Research Article

Monitoring of the Flat-Tailed Horned Lizard With Methods Incorporating Detection Probability

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ABSTRACT Difficulty in monitoring the flat-tailed horned lizard (*Phrynosoma mcallii*) has led to controversy over its conservation status. The difficulty in detecting this species has discouraged large-scale estimates of abundance and led to uncertainty over whether the species exists in population sizes of sufficient size for long-term persistence. We incorporated detection probability into monitoring of this species using closed mark–recapture and distance-sampling methods. Density estimation from mark–recapture abundance estimates was improved using an estimate of the proportion of time lizards were on the plot. We estimated the probability of detection on the line for distance sampling and adjusted density estimates accordingly. We estimated the populations of the Yuha Basin Management Area in 2002 and the East Mesa Management Area, Imperial County, California, USA, in 2003 to be 25,514 (95% CI 14,444–38,970) and 42,619 (95% CI 23,161–67,639), respectively. Two estimates of detection probability on the line in distance sampling by different methods were 0.45 and 0.65. Density estimates derived from distance analyses for 3 East Mesa Management Area plots and the Yuha Basin Management Area were 1.55 per ha (95% CI 0.64–3.76) and 0.41 per ha (95% CI 0.22–0.7), respectively. These are the first large-scale estimates of abundance and density for *P. mcallii*. (JOURNAL OF WILDLIFE MANAGEMENT 71(4):1050–1056; 2007)

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The distribution of the flat-tailed horned lizard (*Phrynosoma mcallii*, hereafter lizard) is limited to southeastern California and southwestern Arizona, USA, and parts of Sonora and Baja California Norte in Mexico (Funk 1981, Flat-tailed Horned Lizard Interagency Coordinating Committee [FTHL ICC] 2003). An estimated 43–49% of historical lizard habitat in the United States has been converted to agriculture, urban areas, or other anthropogenic use (FTHL ICC 2003). Remaining habitat is being impacted by government border activities, utility construction and maintenance, roads, and off-highway vehicles (Turner and Medica 1982, Boyarski 2001). The flat-tailed horned lizard was proposed in 1993 for listing under the federal Endangered Species Act (U.S. Fish and Wildlife Service [USFWS] 1993). In 1997, several state and federal agencies signed a voluntary Rangewide Management Strategy in the hopes of precluding listing (Foreman 1997). The Strategy designated 5 Management Areas (MAs) and one Research Area and requires monitoring of lizard populations within the MAs. In 1997, the proposal to list the species was withdrawn, partially on the premise that the voluntary Management Strategy would provide adequate protection (USFWS 1997). A lawsuit brought against the USFWS a few years later resulted in a court-ordered reconsideration of the proposal to list this species, but the proposal was again withdrawn in 2003 (USFWS 2003). Another lawsuit brought against the USFWS resulted in reconsideration of the proposal to list again, but the proposal was again withdrawn on 28 June 2006 (USFWS 2006). Further litigation is expected.

Resolving controversy over the status of this species has been hampered by a lack of reliable monitoring and abundance data. Estimating the abundance of lizards has relied on methodologies utilizing counts of lizards or lizard scats (Turner and Medica 1982, Rorabaugh et al. 1987, Beauchamp et al. 1998) or utilizing mark–recapture data collected along transects (Boyarski 2001). Scat counts were the preferred method of monitoring from 1979 until the 1990s when the correlation between scat counts and abundance was called into question (Beauchamp et al. 1998; A. Muth and M. Fisher, University of California, Riverside, unpublished report). Scat is produced at different rates during wet and dry years (K. Young and A. Young, Utah State University, unpublished report) and persistence in the environment is variable (A. Muth and M. Fisher, unpublished report). Counts of scat did not correlate with counts of lizards (though both are indices that do not incorporate detection probability; Beauchamp et al. 1998). Estimates of abundance based on lizard detections rather than scat detections are necessary. Further, the low detectability of this lizard indicates that potentially many more lizards are present than are detected. Raw counts fail to account for detection probability, often resulting in biased estimates and misleading results (Thompson et al. 1998, Williams et al. 2002, Anderson 2003). Detectability of lizards also varies by habitat. In sandy habitat, with practice, researchers can track lizards. In hardpan areas tracking is not possible. Thus, methods incorporating detection probability are necessary for valid abundance estimates of this species. Closed mark–recapture methods (Otis et al. 1978) and distance sampling (Buckland et al. 2001) are established methods used to account for detection probability in wildlife surveys. We tested both these methods for efficacy with lizards.

We employed recent developments in closed mark–recapture and distance sampling that are not in wide use.

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Plots in closed mark–recapture studies are typically not enclosed and suffer from lack of geographical closure because animals move on and off the plot. Density estimation is complicated by this fact. To estimate density from closed mark–recapture abundance, estimates require definition of the area used by the population on each plot. The naïve area to use would be the area of the mark–recapture plot. However, the population of animals on the plot uses more area than the plot, thus using the area of the plot for density calculation overestimates density. Typically, a boundary strip is added to the plot to increase the area. The boundary strip may be of width equal to the mean maximum distance moved (Wilson and Anderson 1985) or the radius of the average home range size (Otis et al. 1978). A more rigorous way to control for lack of geographical closure that has not been employed often is to estimate the percentage of time that animals are on the plot (White and Shenk 2001). The average number of animals on a plot at any one time can then be used in density calculations rather than adjusting the area with a boundary strip.

A priori, we hypothesized that standard distance sampling was likely to need adjustment with the lizards. Standard distance sampling assumes that detection on the line [$g(0)$] equals 1. If $g(0) \neq 1$ then density estimates will be biased low. We assessed the detection probability at zero distance and applied this correction factor in distance-sampling analyses to estimate lizard density (Buckland et al. 2004).

Using methods incorporating detection probability we are able to present the first wide-scale population estimates for lizards. While species such as this one that occur in low densities and are difficult to detect will always present challenges, appropriate methods can allay uncertainty in their status.

STUDY AREA

Mark–recapture plots and distance-sampling transects were in Imperial County in southeastern California within the resource area of the El Centro, California, Bureau of Land Management (BLM). The study area was in the Lower Colorado division of the Sonoran Desert (Turner and Brown 1982), which was characterized by low precipitation and high temperatures. The city of Imperial, near the center of the lizard range in California, received an average of 6.5 cm of rain per year (Western Regional Climate Center 2005) and was one of the driest places in North America. The high temperature in July averaged 41.2° C (Western Regional Climate Center 2005) and temperatures greater than 46° C were not unusual. Surface temperatures soar to >60° C from June through August (A. Muth and M. Fisher, unpublished report). Perennial vegetation was sparse and was dominated by combinations of creosote (*Larrea tridentata*), white bursage (*Ambrosia dumosa*), and saltbush (*Atriplex* spp.).

METHODS

Closed Mark–Recapture

We established 12 mark–recapture plots in each of 3 MAs: Yuha Basin MA, East Mesa MA, and West Mesa MA

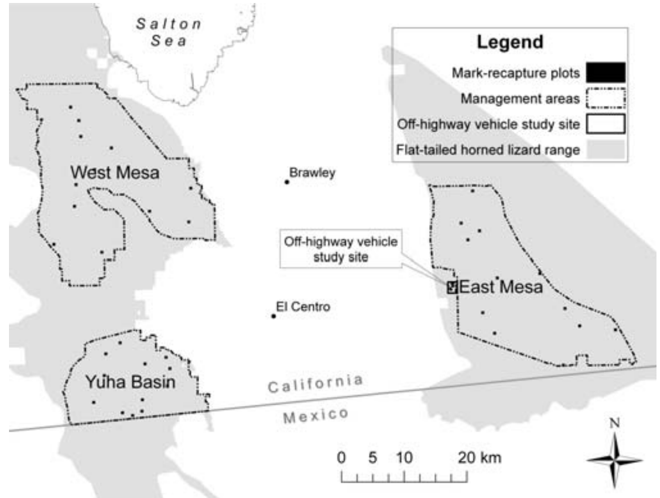

Figure 1. Study areas and plots for closed mark–recapture surveys of flat-tailed horned lizards from 2002 to 2004 in southern California, USA. Three Management Areas are shown (West Mesa, East Mesa, and Yuha Basin) and the site for the mark–recapture portion of the off-highway vehicle study in 2004. Mark–recapture plots are shown to scale.

(Fig. 1). We selected plots in the Yuha Basin MA using stratified random sampling. We chose 3 strata based on substrate type: the flat East stratum (9,280 ha) was defined as covered with fine sand, the Northwest stratum (8,203 ha) was rocky and hilly, and the intermediate Southwest stratum (6,907 ha) was covered with coarse sand and some hills. We randomly chose 4 plots within each stratum. We surveyed these plots in 2002 and 2004. We selected plots on the East Mesa MA and the West Mesa MA using restricted random sampling (Elzinga et al. 2001), in which each MA was split into 12 equal sections and one plot randomly chosen from each section. We surveyed both East Mesa and West Mesa in 2003.

We chose 11 plots for an off-highway vehicle (OHV) study on the western edge of the East Mesa MA (Fig. 1). We did not select the OHV study plots for the purpose of extrapolating to a larger area and estimating the population size of an MA, but for testing for effects of OHVs on lizards (Grant 2005). However, we surveyed these plots using the same protocol used on other plots. Additional information was gained from these plots by using radiotelemeters to estimate the probability of being available for detection, which we denote as $\bar{p}$ (White and Shenk 2001).

Mark–recapture plots were 200 × 200 m (4 ha). We surveyed plots from late May to early September. We assigned 2–4 technicians to a plot and searched the plot each morning for 5 consecutive mornings (excluding weekends). We applied constant effort over the 5 days using the same number of observers. Plot search time varied from 2 hours to 4 hours, depending on the individual characteristics of the plot and the number of lizards found and processed. Searching began as soon as there was enough light to see (generally from 0515 hr to 0600 hr). We divided plots into 10-m lanes for searching. We timed searches to end when the temperature 1 cm above the surface was ≥41° C. Generally, we finished plot searching by 1030 hours.

We marked lizards ventrally with a unique number using a black Sharpie marker (Sanford Corporation, Oakbrook, IL). We measured the snout–vent length (mm) and classified lizards ≥65 mm as adults (Howard 1974; Pianka and Parker 1975; Setser 2004; A. Muth and M. Fisher, unpublished report). We also recorded Universal Transverse Mercator coordinates of the capture location and the observer who found the lizard.

We used Program MARK (White and Burnham 1999) to estimate detection probability (p) and abundance (N). Because we performed the 5 surveys of area-years (Yuha Basin MA 2002, East Mesa MA 2003, West Mesa MA 2003, Yuha Basin MA 2004, and 2004 OHV study) under the same protocol and the data was sparse, data from these plots were analyzed jointly to better estimate p (White 2005). We used Huggins closed mark–recapture models (Huggins 1989, Huggins 1991) rather than the full-likelihood closed-captures models (Otis et al. 1978).

Program MARK uses an information-theoretic approach to rank models according their relative distance from the truth (Burnham and Anderson 2002). We developed 16 a priori models. We modeled detection probability (p) as constant or with combinations of 3 additive effects (area-yr, observer proficiency, and recapture effect). The area-year effect allowed p to vary across the 5 area-years. The second additive effect was a temporal covariate for observer proficiency. Most technicians had little experience with lizards before we hired them for the survey. In contrast, one of us (T. J. Grant) participated in 4 of the 5 area-years and also had previous experience. There appeared to be a difference in detection probability according to experience and other factors; thus, we modeled the effect of an experienced observer with an additive effect on p, denoted by "obs". A recapture effect was also tested. A recapture effect may occur if the lizards respond behaviorally to being captured and become less or more difficult to capture the second time. The recapture effect was one parameter with no structure varying by area-year or other effects. We also employed the heterogeneity estimators of Pledger (2000) to model unexplained variability in the detection process.

We considered the data too sparse to support the estimation of additional parameters in relation to the capture and recapture process. Thus, we created 8 models to model the base detection effects {[π(.) p(.) N(plot)], [π(.) p(area-yr) N(plot)], [π(.) p(obs) N(plot)], [π(.) p(area-yr + obs) N(plot)], [π(.) p(c) N(plot)], [π(.) p(area-yr + c) N(plot)], [π(.) p(obs + c) N(plot)], [π(.) p(area-yr + obs + c) N(plot)]} and we also constructed an additional 8 models to include the heterogeneity models {[p(.) N(plot)], [p(area-yr) N(plot)], [p(obs) N(plot)], [p(area-yr + obs) N(plot)], [p(c) N(plot)], [p(area-yr + c) N(plot)], [p(obs + c) N(plot)], [p(area-yr + obs + c) N(plot)]}. We constructed models using program MARK. We calculated model-averaged parameter and beta estimates for closely ranking models (Burnham and Anderson 2002).

After we estimated abundance (N) for each plot from the above model set, we estimated density for the surveyed area (A) using the probability of availability ($\bar{p}$) following the formula of White and Shenk (2001):

$$\hat{D} = \frac{\hat{N} \times \bar{p}}{A}$$

with variance estimated as:

$$V\hat{a}r(\hat{D}) = \frac{\hat{N}^2 V\hat{a}r(\bar{p}) + \bar{p}^2 V\hat{a}r(\hat{N})}{A^2}$$

We used radiotelemetered lizards to obtain a robust estimate of $\bar{p}$ during 2004. We outfitted all lizards found on the OHV study mark–recapture plots with radiotelemeters on first capture. Each day, during the course of the 5-day plot survey, we used radiotelemetry to determine whether each lizard was on plot and available for detection or off-plot and unavailable. After the plot survey was completed, we also located lizards opportunistically, usually every 2 or 3 weeks, to determine if they were on or off the plot at that time. We estimated the proportion of time spent on the plot for each lizard as the number of relocations that were on the plot divided by the total number of relocations. We took the mean of the individual proportions as the estimate of $\bar{p}$. In our study, $\bar{p} < 1$ is a result only of lizards temporarily leaving the plot. Radiotelemetry studies of lizards demonstrate that they are very seldom underground during the active period of the day (K. Young and A. Young, Utah State University, unpublished report); thus, we assume that if they were on the plot they were available for capture.

Distance Sampling

We conducted 2 distance-sampling (Buckland et al. 2001) surveys in conjunction with the mark–recapture plots. The first distance survey was a pilot study conducted on East Mesa in 2003 to address the $g(0) = 1$ assumption and we did not extrapolate the results to other areas. We performed distance sampling on the 3 most dense mark–recapture plots of East Mesa. Time constraints prohibited surveying on the rest of the plots.

We used the perimeter of the mark–recapture plots and the center line of the plot lanes as the transect lines. We arranged the 3–4 observers such that one observer had responsibility for ensuring all lizards were detected on the line (Buckland et al. 2001) and the other 2 observers also looked for lizards near this line.

On every day but the last day of the mark–recapture survey, we surveyed the perimeter of each mark–recapture plot (800 m). Because the transect formed a square, we were careful not to double-count lizards at the corners. A small area was double-sampled at the corners, which we corrected for by subtracting the double-sampled area from the total area sampled by adjusting the line length.

On the last day, we treated the lanes of the mark–recapture plot as distance-sampling transects. These transects were 4,000 m because plots had 20 lanes each 200 m long. The center of the lane was the zero line. We confined searching to within 5 m of the zero line so as not to search in neighboring lanes. If we found a lizard, we measured the

Table 1. Model selection results for 16 models of detection probability and abundance for flat-tailed horned lizards in southern California, USA, from 2002 to 2004. Models are ranked by Akaike's Information Criterion adjusted for small sample size (AIC_c). The ΔAIC_c is the difference in AIC_c units from the highest ranking model. The AIC_c weights, model likelihood, and number of parameters are also shown.

Model	AIC_c	ΔAIC_c	AIC_c wt[a]	Model likelihood[b]	No. of parameters
[π(.) p(area-yr + obs) N(plot)]	1,258.31	0.00	0.62	1.00	8
[π(.) p(area-yr + obs + c) N(plot)]	1,259.99	1.68	0.27	0.43	9
[π(.) p(obs) N(plot)]	1,263.07	4.76	0.06	0.09	4
[π(.) p(obs + c) N(plot)]	1,264.79	6.49	0.02	0.04	5
[π(.) p(area-yr) N(plot)]	1,266.00	7.69	0.01	0.02	7
[p(area-yr + obs) N(plot)]	1,266.35	8.04	0.01	0.02	6
[π(.) p(area-yr + c) N(plot)]	1,267.64	9.33	0.01	0.01	8
[p(area-yr + obs + c) N(plot)]	1,267.81	9.50	0.01	0.01	7
[p(area-yr) N(plot)]	1,273.02	14.72	0.00	0.00	5
[p(area-yr + c) N(plot)]	1,274.51	16.21	0.00	0.00	6
[p(obs) N(plot)]	1,278.11	19.81	0.00	0.00	2
[p(obs + c) N(plot)]	1,279.12	20.81	0.00	0.00	3
[π(.) p(.) N(plot)]	1,285.33	27.02	0.00	0.00	3
[π(.) p(c) N(plot)]	1,286.70	28.39	0.00	0.00	4
[p(.) N(plot)]	1,301.62	43.31	0.00	0.00	1
[p(c) N(plot)]	1,302.35	44.05	0.00	0.00	2

[a] AIC_c wt sum to one and models with higher likelihood have more wt.
[b] Model likelihood is the likelihood of a model relative to the other models.

distance to the center of the lane (i.e., zero line). We conducted this 4,000-m transect only on the last day.

In 2004, we conducted the second distance-sampling survey in conjunction with the 12 Yuha Basin MA mark–recapture plots. The procedure was the same as for the East Mesa transects, except that we were able to conduct distance sampling 4 of 5 days on the whole plot. We did not conduct any transects on the perimeter of the plots.

We used Distance 4.1 (Thomas et al. 2003) to analyze the data. For the East Mesa data, we truncated distances at 5 m because we focused our search within 5 m of the zero line, so few distances fell outside of 5 m. We truncated distances at 5.5 m for the Yuha Basin data. Because the distance data were sparse, we binned the data for both data sets at the following cutpoints: 0, 1.5, 2.5, 3.5, 4.5, and 5.5. We applied the 6 models recommended by Buckland et al. (2001). We selected the best model using Akaike's Information Criterion adjusted for small sample size (AIC_c).

We estimated $g(0)$ in 2 ways. Radiotelemetry on mark–recapture plots allowed us to estimate probability of detection given availability ($p_{d|a}$). If the detection function using distance sampling was uniform, the probability of detection at any distance from the zero line and at the zero line would be the same. Thus $p_{d|a}$ would be equal to $g(0)$, because $p_{d|a}$ encompasses the entire width of the transect and defines the probability of detection of a lizard at any point. The second way to estimate $g(0)$ was a trial of technician efficiency on 50-m transects. The cryptic behavior of the lizards usually allowed transects to be set up with the lizard in situ, creating the most realistic distance-sampling situation. The lizard was at a random distance along the 50-m transect, within 1 m of the line. Technicians independently walked the entire line and reported detecting the lizard or not. We performed 31 trials in this way. We estimated $g(0)$ as the number of trials in which the lizard was detected divided by the number of trials.

California Department of Fish and Game permitted this study under scientific collecting permit number SC-007201. The Animal Care and Use Committee of Colorado State University approved this study under permit number 03-220A-01.

RESULTS

Closed Mark–Recapture Method

The complete dataset consisted of 228 unique lizards and 363 captures. Two area-years had very sparse data. In the Yuha Basin MA survey of 2004, we captured 44 unique adults. Only 4 of these adults were recaptured. In the West Mesa MA we captured only 9 unique lizards and tallied 14 total captures. A priori we expected the data from these plots to be too sparse to support modeling of detection and abundance well. The observer experience covariate, and data from other plots, improved estimation of p in these cases, but our confidence intervals for the Yuha survey of 2004 were still very wide and must be viewed with caution.

The other area-years were relatively less sparse than the 2 above area-years. In the Yuha Basin MA survey of 2002, we captured 59 unique adults and tallied 108 total captures. In the East Mesa MA survey of 2003, we captured 49 unique adults and tallied 82 total captures. In the OHV study of 2004, we captured 63 unique adults and tallied 99 total captures.

Models with $p = c$ always ranked above models with a recapture effect (combined AIC_c wt = 0.70), providing no support for a recapture effect (Table 1). Models with area-year variation in p were selected over models with constant p (combined AIC_c wt = 0.92), suggesting differences in detection probability between area-years (Table 1). Heterogeneity models always rank higher than nonheterogeneity models (combined AIC_c wt = 0.98), suggesting that there is

Table 2. Model-averaged estimates of $\hat{\beta}$s used in models of detection probability and abundance for flat-tailed horned lizards in southern California, USA, from 2002 to 2004.

Parameter[a]	$\hat{\beta}$	95% LCL[b]	95% UCL[b]
Mixture effect	−1.87	−2.70	−1.04
East Mesa MA 2003	−0.48	−2.04	1.07
Yuha Basin MA 2004	−1.57	−2.81	−0.32
West Mesa MA 2003	0.05	−1.44	1.54
Yuha Basin MA 2002	0.39	−0.36	1.14
Off-highway vehicle study 2004	−0.23	−0.93	0.47
Recapture effect	0.19	−0.46	0.83
Observer effect	0.75	0.25	1.25

[a] The mixture effect models the low proportion of p (p_L) in heterogeneity models (the intercept is the high p). Each Management Area (MA) has a $\hat{\beta}$ in area-year models. The East Mesa MA 2003 $\hat{\beta}$ was modeled as the intercept. The recapture effect is an additive $\hat{\beta}$ effect to model recapture probability (c). The observer effect is whether T. J. Grant was on the plot or not for that capture occasion.

[b] The lower and upper 95% CLs (95% LCL and 95% UCL, respectively) are shown.

Table 3. Total population estimates for flat-tailed horned lizards calculated from closed mark–recapture data with 95% confidence intervals for 4 area-years in southern California, USA, from 2002 to 2004.

Area-yr	N	95% LCL[a]	95% UCL[a]
Yuha Basin MA[b] 2002	25,514	12,761	38,970
East Mesa MA 2003	42,619	19,704	67,639
West Mesa MA 2003	10,849	3,213	23,486
Yuha Basin MA 2004	73,017	4,837	163,635

[a] The lower and upper 95% CLs (95% LCL and 95% UCL, respectively) are shown.

[b] MA = management area.

heterogeneity in capture probabilities (Table 1). Models with the observer experience covariate (combined AIC_c wt = 0.98) were always selected over corresponding models (Table 1). The 95% confidence interval for the model-averaged $\hat{\beta}$ for observer experience ($\hat{\beta}$ = 0.75, 95% CI 0.25–1.25; Table 2) did not overlap zero and neither did the confidence interval for the heterogeneity mixture effect ($\hat{\beta}$ = –1.87; 95% CI –2.70—1.04; Table 2). Only the 95% confidence interval for the model-averaged $\hat{\beta}$ associated with the Yuha Basin MA survey did not overlap zero. Model-averaged capture and recapture probabilities varied among area-years and by observer experience, and ranged from 0.03 to 0.65.

To estimate $\bar{p}$, we relocated 46 lizards on 9 plots a total of 226 times during the OHV study in 2004. Mean $\bar{p}$ was 0.60 (95% CI 0.49–0.71). We adjusted abundance estimates $\bar{p}$ (White and Shenk 2001) to estimate plot densities. Because some of the lower confidence limits for plot N estimates were <0, we used the average number of lizards found per occasion per plot, if it was greater than the lower confidence limit. It was then divided by 4 ha and used as the lower confidence limit of density for each plot. We extrapolated density to the entire sampling frame to obtain a total population estimate for the 4 monitoring surveys (Table 3).

We surveyed the same plots in the Yuha Basin MA in 2002 and 2004. No overall trend can be inferred in the Yuha Basin MA from 2002 to 2004.

Distance Sampling

We used 2 $g(0)$ estimates in the analysis. Estimates of $g(0)$ were calculated from radiotelemetry and from distance-sampling trials. Of 56 lizards found to be on the mark–recapture plot using radiotelemetry, we found 24 during the search of the plot. Hence, $g(0)$ was estimated as 0.43 (95% CI 0.30–0.56), assuming the detection function is uniform (see below). Of 31 50-m-transect trials, lizards were detected 20 times. Hence, $g(0)$ was estimated as 0.65 (95% CI 0.48–0.81). We applied these estimates to the 2 distance-sampling surveys.

East Mesa MA 2003.—We recorded 26 distances to lizards. Because not all models fit a uniform detection function, we used the estimate of $g(0) = 0.65$ from the distance-sampling trials. The data were heaped near the line and near the 5-m distance. The model selected by AIC_c was the uniform key function (no series expansions were added to any models). Density was estimated as 1.55 lizards per ha (95% CI 0.64–3.76).

Yuha Basin MA 2004.—We recorded distances for 43 lizards. The $g(0)$ estimate of 0.43 was used because the detection function for the Yuha Basin was always uniform. The uniform key function with no adjustment terms ranked highest, though all density estimates were equal to 2 decimal places. Density was estimated to be 0.41 lizards per ha (95% CI 0.22–0.77) and the population of the Yuha Basin MA in 2004 was estimated as 10,001 (95% CI 5,321–18,798).

DISCUSSION

Our results are the first large-scale abundance estimates of flat-tailed horned lizards. We successfully estimated population sizes for this difficult species. The point estimates generally indicate larger populations than were expected. A population viability analysis on this species used initial population sizes of 5,000 and assumed a carrying capacity of 15,000 (Flat-tailed Horned Lizard Conservation Team, USFWS, unpublished report). Closed mark–recapture methods seem better suited to this species than distance sampling, because of the difficulty in estimating $g(0)$. However, the mark–recapture plots suffered from large amounts of movement on and off the plots, a violation of the assumption of geographical closure, as shown by the fact that we estimated lizards to be on the plot only 60% of the time. Closed-capture models assume no emigration or immigration, though if a lizard's status as on or off the plot is random and not dependent on its previous status, lack of geographical closure will not affect the point estimate of abundance. Lack of closure will bias estimates of abundance if the movement on and off the plot is not random (Kendall 1999). Movement on and off the plot essentially induces heterogeneity, which tends to underestimate abundance (Pledger 2000). Thus, heterogeneity is preferably avoided.

Probability of availability ($\bar{p}$) refers to the probability that a lizard is available for capture during a capture occasion. Because plots were large and not enclosed, lizards were free to move on and off the plots and became temporarily unavailable for capture when off the plot. This has often been referred to as temporary emigration (e.g., Kendall and Nichols 1995). Traditionally, $\bar{p}$ has been implicitly accounted for by expanding the area of the survey plot by the radius of a home range (Otis et al. 1978) or mean maximum distance moved (Wilson and Anderson 1985) from capture data. However, these are ad hoc solutions to the problem and incorporate none of the variance associated with this process. Our use of $\bar{p}$ is a more robust approach to estimating density.

Four-hectare plots are probably the largest size plot that can be surveyed in one morning with one team of 3 people, but lizard home ranges may be larger than the plot size. In the Yuma Desert MA, female average home-range size varied from 1.3 ha in a very dry year to 1.9 ha in a very wet year, but male average home-range size varied from 2.5 ha in a very dry year to 10.5 ha in a very wet year (K. Young and A. Young, Utah State University, unpublished report). Home range size during the summer at the Ocotillo Wells State Vehicle Recreation Area in California ranged from 0.4 ha to 0.6 ha in females and 0.96 ha to 1.1 ha for males during the 2 dry summers of 1999 and 2000 (Setser 2004). Precipitation for the previous September to May was only 11 mm and 18 mm, respectively (Grant 2005). East Mesa is more similar to the Yuma desert, however. East Mesa in 2004 received 4.7 cm in the 12 months prior to May, a few cm below the yearly average of 6.5 cm. East Mesa in 2003 had a similar amount (5.0 cm), but the Yuha Desert in 2002 had only a trace of precipitation. Thus, using $\bar{p}$ from 2004 on 2003 is mitigated by the fact that precipitation, and therefore home range sizes, were similar, and using $\bar{p}$ from 2004 on 2002 data is likely overly conservative.

Possibilities are available to ameliorate or eliminate the violation of closure on mark–recapture plots, namely, larger plots or enclosed plots. If larger plot size or the current plot size is used, radiotelemeters ought to be employed to estimate $\bar{p}$ in different areas and years, as $\bar{p}$ will likely differ. Enclosing plots for the length of the survey would be ideal, as this would prohibit movement across the boundaries and essentially create a snapshot of the density at the time the plot was enclosed.

The effect of the observer experience covariate shows a situation of strong observer variation. If there are large differences in technicians' ability to find lizards, a covariate might be used for each of the technicians. In this case, because T. J. Grant was present for many of the surveys over the 3 years, the observer experience covariate helped model p across area-years, but it was also useful in that it controlled for the higher rate of finding lizards by one with more experience. We believe this higher rate can be attributed to experience and perhaps because T. J. Grant is colorblind. Color-blindness may encourage a person to seek out patterns rather than colors, which may increase ability to detect cryptic objects (Morgan et al. 1992).

Distance sampling suffered from low sample sizes and a low $g(0)$. Future use of distance sampling would need to incorporate estimates of $g(0)$. We suspect both estimates of $g(0)$ are biased high for the context in which we applied them. Detectability in the Yuha Basin is likely to be less than on East Mesa because the color of the substrate and often coarser substrate of the Yuha Basin decreases detectability. The use of $p_{d|a}$ as an estimate of $g(0)$ also relies on the assumption that the detection function is uniform. The search pattern of the technicians would theoretically generate a uniform detection function because the lanes are narrow (10 m) and with 3 technicians searching, the entire lane receives almost equivalent effort. However, we likely did not have the sample size and power to detect if the detection curve was not uniform, analogous to detecting if a null hypothesis is false. It is very unlikely that the detection function was exactly uniform, but larger sample sizes would be required for AIC model selection to select a nonuniform model as most parsimonious.

A potential problem with our $g(0)$ distance-sampling trials is that the trials are artificial situations in which diligence and thus, detection probability, were likely increased by pressure from peers and the observing supervisor. This would result in a $g(0)$ correction factor that is biased high, resulting in densities that are biased low. Trials such as we describe might be advantageous to bound the magnitude of $g(0)$ in different areas, but combining mark–recapture and radiotelemetry with distance sampling and using $p_{d|a}$ as the estimate of $g(0)$ would be more desirable.

Distance-sampling density estimates are lower than corresponding mark–recapture estimates. On the 3 East Mesa MA plots of 2003 where distance sampling was done, the average density estimated from mark–recapture was 2.83 (95% CI 0.68–4.97, individual densities were 1.52, 2.17, and 4.78), whereas the distance-sampling estimate was 1.55 (95% CI 0.64–3.76). This suggests that distance sampling may be underestimating the density, likely because $g(0)$ is actually even lower than 0.65.

MANAGEMENT IMPLICATIONS

Mark–recapture methods of flat-tailed horned lizards have been employed successfully and with proper planning, can continue to be successful in the future. Improvements to estimation of density, such as use of $\bar{p}$ to adjust for lack of geographical closure, will increase the validity of density estimates and total population estimates. Distance sampling will require ancillary data to estimate $g(0)$. Managers will need to address these issues. Population estimates presented here may provide the baseline for future monitoring. The persistence of lizard populations depends on many factors, but the populations we studied currently appear to be large. Additional work on explaining variation in density across the range (Grant 2005) could be useful in better understanding the biology of this little-known species. Continued mitigation of threats by prudent management will ensure their persistence.

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