovery unit had very different initial densities, trends were more similar within recovery units than between them. Only one of the five recovery units (Northeastern Mojave) exhibited population increases across all TCAs; this recovery unit also had the lowest densities at the start of our study period in 2004.

The trends we describe are consistent with published observations within some TCAs. In the Upper Virgin River Recovery Unit, RC experienced catastrophic wildfire as well as a drought-related die-off of tortoises during the period of this study (McLuckie et al., 2014). The vulnerability of this smaller recovery unit in the face of such large-scale impacts remains of paramount concern. In the Western Mojave Recovery Unit, decreasing population trends in the decades before 2004 were described based on multiple widespread but local mark-recapture plots (Doak et al. 1994, Berry and Medica 1995); other evidence of population declines came from comparison of the frequency of live and dead tortoise sightings in the Western Mojave TCAs (Tracy et al. 2004).

In other parts of the desert, earlier research on small plots sometimes described population trajectories that differ from declines reported here, such as static adult tortoise numbers on 2.59-km^2 plots in IV in the Eastern Mojave Recovery Unit, and in PV and FE in the Colorado Desert Recovery Unit (Berry and Medica, 1995). The data in these cases were for earlier decades and describe patterns on single local plots that were also not selected to be representative of the larger TCA (Corn, 1994; Anderson et al., 2001; Tracy et al., 2004). Ongoing and long-term declines on a 2.59- km^2 plot in the JT TCA of the Colorado Desert Recovery Unit (Lovich, et al. 2014) may reflect drought impacts they describe, in addition to consequences from the unimproved road that bisects the plot, and predator impacts reported elsewhere in a low relief site (Berry et al., 2013). These characteristics of the plot differ from large areas of the TCA, which are in more rugged terrain and where we characterize populations as increasing (Table 9).

This report does not test for population trends by comparing a trend model to a null model of static population size. That approach unnecessarily restricts the usefulness of monitoring programs by only tasking them with acquiring enough information to rule out no-action (Wade, 2000; Taylor et al., 2007; Gerrodette, 2011). Instead, we used an information-theoretic approach in which the data are applied to each competing model; we drew conclusions based on the relative support for each model given the data (Burnham and Anderson, 2002). This mirrors the structured decision-making process of selecting among alternatives, allowing monitoring data to support adaptive management (Nichols and Williams, 2006). In this case, regional trend models best described the data in hand. Our current analysis strongly concludes that there are similar population trends within recovery units, with different trends between recovery units.

The range-wide scope of our analysis also uses the power of replication in space to underline regional trends rather than attempting to describe one local trend in isolation (*cf*. Freilich et al., 2005; Inman et al., 2009). We would have reached less definitive conclusions if the monitoring effort had continued exclusively in a few dozen 2.59-km^2 study plots that had been initiated in the 1970s and 1980s or if fewer TCAs had been surveyed, perhaps in a less coordinated effort. Instead, the current range-wide distance sampling program provides fairly coarse but clear summaries of patterns in tortoise density and abundance, definitive because they sample regionally and range-wide.

Monitoring of declining populations should be deeply integrated in conservation and recovery programs. Although these surveys were designed to provide a 25-year description of a positive population growth trend, it is clear that this single purpose would be an underutilization of the program which can certainly address interim management questions (Nichols and Williams, 2006). Population recovery will necessitate accelerated, prioritized recovery activities (Darst et al., 2013). Targeted effectiveness monitoring (Lyons et al., 2008; Lindenmayer et al., 2010), where possible, will complement this larger monitoring program that provides a composite view of all recovery activities. Both types of monitoring will be needed to characterize the effectiveness of recovery activities where the list of threats is so large and varied.

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