

## Regional-Scale Estimation of Density and Habitat Use of the Desert Tortoise (*Gopherus agassizii*) in Arizona

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**ABSTRACT.**—Desert Tortoise surveys and management in the Sonoran Desert typically exclude intermountain valleys, where tortoises are generally thought to be absent. Furthermore, few regional-level surveys have been conducted because of difficulties in sampling in the complex landscape of Sonoran Desert upland habitat. We used distance-sampling to document macrohabitat use and regional density of Desert Tortoises across the 76,800-ha Ironwood Forest National Monument in Arizona. We observed 42 tortoises on transects, and distance sampling produced an estimate of 17,997 tortoises  $\geq$  150 mm carapace length (coefficient of variation = 41.5%) on the monument. Stratification by habitat type (steep topography with boulders, incised washes, or neither of these components) improved precision slightly (37.2%). Detection probability contributed least to density variance, compared to encounter rate and tortoise detectability on the transect line, indicating that assumptions of the technique were met during sampling. We found tortoises or their sign on 92% of transects in boulder habitat, on 71% that included incised washes, and on 25% in habitat with neither of these features (up to 1.7 km away from the nearest slope). Our results indicate that Desert Tortoises in the Sonoran Desert occur at low density, but are not absent, from intermountain valleys, and the maintenance of these valleys for tortoise movement between local populations may be important for long-term population viability. With this in mind, concentrating survey effort in areas with steep topography and boulders will increase tortoise encounter rate, result in better precision of regional density and trend estimates, and may also reduce survey effort.

Desert Tortoises (*Gopherus agassizii*) are known to occupy a diversity of habitats. In the Mojave

Desert (Turner, 1982), including the Colorado Desert (or Lower Colorado River Valley subdivision of the Sonoran Desert; Turner and Brown, 1982) of southeastern California, tortoises generally occur in creosotebush, alkali, or cactus scrub in valley bottoms, extending up washes on the lower slopes of bajadas (Luckenbach, 1982;

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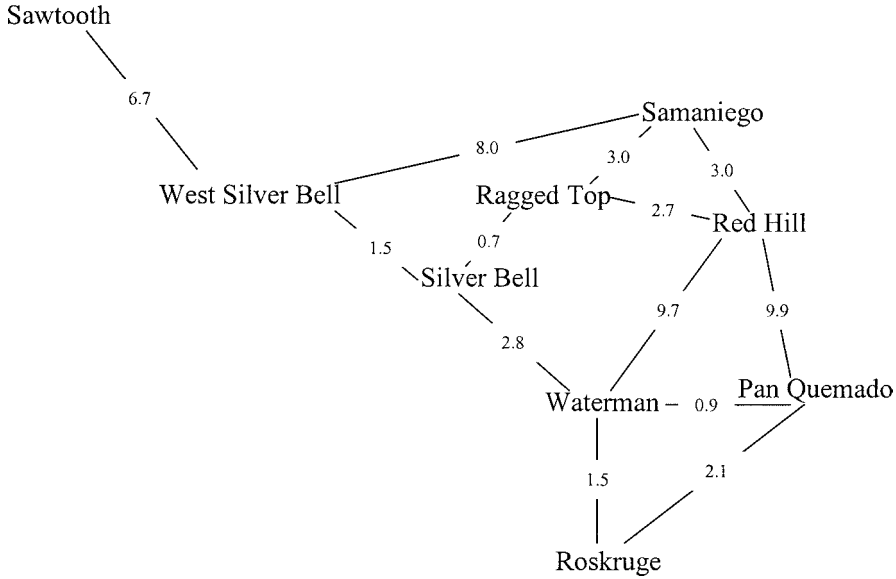


FIG. 1. Schematic diagram of mountain ranges and hill complexes on Ironwood Forest National Monument, Arizona. Distances between adjacent ranges are shown to nearest 0.1 km. Map not to scale.

Bury et al., 1994). Bury et al. (1994) noted that tortoises were absent in relatively few areas of the eastern Mojave Desert but that rocky slopes and steep terrain were seldom surveyed. Tortoises in the Sonoran Desert (Turner and Brown, 1982) are generally absent in valleys and are instead found mostly on rocky hillsides and mountain foothills, most abundantly in the Arizona Upland subdivision, as well as multi-dissected, sloping plains (Burge, 1979, 1980; Barrett, 1990; Germano et al., 1994). In both the Sonoran Desert of Arizona and extending into Mexico, Desert Tortoises are apparently absent from or occur in low densities in valley floors and other flat areas (Fritts and Jennings, 1994; Van Devender, 2002). Germano and Bury (1994) noted that the lack of surveys in hills and on mountains in the Mojave Desert has probably biased our understanding of where tortoises live and how they use their habitats. They called for random surveys in all potential habitats to gather the quantitative information that will best answer questions of habitat selectivity and use by tortoises, and the same recommendation can be made for surveys in the Sonoran Desert.

Attempts to quantify regional-scale tortoise population sizes and trends have not been made in the Sonoran Desert because of the difficulty of sampling in the topographically and vegetationally complex landscape of "typical" tortoise habitat in rocky uplands. Distance sampling has been used extensively for regional monitoring of Desert Tortoises in the Mojave Desert since 1996, but until recently the method has been untested

in the Sonoran Desert (Anderson et al., 2001). A recent study conducted near Saguaro National Park, Pima County, Arizona, demonstrated that distance sampling could be an effective means of estimating tortoise density in the Sonoran Desert, despite denser vegetation and more complex topography, at least on a relatively small scale (<370 ha; Swann et al., 2002). Our objectives were to (1) document habitat use of Desert Tortoises across the 76,800-ha Ironwood Forest National Monument (IFNM) using a distance-sampling protocol, and (2) evaluate effectiveness of distance sampling in estimating density of Desert Tortoises at a regional scale in the Sonoran Desert.

#### MATERIALS AND METHODS

*Study Site.*—IFNM, located in Pima and Pinal counties, Arizona, includes five mountain ranges (Sawtooth, West Silverbell, Silverbell, Waterman, and Roskrige Mountains), as well as intervening desert valleys and several hill complexes (Pan Quemado, Red Hill, Samaniego Hills; Fig. 1). Mean distance between nearest neighboring ranges is  $2.4 \text{ km} \pm 0.78 \text{ SE}$ , as measured from the base of slopes identified on topographic maps in ArcView (ESRI, Redlands, California). The predominant vegetation on hills and mountains is typical of the Arizona Upland subdivision of the Sonoran Desert, including *Olneya tesota*, *Cercidium microphyllum*, *Acacia constricta*, *Prosopis velutina*, *Carnegiea gigantea*, *Ambrosia deltoidea*, and many *Opuntia* species (Wiens, 2000). In-

tervening desert valleys have vegetation more characteristic of the Lower Colorado River Valley subdivision, such as *Larrea tridentata* and *Ambrosia deltoidea* (Wiens, 2000). Desert washes extend from slopes into valleys, are characterized by ephemeral water and denser vegetation and often contain incised banks with naturally eroded or animal-modified caliche caves. Some plant species, such as *Cercidium floridum*, are found almost entirely, if not exclusively, in these washes (Wiens, 2000).

**Sampling Design.**—We stratified and randomly located transects, each a square measuring 250 m (map distance) on each side for a total length of 1 km (Swann et al., 2002), into three categories based on specific habitat features. Category B was characterized by steep topography with boulders ( $N = 26$ , 24%). Category W included transects that crossed or ran along incised washes and contained few to no boulders (with or without topographic relief;  $N = 24$ , 22%). Category X was relatively flat and contained neither incised washes nor boulders ( $N = 59$ , 54%; Fig. 2). A transect was considered type B or W if any portion of the transect met the relevant criteria. Therefore, these landscape features were not necessarily the primary component of a transect, but we assumed the proximity of boulders and washes were immediately available to tortoises found on such transects. We shifted or moved the location of 14 transects because they either fell partially off monument land or across a sheer cliff face.

We surveyed for Desert Tortoises on 53 days between 16 July and 11 October 2001, which coincides with the Sonoran Desert monsoon season and the period of greatest tortoise activity (Averill-Murray et al., 2002b). Because our study site was large and some areas were not easily accessible, we did not randomly select the order in which to survey transects. We did, however, select transects such that each major area of the monument (e.g., mountain range) was surveyed periodically throughout the study. Daily time constraints during a survey occasionally prevented us from completing a transect.

**Survey Protocol.**—We surveyed for tortoises in the morning (74.95 km of transects) and evening (33.3 km of transects), for a total of 108.25 km of transects. We conducted most morning surveys between 0630 and 1200 h and most evening surveys between 1630 and 1830 h, with exact times depending on weather conditions, sunrise/sunset, and travel distance from camp. Most transects were surveyed by three experienced people (see Swann et al., 2002). We extracted tortoises found inside burrows by hand or by using a snake hook. We measured midline carapace length (CL) of each tortoise using calipers and a ruler, identified sex (juvenile if

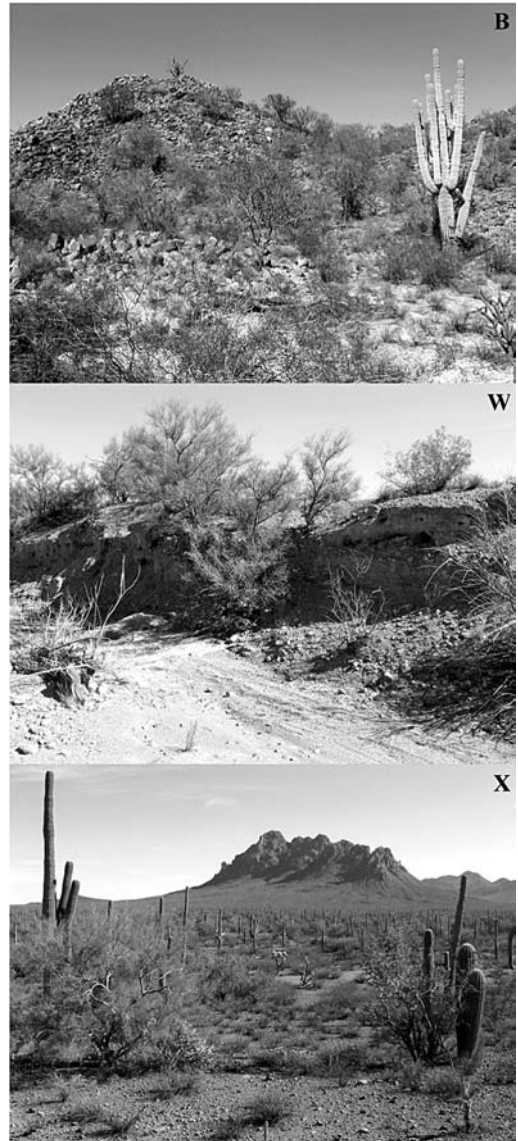


FIG. 2. Representative *Gopherus agassizii* habitat at Ironwood Forest National Monument: (B) Category B, steep topography with boulders; (W) Category W, incised wash; and (X) Category X, lacking boulders or incised washes.

CL < 180 mm; Germano, 1994), and gave each tortoise a unique mark by notching the marginal scutes. We wore latex gloves while handling tortoises and washed equipment with the disinfectant chlorhexidine diacetate (Nolvasan, American Home Products Corp., Madison, New Jersey) after processing each tortoise. If we were unable to extract a tortoise from a burrow, we estimated whether its CL was greater or less than 150 mm. Tortoises with CL < 150 mm are

more easily overlooked (e.g., Averill-Murray [2002] found that recapture rates fell below 50% at about this cut point); hence, they were not included in analyses estimating density.

We noted all tortoise carcasses found, including partial skeletons and isolated scutes, as well as scat, tracks, pallets, and burrows likely excavated by tortoises. We measured the distance between the center of any Category X transect on which a tortoise or sign was found and the base of the nearest mountain or hill slope on topographic maps in ArcView. One observation of tortoise scat found en route to a Category X transect was measured from the point of observation to the nearest mountain.

*Distance Sampling Assumptions.*—Unbiased density estimation using distance sampling rests on three major assumptions: (1) objects on the centerline are always detected; (2) objects are detected at their initial location, prior to movement in response to the observer; and (3) perpendicular distances are measured accurately (Buckland et al., 2001). In using the distance sampling approach for Desert Tortoises, the latter two assumptions are relatively easy to meet. Desert Tortoises generally do not move in response to approaching observers, and perpendicular distances can be accurately measured if the centerline is clearly marked (Anderson et al., 2001). However, field protocols must address the first assumption.

Because Desert Tortoises spend a significant amount of time underground, it may be impossible to detect all tortoises on the centerline regardless of how thoroughly the area is searched. Therefore, the proportion of the population visible must be independently estimated to meet the first assumption. We defined tortoise detectability ( $g_0$ ) at IFNM as the proportion of time that a tortoise would be visible to an observer during distance sampling, with or without supplemental light, inside or outside a shelter. To determine  $g_0$ , we affixed radio transmitters to 10 individuals at a central location within the monument and tracked them concurrent with transect surveys. Telemetered tortoises typically occupied boulder slopes or incised washes.

On 30 June and 1 July 2001, volunteers located seven tortoises large enough ( $> 150$  mm CL) for transmitters. We found an additional tortoise the following week and the remaining two tortoises by mid-August. Of these tortoises, five were female and five were male; CL ranged from 185–256 mm. We affixed transmitters (AVM Instrument Co., Colfax, California; Advanced Telemetry Solutions, Isanti, Minnesota) to the right front (for females and some males) or rear (for males only) of the carapace with quick-drying epoxy.

We tracked tortoises using a directional antenna and receiver (Telonics Model TR-2, Mesa, Arizona) on 30 of the 50 mornings (60%) and 21 of the 38 evenings (55%) that we also conducted distance sampling. We did not track all tortoises during each session and only counted sessions in which more than four tortoises were found (morning average =  $8.3 \pm 0.28$  SE,  $N = 28$  days; evening average  $6.0 \pm 0.44$ ,  $N = 18$  days). Tortoises not found during a morning session were located that evening, and tortoises not found one evening were located the following day when possible. When we located a tortoise, we recorded whether it was visible with the naked eye, supplemental light, or not at all.

We calculated  $g_0$  as the mean daily proportion of tortoises visible with the naked eye or supplemental light during morning surveys, evening surveys, and overall. We estimated the standard error of  $g_0$  as the mean of the daily binomial standard errors of the proportion visible (Zar, 1984). We used the overall  $g_0$  as a correction factor in estimating the detection probability curve, from which density is computed (see below), because sample sizes were too small to run separate analyses for morning and evening surveys.

*Density Estimation.*—We used Program DISTANCE 3.5 (University of St. Andrews, U.K., 1998) to estimate density of tortoises  $\geq 150$  mm CL. We used the detection-function models (key function/series expansion) recommended by Buckland et al. (2001): uniform/cosine, uniform/simple polynomial, half-normal/cosine, half-normal/hermite polynomial, hazard-rate/cosine, and hazard-rate/simple polynomial. We truncated 5% of the largest observations ( $N = 2$ ; Buckland et al., 2001) to eliminate spikes on the tail of the curve and improve model fit. We analyzed the data in two ways: without stratification and stratified by habitat categories. In the stratified analysis, density pooled across strata was estimated based on weighting by search effort in each stratum, because the area of each habitat category (especially incised washes and many boulder slopes) across IFNM could not be determined from maps. We chose the model with the lowest Akaike Information Criterion (AIC) as the best fitting model (Buckland et al., 2001). Density variance was computed by Program DISTANCE with 999 bootstrap samples; upper and lower confidence intervals were taken as the 2.5% and 97.5% quantiles of the bootstrap estimates. Program DISTANCE converted density estimates to estimates of absolute abundance based on the study site's area of 767.9 km<sup>2</sup>. Means are given  $\pm 1$  SE, and DISTANCE output is reported with coefficients of variation (%CV) and 95% confidence intervals (CI).

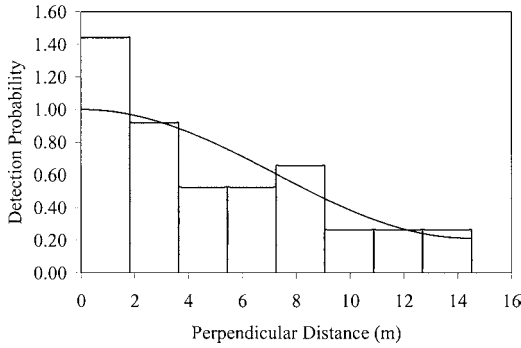


FIG. 3. Detection probability plot for the uniform-cosine model for Desert Tortoises at Ironwood Forest National Monument, Arizona ( $P = 0.7720$ ).

RESULTS

We observed 36 subadult-adult ( $\geq 180$  mm CL) and six juvenile ( $< 180$  mm CL) tortoises on 23 transects on IFNM. We found 31 tortoises during morning surveys (on 39% of morning transects surveyed) and 12 tortoises, including one recapture, during evening surveys (on 30% of evening transects surveyed). We found 19 males and 15 females, excluding juveniles and two individuals that we could not extract from burrows. Carapace length ranged from 115–265 mm; 39 tortoises had a CL  $> 150$  mm and were subsequently used in DISTANCE analysis.

The mean overall proportion of tortoises visible during radio telemetry throughout the study was  $0.83 \pm 0.119$ . The mean proportion visible was higher and less variable for evening surveys ( $0.92 \pm 0.068$ ) than for morning surveys ( $0.78 \pm 0.152$ ). The uniform/cosine model resulted in the best fit for the data (AIC = 190.68; Fig. 3). The hazard rate and half-normal models, without series expansions, followed with AIC = 191.10, and the uniform/simple polynomial model provided the worst fit (AIC = 192.65). The effective strip width was 8.8 m (CV = 10.9%, 95% CI = 7.0–11.0). In the unstratified analysis, the estimated encounter rate was 0.34 tortoises  $\text{km}^{-1}$  (Table 1). Stratification resulted in fairly similar encounter rates in habitat categories B (0.77 tortoises  $\text{km}^{-1}$ ) and W (0.62 tortoises  $\text{km}^{-1}$ ), compared to the much lower 0.03 tortoises  $\text{km}^{-1}$  in category X.

Unstratified analysis resulted in a density estimate of 0.23 tortoises  $\text{ha}^{-1}$  with poor precision and an estimate of 17,997 tortoises across the monument (Table 1). Precision improved slightly in the pooled, stratified analysis. Variance was extremely high for estimates from each of the habitat categories (CV  $> 42\%$ ; Table 1), but density is much greater where tortoises have boulders or incised washes for shelter. Abun-

TABLE 1. Distance sampling results for Desert Tortoises on Ironwood Forest National Monument, Arizona. Encounter rate = tortoises  $\text{km}^{-1}$ . CV = coefficient of variation. CI = confidence interval.

Stratum	Estimate	CV	95% CI
Unstratified (overall, 108.25 km)			
Encounter rate	0.34	26.4%	0.20–0.57
Density	0.23	41.6%	0.13–0.50
Abundance	17,997	41.5%	9616–38,757
Stratified			
B (26 km)			
Encounter rate	0.77	35.8%	0.38–1.56
Density	0.53	47.3%	0.23–1.22
Abundance	40,503	47.3%	17,654–93,717
W (24 km)			
Encounter rate	0.62	31.8%	0.33–1.18
Density	0.43	42.8%	0.15–0.84
Abundance	32,909	42.8%	11,590–64,379
X (58.25 km)			
Encounter rate	0.03	67.9%	0.01–0.12
Density	0.02	94.1%	0.00–0.08
Abundance	1808	94.1%	0–6449
Pooled Categories (108.25 km)			
Encounter rate	—	—	—
Density	0.23	37.2%	0.12–0.46
Abundance	17,997	37.2%	9394–35,414

dance estimates for each habitat category should be viewed with caution, because they are based on effort instead of actual habitat area.

In the unstratified analysis, component percentages of density variance were 68.2% for encounter rate, 20.1% for  $g_0$ , and 11.7% for detection probability (that is, the fit of the detection function). Encounter rate also contributed the most to density variances when we analyzed the data by stratum (W = 75.7%, B = 79.7%, X = 93.4%). Tortoise detectability ( $g_0$ ) contributed only moderately to density variances (X = 4.2%, B = 12.8%, W = 15.4%). Detection probability contributed least (X = 2.4%, B = 7.4%, W = 9.0%), indicating that our curve fit well relative to other sources of variation.

We found tortoises on 11 (42%) Category B transects, 10 (42%) Category W transects, and two (3%) Category X transects. We found tortoise sign on 31 transects where we did not find live tortoises. Overall, we found combined tortoises and sign on 92% of the transects on slopes with boulders, 71% with incised washes, and 25% with neither of these habitat features. The 15 tortoise-sign observations on Category X transects were eight scat, three burrows, two tracks, and two live tortoises. The distance between tortoises or sign found on Category X transects and the nearest mountain or hill slope

TABLE 2. Survey effort (kilometers) needed to achieve specified precision (%CV) of Desert Tortoise density estimates. 2001 encounter rates at Ironwood Forest National Monument are given in parentheses.

Stratum	Precision			
	20% CV	25% CV	30% CV	50% CV
Unstratified				
Overall (0.34)	294	188	131	47
Stratified				
B (0.77)	130	83	58	21
W (0.62)	161	103	72	26
X (0.03)	3333	2133	1480	533

ranged from 0.1–1.7 km (mean = 0.7 km  $\pm$  0.12).

#### DISCUSSION

*Distance Sampling.*—Examination of the detection probability plot for Desert Tortoise surveys on IFNM (Fig. 3) indicates that our distance-sampling protocol worked well at a scale two orders of magnitude larger than previously applied in the Sonoran Desert (Swann et al., 2002). The model fit the raw data despite a narrow shoulder to the data. Additionally, detection probability contributed least to our density variance, indicating that we were likely finding visible tortoises at and near the centerline, with the detection probability decreasing with increasing distance from the centerline.

Our results indicate tortoise densities of 0.23 tortoises per hectare (~18,000 tortoises across the monument), but precision was low. Buckland et al. (2001) recommend stratification by geographic region or environmental conditions to minimize heterogeneity in the data, improve precision, and reduce bias of density estimates. Stratifying the data by landscape features increased the precision of the overall density estimate only slightly, and the precision was low within each stratified habitat category. This is because we placed the majority of transects in Category X, where there were few tortoises, in an effort to document tortoise occurrence in this habitat type.

It would be difficult to discern trends in anything but large population declines with the level of precision we achieved in our study. The total line length of surveys to achieve a specified precision can be calculated using the following formula (Buckland et al., 2001):

$$L = [b/\{CV_i(D)\}^2]/(n/L),$$

where  $L$  = total line length,  $b$  = dispersion parameter or variance inflation factor,  $CV_i(D)$  =

target value for coefficient of variation, and  $n/L$  = encounter rate of objects of interest. We calculated the total line length needed to obtain various levels of precision (Table 2) using encounter rates for desert tortoises based on our surveys at IFNM. We used a dispersion parameter ( $b$ ) of 4. Whereas this value typically falls between 1.5 and 3, Buckland et al. (2001) recommend using a value greater than 3 for surveys where the detection function has a narrow shoulder, such as we have with our data. This value appears reasonably close, as our survey effort (108.25 km) and precision values fall between the 30% and 50% levels (Table 2).

To achieve a 20% CV, we would need to survey almost 300 km with an unstratified sampling design, or 2.7 times what we surveyed in 2001 (Table 2). A total of 291 km of transect line needs to be surveyed to achieve a 20% CV in both habitat categories B and W, which is similar to the overall effort needed with an unstratified design. Alternatively, a concentrated effort on boulder slopes would require only 130 km to be surveyed to achieve this level of precision for the predominant habitat type of tortoises in the Sonoran Desert (Table 2). Because tortoise density is very low in Category X, and the effort needed to survey this habitat type is likely cost prohibitive, this category could be ignored without losing much in terms of accuracy in the density estimate. In addition, locating incised washes (as opposed to nonincised washes) prior to sampling and determining the actual geographic area of inference for which abundance might be estimated from incised wash transects are problematic. Thus, stratification by a combination of topography and the presence of boulders is the best strategy for Desert Tortoise surveys over large geographic areas at IFNM and perhaps throughout the Sonoran Desert. If the shoulder of the detection function is broadened in the process of increasing the total number of encounters, as would be expected under such a sampling strategy, a given level of precision will be met after a shorter total line length is surveyed.

Surveys to determine tortoise density in specific mountain ranges may also be useful for management. Obtaining these estimates will require intensive surveys. The 130 km of transects needed for a 20% CV would need to be concentrated within the particular mountain range of interest. Effort concentrated within individual mountain ranges would be more efficient than the current study, in which we traveled between ranges across the entire monument. Also, telemetry may not be needed to estimate  $g_0$ -based on results from this and other studies, greatly reducing the cost and effort required. Surveys at the Rocking K Ranch and Saguaro National Park in 2000 and 2001 pro-

duced  $g_0$  estimates of  $0.82 (\pm 0.125)$ ; Swann et al., 2001) and  $0.79 (\pm 0.122)$ ; RAM and D. E. Swann, unpubl. data), respectively. Within environmental conditions and tortoise activity similar to those of 2000 and 2001, using the overall average of the three studies ( $0.84 \pm 0.105$ ) may be adequate. Additional study quantifying  $g_0$  and correlating it with geography and environmental conditions would be beneficial to future distance sampling of tortoises in the Sonoran Desert (e.g., we found tortoise observability to be higher and less variable during evening surveys than in the morning).

*Tortoise Habitat Associations.*—Where boulders are present on IFNM (major hills and mountain ranges), there is a good chance that tortoises occur at least at low density, depending on the degree of soil development conducive to burrow construction. Desert Tortoises in the Sonoran Desert are not limited exclusively to rock-pile habitat; they also construct burrows in the banks of washes (Germano et al., 1994). Tortoise density at IFNM in areas with incised washes was similar to that in boulder habitat. Desert Tortoises at the Florence Military Reservation, Pinal County, Arizona, extend well away from rocky hillsides into the lower bajada and valley floor, where they also appear to be most concentrated near incised washes and caliche caves (J. D. Riedle, R. C. Averill-Murray, and D. K. Bolen, NGEWP, Technical Report 194, Arizona Game and Fish Department, Phoenix, 2002). Tortoise activity at that site was centered around washes with caliche caves, but individuals also spent substantial time in *Ambrosia*-dominated flats.

Notably, tortoises also occur at very low density, but are not absent, in the valley floors of IFNM, outside of areas with boulders or washes. Mean home range size (typically measured over approximately 2 yr) of tortoises in the Sonoran Desert vary from 2.6–25.8 ha, depending on site and sex (Averill-Murray et al., 2002b). Assuming roughly circular to square home ranges, the mean distance we observed tortoises or sign away from mountainous slopes (0.7 km) was slightly greater than the diameter of the largest mean home-range size reported for Desert Tortoises in the Sonoran Desert (0.5 km), suggesting that some of our observations were not merely at the edge of a tortoise's home range peripheral to the base of a mountain. Although we committed much effort to document relatively few signs of tortoises in the intermountain valleys, the number of observations and diversity of signs (scat, tracks, and burrows, as well as live tortoises) indicates that the use of valleys may be more significant than generally believed. At other sites, radio-telemetered or otherwise permanently marked tortoises have been observed making, or found after making, movements from

one mountain range to the next, across intermountain valley floors (Edwards, 2003; Arizona Game and Fish Department, unpubl. data).

Tortoises making movements across or occupying valley-floor habitat may provide connections between adjacent, otherwise disjunct, rock-pile populations. Gene flow estimates based on microsatellite DNA data indicate that Desert Tortoise populations in the Sonoran Desert historically exchanged individuals at a rate greater than one migrant per generation (Edwards, 2003). A positive correlation between geographic and genetic distances of sampled population pairs suggests that tortoise populations on adjacent mountain ranges are more closely related than distant ranges (isolation-by-distance pattern of gene flow). Because of the naturally small size and isolation of most Sonoran Desert populations, occasional exchange of individuals may be important for recolonization and prevention of genetic deterioration (Howland and Rorabaugh, 2002). However, desert mountain ranges, and the tortoises that occupy them, are increasingly fragmented by urban development and other anthropogenic activities (Howland and Rorabaugh, 2002). This suggests that dismissing valleys as "unsuitable habitat" in Desert Tortoise conservation efforts in the Sonoran Desert may be harmful to long-term population viability, regardless of actual tortoise density within valley habitat (Averill-Murray et al., 2002a).

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