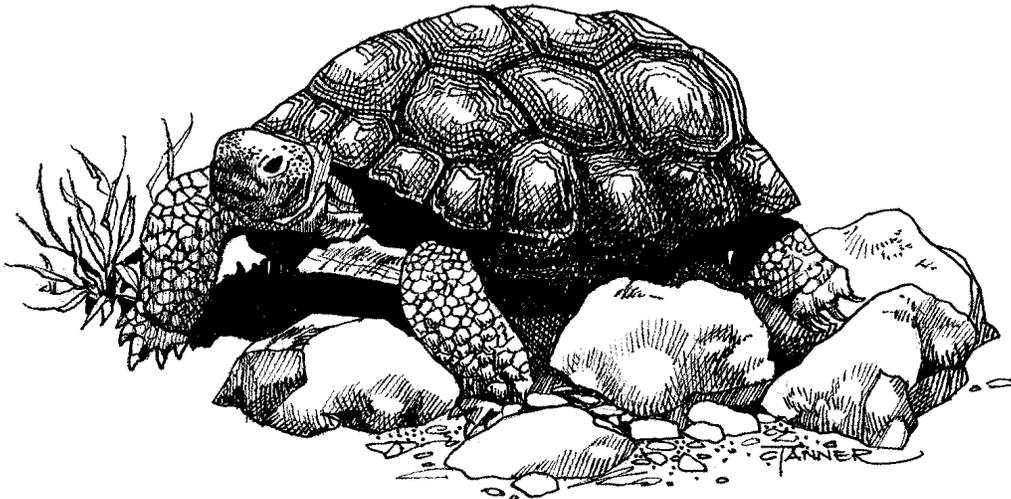


MONITORING AND ECOLOGY OF SONORAN DESERT TORTOISES IN ARIZONA

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EXECUTIVE SUMMARY

The U.S. Fish and Wildlife Service listed the Mojave Desert population of the desert tortoise as threatened in 1990. In the same year, a status determination for the Sonoran population indicated that, though large gaps in baseline information existed, the current data suggested that listing was not warranted. Research and monitoring have since continued in order to more accurately assess the status of the Sonoran population. The objective of this report is to summarize population monitoring results since 1987 across the tortoise's range in the Sonoran Desert in Arizona, as well as intensive ecological research conducted since 1991 at one site in the northeastern Sonoran Desert.

To date, 24 Sonoran population plots have been surveyed (18 at least twice each). Tortoise densities within local populations vary widely, ranging from 15 to more than 100 adults per square mile. Density is apparently related to habitat features providing burrow sites. Symptoms of upper respiratory tract disease have occasionally been observed on plots, and cutaneous dyskeratosis is present in virtually all populations. However, disease has not impacted Sonoran populations as it recently has in the Mojave Desert. Notable human-related impacts to some populations include predation by feral dogs, burrows trampled by cattle, tortoises trapped in a mining pit, adjacent development, and shot and vandalized tortoises (or a released pet). Only one documented population crash has occurred in the Sonoran Desert in Arizona during the last 13 years, and it appears to have been related to drought rather than disease.

At one intensively studied site, female tortoises laid a single clutch of eggs near the onset of each summer rainy season. Not all females reproduced every year, with the proportion reproducing correlated with winter and spring rainfall. Minimum reproductive size each year was negatively correlated with winter rainfall. Mean clutch size ranged from 3.8 to 5.7 eggs and was not related to female body size or rainfall. Mean egg width was not related to year or clutch size, but large females laid larger eggs than small females. The lack of a correlation between clutch size and female body size indicates that larger tortoises in the northwestern Sonoran Desert may not lay more eggs per female on average than smaller tortoises in southern populations, but large-tortoise populations might produce larger hatchlings. Relatively large tortoises in the northwestern Sonoran Desert might also store more nutrient reserves and reproduce under drier conditions than smaller tortoises in more mesic parts of the distribution.

Peak tortoise activity occurs during the summer monsoon season, but spring and winter activity increases with increasing rainfall during those seasons. Spring foraging appears to be important, especially for females, since ovarian follicles mature during spring. Males also appear to be more active during spring than previously thought. Some individuals may make long-distance movements outside their "normal" home ranges. Some of these movements represent temporary excursions to specific resource sites, such as nesting burrows. Others are more difficult to explain, but some may represent dispersal.

How disjunct tortoise populations in the Sonoran Desert persist remains poorly understood. High variability in existing data and important data gaps (for example, juvenile growth and survival) preclude effective population viability analysis at present. However, observed long-distance

movements suggest a potential meta-population relationship between local populations. A large cohort of young tortoises that experiences a relatively wet and productive environment, with high survival, may provide the stock for dispersal between populations as they approach sexual maturity, in addition to replacing aging adults within the local population.

Sonoran desert tortoise populations currently appear to be stable in Arizona. However, existing trend data are insufficient to draw secure conclusions about population trajectories, especially with increasing urban growth and habitat fragmentation. The unknown significance of high incidence of cutaneous dyskeratosis within tortoise populations poses another concern; apparently healthy populations in the Mojave Desert have suffered dramatic declines in the presence of this disease. Continued monitoring across the range is essential to better quantify population trends, and implementation of several changes to the monitoring plot protocol will make this a more efficient process. Individual and cooperative efforts by land and wildlife management agencies must continue to ensure that sufficient habitat area and quality remain for the survival of tortoise populations. Additional research should be conducted to answer questions about population dynamics, habitat impacts (especially fire and invasion of exotic grasses), and disease, so managers can better direct conservation efforts. Specific management recommendations include 1) continue state-wide population monitoring using the described revisions to the monitoring protocol; 2) continue life history studies at multiple sites, with an increased emphasis on monitoring juveniles, and conduct population viability analyses of local populations; 3) conduct studies of tortoise energy budgets to determine how females allocate energy to reproduction; 4) continue long-term monitoring of individual tortoises (males, females, and juveniles) to better understand home ranges, habitat use, and long-distance movements; 5) determine genetic relationships between adjacent local populations and estimate rates of genetic interchange; 6) determine the prevalence and cause of diseases within populations; and 7) implement management options identified by the Arizona Interagency Desert Tortoise Team.

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MONITORING AND ECOLOGY OF SONORAN DESERT TORTOISES IN ARIZONA

Roy C. Averill-Murray
and
Christopher M. Klug

CHAPTER 1 INTRODUCTION

The Sonoran desert tortoise *Gopherus agassizii* is included on the state list of Wildlife of Special Concern in Arizona (Arizona Game and Fish Department [AGFD] in prep.) but has no federal status as endangered or threatened. Population declines have been documented in a substantial portion of the desert tortoise's occupied and historical range in the United States. The declines were sufficient to warrant emergency listing of the Mojave Desert population in 1989 (U.S. Fish and Wildlife Service [FWS] 1989), followed in 1990 by listing through the normal process as a threatened species (FWS 1990). A status determination for the Sonoran Desert population in 1990 indicated that, though large gaps in baseline information existed, neither population declines nor known or potential threats were yet sufficient to warrant listing (Barrett and Johnson 1990; FWS 1991). Even so, the existence and impacts of disease in wild populations in the Mojave Desert, west and north of the Colorado River, was an indication of the precarious status of the Sonoran population (Howland 1994). Therefore, continued population monitoring to estimate population trends and collection of life history data to develop life tables and predictive population models are needed to assess the status of the Sonoran population. This report summarizes population monitoring results since 1987 across the tortoise's range in the Sonoran Desert in Arizona, as well as intensive ecological research conducted since 1991 at one site in the northeastern Sonoran Desert.

ORGANIZATION OF THE REPORT

The body of this report is organized into 4 chapters. Chapter 2 (Long-term monitoring of Sonoran desert tortoise populations) summarizes results of monitoring plot surveys since 1987 and covers population characteristics, including abundance, sex ratios, growth, and survivorship; incidence of disease; aspects of population regulation; and describes revisions to the monitoring protocol. An appendix includes individual summaries of monitoring results from each plot. The bulk of Chapter 2 is based on a manuscript submitted for publication in the book, *The Sonoran Desert Tortoise: Natural History, Biology, and Conservation* (Averill-Murray and others, *in press a*). The monitoring protocol was more completely reviewed and revised in Averill-Murray (2000).

Chapter 3 (Reproduction of *Gopherus agassizii* in the Sonoran Desert) summarizes reproductive ecology data gathered from a population northeast of Phoenix from 1993 and 1997 to 1999, with additional data from one year at a second population. This chapter is reformatted from a manuscript submitted in 2000 for publication in the journal, *Chelonian Conservation and*

Biology, as part of a special issue commemorating the 25th Anniversary of the Desert Tortoise Council.

Chapter 4 (Desert tortoise activity, behavior, and home ranges) describes the referenced aspects of desert tortoise ecology for which data were gathered during the reproductive ecology study. This chapter includes 6 years of data, from 1992 to 1993 and 1996 to 1999. Finally, Chapter 5 (Conclusion) synthesizes chapters 2 through 4 and identifies specific recommendations for research and management of Sonoran desert tortoises.

CHAPTER 2
LONG-TERM MONITORING OF SONORAN DESERT TORTOISE POPULATIONS

INTRODUCTION

Desert tortoise (*Gopherus agassizii*) populations have been studied in Arizona since the mid-1970s. However, the systematic study of specific long-term monitoring plots in the Sonoran Desert began later, as concern for the rangewide status of the species was building toward eventual emergency listing of the Mojave population as an endangered species in 1989 (FWS 1989). The U.S. Bureau of Land Management (BLM) funded the initial 3 standardized monitoring plot surveys in the Sonoran Desert in 1987 and 3 more in 1988. In 1990 the FWS listed the Mojave population of the tortoise as threatened under the normal Endangered Species Act (ESA) rule-making process and agreed to continue evaluating the status of the Sonoran population (FWS 1990). No Sonoran monitoring plots were surveyed in 1989, but FWS provided funding under Section 6 of the ESA which, combined with AGFD Nongame Checkoff funds and a donation from the Gladys Porter Zoo, allowed 4 monitoring plot surveys in 1990.

In 1991 the FWS determined that the Sonoran population of the desert tortoise did not warrant listing under the ESA (FWS 1991). This decision was based largely on transect and plot surveys conducted to date, but sufficient data to determine population trends (whether positive, negative, or stable) were unavailable (Barrett and Johnson 1990). As a result, AGFD continued monitoring plot surveys through 1993 using Section 6 and BLM funding, as well as the Nongame Checkoff Fund, Nongame Donations Fund, and Heritage Fund. Fifteen plots had been established through 1993. Only 6 of these plots had been surveyed more than once for even preliminary trend estimates, although relatively large numbers of carcasses found at 2 plots indicated at least short-term declines in those populations (Howland 1994). AGFD surveyed up to 4 plots each year from 1994 through 1999 with funding from BLM, Partnerships for Wildlife administered by FWS and the National Fish and Wildlife Foundation, and the AGFD Heritage Fund. All but one of these plots have now been surveyed at least twice, and some have been surveyed 6 or more times. The surveys were primarily contracted by AGFD to private biological consultants and are summarized in annual plot reports (Table 1). This chapter synthesizes results of the last 13 years of monitoring these 15 plots. Additional plots have been surveyed by other agencies, and we discuss results from these studies within an overall, state-wide perspective. Finally, this chapter summarizes recommendations from Averill-Murray (2000) for revising the monitoring plot protocol.

METHODS

The plots discussed in this chapter are located across the range of the desert tortoise in the vicinity of the Sonoran Desert of Arizona (Fig. 1). The plots include a variety of biotic communities within or extending from the Sonoran Desert, including the Arizona Upland Subdivision, Lower Colorado River Subdivision, desert grassland, and ecotonal areas consisting

of Sonoran desertscrub with elements of Mojave desertscrub and juniper woodland, interior chaparral, and desert grassland (Brown 1982). One population on the east bajada of the Black Mountains (hereafter, referred to as East Bajada; Fig. 1) is included in the 'Sonoran population' south and east of the Colorado River for purposes of the ESA (FWS 1990) even though it occurs in the Mojave Desert proper. Specific plot descriptions can be found in individual plot sections in the appendix and in the primary plot reports (see Table 1).

PLOT CONFIGURATION AND COVERAGE

The typical monitoring plot is 1 mi x 1 mi (1.6 km x 1.6 km) in size, with plot corners marked with green metal t-posts. A 0.1-mi² (0.16-km²) grid was overlaid on each topographic map for geographic reference. Grid cells were generally numbered according to their position within U.S. Geological Survey (USGS) sections, with the northwest cell of a USGS section numbered 00, the northeast cell numbered 09, the southwest cell numbered 90, and the southeast cell numbered 99. Plots may overlap one or more sections, but grid cell numbering was based on the particular USGS section the cell lies in. Field effort during a typical plot survey consisted of workers searching for tortoises for 60 person days during 45 calendar days of the summer monsoon season (peak tortoise activity). A person day equaled 8 hours of field effort in 1 day. Search routes varied according to the topography of the site, and field workers spent more time searching areas that had resulted in finding tortoises previously, either during the current survey or surveys in prior years. Burrows were flagged and rechecked periodically throughout a survey (Shields 1994). Search effort was generally split between morning and evening during the hottest part of the season but included more time in mid-afternoon as temperatures began to cool in the fall. During and following rain, emphasis was placed on finding smaller tortoises (juveniles and immatures) by concentrating on previously located shelters and what was perceived to be good tortoise habitat (Shields 1994).

Several exceptions have been made to the standard survey duration and plot configuration. Limited habitat or concentrated tortoise populations allowed shorter surveys (approximately 35 person days) to be conducted on the Eagletail Mountain (Hart and others 1992; Woodman and others 1993, 1994, 1995) and Bonanza Wash (Woodman and others 1998) plots. An additional rocky hill (approximately 0.06 square mi [0.01 square km]) was incorporated into the square-mile plot at the Arrastra Mountains (Wirt 1988), and surveys were reduced to 35 person days (Woodman and others 1998). The Granite Hills plot totals about 1 square mile of area but is configured as approximately 0.7 mi x 1.6 mi (1.1 km x 2.6 km; Hart and others 1992; Woodman and others 1993, 1994, 1995). The Harquahala Mountain plot is 1.5 square miles (3.9 sq. km) in area (Holm 1989; Woodman and others 1995).

LIVE TORTOISES

Each tortoise encounter was categorized by capture type (CT): CT-1 includes the first encounter of a tortoise; CT-2, a subsequent capture of a tortoise previously processed during the current

year; and CT-3, the first encounter in the current year of a tortoise marked during a previous survey. Carcasses of marked individuals were classified as CT-5. There is no CT-4.

Table 1. Desert tortoise monitoring plots surveyed in the Sonoran Desert, Arizona. Estimated density of adults (≥ 180 mm straight midline carapace length [MCL]) are scaled to one square mile (95% confidence limits). Observed tortoise numbers: F = female; M = male; U = unsexed (< 180 mm MCL); X = carcass. Specific plot report citations are listed numerically at the end of the table. Locality codes in parentheses refer to subsequent tables and figures. Plots funded by FWS, BLM, or AGFD are indicated with an asterisk.

Locality	Year	Density	F:M:U:X	Citation
*Arrastra Mountains (am)	1987	20 (15-25)	9:6:3:16	15
	1997	24 (18-30) ^A	8:5:1:2	24
*Bonanza Wash (bw)	1992	---	6:8:3:13	19
	1997	27 (16-38) ^A	4:6:3:2	24
*Eagletail Mountains (et)	1987	---	22:12:8:8	8
	1990	31 (26-36)	21:8:3:1	11
	1991	30 (28-32) ^A	16:9:7:5	3
	1992	29 (27-31) ^A	12:10:5:1	19
	1993	30 (26-34) ^A	13:10:14:3	20
	1994	30 (28-32) ^A	17:11:19:9	21
	1998	39 (35-43) ^A	17:14:8:5	25
*East Bajada (eb) ^B	1990	---	12:21:12:5	13
	1993	67 (51-83) ^A	14:29:3:10	20
	1997	61 (50-72) ^A	23:20:2:6	24
*Granite Hills (gh)	1990	68 (24-112)	16:16:15:8	11
	1991	63 (50-76) ^A	30:19:21:4	3
	1992	60 (56-64) ^A	23:22:30:2	19
	1993	90 (78-102) ^A	31:24:40:2	20
	1994	69 (66-72) ^A	31:29:49:3	21
	1998	60 (59-61) ^A	20:16:20:13	25
*Harcuvar Mountains (hm)	1988	---	22:33:5:8	18
	1993	72 (65-79) ^A	15:29:2:5	20
	1997	77 (67-87) ^A	23:27:4:6	24
*Harquahala Mountains (hq)	1988	---	9:8:4:4	4
	1994	15 (13-17) ^A	10:7:2:0	21
*Hualapai Foothills (hf)	1991	---	13:19:5:8	3
	1996	52 (44-60) ^A	13:21:2:6	23
*Little Shipp Wash (ls)	1990	85 (71-100)	42:26:16:9	11
	1991	79 (75-83) ^A	37:30:15:2	3
	1992	107 (97-117) ^A	42:34:12:2	19
	1993	107 (100-114) ^A	47:36:20:9	20
	1994	97 (91-103) ^A	34:27:16:3	21
	1998	98 (90-106) ^A	30:18:10:9	25
*Maricopa Mountains (mm)	1987	146 (69-223)	24:33:1:65	15
	1990	---	6:7:4:54	11

Table 1. Continued.				
Locality	Year	Density	F:M:U:X	Citation
Mazatzal Mountains (mz), Tonto National Forest	1992	150 (83-218)	19:27:5:8	5
	1995*	114 (91-137)	24:25:17:3	6
*New Water Mountains (nw)	1988	---	8:7:1:2	10
	1999	32 (30-35) ^A	9:8:5:3	26
Organ Pipe Cactus National Monument (orpi):				
Ajo Mountain Drive	1996	75 (21-225)	11:12:6:8	16
Quitobaquito Hills	1997	34 (18-60)	16:6:3:1	16
Twin Peaks	1996	28 (8-73)	9:6:0:0	16
Rincon Mountains (rm), Saguaro National Park:				
Rincon Burn	1996	84 (26-220)	13:12:9:7	17
Javelina Campground	1996	127 (67-220)	18:29:15:2	17
	1997	127 (75-194)	29:29:18:2	17
*San Pedro Valley (sp)	1988	---	9:10:1	7
	1991	---	18:16:9:11	3
	1995	125 (103-147) ^A	36:48:6:9	22
Sand Tank Mountains (st), Barry M. Goldwater Range	1992	---	19:15:0:31 ^C	2
	1994	---	2:5:6:32	1
*Santan Mountains (sn)	1990	---	3:4:1	12
	1991	---	16:10:3:3	14
*Tortilla Mountains (tl)	1992	---	29:20:3:12	19
	1996	97 (82-112) ^A	34:26:12:9	23
Tucson Mountains (tm), Saguaro National Park	1996	104 (62-166)	26:23:21:12	17
	1997	101 (67-142)	34:22:25:?	17
*West Silverbell Mountains (ws)	1991	---	39:20:5:11	3
	1995	134 (112-156) ^A	40:35:16:8	22
*Wickenburg Mountains (wm)	1991	---	5:10:0:2	3

Citations: 1, Dames and Moore, Tucson (1994); 2, Geo-Marine, Inc. (1994); 3, Hart and others (1992); 4, Holm (1989); 5, Murray (1993); 6, Murray and Schwalbe (1997); 7, Schnell and Drobka (1988); 8, Shields and Woodman (1987); 10, Shields and Woodman (1988); 11, Shields and others (1990); 12, SWCA Inc. (1990a); 13, SWCA Inc. (1990b); 14, SWCA Inc. (1992); 15, Wirt (1988); 16, Wirt and others (1999); 17, Wirt (pers. comm., 1999); 18, Woodman and Shields (1988); 19, Woodman and others (1993); 20, Woodman and others (1994); 21, Woodman and others (1995); 22, Woodman and others (1996); 23, Woodman and others (1997); 24, Woodman and others (1998); 25, Woodman and others (1999); 26, Woodman and others (2000).

^ADensity calculated using tortoises marked from previous and current surveys; therefore, estimates are not independent between surveys.

^BPlot is located in the Mojave Desert proper but is regarded by FWS as part of the Sonoran Desert population in Endangered Species Act decisions (FWS 1990).

^CCombined data from 2, 4-square-km, plots within 2 km of each other.

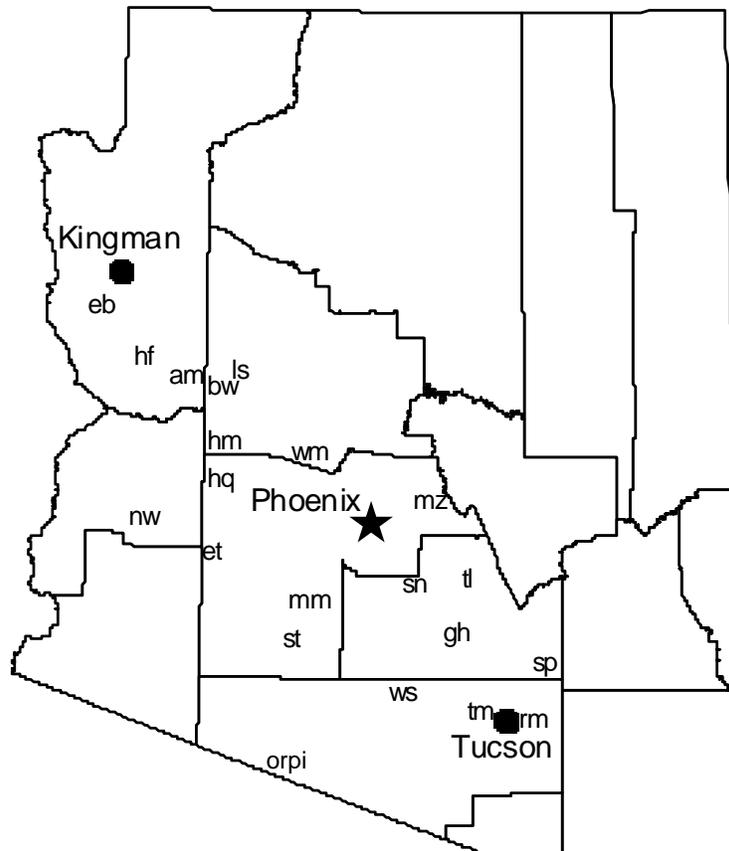


Figure 1. Sonoran desert tortoise populations studied in Arizona. Codes are defined in Table 1.

For every tortoise encounter, field workers completed a data sheet including the following data: capture type; location, referenced to position within grid cell; temperatures taken with a shaded bulb at ground surface, 1 cm above ground, and 1.5 m above ground, and temperature 0.5 m deep inside the sheltersite, if applicable. Sheltersite type, location, dimensions (length and opening width and height), orientation of slope and sheltersite entrance, and beginning in 1992, identification number (pre-stamped aluminum tag attached to sheltersite structure) were also recorded. Finally, activity and social interactions; foods eaten; whether new growth was visible on the shell; estimated volume, color, and viscosity of voided urine; and the beginning and end times for the process were noted.

Field workers visually inspected each tortoise for injuries, morphological anomalies, ectoparasites, and symptoms of cutaneous dyskeratosis and upper respiratory tract disease (URTD). Field workers handled all tortoises with disposable latex gloves to minimize the

potential spread of pathogens between individual tortoises. Any instruments coming into contact with a tortoise during handling were disinfected with bleach prior to use on another tortoise.

Physical data recorded for each tortoise depended on the capture type. For CT-1 tortoises, field workers typically recorded weight (corrected for the estimated mass of urine or feces voided prior to weighing) plus 8 shell measurements: straight midline carapace length (MCL), midline plastron length (between the gular and anal scute notches), greatest plastron length (the longest distance between tips of the gular and anal scutes on the left or right side), carapace width between the third marginal scutes, width between the fourth marginals, width between the seventh/eighth marginal seams, maximum width, and maximum height. Lengths were measured to the nearest millimeter and weight to the nearest gram. The tortoise was assigned a number, and marginal scutes were notched accordingly (with triangular files) based on a code adapted by Berry (1984). Bridge marginals were not notched on tortoises <120 mm MCL. The identification number was also written on a dot of correction fluid on the right fourth costal scute and covered with clear epoxy. Gender was determined for tortoises ≥ 180 mm MCL. Close-up photographs were taken of the full carapace, full plastron, and left fourth costal; a label indicating study plot, date, tortoise number, and investigator was included in each photograph. Finally, a shell wear class was assigned based on the system of Berry and Woodman (1984a).

Usually, field workers did not record physical data for CT-2 tortoises, but weight and MCL were recorded for tortoises <180 mm MCL if more than 14 days had elapsed or rain had fallen since it was last processed. Field workers identified CT-3 tortoises by their notches and epoxied numbers, if still present. File marks and epoxy numbers were redone, if necessary, and all other measurements were taken as for CT-1 tortoises.

CARCASSES

Field workers photographed each carcass in situ (with a label indicating study plot, date, carcass number, live tortoise number [if applicable], and investigator) and filled out a data sheet (2 copies) for each. Data recorded included shell position and percent daylight hours exposed to sun; location, as with live tortoises; sex, MCL, and identifying marks (when possible); and notes on signs of cause of death. Carcasses were collected in reclosable plastic bags, with one of the data sheets, and deposited at AGFD. When MCL could not be measured directly, it was estimated with a regression formula developed by Berry and Woodman (1984b) from tortoises in the Mojave Desert. Time since death was also classified as <1 year, 1-2 years, 2-4 years, or >4 years, based on a key developed by Berry and Woodman (1984b), also from tortoises in the Mojave Desert.

DATA ANALYSIS

Size Distributions

Size distributions were summarized in 10-mm increment histograms and tabulated according to the classification of Turner and Berry (1984): Hatchling, no growth rings; Juvenile 1, ≤ 59 mm

MCL; Juvenile 2, 60-99 mm; Immature 1, 100-139 mm; Immature 2, 140-179 mm; Subadult, 180-207 mm; Adult 1, 208-239 mm; and Adult 2, ≥ 240 mm.

Abundance and Survival Estimation and Other Analyses

The primary statistical analysis was estimation of abundance. Abundance of tortoises ≥ 180 mm MCL was estimated with the Lincoln-Petersen estimator (Lincoln 1930; Petersen 1896). Typically, not enough tortoises < 180 mm MCL were found to derive estimates for that size class, and differences in capturability between tortoises greater than or less than 180 mm preclude combining them into an overall abundance estimate for the entire population (Murray 1993; Schneider 1980). Abundance was usually only estimated for plots surveyed 2 or more times. The most recent survey served as the “mark” sample, and the current survey served as the “recapture” sample.

Survival was separately estimated for adult (≥ 180 mm) and juvenile (< 180 mm) tortoises from the 1990-1994 surveys of the Eagletail Mountain, Granite Hills, and Little Shipp Wash plots using Program JOLLY (Howland and Klug 1996; Pollock and others 1990). We also used mark-recapture data to construct growth curves for each sex within these 3 populations. We input the first and last MCL for every tortoise captured in more than 1 year into a nonlinear regression analysis. Individuals < 180 mm MCL in both years (that is, those of undetermined sex) were included in the curves for both sexes. We used Richards' (1959) equation modified by Bradley and others (1984) and the mark-recapture interval equation given by Schoener and Schoener (1978):

$$1) \text{MCL} = A(1 + [m - 1]e^{-k(t - I)})^{1/(1 - m)} \text{ and}$$

$$2) \text{MCL}_2 = A(1 - e^{-kt} [1 - (\text{MCL}_1^3 / A^3)^{1 - m}])^{1/(3 - 3m)},$$

where A = asymptotic carapace length, m = a shape constant, k = intrinsic growth rate, t = time interval between first and last captures, and I = the time to reach the inflection point in the curve (Fig. 2). We used the estimates of A , k , and m derived from the interval equation (equation 2) to solve for I in equation 1 in order to complete the growth equation and develop a curve. In so doing, we set $t = 0$ and estimated $\text{MCL} = 46$ mm at hatching (unpublished data). We computed 95% “support plane” confidence intervals for A , k , and m , which are the maximum symmetrical confidence intervals about the parameters regardless of the values of the other parameters (Marquardt 1964). We considered parameter estimates to be different if these intervals did not overlap. We also computed the following, more biologically meaningful statistics (Bradley and others 1984; Richards 1959): weighted mean growth rate (R), percentage of asymptotic size achieved at inflection (P), and time to pass from 10% to 90% total growth (G) (Fig. 2):

$$3) R = k/m,$$

$$4) P = m^{1/(1 - m)},$$

$$5) G = \ln([1 - .10^{1 - m}] / [1 - .90^{1 - m}]) / k.$$

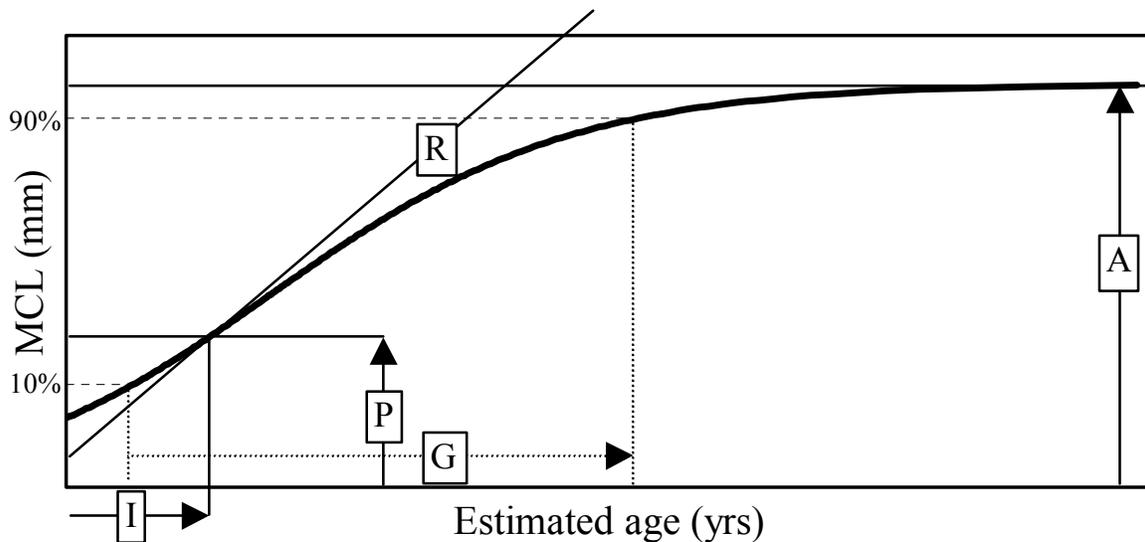


Figure 2. Statistics computed from Richards growth curve. A = asymptotic carapace length, R = weighted mean growth rate, I = time to grow from hatching to the inflection point of the curve, P = percent of A reached at the inflection point of the curve, and G = time to pass from 10% to 90% total growth.

Unfortunately, measures of variance and confidence intervals for R , P , and G must be computed with jackknife or bootstrapping procedures. Bradley and others (1984) had developed a jackknife program to estimate these statistics, but the program is not available for modern computers (D.W. Bradley, pers. comm. 1996). Therefore, we present the point estimates for these parameters for illustrative purposes only.

Numbers of marked tortoise burrows were compared to population density with linear regression. Other statistical procedures included comparison of sex ratios with Chi-square or log-likelihood ratio tests, regression of mean annual growth against carapace length, and regression of carapace length against shell wear class.

This chapter reports general trends and synthesized results from the last 13 years of monitoring plot surveys. Detailed results from annual surveys for each plot, including vegetation sampling, may be found in the primary plot reports (Table 1).

RESULTS AND DISCUSSION

POPULATION CHARACTERISTICS

Abundance and Sex Ratios

Local desert tortoise population densities vary widely within the Sonoran Desert, ranging from 15 to more than 100 adults per square mile (2.6 square km; Table 1). Three caveats should be considered regarding these estimates. First, various methods have been used to calculate tortoise abundance and density, especially in surveys conducted outside this project (details are included in the plot sections). Second, most of the plots contain some areas used by few to no tortoises, affecting the accuracy of estimates of density within occupied habitat. Third, except for the Mazatzal Mountains population, density was derived simply by dividing estimated abundance by plot area. This method of density estimation disregards the fact that tortoise habitat usually extends beyond the study plot boundaries, and tortoises living near the plot boundaries range both inside and outside the plot. Dividing abundance by plot area assumes that all the tortoises actually live *within* the plot boundaries and usually produces overestimates of density; that is, tortoises are actually distributed over a larger area than estimated in this way. Regardless, these estimates do illustrate the magnitude of geographic variation in tortoise density in Arizona.

The range of tortoise densities observed on Sonoran Desert monitoring plots falls within the range historically observed in the Mojave Desert. Since 1977, 13-219 adult tortoises have been found on plots (generally 1 square mile) in the eastern Mojave Desert, while 19-402 have been found on plots in the western Mojave (data summarized by Corn 1994). However, in some cases the low ends of these ranges may reflect previous declines in Mojave Desert populations (FWS 1994).

Most high tortoise densities observed in the Mojave Desert have occurred within intermountain valleys, where friable soils allow the construction of deep burrows (Luckenbach 1982; Germano and others 1994). At least in the past, such populations may have been quite expansive, spanning from one valley to the next (Luckenbach 1982). In the Sonoran Desert, highest tortoise densities occur on steep, rocky hills and desert mountain slopes; tortoises are generally absent from the intermountain valleys (Germano and others 1994). As a result, local tortoise populations appear to be smaller and more isolated in the Sonoran Desert than historically in the Mojave. Tortoise occupation of valley floor habitats in the Mojave Desert may be a relatively recent occurrence relative to their evolutionary history; the desert tortoise's tropical ancestors lived in a warmer climate where burrowing was less important for avoiding temperature extremes (Van Devender, *in press*).

With few exceptions, sex ratios are typically balanced (Table 1). About twice as many males as females were found on the Harcuvar Mountains plot in 1993. In contrast, females have outnumbered males by similar margins on the West Silverbell (1991) and Eagletail mountains plots. Cumulative sex ratios (over all years surveyed) in the Sonoran Desert do not differ statistically from 1:1 for any plot ($P > 0.05$). Mojave Desert populations also typically have 1:1

sex ratios (Goodlett and others 1996, 1997). Although males outnumbered females by about two to one in 1990 and 1993 surveys of the East Bajada plot, combined data from all surveys resulted in approximately equal numbers of males and females.

Abundance of individuals and sex ratios may be illustrated together in size distribution histograms for visual comparison of populations (Fig. 3). Size distributions observed from desert tortoise populations across Arizona share some similar characteristics, while regional variation in other characteristics is also evident. A distinct gap is typically present in the distributions at the smaller adult and larger juvenile sizes (around 180 mm; Fig. 3). In fact, among all plots on which at least 20 tortoises were marked, only the Granite Hills population in south central Arizona lacks this characteristic gap (Fig. 3B). The number of tortoises found between 180-189 mm MCL on the Granite Hills increased from 0 in 1990 to 6 in 1993 before dropping back to 4 in 1994. In contrast, only 6 of 16 populations in California exhibit a comparable gap in size distributions (Figs. 5-1 through 5-30 in Berry and Nicholson 1984). No tortoises 180-199 mm MCL were found in a 1996 survey of the Beaver Dam Slope population in the Mojave Desert, extreme northwestern Arizona bordering southwest Utah; however, 8 150-179 mm tortoises were found (Goodlett and others 1996). This population has experienced high turnover and has a high incidence of disease symptoms (Goodlett and others 1996). It remains to be seen if younger, smaller tortoises will fill in the adult size distribution.

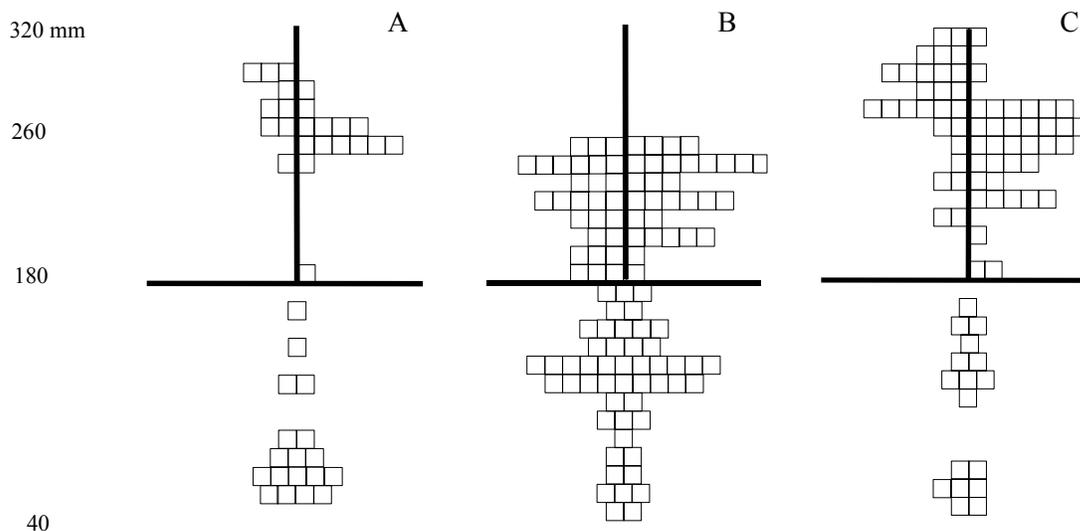


Figure 3. Representative size distributions (frequency histograms) of individuals from 3 Sonoran desert tortoise populations in 1994: Eagletail Mountains (A), Granite Hills (B), and Little Shipp Wash (C). Each row represents a 10-mm increment in midline carapace length (MCL). Males are on the left side of the vertical lines, females on the right; individuals <180 mm MCL, below the horizontal lines, are of undetermined sex.

Small individuals are under-represented in size distributions, because they are more difficult to find in the structurally complex habitat in the Sonoran Desert. As Figures 3A and 3B illustrate, however, relatively large numbers of juveniles may be found in some populations during some years, usually characterized and preceded by above average rainfall and forage availability. Even in these cases each juvenile is recaptured fewer times on average, if at all, than the adults, making density estimation of juveniles impossible. Finally, differences in tortoise growth characteristics at different populations result in population-specific maximum sizes and sexual size dimorphism (Figs. 3 and 4; see Growth, below).

Growth

Desert tortoises grow most rapidly early in life and reach 36-47% of their maximum carapace length before growth begins to slow (Fig. 4; Murray and Klug 1996). Rapid early growth contributes to relatively high juvenile survivorship compared to slower-growing juveniles (see Survivorship, below). Maximum sizes, however, differ between sexes and among populations. For example, Hart (1996) found that individuals in populations north of the Gila River tend to reach larger sizes than individuals in populations south of the Gila. Additionally, Murray and Klug (1996) found that males reach larger average maximum sizes than females at Little Shipp Wash (299 and 267 mm MCL, respectively) and the Eagletail Mountains (288 and 268 mm) (Fig. 4). In fact, males reach larger average sizes than females at all 13 monitoring plots surveyed to date north of the Gila River. On the Granite Hills plot, the sexes reach about the same size (244 and 243 mm), which is significantly smaller than in the Eagletail Mountains and Little Shipp Wash populations (Figs. 3 and 4). Females reach the same or larger average sizes at three other plots south of the Gila River (Sand Tank Mountains, San Pedro Valley, West Silverbell Mountains), but males are larger than females in the Maricopa Mountains. The underlying reasons for these patterns are currently unknown.

The largest desert tortoise on record from the Sonoran Desert of Arizona is a 322-mm MCL female found on the Harcuvar Mountains plot in 1997. The large size of this female tortoise is anomalous given the trend for males to reach larger sizes than females at “northern” populations. Interestingly, the largest wild tortoise found in the Mojave Desert is also a female from the Lucerne Valley, California, with a carapace length of 378 mm (P. Woodman, pers. comm. 1998).

Growth of tortoises in the Mojave Desert is generally similar to that in the Sonoran Desert. Annual growth declines as carapace length increases (Germano 1994a; Karl 1998), and maximum size varies geographically; tortoises in the western Mojave reach larger sizes than those in the eastern Mojave (Germano 1994a). Geographic variation in size does not follow a smooth trend across the entire range of the desert tortoise, however (Table 2). The largest tortoises seem to be found at both ends (western Mojave Desert and Sinaloa, Mexico) and the middle of the distribution (northern Sonoran Desert), with smaller tortoises distributed in between (eastern Mojave and eastern/southern Sonoran deserts). Males reach larger sizes on average than females across the Mojave Desert (Berry and Nicholson 1984; Goodlett and others 1996, 1997; Karl 1998; Minden and Keller 1981). Even though growth varies each year with rainfall and forage availability within populations (Karl 1998; Medica and others 1975), factors

controlling growth relative to different populations (and species) of tortoises are unknown (Germano 1994a).

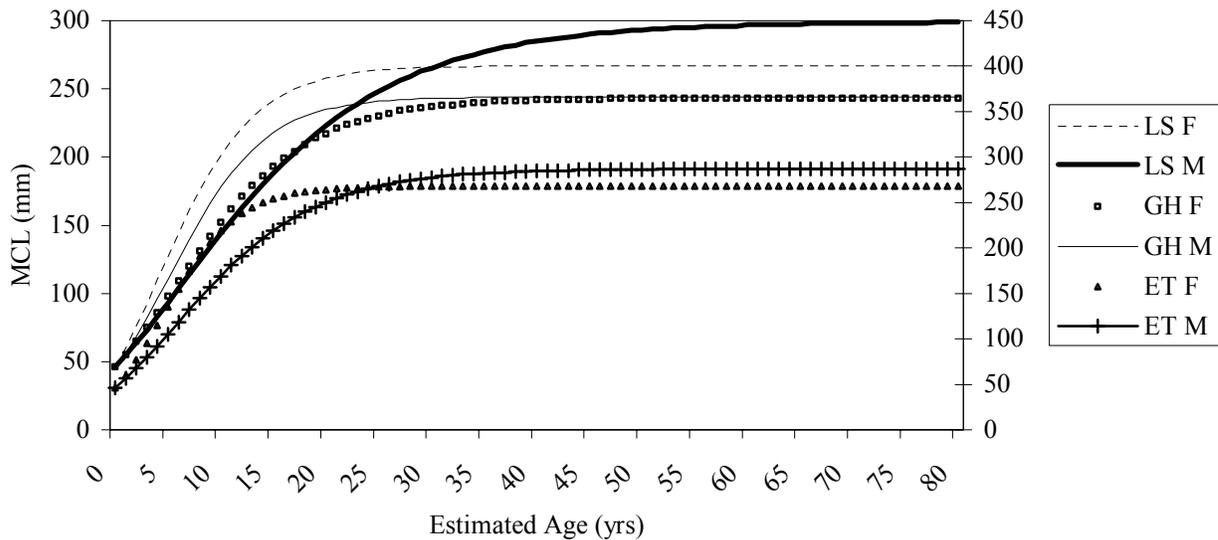


Figure 4. Growth curves for female (F) and male (M) desert tortoises on the Little Shipp Wash (LS), Granite Hills (GH), and Eagletail Mountains (ET) plots. LS and GH curves are scaled to the left axis; ET curves are scaled to the right axis.

Table 2. Upper size estimates for desert tortoises across their range. Estimates are mean upper decile carapace lengths, unless otherwise indicated. Sample size given in parentheses.		
Location	Males	Females
Western Mohave	283 (24) ^A	246 (15) ^A
Eastern Mohave	260 (54) ^A	233 (34) ^A
Northwestern Sonoran		
Little Shipp Wash	311 (27) ^B	290 (35) ^B
Eagletail Mountains	299 (54) ^C	267 (83) ^C
Eastern Sonoran		
Granite Hills	301 (11) ^B	287 (17) ^B
	287 (23) ^C	268 (34) ^C
Sinaloan	254 (29) ^B	255 (31) ^B
	244 (69) ^C	243 (77) ^C
	282 (22) ^A	265 (10) ^A

^AGermano (1994b).

^BData from 1994 survey (Woodman and others 1995).

^CGrowth curve estimates using data from all surveys through 1994 (Murray and Klug 1996).

Survivorship

Desert tortoises may exceed 35 years of age in the Sonoran Desert (Germano 1992) and have been observed to live at least 50 years in the eastern Mojave Desert (Hardy 1976). As expected in a long-lived animal, adult desert tortoises have exceptionally high survivorship. Annual survival estimates at the 3 most studied plots were 94% or higher for adult tortoises (Table 3; Howland and Klug 1996). Confidence intervals generally indicate these estimates are not significantly different from the 98% level estimated necessary for long-term persistence of tortoise populations in the Mojave Desert (FWS 1994). Although less precise, estimates of mean annual survivorship for juvenile tortoises (that is, all tortoises <180 mm MCL) are only slightly lower than those for adults, ranging from 84-93% (Table 3). However, the data supporting these estimates are biased toward larger juveniles. Survivorship of hatchlings and 1-2 year-olds is probably much lower, and rates of nest survivorship are unknown. Studies specifically addressing the ecology of these small tortoises have yet to be conducted in the Sonoran Desert because of their secretive nature and cryptic appearance.

Table 3. Mean survivorship of desert tortoises at the Eagletail Mountains, Granite Hills, and Little Shipp Wash plots. Estimates computed with Program Jolly (Model A; Pollock and others 1990). Juveniles <180 mm MCL; adults ≥180 mm MCL. Data from Howland and Klug (1996).			
Plot	Size Class	Survivorship	95% Confidence Interval
Eagletail Mountains	Juvenile	0.84	0.55-1.00
	Adult	0.97	0.93-1.00
Granite Hills	Juvenile	0.93	0.75-1.00
	Adult	0.95	0.91-0.99
Little Shipp Wash	Juvenile	0.85	0.26-1.00
	Adult	0.94	0.90-0.97

Life history traits of turtles (delayed sexual maturity, iteroparity) require high survival for adults, as well as relatively high survival for juveniles, to maintain viable populations (Congdon and others 1993). In fact, viability of tortoise populations in the western Mojave Desert is most sensitive to survival of large adult females (Doak and others 1994). While specific reproductive traits differ between tortoises from the Sonoran and Mojave deserts (Chapter 3), the same general pattern of survivorship undoubtedly contributes to population persistence in the Sonoran Desert.

Potentially higher survivorship of juvenile tortoises in the Sonoran Desert may actually make population persistence less tenuous than in the Mojave. Even though hatchlings have enough energy reserves from the embryonic yolks to survive through late summer and winter, they potentially can accumulate additional energy by foraging. With Sonoran females laying a single clutch prior to the summer rainy season, the eggs hatch at the end of the rainy season when annuals and herbaceous perennial forage are available in most years. In the Sonoran Desert a few hatchlings have been observed foraging up to late September (Holm 1989; Hart and others 1992;

Woodman and others 1994). In years with late summer and fall rains, food plants may remain green until the first frost in late November or early December. The importance of summer-fall foraging in Sonoran tortoise hatchlings needs to be evaluated but may be important in enhanced survivorship. In the western Mojave Desert where females produce multiple clutches, the situation is very different. Hatchlings rarely have green annuals available and wait until the next spring to feed. The primary function of hatchling emergence in August and September may be dispersal up to 1.5 km away from the nest site, not foraging (David J. Morafka, pers. comm. 1999). However, eastern Mojave females appear to lay their eggs early enough for hatchlings to take advantage of late summer forage resulting from unpredictable summer rains (Wallis and others 1999).

The only documented exception to high survivorship in Sonoran tortoise populations occurred in the Maricopa Mountains, where the tortoise population suffered a major decline in the mid- to late 1980s. Wirt (1988) found 57 live adult tortoises and 65 carcasses on the square-mile Maricopa plot in 1987. Only 3 years later, Shields and others (1990) found only 17 live tortoises and 54 additional carcasses on the plot, including at least 15 carcasses of tortoises that had been marked alive in 1987. The reasons for this decline are unclear, but a major drought affecting the Maricopa Mountains from 1984 to 1992 may have contributed to increased mortality (Wirt and Holm 1997). A relatively high proportion of tortoises at this plot was also observed with a shell disease (Woodman, pers. comm. 1998), which has been correlated with a decline in one Mojave Desert population (Berry 1997). This condition, however, has been observed in varying proportions in virtually all tortoise populations studied in Arizona to date, with no apparent detrimental effects to those populations or individuals (see Appendix). Relatively high numbers of carcasses compared to live tortoises have also been found on the Arrastra Mountain, Bonanza Wash, and Sand Tank Mountain plots. These cases could represent either: accumulated mortality over a number of years, especially for the Arrastra Mountains and Bonanza Wash plots, at which few carcasses have been found in subsequent surveys; a previous short-term decline; or a longer-term decline in progress.

Specific causes of mortality are usually impossible to determine. Disease has contributed to widespread mortality of tortoises in the Mojave Desert (FWS 1994), but no population-level effects have been determined in the Sonoran Desert. Predation occurs to varying degrees in all tortoise populations. For example, of 13 adult mortalities estimated to have occurred on the Little Shipp Wash plot between 1986 and 1993, most were attributed to mountain lion *Felis concolor* predation, including 7 out of 8 carcasses found in 1993. Mountain lions are one of the few, if not only, natural predators capable of breaking through an adult tortoise's shell. Other carnivores, including coyotes *Canis latrans* (Hohman and Ohmart 1980), kit foxes *Vulpes macrotis* (Coombs 1977), bobcats *Felis rufus* (Woodbury and Hardy 1948), gray foxes *Urocyon cinereoargenteus*, and badgers *Taxidea taxus*, may prey on hatchlings, juveniles, or eggs, or kill adults by chewing exposed limbs. Feral dogs have been implicated in tortoise mortality on the East Bajada and Bonanza Wash plots.

Other potential predators of smaller tortoises include golden eagles *Aquila chrysaetos* (Luckenbach 1982) and other raptors, common ravens *Corvus corax*, and greater roadrunners *Geococcyx californianus*. Although increased predation on hatchling and juvenile tortoises by ravens near urban areas and along power lines crossing the desert has contributed to the decline of Mojave tortoise populations (FWS 1994), predation by aerial predators has not resulted in any noticeable population effects in the Sonoran Desert, probably because of the relative complexity of Sonoran tortoise habitat. Although not documented, some snakes, including coachwhips *Masticophis flagellum*, gopher snakes *Pituophis melanoleucus*, and kingsnakes *Lampropeltis getula*, may also eat tortoise eggs or juveniles. Finally, Gila monsters *Heloderma suspectum* are known to eat tortoise eggs (Barrett and Humphrey 1986).

HEALTH AND DISEASE

Most tortoises at populations studied to date in Arizona's Sonoran Desert appear to be in good health. Very few definitive signs of URTD have been recorded, and certainly no epidemic levels of disease have been seen. Virtually every tortoise population studied so far has at least some proportion of tortoises with cutaneous dyskeratosis, although we have observed no detrimental effects to the individual tortoises or populations. More detailed records of disease symptoms may be found in the appendix and from each specific plot report.

POPULATION REGULATION

As previously discussed, desert tortoise abundance and density varies widely across the Sonoran Desert. One hypothesis to explain this variation suggests that a relatively fixed number of sheltersites available to the population ultimately limits its size. Only a weak correlation ($r^2 = 0.05$) currently exists between the number of burrows marked on a plot and tortoise density, but only half the sites have had burrows marked in more than one survey (Fig. 5). Not all burrows are found in a single survey, and only those with tortoises actually inside or nearby are marked. A much stronger correlation exists between the number of burrows and tortoise density on those plots on which more intensive effort has been made to find, confirm, and number tortoise burrows ($r^2 = 0.76$; Fig. 5).

Tortoises use burrows to regulate heat and moisture, and females require adequate soil development to excavate nests, usually inside the burrow. In most Sonoran populations, tortoise burrows are relatively permanent sheltersites usually found below large rocks or boulders. Researchers rarely find newly excavated burrows, because existing rock crevices and patches with suitable friable soil that tortoises can excavate already have burrows. Only some burrows have soil deep enough for nesting.

Closer examination of intensively studied sites augments the available evidence that sheltersite abundance limits tortoise abundance. On the Eagletail Mountains plot, for example, individual tortoises have often been found in the same burrow repeatedly within an annual survey. Some individuals have even been found in the same burrows during 6 consecutive annual surveys, an

exceptional degree of sheltersite fidelity relative to other plots. A volcanic dike running across the Eagletail Mountains plot has many large rocks but relatively little soil development, resulting in few quality sheltersites and a small population. In comparison, the Little Shipp Wash and Mazatzal Mountain study sites with large populations are in areas where rapidly-eroding granitic bedrock forms extensive soils and abundant suitable sheltersites.

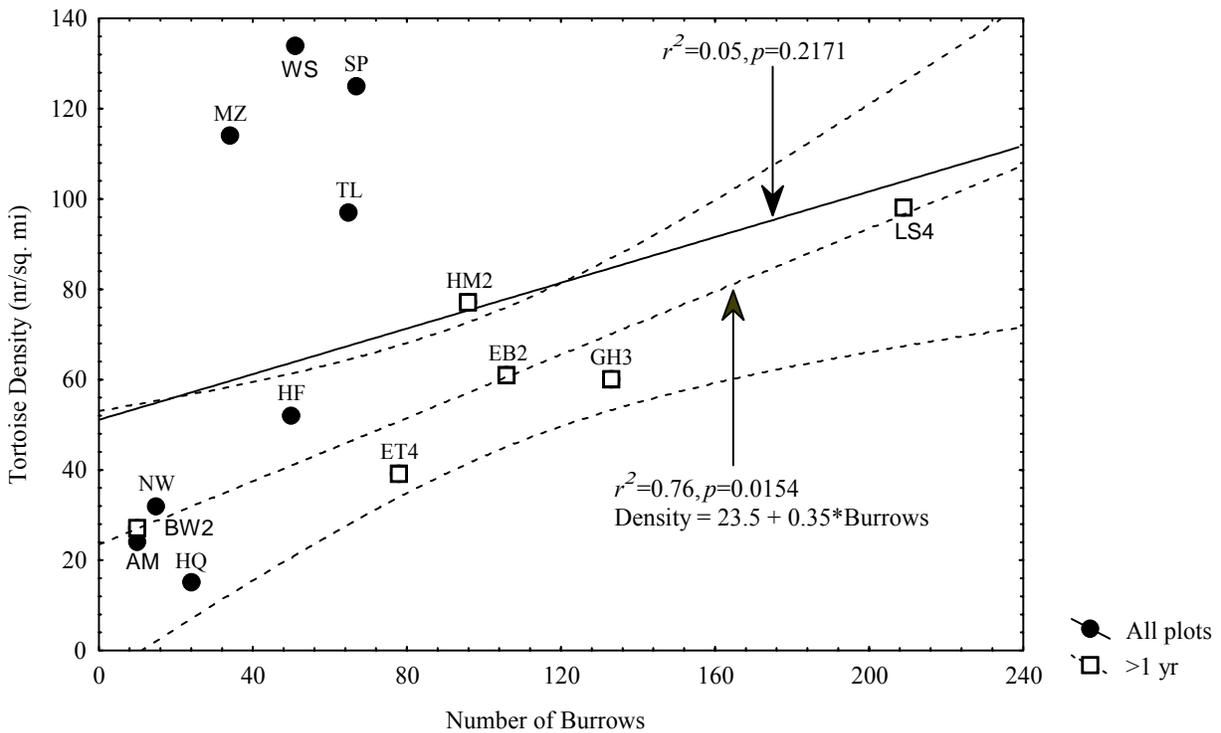


Figure 5. Correlation of the number of desert tortoise burrows to population density in the Sonoran Desert of Arizona. Codes refer to study sites listed in Table 1. Burrow numbers were obtained from monitoring plot surveys in a single year (closed circles) or multiple years (open squares). The number of surveys is indicated after the plot codes for those plots surveyed >1 time.

Given natural limitations on sheltersite availability, especially on those with burrows suitable for nesting, sheltersite usage is complex. Individual tortoises use multiple burrows, including those used by other tortoises. However, Murray and Klug (1996) found that over a 2-3 year period, female tortoises were found in other female's burrows (that is, those in which another female had previously been found) significantly less often than in burrows used by males. Other short-term studies have shown the same pattern in both the Mojave (Burge 1977) and Sonoran deserts

(Bailey and others 1995). At one northeastern Mojave Desert site, female tortoises shared burrows with other females less often than males with other males or than males with females (Bulova 1994). During the nesting season at this same site, female tortoises avoid burrows containing another female's feces, suggesting that chemical cues may indicate whether another female has already nested in a particular burrow (Bulova 1997). Avoiding burrows in which another female has already nested might be advantageous if females risk breaking their own or another female's previously-laid eggs. Broken eggs might also result in bacterial infection of embryos or an increased chance of detection by egg predators.

Another hypothesis may also help explain tortoise population regulation. Variation in rainfall may influence reproductive success, juvenile survivorship, and recruitment. Ten years or so of relatively low juvenile survivorship will gradually deplete new generations, so few tortoises in a given cohort reach sexual maturity to be recruited into the adult population. Wirt and Holm (1997) reported a low proportion of Sonoran tortoises reproducing in the Maricopa Mountains following an extended drought, and Karl (1998) and Turner and others (1986) showed that clutch frequency of Mojave tortoises was correlated with winter rainfall and spring forage in California populations. A series of dry years may limit reproductive output or result in high mortality among smaller tortoises, resulting in smaller surviving cohorts from those years. These 'missing' cohorts may be reflected as gaps in size distributions in the smaller adult sizes (Fig. 3A, 3C). On the other hand, successive years with precipitation producing adequate forage may result in high reproductive output and juvenile survivorship (Morafka 1994). Although such years may be those represented by bulges in juvenile size distributions (Fig. 3A, 3B), we have not studied those populations long enough to see increases in adult densities.

How individual populations in the Sonoran Desert interrelate is even less understood than their local dynamics. Tortoises in the Sonoran Desert occur naturally in disjunct local populations, generally in low, desert mountain foothills (Germano and others 1994). Although observations of Sonoran tortoises dispersing far away from rocky ridge habitats are rare, populations, at least theoretically, may depend on occasional cross-valley immigration for genetic interchange and long-term survival. Local tortoise populations receiving high precipitation for 2-3 years may increase, increasing the probability of individuals at or approaching sexual maturity dispersing across the valleys (Morafka 1994). We have observed such tortoises of both sexes make relatively long-distance movements away from their normal observed activity centers (see Chapter 4). They crossed areas of atypical tortoise habitat, including an approximately 1-km wide alluvial fan and steep, boulder-free slopes occupied by few to no resident tortoises.

Most local tortoise populations in the Sonoran Desert appear stable at present, but they are increasingly fragmented by urban and agricultural development. Given the fact that individual tortoises live for decades, potential impacts of population isolation may not be seen for many years. The degree to which local populations depend on interchange with other populations for long-term persistence is unknown, as are the effects of dismissing intermountain valleys as "unsuitable" habitat in Sonoran desert tortoise conservation efforts.

REVISIONS TO THE MONITORING PROTOCOL

Averill-Murray (2000) reviewed and revised the current protocol for monitoring desert tortoise populations. The most important points are summarized here.

PLOT CONFIGURATION

Many of the unique configurations and survey durations of current plots were constructed or modified to account for the fact that tortoises often do not occur throughout an entire standard 1-mi² plot, at least in the Sonoran Desert. In fact, any configuration of an entire square mile will usually include a significant proportion of area unused by tortoises. An exception is the 1-square-mile Granite Hills plot, which is narrow and elongate to encompass a narrow, rocky ridge and to exclude as much of the surrounding creosotebush flats as possible (Hart and others 1992). Localized tortoise distributions within plots led to spatially and temporally reduced surveys at the Eagletail Mountains, Bonanza Wash, and the Arrastra Mountains (see references in Table 1).

Still, new study plots should be configured and surveyed similarly to current standard methods on 1-square-mile areas. Surveys of square-mile plots will allow researchers to determine and map tortoise distribution in the general area. This information can then be used to modify plot configuration for more efficient future surveys. Boundaries for *subsequent* surveys of a plot should be drawn to include as many tortoises as possible within approximately 1 square km. However, the actual area of the plot is less important than a configuration that contains tortoises distributed throughout the plot and that can be completely surveyed 4 to 6 times.

Plot configuration need not be square but should be shaped to best fit presumed tortoise habitat (for new plots) or observed tortoise distribution (for existing plots) in the chosen area (for example, the Granite Hills). A low perimeter/area ratio is best for plots susceptible to edge effect (that is, plots with contiguous habitat outside plot boundaries; Thompson and others 1998).

PLOT COVERAGE

Specification of a 60 person-day field effort over 45 calendar days results in up to 30 days spent on the plot by a single person working alone. Although no major accident has occurred on a plot of this design, the rigorous terrain of most plots raises important safety issues (Murray and Schwalbe 1997). It may be desirable to allow surveys to occur over fewer calendar days with field personnel working in teams, as long as the surveys occur during high activity periods of tortoises.

To the maximum extent practicable, new (1-square-mi) plots should be surveyed during the summer monsoon season. Each survey should include 2 complete and independent coverages to allow population size estimation (see below) and an unbiased evaluation of tortoise distribution within the plot. Existing plots (reconfigured to approximately 1-square-km) will be surveyed during the monsoon season with a minimum of 4 and maximum of 6 complete, independent

coverages; the actual number of coverages will be determined by plot size, topography, and complexity (Averill-Murray 2000). Each separate coverage should occur in the shortest amount of time possible to more closely approximate an “instantaneous” sample, as desired for the population closure assumption (see Abundance Estimation, below). In general, total field effort on both new and existing plots will consist of 60 person days during no fewer than 30 calendar days per survey, with field personnel working in teams of 2. However, 4 coverages of plots with relatively simple (not necessarily flat) topography with highly localized populations, such as the Eagletails plot, may be performed in 40 person days (4 separate plot coverages of 10 days each) but including no fewer than 20 calendar days (Averill-Murray 2000). A calendar day is an actual day spent in the field (>4 hours); a person day equals 8 hours of field effort. A 60-person-day survey over 44-45 calendar days is also acceptable (Averill-Murray 2000), but extra caution must be exercised when working alone.

TORTOISE DATA

Special precautions should be taken to minimize the number of tortoises voiding their bladder during processing, as well as the amount of urine voided. Averill-Murray (1999a) found that tortoises that void their bladders during handling were less likely to be recaptured in subsequent years, at least for some plots and years, suggesting that survival might be compromised by the fluid loss.

Re-evaluation of the types of data recorded on live tortoises presents opportunities to reduce handling and risk of tortoises voiding their bladders. A large database, compiled from monitoring plot surveys through the present, exists on tortoise shell morphology, so most shell measurements currently recorded should be eliminated. A measure of size (length) is needed to characterize population demographics, so MCL should still be recorded. Tortoise weight is extremely variable within individuals and depends on each individual’s hydration state, making it an unreliable indicator of tortoise health (Jacobson and others 1993); therefore, handling could be minimized by eliminating tortoise weights from the data recorded.

Files should be replaced after marking no more than 10 tortoises (or 10 uses/edge of triangular files) to ensure that only sharp files are used; a system of tracking file use should be implemented, such as making tick marks on the file with a marker after each use. Plastron photographs should be taken as quickly as possible, and tortoises should be handled carefully at all times. To further minimize the risk of tortoises voiding their bladders, individuals recaptured during the same survey should not be handled at all except to verify their identification number, if necessary. This is especially true if the tortoise is in a burrow and its epoxied number is visible. If a tortoise does void its bladder, the processing activity at the time of voiding should be recorded on the data sheet.

DATA ANALYSIS

Size Distributions

Turner and Berry's (1984) size categories have been used to describe tortoise population structure and to compare populations for almost 20 years (Woodman and others 1998). However, tortoise growth varies temporally (Medica and others 1975; Turner and others 1987) and geographically (Germano 1994a; Murray and Klug 1996). Therefore, comparisons of artificial size categories between populations and years can confound accurate inferences. For example, tortoises at the Granite Hills grow to significantly smaller sizes than those at Little Shipp Wash (Murray and Klug 1996). The low numbers of "Adult 2" tortoises at the Granite Hills do not imply that this population has lost its oldest individuals; likewise, smaller-size categories (for example, Immature 1, 2) may be compressed relative to other populations. Apparent differences in number within juvenile or immature classes between years or plots may reflect annual differences in growth rates rather than in age structures, as implied by the category labels. Size distributions should instead be tabulated in 10-mm increments and graphically presented in a histogram.

Abundance Estimation

Generally, abundance estimators make 3 basic assumptions. First, the population under study must be "closed," both demographically (no births, deaths, immigration, or emigration) and geographically (no edge effect, movement of animals across the plot boundaries). Failure of this assumption leads to overestimates of the true population size due to an inflated ratio of unmarked to marked individuals. Minimizing the sampling period and maximizing the size of the study plot compared to the average movements of the target animals during each sample may satisfy, at least approximately, the geographic closure assumption (Thompson and others 1998). Edge effects result in abundance estimates associated with unknown sample areas or overestimates of density within the plot (Thompson and others 1998), but it is minimized on plots with unsuitable tortoise habitat outside the plot boundaries (for example, Granite Hills). Density estimates may be corrected for minor edge effects with the mean maximum distance moved method of Wilson and Anderson (1985; see Density Estimation, below).

Tortoise longevity allows adult (≥ 180 mm MCL) tortoise populations to be considered demographically closed within a given sampling season (Murray 1993). Mortality is low for mature tortoises in healthy populations, and slow growth rates prevent significant recruitment into this size class within a single season. Demographic closure will begin to break down as the number of seasons included in a given analysis increases, for example by using different years as "mark" and "recapture" samples. Most Sonoran desert tortoise populations may be considered geographically closed due to small annual home ranges (Bailey 1992; Barrett 1990; Martin 1995).

The second and most important assumption requires each animal to have a constant and equal capture probability during each trapping occasion (Otis and others 1978). This assumption may fail due to 3 sources of variation: temporal differences in capturability between sample periods;

behavioral responses to capture, such as trap-shyness and trap-happiness; and individual heterogeneity (that is, innate differences in capturability between individuals). If heterogeneity is present in the population, individuals with higher capture probabilities will be marked earlier and caught more often than those with low capturability, resulting in an underestimate of the ratio of unmarked to marked individuals and, thus, the true population size (Pollock and others 1990). Similar results occur when animals are trap-happy, while trap-shy animals produce overestimates due to the opposite effect (Pollock and others 1990).

Larger tortoises are easier to find than smaller ones (Shields 1980), so it has been common practice to compute estimates separately for adult and juvenile tortoises. Schneider (1981) provided evidence for unequal capturability for tortoises within size classes, possibly due to differences in home range and activity patterns, but this problem has since received very little attention. Hart (1993) presented preliminary data suggesting differences in capturability between sexes. Individual tortoises may also be differentially subject to capture depending on the complexity of the habitat in their home ranges, especially in topographically diverse areas with varying concentrations of boulders (Murray 1993).

The third primary assumption in estimating animal abundance requires permanent marks which are recorded correctly at each trapping occasion (Otis and others 1978). Failure of this assumption leads to overestimates because of the loss of marks. Notching the marginal scutes results in permanent marks in large tortoises (unless the tortoise is chewed by a predator), but growth of young individuals between recaptures may obscure the notches. Correctly recording identification numbers is simply a matter of working carefully.

Abundance of tortoises ≥ 180 mm MCL should be estimated with the Lincoln-Petersen estimator (see Pollock and others 1990), using capture data pooled from the first 3 plot coverages (2 for plots with localized populations and on which only 4 coverages are completed) as the “mark” sample (Murray and Schwalbe 1997). Data pooled from the remaining coverages will comprise the “recapture” sample (Murray and Schwalbe 1997). Individuals will only be counted once in each sample, regardless of the actual number of times found. This method minimizes variation in individual capture probabilities. That is, even tortoises that are less likely to be captured during 1 plot coverage may be captured after 2 or more coverages (but still within 1 sample), giving tortoises the same weight whether they were captured after 1, 2, or more opportunities (Murray and Schwalbe 1997). This provides a similar benefit to the current method of pooling tortoises within an entire season into either a mark or recapture sample but has the advantage of producing an abundance estimate within a single season. Therefore, violations of the Lincoln-Petersen method’s assumption that the population is closed are minimized compared to between-year estimates, especially when plot surveys occur in non-consecutive years.

Density Estimation

Dividing estimated abundance by study plot area to calculate density overestimates true density by as much as 99% by not accounting for “edge effects” of plot boundaries (Wilson and Anderson 1985). Wilson and Anderson (1985) provided an unbiased method of estimating

animal density based on mark-recapture methods, and this has been applied to one tortoise plot in Arizona (Murray 1993; Murray and Schwalbe 1997). See Averill-Murray (2000) for more specific details.

Trends in Abundance

Trend estimation requires multiple surveys, and for a long-lived animal like the desert tortoise, this requires many years to be meaningful. So far, individual tortoise populations in Arizona have been monitored for a relatively short time. However, managers still need to know if any short-term changes in population size have occurred while the long-term data are accumulating. This has typically been done in the past by comparing 95% confidence intervals of point estimates for the first and second surveys of a given tortoise plot. Statistically, this type of comparison does not test whether the population sizes at each time are equal (that is $N_1 = N_2$) or whether they have even changed significantly. This comparison is based on an incorrect assumption that each confidence interval has a 95% chance of including the true population size and that overlapping intervals are thus not significantly different at the 95% confidence level. In fact, each interval indicates only that, on average, 95 out of 100 confidence intervals obtained from similar samples would include the true population size (Sokal and Rohlf 1995). Whether or not two intervals overlap indicates nothing about actual differences in population size.

Testing whether abundance is higher (or lower) between 2 surveys can be done with proportional abundance estimation. This method estimates the proportion by which population size during the second survey differs from size during the first survey; a confidence interval for this proportion that includes zero indicates that there has been no detectable change in population size (Skalski and Robson 1992). Precision of the proportional abundance estimate, however, is a function of the precision of abundance estimates, which may limit the ability to detect changes between 2 surveys (Murray and Schwalbe 1997).

Current monitoring methods also have little power (ability) to detect trends in tortoise abundance over 3 or more years (Averill-Murray 1999b). Since current abundance estimation uses 1 year as the “mark” sample and the subsequent year as the “recapture” sample, annual estimates are not independent of each other, and temporal variation is underestimated (Averill-Murray 1999b; Murray and Schwalbe 1997). In addition to invalidating the use of proportional abundance estimation, the lack of independent abundance estimates makes trend estimates less reliable (Harris 1986). An important step to improve the power to detect trends is to minimize temporal variation in estimates within plots. By reducing plot size and excluding areas with few to no tortoises, multiple systematic (complete) coverages of the plot may be conducted within a single survey. This will increase recaptures in the sampled population and produce precise abundance estimates within a single year by providing multiple sample periods within each year (Averill-Murray 1999b; Murray and Schwalbe 1997). The importance of minimizing sampling variation cannot be overstated, because poor precision from an inadequate survey means there will be no power to reject the null hypothesis of no trend, resulting in a default decision of no action (Thompson and others 1998).

A long-term commitment to monitoring tortoise populations is also necessary to detect anything other than a catastrophic population decline (Averill-Murray 1999b). Power to detect trends is negligible if populations are only surveyed 2 or 3 times. With the exception of 1990-94 when 3 plots were surveyed annually, monitoring efforts have been haphazard (Table 1). Inconsistent funding will result in an increased period of time before trend estimation is possible for each plot. Long survey intervals could result in gradual declines over several years not being detected until a significant absolute decline in abundance has already occurred. Catastrophic declines (such as that at the Maricopa Mountains; Shields and others 1990) might not be recognized as such, reducing the ability to identify and correct the cause of the decline (Averill-Murray 1999b).

A consistent schedule is needed to obtain the most useful trend estimates for each tortoise population monitored. The monitoring program should include plots from populations across the tortoise's distribution in Arizona. Most plots should be surveyed on a consistent 4-year rotation. For example, a set of 16 plots could be surveyed with a 4 plot/year rotation. Trends in population size should be estimated for plots with 3 or more independent abundance estimates with linear regression after \log_e -transforming the data. Significant trends will be determined as those regression slopes whose 95% confidence interval do not include zero. If the regression assumption of normally distributed random errors is not met, randomization or nonparametric methods may be used (Thompson and others 1998). Individual survival can be estimated with Program MARK (White 1999) with which models can be developed and tested to detect differences between groups or survey intervals and trends over time.

Rangewide Inferences

It is important to note that the current set of plots (Table 1, Fig. 1) does not represent a random sample from the entire range in Arizona, or even within individual land management agencies. Most plots were selected largely on relatively high evidence of tortoise sign and a likelihood of finding tortoises; other criteria included public land ownership, which was not likely to get traded or mined; distribution across the tortoise's range in Arizona; and relative "representativeness" of an area or habitat type (T. Cordero, pers. comm. 1999). The advantage of this approach was the minimization of effort spent on randomly selected plots with few to no tortoises. A serious disadvantage is the inability to extrapolate results to the entire Sonoran population in Arizona; inferences are limited to the selected plots themselves (Thompson and others 1998).

Four possible scenarios could occur if patterns in population trends on the plots are extrapolated regionally or rangewide. 1) Plot results may indicate a stable or increasing trend in tortoise numbers or survival, and regional populations are also stable to increasing. 2) A negative trend on plots occurs concurrently with a negative regional trend. 3) A negative trend on plots may occur while regional tortoise populations are actually stable or increasing. 4) Tortoise numbers on plots appear to be stable or increasing but are actually declining outside the plots. Scenarios 1 and 2 would generally provide correct information to managers regarding regional tortoise status, but the degree of change may differ within and outside plots. Scenario 3 would indicate that regional tortoise populations are in worse shape than they really were, possibly leading to more conservative management policies than necessary, rather than site-specific actions appropriate to

particular areas containing declining populations. Under scenario 4, regional tortoise populations could suffer large-scale, catastrophic declines before they were observed on the plots.

The wide distribution of plots across the tortoise's distribution could possibly buffer against incorrect inferences, as in scenarios 3 and 4. However, since the plots were selected based on a perceived chance of finding many tortoises in an area, they may not be representative of tortoise populations at a larger scale. Scenario 3 could result because tortoise populations on the plots are at or near carrying capacity; a negative trend on a plot may be a short-term demographic effect resulting from an inability to pack more tortoises into the population, while surrounding populations may actually be increasing (possibly even partly via emigration from the plot). On the other hand, scenario 4 would result if a plot was placed in the best tortoise habitat in the area and was buffered more strongly against negative impacts occurring to populations elsewhere. Regional populations may be in decline long before recognized. It is important to continue to monitor the current plot set and to possibly add additional plots, but managers must be alert for potential population impacts or declines in tortoise habitat between individual plots. Additional plots should be surveyed opportunistically as funding allows, serving as "check-ups" within the intervening tortoise distribution between regularly surveyed plots. Observations of multiple fresh tortoise carcasses on transects or other local surveys in areas between plots may provide an indication that a problem may be present in a particular population, so that population may merit more intensive surveys.

CHAPTER 3
REPRODUCTION OF *GOPHERUS AGASSIZII* IN THE SONORAN DESERT

INTRODUCTION

Life history traits within chelonian species may vary over both geographically broad or local scales. Variation in body size, clutch size, clutch frequency, and age at maturity in painted turtles *Chrysemys picta* corresponds with taxonomic divisions of recognized subspecies, but local variations may be influenced by environmental conditions (Christiansen and Moll 1973; Moll 1973; review by Wilbur and Morin 1988). Other studies have reported geographic variation in reproduction in common musk turtles *Sternotherus odoratus* and green turtles *Chelonia mydas* (Wilbur and Morin 1988). On more local scales, *C. p. bellii* vary in body size and clutch size in 3 habitats in Michigan (Gibbons and Tinkle 1969), and Rowe (1994) described variation in egg size and shape among *C. p. bellii* populations in Nebraska. Female red-eared sliders *Trachemys scripta* in a heated pond mature at larger sizes and have larger clutches as a result when compared to natural ponds in South Carolina (Gibbons and others 1981). Within the Testudinidae, reproductive parameters vary with population density among 3 populations of Aldabra tortoise *Geochelone gigantea* on Aldabra Atoll (Swingland 1977; Swingland and Coe 1978; Swingland and Lessels 1979). Hermann's tortoise *Testudo hermanni* laid larger eggs in smaller clutches, on average, in France than in Greece (Swingland and Stubbs 1985), and egg size, clutch size, and clutch mass varied among 3 populations in Greece (Hailey and Loumbourdis 1988).

The desert tortoise *Gopherus agassizii* has the broadest range of latitude and habitats of the 4 species of North American tortoises (Auffenberg and Franz 1978; Patterson 1982; Germano and others 1994), but reproductive biology and ecology is known from wild populations primarily within the Mojave Desert (Hampton 1981; Turner and others 1984, 1986; Roberson and others 1989; Rostal and others 1994; Henen 1997; Karl 1998; Mueller and others 1998; Wallis and others 1999). Even though Mojave and Sonoran desert populations differ genetically, morphologically, and ecologically (Luckenbach 1982; Lamb and others 1989; Glenn and others 1990; Germano 1993), little is known about geographic variation in reproduction across the range. Murray and others (1996) summarized 1 year of reproductive output of *G. agassizii* from a population in the Sonoran Desert, Arizona. This paper builds on that study by providing an additional 3 years of data from the same population, as well as a year of data from a second population in the Sonoran Desert. We then compare reproductive strategies among populations of the species and among the 4 species of *Gopherus*.

METHODS

STUDY AREA AND SEASONS

Our primary study site was near Sugarloaf Mountain on the Tonto National Forest, Maricopa County, Arizona. Elevations at Sugarloaf range from 549-853 m (1800-2800 ft) with steep, rocky

slopes divided by many arroyos. Boulders up to 4-m (13-ft) diameter occur on many slopes. In 1997 we also sampled tortoises from a second site, about 100 km (62 mi) to the south in the Granite Hills, Pinal County, Arizona. Elevations at the Granite Hills range from 600-702 m (2000-2300 ft), and topography is similar to Sugarloaf. Both sites occur in the northeastern Sonoran Desert with vegetation classified in the paloverde-mixed cacti series of the Arizona Upland subdivision (Turner and Brown 1982).

We recorded rainfall each week from a rain gauge at Sugarloaf, and we summarized long-term (1939-1999) rainfall data from the National Oceanic and Atmospheric Administration's nearest weather station, about 13 km (8 mi) to the south (Stewart Mountain). We summarized annual rainfall data according to 3 seasons defined by average environmental conditions and tortoise activity. Summer includes the months of July through October, containing the monsoon rainy season and peak tortoise activity. Winter includes November through February and is usually also wet, but cool and with little tortoise activity. Spring includes March through June and is generally characterized by increasing temperatures, decreasing rainfall, and variable tortoise activity.

TELEMETRY AND X-RADIOGRAPHY

Each year at Sugarloaf we monitored female tortoises (184-289 mm straight midline carapace length [MCL]) weekly using radio telemetry. We attached radio transmitters (AVM Instrument Company, Telonics, or Wildlife Materials) to the anterior carapace using 5-minute gel epoxy (Devcon). We radiographed tortoises with an HF-80 (MinXray) portable X-ray machine powered by a gasoline generator. We placed tortoises upright on loaded film cassettes (high speed cassettes refurbished by Custom X-Ray Imaging Services) at a constant "focus to film" distance of 61 cm (24 in). We used Custom X-Ray high speed blue private practice film. X-ray exposure times ranged from 0.12-0.24 sec at 65 kVP, depending on tortoise size (MCL). See Murray and others (1996) for slight deviations in 1993 from the methods described above.

In 1993 we radiographed 10 tortoises approximately weekly between 12 June and 11 July, then biweekly through 12 September. In 1997 we radiographed 13 tortoises weekly between 15 May and 12 August, then once each in mid-September and mid-October. In 1998 we radiographed 22 tortoises biweekly (approximately 1/2 each week) between 21 May and 6 August. Finally, in 1999 we radiographed 20 tortoises biweekly between 28 May and 23 July, although 2 tortoises that retained their eggs longer than expected were periodically radiographed until as late as 2 October.

We also randomly sampled tortoises from our telemetered population in late summer 1997, spring 1998, summer 1998, and spring 1999 to determine whether tortoises developed shelled eggs outside the radiography focal periods described above. Occasionally, we could not retrieve randomly selected tortoises from their burrows for radiography, so we simply selected the next tortoise on the list of random numbers. We assumed that those we did radiograph represented random samples of the population. In late summer 1997, we sampled 9 tortoises on 16 September

and 8 on 21 October. In spring 1998, we sampled 10 tortoises on 1 April and 16 on 1 May. On 7 May, we radiographed 4 of the 6 tortoises not previously sampled plus 1 which was sampled on 1 May. In summer 1998, we radiographed 10 tortoises on 14 August, 3 September, and 6 October. In spring 1999, we radiographed 8 tortoises on 1 April and 11 on 6 May; several tortoises that had not yet left hibernation in spring 1999 (5 and 2 on each date, respectively) were not sampled. We calculated the minimum overall probability that we would detect eggs in each season, if any female in the telemetered population actually had eggs, based on our samples of negative radiographs. We limited this analysis to tortoises ≥ 220 mm MCL; tortoises below this size have not been observed to produce eggs at this site. First, we determined the maximum probability of each sample containing no gravid females (P_0), given at least 1 of the total number of telemetered females is gravid, based on the hypergeometric distribution:

$$P_0 = [(qn)!*(n-k)!]/[n!*(qn-k)!],$$

where q is the proportion of tortoises without eggs (set to $[n-1]/n$), n is the size of the telemetered population, and k is the size of the random sample. The overall power of detecting a gravid female in a seasonal sample of tortoises is then 1 minus the product of each sample's P_0 within that season.

In all years, if we could detect eggs by palpation after we had confirmed clutch size on a previous radiograph, that tortoise was not radiographed during its normal rotation; this procedure allowed us to minimize handling, cumulative radiographic exposure, and stress to individual tortoises. For the same reasons, beginning in 1998 we provided tortoises that voided their bladders during processing an opportunity to rehydrate by placing them in a plastic container with water for several minutes before returning them to their capture location; containers were rinsed, disinfected with chlorhexidine diacetate (Nolvasan), and sun-dried between uses. In 1999 we processed tortoises ($n = 3$) below the minimum reproductive size observed in the 3 prior years every third week instead of second, and the use of ultrasonography on 4 weeks during the 1999 season allowed us to prevent radiographic exposure to tortoises known not to have eggs (ultrasound results will be presented elsewhere).

Tortoises at the Granite Hills were individually marked but not telemetered, so we searched for as many females as possible during 1 evening and morning survey each week in 1997. We radiographed a total of 16 females up to 5 times each at the Granite Hills from 4 June to 14 August.

Clutch size was determined directly from radiographs, and egg width was measured with calipers to the nearest 0.05 mm and corrected for magnification (Graham and Petokas 1989). We estimated the "egg to film" distance for this correction to be 30 mm (1.2 in; Wallis and others 1999). We estimated oviposition date for each gravid tortoise as the midpoint between the date eggs were last recorded by radiography or palpation and the date eggs were confirmed to have been laid.

STATISTICAL ANALYSIS

After confirming a significant correlation between seasonal rainfall at Sugarloaf and Stewart Mountain ($r^2 = 0.941$, $t_{15} = 14.41$, $P = 0.000$), we evaluated potential deviations of seasonal rainfall during the study from the long-term (1939-1999) norm by analyzing residuals. We square-root-transformed the Stewart Mountain data to achieve normality, then considered seasonal rainfall for a given year to be significantly abnormal if the absolute value of its standardized residual was >1.96 .

We examined reproductive patterns with analysis of covariance (ANCOVA), controlling for MCL, or correlation analysis. We did not control for potential effects of partial repeated measures, because individuals were added and lost during the 4 years of study and only 6 of 21 individual tortoises that we observed to lay eggs reproduced in more than 1 year. We conducted analyses with Statistica '99 (StatSoft, 1999), considered results significant at $P < 0.05$, and report all means ± 1 standard deviation (SD).

RESULTS

RAINFALL

Residual analysis of Stewart Mountain rainfall since 1939 revealed that seasonal rainfall was abnormally high during spring 1941, winter 1979, and winter 1993 and abnormally low during spring 1947, 1955, and 1959; winter 1961; and winter and spring 1972 ($|z \text{ residuals}| > 1.96$). Even though rainfall varied substantially during the study, the extremely wet winter of 1993 was the only significant deviation from average (Table 4).

Table 4. Seasonal rainfall (mm) at Sugarloaf and Stewart Mountain, Arizona. Winter = November–February; Spring = March–June; Summer = July–October. Asterisk indicates rainfall significantly above average ($z \text{ residual} = 2.976$).						
Year	Sugarloaf			Stewart Mountain		
	Winter	Spring	Summer	Winter	Spring	Summer
1992	---	96.1 (Apr-Jun)	221.2	224.0	131.1	186.2
1993	367.0	92.6	---	413.8*	74.9	83.3
1996	---	0.0 (Apr-Jun)	68.6	82.8	16.0	72.9
1997	76.5	50.5	83.3	102.9	13.5	61.7
1998	252.4	74.1	96.1	257.8	78.2	115.3
1999	72.1	61.2	128.6	74.2	33.8	126.8
Mean (SD)	192.0 (143.7)	62.4 (35.3)	119.6 (61.0)	192.6 (132.9)	57.9 (45.5)	107.7 (45.8)
1939-1999 (SD)				136.9 (82.4)	48.9 (39.0)	123.5 (61.7)

EGG DEVELOPMENT

Few tortoises at Sugarloaf had shelled eggs outside of June through August. Eggs were first visible on radiographs from late May to early July (Table 5). Our samples of negative radiographs gave us a $\geq 88\%$ chance of detecting eggs in the spring and late summer samples, if any tortoise in the telemetered population was actually gravid (Table 6). The April 1998 radiography sample revealed no gravid tortoises, but 1 tortoise (#77) was found with a single egg on 1 May. The 7 May sample resulted in no additional gravid females. We had 94% probability of detecting eggs in spring 1998, if any tortoise (other than #77) was gravid. Tortoise #77 was not telemetered during the 1997 reproductive season, however we believe this egg was retained from 1997. We excluded this observation from all analyses based on the following evidence. First, tortoise #77 laid this egg on approximately 12 June, while clutches from all other tortoises that reproduced that year did not even appear on radiographs until 4-26 June. Second, 1997 was a dry year, during which most females did not reproduce and those that did had small clutch sizes (see below). Most tortoises did reproduce in 1998, and mean clutch size increased (see below); tortoise #77's clutch of 1 egg in 1998 does not fit this pattern.

	1993	1997	1998 ^A	1999
Eggs first visible	<12 Jun ^B	31 May \pm 6 d (28 May–10 Jun)	17 Jun \pm 9 d (4 Jun–1 Jul)	19 Jun \pm 11 d (28 May–2 Jul)
Egg layers (% , n)	8 (80%, 10)	4 (36%, 11)	13 (68%, 19)	7 (44%, 16)
Oviposition date	27 Jun \pm 14 d (9 Jun–25 Jul)	1 Jul \pm 7 d (20 Jun–4 Jul)	13 Jul \pm 9 d (12 Jun–3 Aug)	25 Jul \pm 21 d (9 Jul–30 Aug) ^C
Mean MCL (mm) ^D	247 \pm 12.9 (220-260)	253 \pm 11.5 (184-288)	248 \pm 16.0 (171-287)	260 \pm 16.8 (180-289)
Min. MCL (mm) ^D	220	239	229	239
Clutch size	5.7 \pm 2.43 (3-9) ^E	3.8 \pm 1.26 (2-5)	5.7 \pm 1.49 (4-9)	4.6 \pm 1.51 (3-7)
Egg width (mm)	35.7 \pm 1.74 (32.1-37.7) ^E	34.9 \pm 1.18 (33.5-36.4)	35.4 \pm 1.72 (32.8-39.7)	36.2 \pm 2.12 (33.8-39.6)

^AExcludes 1 clutch presumed to have been retained from the previous year but includes data from an untelemetered female (except for eggs first visible and oviposition date).

^BRadiography initiated on 12 June, after eggs had shelled.

^CExcludes 1 clutch retained over winter and 1 tortoise lost prior to oviposition.

^DReproductive females only (except range).

^EExcludes 1 clutch laid prior to initiation of radiography (Murray and others 1996).

Season	n	N	k	Probability
Late summer 1997 (Sep – Oct)	11	2	9, 8	95%
Spring 1998 ^A (Apr – May)	17	2	8, 15	94%
Summer 1998 (Aug – Oct)	18	3	10, 10, 10	91%
Spring 1999 (Apr – May)	15	2	8, 11	88%

^AExcludes 1 clutch retained from 1997 (see text).

CLUTCH FREQUENCY AND OVIPOSITION

Annual clutch frequency ranged from 0.36 to 0.80 (Table 5: Egg layers). Female tortoises generally laid their eggs near the beginning of the summer monsoon season, which usually occurs in early July. However, mean oviposition occurred later during each year of the study (Table 5), and ANCOVA revealed significant differences in oviposition date by year ($F_{3,24} = 4.94$, $P = 0.008$) and MCL ($F_{1,24} = 4.65$, $P = 0.041$). Larger females tended to lay later than smaller females ($r = 0.440$, $t_{29} = 2.54$, $P = 0.017$, combined years; Fig. 6). Mean annual oviposition date was not correlated with prior summer, winter, or spring rainfall ($P \geq 0.478$).

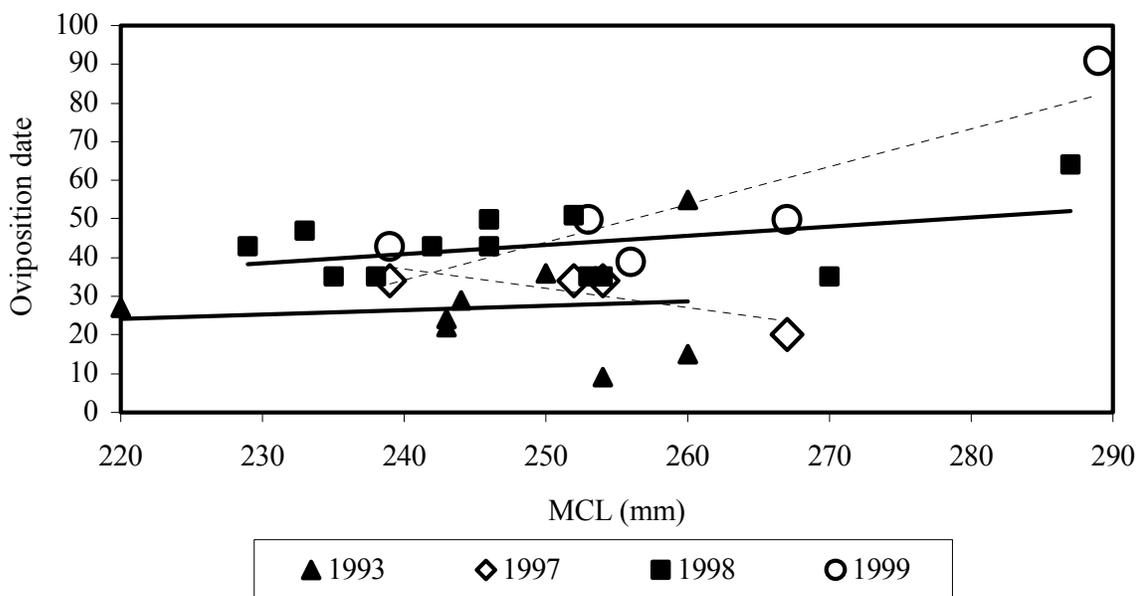


Figure 6. Oviposition date (d > May 31) vs midline carapace length (MCL) for Sugarloaf desert tortoises. Solid lines correspond to solid symbols, and dashed lines correspond to open symbols.

The proportion of females reproducing each year was positively correlated with both winter ($r = 0.983$, $t_4 = 7.58$, $P = 0.017$) and spring ($r = 0.975$, $t_4 = 6.23$, $P = 0.025$) rainfall (Fig. 7), but these seasonal measures of rainfall were nearly significantly correlated with each other during the years of the study ($r = 0.932$, $t_4 = 3.64$, $P = 0.068$). Proportion reproducing was not correlated with prior summer rainfall ($P = 0.219$).

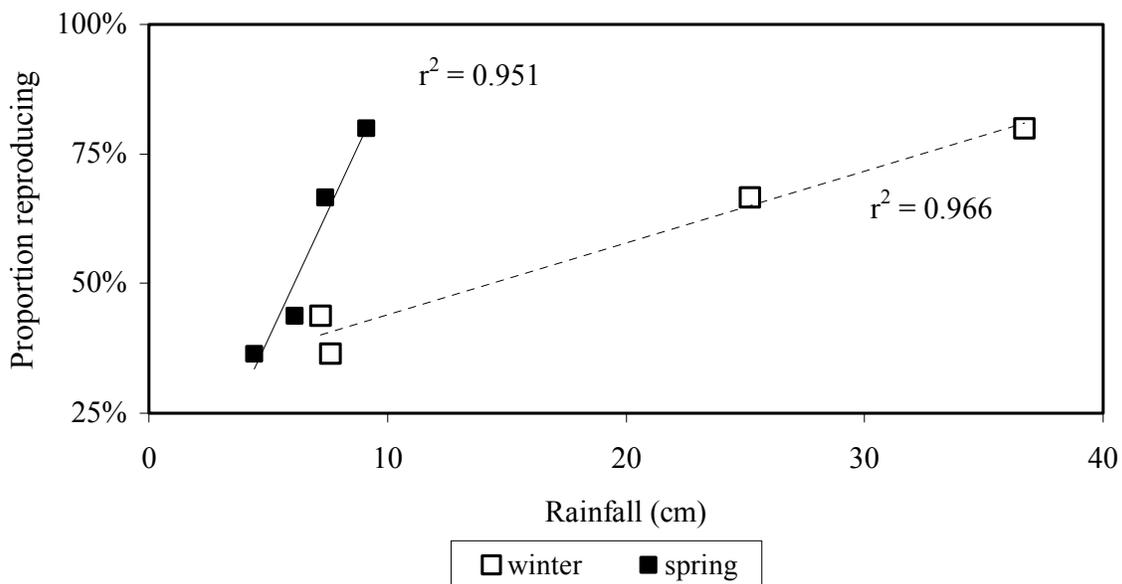


Figure 7. Clutch frequency vs seasonal rainfall for Sugarloaf desert tortoises. Winter = November – February; Spring = March – April.

BODY SIZE

Reproductive females averaged 247 (± 12.9) mm MCL in 1993 to 260 (± 16.8) mm in 1999 (Table 5). The smallest reproductive females in the study ranged from 220 mm MCL in 1993 to 239 mm in both 1997 and 1999 (Table 5). Mean body size of reproductive females was not significantly correlated with seasonal rainfall ($P \geq 0.146$), but minimum reproductive size was negatively correlated with winter rainfall ($r = -0.997$, $t_4 = 17.23$, $P = 0.003$; Fig. 8), nearly so with spring rainfall ($r = -0.937$, $t_4 = 3.79$, $P = 0.063$; Fig. 8), and not with prior summer rainfall ($P = 0.152$). These rainfall effects resulted in a negative correlation between minimum reproductive size and clutch frequency ($r = -0.977$, $t_4 = 6.41$, $P = 0.023$).

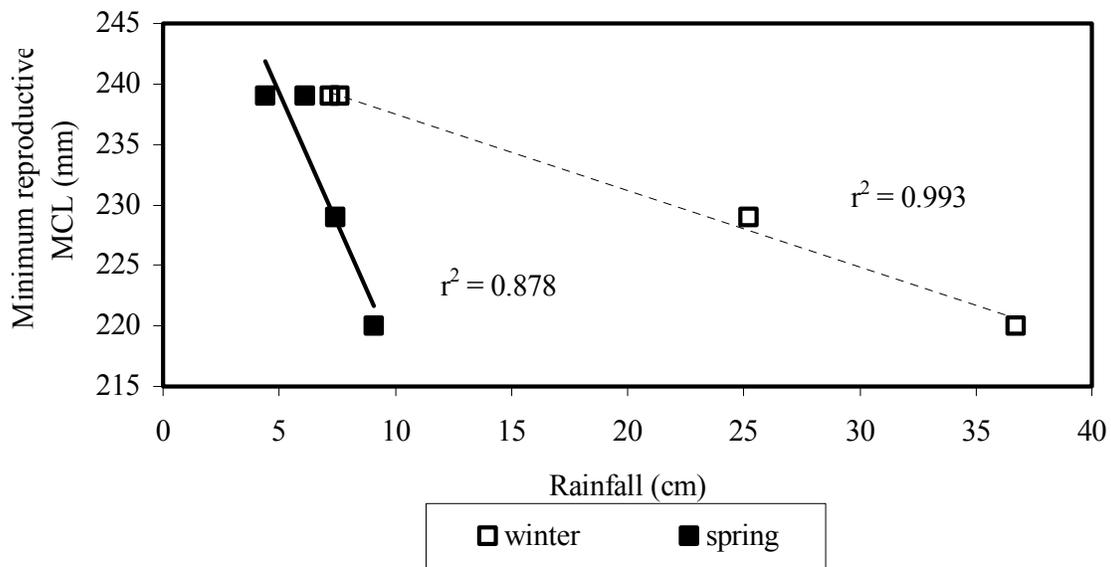


Figure 8. Minimum size of reproductive female desert tortoises vs seasonal rainfall at Sugarloaf. Winter = November – February; Spring = March – April.

CLUTCH AND EGG SIZE

Mean clutch size ranged from 3.8 (± 1.26) eggs in 1997 to 5.7 eggs in both 1993 (± 2.43 eggs) and 1998 (± 1.49) (Table 5). ANCOVA revealed no relationship between clutch size and year ($P = 0.122$) or female body size ($P = 0.315$; Fig. 9), but the correlation between mean clutch size and seasonal rainfall approached significance for spring ($r = 0.937$, $t_4 = 3.80$, $P = 0.063$). Mean clutch size was not correlated with winter ($P = 0.120$) or summer rainfall ($P = 0.408$). Increased summer rainfall appeared to result in increased variability (standard deviation) in clutch size, however ($r = 0.995$, $t_4 = 13.92$, $P = 0.005$).

Annual mean egg width ranged from 34.9 (± 1.18) mm in 1997 to 36.2 (± 2.12) mm in 1999 (Table 5). ANCOVA showed that individual females' mean egg width was not related to year ($P = 0.410$), but larger females laid larger eggs than smaller females ($F_{1,26} = 24.64$, $P = 0.000$; $r = 0.680$, $t_{31} = 5.00$, $P = 0.017$; Fig. 9). Egg width was not correlated with clutch size ($P = 0.065$) or seasonal rainfall ($P \geq 0.599$).

NESTS

In 1997 and 1998, we attempted to find as many nests at Sugarloaf as possible and monitor them to determine their outcome. We only found nests laid inside burrow entrances. Of 4 nests laid in 1997, 3 appeared to have been destroyed by predators; 1 (which was never found) had an unknown outcome. Of the 13 clutches laid in 1998, we confirmed 4 nests inside burrows and

suspected 2 others based on the females' occupation of the same burrows for several weeks after ovipositing (Murray and others, 1996); we were unable to find the remaining 7 nests. Of the 4 confirmed nests, 2 appeared to have been destroyed by predators, and 2 appeared to have successfully hatched. We observed 2 hatchlings in 1 of these nests between 15 and 29 October 1998. The last hatchling (43.5 mm MCL, 16 g) was observed leaving the nest on 29 October.

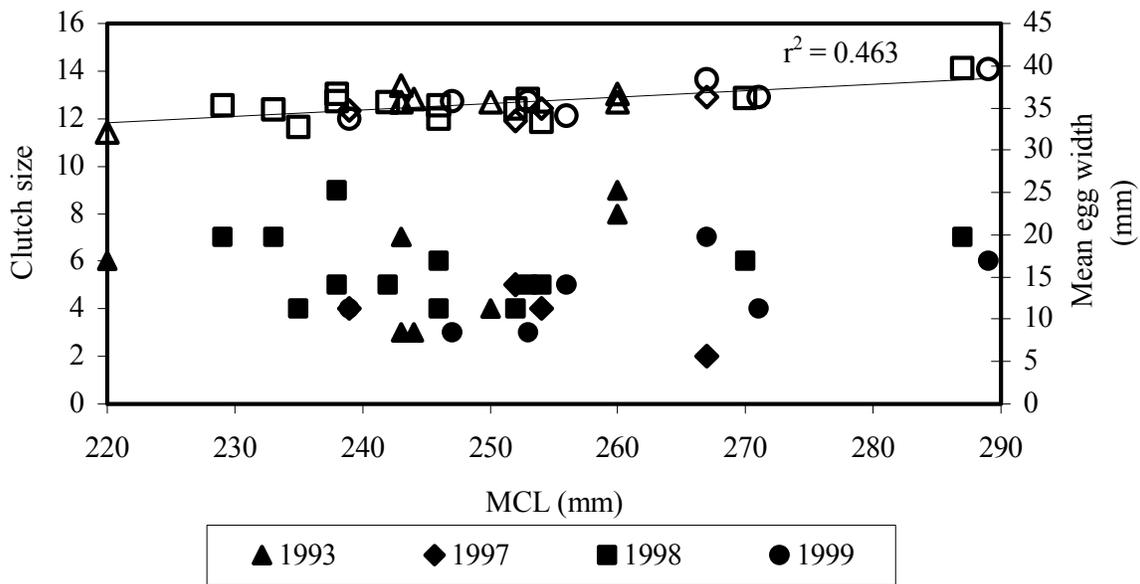


Figure 9. Clutch size (closed symbols) and mean egg widths (open symbols) vs midline carapace length (MCL) for Sugarloaf desert tortoises.

GRANITE HILLS

Four of 16 females radiographed at the Granite Hills (MCL ranged from 172-249 mm; 9 \geq 220 mm) were found to be gravid (Table 7). Since these tortoises were not telemetered and we were unable to locate the same tortoises each week, we make no estimates of clutch frequency or the proportion reproducing in the population. Oviposition would have occurred as early as late June to early August, based on dates on which eggs were visible on radiographs (Table 7). Reproductive females ranged from 226-249 mm MCL (mean = 236 \pm 10.6; Table 7). Clutch size was unrelated to female body size ($P = 0.917$), and mean egg width was unrelated to clutch size ($P = 0.540$) (Table 7). The positive correlation between mean egg size and female body size approached significance for this small sample ($r = 0.90$, $t_4 = 2.86$, $P = 0.104$).

ID	MCL (mm)	Clutch size	Mean egg width (mm)	Eggs visible
126	226	5	32.1	4 Jun-10 Jul
164	229	2	30.1	19 Jun
125	240	1	32.3	23 Jul-7 Aug
205	249	5	35.0	4-19 Jun
Mean (SD)	236 (10.6)	3.3 (2.06)	32.4 (2.01)	---

DISCUSSION

Virtually nothing is known about reproduction in *Gopherus agassizii* in the southern half of its range in Mexico (Germano 1994a), as its habitat grades from the Sonoran Desert through Sinaloan thornscrub and into Sinaloan deciduous forest (Germano and others 1994). Reproductive output is highly variable throughout the southwestern U.S., however, both within and among populations. Individual variation within the unpredictable environments of the Mojave and Sonoran deserts can obscure underlying patterns and life history characteristics (*cf.* Gibbons and Greene 1990), but the current study reinforces some conclusions derived from previous work in the Mojave Desert. It also suggests important intraspecific differences in life history strategy between the 2 deserts.

Winter rainfall and subsequent spring annual plant production can influence mean clutch frequency (Turner and others 1986) and annual egg production (Henen 1994) in the Mojave Desert through the amount of energy available from forage. However, simple correlations between environmental condition and reproductive output do not always occur (Karl 1998; Mueller and others 1998). Reproductive output reaches asymptotic levels and may be constrained by other factors, such as body size and maternal nutrient reserves, in especially productive years (Wallis and others 1999). Mojave females typically lay 1-2 clutches (occasionally 3) each year (*op. cit.*); most lay at least some eggs even following relatively dry seasons by sacrificing nutrient reserves and body condition (Henen 1997). The extent that reserves are expended for reproduction can also affect energy available for egg production the next year (Henen 1997).

No tortoise laid more than a single clutch during any year of the current study, and most skipped reproduction completely during at least 1 year. The proportion of females reproducing during a given year was correlated with prior winter and spring rainfall (and presumably subsequent plant production). Neither clutch nor egg size was clearly related to seasonal rainfall, although a marginally non-significant correlation suggests that relatively wetter springs with abundant forage may allow reproductive females to produce more eggs that year. Annual variability in clutch size was correlated with summer rainfall the previous year. Ongoing study should help resolve relative contributions of seasonal rainfall and plant production to reproductive output, especially since more rain fell in summer 1999 than in any year other than the first of the study

(Table 4), almost no rain fell during winter 2000, and substantial rain fell in early spring 2000 (unpubl. data).

Maternal body size of *G. agassizii* in the Mojave Desert affects reproductive output in various ways, including clutch frequency (Turner and others 1986; Karl 1998; Wallis and others 1999), clutch size (Turner and others 1986; Karl 1998; Mueller and others 1998; Wallis and others 1999), total annual egg production (Karl 1998; Mueller and others 1998; Wallis and others 1999), and egg size and clutch volume (Wallis and others 1999). Interestingly, Wallis and others (1999) found that the size of the first clutch, but not the second, was correlated with body size, while Karl (1998) found the opposite pattern. Physical constraints of a female turtle's shell limit the maximum number of eggs she can carry (Congdon and Gibbons 1987), but female size otherwise usually explains relatively little variation in clutch size within populations (Wilbur and Morin 1988; *op. cit.*). In fact, we found no relationship between body size and clutch size in our study. Female body size affected clutch frequency (0 or 1) at Sugarloaf in that smaller tortoises failed to produce eggs following dry seasons, but still not all large females reproduced every year. Larger females did lay larger eggs, though there was much unexplained variation ($r^2 = 0.462$).

Ovarian follicles of *G. agassizii* in the Mojave Desert mature to near-ovulatory size prior to hibernation (Rostal and others 1994). Thus, Mojave tortoises emerge from hibernation almost ready to lay eggs. Smaller tortoises tend to lay their clutches later in the spring than larger tortoises, probably because small tortoises have relatively less nutrient reserves, relying more on spring forage to obtain energy for egg production (Wallis and others 1999). Large females may benefit by having greater reserves to produce eggs shortly after emerging from hibernation and then still have time during the nesting season to lay a second or third clutch, at least during favorable conditions. Ovarian follicles do not mature until after hibernation at Sugarloaf (unpubl. data), and ovulation does not typically occur until May or June when Mojave tortoises are already laying their first clutches. Oviposition at our sites occurred near the onset of the summer rainy season, from June through August, so all females had the opportunity to forage during the spring before egg-laying. It remains unclear why larger females tended to lay their eggs later than smaller tortoises, but again there was a great deal of variation ($r^2 = 0.194$); additional study may prove that this initial correlation was spurious. Late oviposition dates at Sugarloaf in 1998 and 1999 suggest that some hatchlings may overwinter in the nest before emerging.

DERIVED MOJAVE CHARACTERISTICS

The fossil record suggests that *G. agassizii* evolved in a more mesic climate, and the formation of the current Sonoran and Mojave deserts during glacial climates 9,000-10,000 years ago left tortoises in an increasingly dry and unpredictable environment (Van Devender, *in press*). Mean winter rainfall values broadly overlap between the Mojave and Sonoran deserts, but summer rainfall decreases from the Sonoran Desert, through the eastern Mojave, to the extremely dry western Mojave (Turner 1982; Turner and Brown 1982; Germano 1994b; Wallis and others

1999). If we assume that Sonoran tortoises are most similar to the ancestral *G. agassizii* stock, we can form hypotheses for the evolution of derived reproductive traits in Mojave tortoises.

Females as small as 220 mm MCL produced eggs in our study. The minimum recorded size at first reproduction in the western Mojave Desert is 176 mm MCL (Germano 1994a) and 180 mm in the eastern Mojave (Karl 1998). Though precise data on growth are lacking across the range of the desert tortoise, Mojave tortoises also appear to mature at earlier ages than Sonoran tortoises (Germano 1994a). Adult survival appears to be similar between the 2 deserts (Howland and Klug 1996; FWS 1994), but the small size of hatchlings and juveniles might predispose them to lower average survival under the harsher conditions of the Mojave Desert. Therefore, earlier maturation and production of offspring in Mojave tortoises might balance higher juvenile mortality compared to Sonoran tortoises (*cf.* Stearns 1992:123-124).

Sonoran tortoises investing their entire reproductive output in a single clutch during the relatively predictable summer rainy season may produce hatchlings that experience greater survival than those in the Mojave Desert. Limited data from this study suggest a high rate of nest predation, but no data exist on hatchling survival in the Sonoran Desert. Drier conditions in the Mojave Desert may have resulted in tortoises adaptively producing a second and sometimes third clutch, thus maximizing the chance that at least some hatchlings will emerge coincident with favorable conditions. If this is true, hatchling cohorts from the same year but different clutches should exhibit differential average survival rates.

Tortoises in the eastern Mojave Desert produce relatively smaller eggs, produce more eggs overall, and lay their second clutches earlier than tortoises in the western Mojave Desert (Wallis and others 1999). Tortoises in the Sonoran Desert produce even smaller eggs relative to their body size than in the eastern Mojave (Fig. 10), but they produce fewer eggs overall. Average annual egg production ranged from only 3.3 to 5.7 eggs/female at our Sonoran sites, compared to 4.9 (in a drought year) to 8.4 in the eastern Mojave (Karl 1998; Wallis and others 1999) and 7.0-7.1 in the western Mojave Desert (Wallis and others 1999). Increasing relative egg size from east to west, through an increasingly dry summer climate, may have improved reproductive success, because eggs in the eastern and western Mojave Desert are more likely to hatch during unfavorable conditions (Murray and others 1996; Wallis and others 1999). Greater parental investment per offspring could provide nutrient reserves necessary to survive both a harsh summer with limited rainfall and then the following winter. Smaller hatchlings toward the east are more likely to have an opportunity to forage before entering hibernation and to require less nutrient reserves to survive their first winter than hatchlings in the western Mojave Desert (Wallis and others 1999). Late-hatching tortoises in the western Mojave, compared to the eastern Mojave, could also better conserve their larger nutrient reserves for surviving through winter (Wallis and others 1999). This hypothesis fits within the central idea on evolution of offspring size, that the trade-off between number and size of young should be at evolutionary equilibrium when the gain in parental fitness of adding 1 more offspring is less than the overall decrease in fitness due to lowered success of each individual offspring that results from lower investment per offspring (Stearns 1992). Mojave tortoises increased their fitness in an increasingly unpredictable

(or predictably harsher) environment by increasing both the size and number of offspring. As the Mojave Desert continued to dry to the west, larger egg and hatchling size may have become adaptive to survive even harsher conditions than in the eastern Mojave (Morafka 1994), while balanced by slightly reduced clutch size.

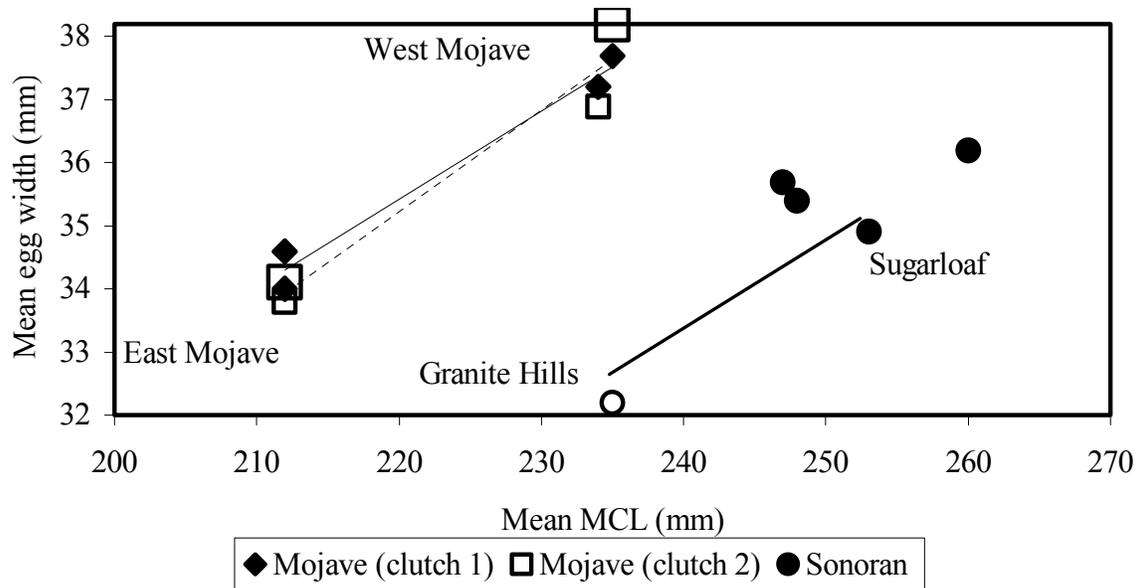


Figure 10. Mean egg width vs mean midline carapace length (MCL) for Mojave and Sonoran desert tortoises. Mojave Desert data are from 2 populations, 1992-93 (Wallis and others 1999). Trend lines are for Mojave clutch 1 (solid symbols and line) and Mojave clutch 2 (open symbols and dashed line) for combined years and 1997 clutches for Sonoran sites (bold).

REPRODUCTIVE STRATEGIES

Deserts are inherently unpredictable environments with high variation in resource availability. An organism might maximize its fitness in such a highly variable environment by increasing reproductive events at reduced cost to increase the number of offspring born into good conditions (“bet-hedging” strategy: Stearns 1992; Kuchling 1999). Mojave tortoises have adopted this strategy by producing multiple annual clutches, when resources allow, so at least some hatchlings might emerge during less predictable favorable conditions (Wallis and others 1999).

Reproductive strategies may also be classified according to relative use of “income” or “capital” energy sources (Stearns 1992). Capital breeders rely on stored energy for reproduction, while income breeders use energy acquired during the reproductive period. Closely related species inhabiting environments of varying predictability may exhibit differing reproductive strategies.

For example, 3 species of chelid freshwater turtles in western Australia have varied strategies depending on their microhabitat (Kuchling 1999). The narrow-breasted snakeneck turtle *Chelodina oblonga*, which lives in (semi-) permanent aquatic habitats, initiates its reproductive cycle 8 to 10 months prior to the breeding season when vitellogenesis starts and produces eggs regardless of environmental conditions, according to the capital breeding strategy. Steindachner's snakeneck turtle *C. steindachneri* occurs in more arid regions of western Australia in ephemeral river pools that may only contain water for 4 to 6 weeks at a time; rains are infrequent and unpredictable. In addition to aborting reproduction during poor conditions, *C. steindachneri* can delay reproduction many months at either the ovulation or oviposition stages until conditions become suitable. The western swamp turtle *Pseudemydura umbrina*, which inhabits seasonal, ephemeral swamps, may also abort reproduction in the short term if environmental conditions are unsuitable, but different reproductive characteristics of *P. umbrina* fall near either extreme of the capital-income spectrum. *P. umbrina* allocates energy to follicles in most years when the females are dormant and not feeding (capital strategy), but they only produce eggs after amassing energy at a high rate just prior to the nesting season (income strategy).

G. agassizii has apparently adapted different strategies depending on regional climate. Sonoran tortoises generally follow the income breeding strategy of producing eggs only after acquiring a certain, unknown amount of energy; otherwise, they skip reproduction completely. The bet-hedging approach of Mojave tortoises fits within the capital breeding strategy of usually investing at least a little energy every year to produce at least a few eggs. The degree to which patterns of investment in vitellogenesis parallel those of ovulation in desert tortoises (or not, as in *P. umbrina*) relative to the capital-income breeding paradigm requires further research.

COMPARISONS WITH OTHER *GOPHERUS*

The Texas tortoise *Gopherus berlandieri* occurs at low elevations in habitats ranging from near-desert in Mexico to Tamaulipan thornscrub in humid and subtropical parts of southern Texas (Ernst and others 1994). Female *G. berlandieri* mature as early as 140 mm MCL (Judd and Rose 1989) at around 11 to 17 years of age (Germano 1994a). *G. berlandieri* is the smallest of the 4 species of North American tortoises, rarely exceeding 180 mm MCL (Rose and Judd 1991; Germano 1994b). *G. berlandieri* lays correspondingly small clutches of 1 to 7 eggs (annual means range from 1.4 to 4.3) and probably lays a single clutch per year, although about 1/3 may not reproduce during a given year (Judd and Rose 1989). The eggs are relatively large (about 34.1 mm wide: Judd and Rose 1989), and can only be passed from the body through an enlarged pelvic girdle opening made possible by a xiphiplastral-hyoplastral hinge (Rose and Judd 1991). Neither clutch size nor egg size increase with female body size, but egg length was negatively correlated with clutch size (Judd and Rose 1989). Nothing has been reported on reproduction from the Mexican part of the range.

The gopher tortoise *Gopherus polyphemus* occurs in the southeastern U.S. on well-drained sandy soils of pine-oak, beach scrub, oak hammocks, or pine flatwoods (Ernst and others 1994). *G. polyphemus* is relatively large compared to *G. agassizii* and *G. berlandieri* (Germano 1994b).

Females mature at 220 to 265 mm MCL (10-21 yrs), with minimum size and age at maturity generally increasing as mean body size increases from south to north (Germano 1994a). Mean clutch sizes typically range from 5 to 9 eggs throughout its distribution (Germano 1994a). *G. polyphemus* lay a single clutch throughout the range (Germano 1994a), but <75% of all females may reproduce every year (Diemer and Moore 1994). Egg width is usually around 41 mm (Ernst and others 1994), but eggs from a northern population were larger than those from a southern population due to body size differences (Landers and others 1980). Clutch size also increases with body size within populations but is highly variable (Landers and others 1980; Smith 1995).

The Bolson tortoise *G. flavomarginatus* occurs in the arid Chihuahuan Desert of northeastern Mexico (Morafka 1982). Virtually nothing is known about reproduction in *G. flavomarginatus* (Germano 1994a), but the majority of wild females (56%) apparently do not lay eggs in any given year (Adest and others 1989). Minimum age and size at maturity are unknown but are probably greater than for other *Gopherus*, since this is the largest species within the group (Germano 1994b). Data from captive individuals indicate that clutch size ranges from 3 to 9 eggs (mean = 6), females may lay up to 3 clutches in a year, and maximum annual egg production may reach 16 eggs/female (Morafka 1982). Females in the wild may have a lower mean clutch frequency of about 1.4 (Adest and others 1989).

Annual precipitation levels are highest for *G. polyphemus* and *G. berlandieri* among the 4 species within the genus (Germano 1994b). Rainfall is somewhat lower within the range of *G. flavomarginatus* and is usually concentrated during the summer months, even more so than Sonoran *G. agassizii*. Even though annual rainfall is fairly high, *G. berlandieri* occupies the most variable and unpredictable environment with respect to precipitation. *G. polyphemus* experiences relatively constant rainfall throughout the year (Germano 1994b).

Incomplete data preclude a thorough analysis of life history evolution within the genus, but a few patterns are apparent. Most obvious is the fact that all *Gopherus*, like other turtles, are characterized by delayed reproduction, longevity, and iteroparity. Survival of eggs, hatchlings, and juveniles is low (Germano 1994a). Sonoran *G. agassizii*, *G. polyphemus*, and *G. berlandieri* all appear to share an income-breeding strategy in which they produce a single clutch of eggs under relatively wet and productive environmental conditions; individuals may skip reproduction during unfavorable years. Although data are limited, *G. flavomarginatus* may have adopted an intermediate strategy with individuals withholding reproduction during unfavorable years (income strategy) but hedging their bets against the uncertainty of future conditions by producing multiple clutches when conditions improve. Finally, the more extreme and unpredictable environments of the Mojave Desert resulted in Mojave *G. agassizii* adopting the capital-breeding strategy of usually investing some energy into reproduction every year.

CHAPTER 4
DESERT TORTOISE ACTIVITY, BEHAVIOR, AND HOME RANGES

INTRODUCTION

Only a few short-term studies on Sonoran desert tortoises have described their activity, behavior, and home ranges in detail. Much anecdotal information on activity and behavior has been obtained from the monitoring plot surveys described in Chapter 1, but these observations were opportunistic and concentrated during the summer. Vaughan (1984) conducted the first intensive study of Sonoran desert tortoises with radio telemetry and quantified home range and habitat use over a 2-year period in the Picacho Mountains, Pinal County, Arizona (see also Barrett 1990). Bailey (1992) described hibernaculum use and home range of tortoises in another 2-year study on the western slope of the Galiuro Mountains, Pinal County (see also Bailey et al. 1995). Murray and others (1995) reported 2-year home ranges of female tortoises in their reproduction study in the Mazatzal Mountains, Maricopa County. Martin (1995) reported on aspects of all these topics from another 2 years of telemetry data from the Tortolita Mountains, Pinal County, as did McLuckie and others (1996) from the Black Mountains, Mohave County. The Black Mountain study site actually occurs within the Mojave Desert, but within the Sonoran population of desert tortoises as defined by FWS (1990). This chapter builds specifically on the work reported by Murray and others (1995) by quantifying tortoise home ranges for the 4-year period from 1996 to 1999 and activity and behavior from 1992 to 1993 and 1996 to 1999 at the same site in the Mazatzal Mountains.

METHODS

The data in this chapter come from the same tortoise population described in Chapter 3, near Sugarloaf Mountain on the Tonto National Forest, Maricopa County. As in the reproduction study, we summarized annual rainfall data according to 3 seasons defined by average environmental conditions and tortoise activity. Summer includes July through October, winter includes November through February, and spring includes March through June.

We primarily monitored female tortoises (184-289 mm MCL) each week throughout the year using radio telemetry, but some males were also included in the study during various times (methods as described in Chapter 3). We uniquely marked all tortoises found on the site according to the system developed by Ernst and others (1974). Each time we located a tortoise, we noted its activity. We considered tortoises "active" if found outside a shelter, in an unmodified cover site (that is, lacking any evidence of digging or "settling in," usually under a tree, shrub, or rock), or actively digging a nest or burrow. We considered tortoises "inactive" if found inside a shelter. We found most active tortoises motionless, but we noted other behaviors as follows: courting, mating, combat, digging, walking, drinking, and foraging. We also noted evidence of recent foraging by each tortoise, if their beaks were stained with plant material. We often found tortoises basking, with their limbs extended in full sun and occasionally asleep, but

we do not attempt to quantify the behavior here due to frequent uncertainty as to whether a tortoise was actually basking or sitting motionless. We defined spring (SpAI) and summer (SuAI) activity indices as the number of “active” observations plus the number of times a tortoise changed locations from the previous week within each season.

We continued to monitor telemetered tortoises weekly through the winter and determined hibernation onset, end, and duration. We defined hibernation onset as the first date in late summer/winter after which a tortoise did not emerge from a shelter for >14 days. We defined hibernation end as the last recorded day a tortoise was observed inside or <10 m from its hibernaculum. Some tortoises moved during the winter, so we defined each winter shelter as a separate hibernaculum for that year if they met the onset and end definitions above. Hibernation duration includes the number of days between onset and end (from first to last hibernaculum), less the number of days between different hibernacula. We measured the depth of each hibernaculum to the nearest cm with a metal tape measure and used a compass to determine the aspect of the slope on which each hibernaculum was located with a compass. We also coded aspect categorically as north- or south-facing and east- or west-facing, after correcting for magnetic declination, as follows: N = 257-76° or S = 77-256° and E = 347-166° or W = 167-346°. By placing sticks upright at the entrance of each hibernaculum, we also quantified winter activity; we defined “winter activity index” (WAI) as the number of times a tortoise changed locations between weekly visits plus the number of times the hibernaculum sticks were knocked down.

We recorded each tortoise’s position with a global positioning system receiver (Basic+ or GeoExplorer II, Trimble Navigation Ltd.), post-processed the data for accuracy with Pathfinder Office (Trimble Navigation Ltd.), and mapped the locations with ArcView GIS 3.2 (Environmental Systems Research Institute, Inc.). We marked burrows with individually numbered aluminum tags epoxied to rock faces above the burrow or wired to overhanging shrubby cover. We generally only marked relatively permanent burrows, defined as modified shelters $\geq 1/2$ the tortoise’s shell length. We did not include pallets (shallow, scraped out areas <1/2 tortoise length), boulder piles, or other temporary shelters unmodified by the tortoise (for example, trees, shrubs, or rocks). We estimated minimum convex polygon (MCP) home ranges with the Animal Movement extension to ArcView (Hooge and Eichenlaub 1997). Other home range studies have applied Jennrich and Turner’s (1969) correction for sample size bias to MCP estimates (for example, Barrett 1990), but Rautenstrauch and Holt (1995) reported that this correction routinely overestimated home range size, sometimes as much as 200%. Because of this overestimation and the fact that our MCP estimates were uncorrelated with sample size, we chose not to apply this correction factor.

We conducted statistical analyses with Statistica ’99 (StatSoft 1999). Since we monitored few males, all analyses include females only. We examined most potential patterns by year with analysis of covariance (ANCOVA) or correlation analysis. We compared differences in seasonal activity indices with repeated measures analysis of variance (ANOVA) categorized by year. We investigated effects of season and seasonal rainfall on activity with logistic regression; we used

the best subsets search method and evaluated model fit with the Akaike Information Criterion (StatSoft 1999). We examined seasonal patterns of burrow use with ANOVA, with season nested within year, and used Bonferroni's test to determine significant differences between seasons. For circular data, we tested the significance of mean angles by hand with Rayleigh's test and evaluated combined annual results with a X^2 test (Batschelet 1981). We used circular-linear rank correlation (Batschelet 1981) to test the relationship between hibernaculum depth and slope aspect; we combined all years but deleted multiple uses of individual hibernacula for this test. We considered results significant at $P < 0.05$ and report all means ± 1 standard deviation (SD), or ± 1 angular deviation (s) for circular data.

RESULTS

ACTIVITY AND BEHAVIOR

We recorded 3473 observations of female tortoises from September 1991 – September 1993 and April 1996 – December 1999; 3442 of these observations were of telemetered individuals (plus initial captures of individuals receiving a transmitter). We recorded 282 observations of male tortoises and 36 observations of juvenile tortoises during the same period. Inactive (inside shelters) observations accounted for 84%, 67%, and 8% of all observations for female, male, and juvenile tortoises, respectively. The decreasing proportions of inactive tortoises for males and juveniles reflect the difficulty of finding well-hidden tortoises without the aid of radio telemetry rather than actual differences in activity levels between groups. Untelemetered tortoises, especially juveniles, are much more easily found when outside.

Logistic regression revealed a significant interaction between season and rainfall affecting female tortoise activity ($P = 0.000$; Fig. 11). Observations of active tortoises increased with increasing rainfall in both spring and winter, but more dramatically in spring, and showed no strong trend relative to rainfall during summer (Fig. 11). Overall, tortoises appeared to be about twice as active in summer than in spring (Fig. 12, Table 8). Little activity occurred during the winter, but we observed some activity in all months. Monthly activity of females was low through winter, increased to 25% in March, but gradually declined through the spring to 11% in June (Fig. 13). Activity increased again during the summer monsoon season, peaking at 35% in August. The general pattern was similar for males, but the spring peak occurred a month later at 54% in May (Fig. 13). We typically found only active juveniles, so relative seasonal activity of juveniles remains unclear (Fig. 13).

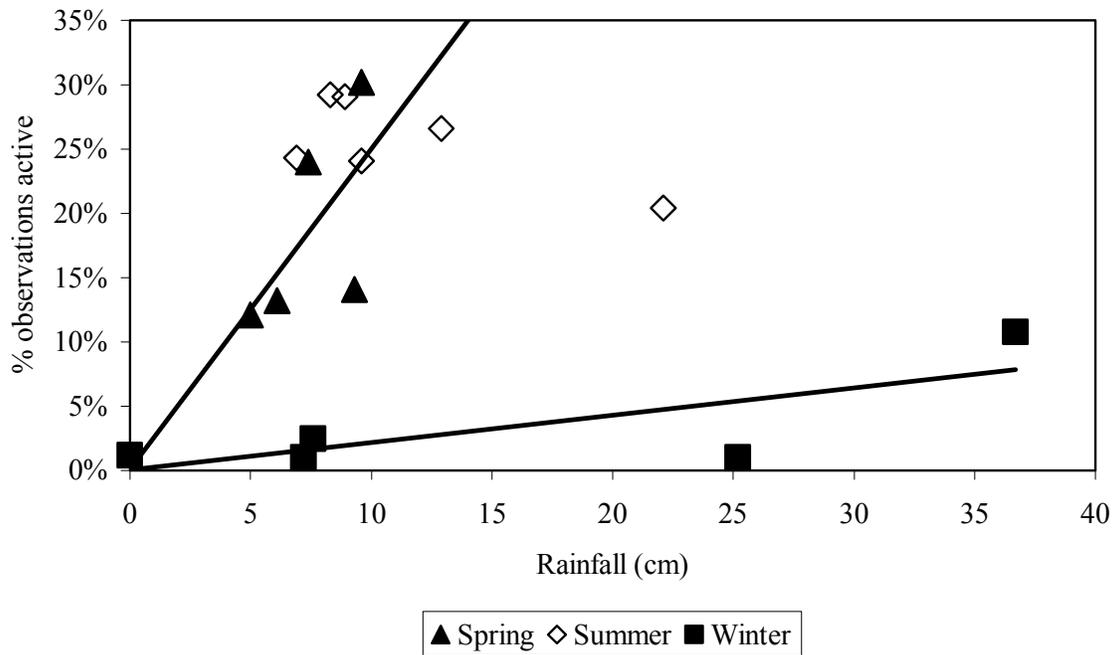


Figure 11. Seasonal activity of female desert tortoises at Sugarloaf vs rainfall. Spring = March-June, Summer = July-October, Winter = November-February.

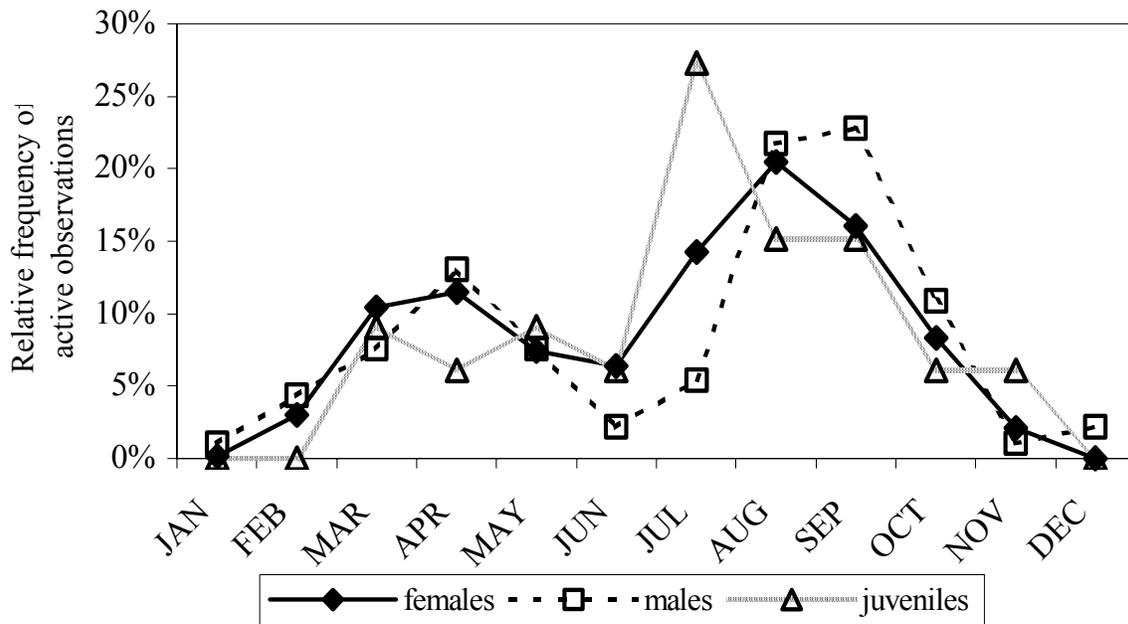


Figure 12. Frequency of active tortoise observations each month at Sugarloaf relative to total number of active observations (567, 92, and 33 for females, males, and juveniles, respectively), all years combined.

	Spring	Summer	Winter	Total active obs.
Females	36% (202)	59% (335)	5% (30)	567
Males	30% (28)	61% (56)	9% (8)	92
Juveniles	30% (10)	64% (21)	6% (2)	33

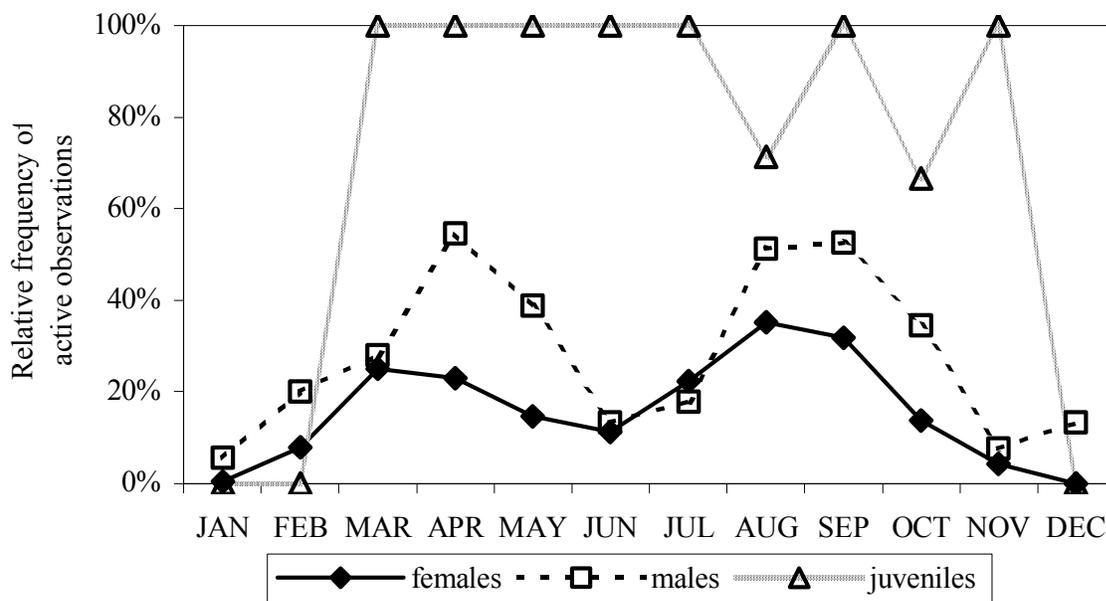


Figure 13. Relative frequency of active tortoise observations each month at Sugarloaf, all years combined.

Activity indices revealed similar patterns, although differences in spring and summer activity were not as striking (Table 9). Repeated measures ANOVA revealed significant differences between seasons ($F_{3,35} = 448.47, P = 0.000$) but not between years ($F_{6,70} = 1.15, P = 0.342$). Both SpAI and SuAI were obviously greater than WAI, and SuAI was slightly greater than SpAI each year, especially so in 1999 (Fig. 14).

Even of the “active” observations, most tortoises were simply sitting (or basking, which we did not distinguish here). Of those not stationary, most were walking or foraging (Table 10). Seasonal patterns of the frequency of tortoises found walking or foraging generally followed those illustrated in Figure 12, peaking in the spring during April, then with larger peaks during the summer monsoon season (Table 10). We observed 2 instances of courtship and mating, both

during the summer, and we observed tortoises drinking from puddles or the ground surface (5 instances) both during spring and summer (Table 10). We observed 4 tortoises actively digging burrows or nest cavities (Table 10).

A closer look at the foraging observations reveals that while tortoises were less active during spring than summer, they spent similar amounts of time foraging in each season, based on our weekly observations (Table 10, Fig. 15). The frequency of foraging observations of female tortoises peaked during summer with 28% in September, but observations of foraging plus tortoises with food in their beaks or with stained beaks peaked in spring with 18% in April (Fig. 15). Overall, we found tortoises actively foraging 36 times in spring and 46 times in summer, but we recorded tortoises with food or stained beaks 414 times in spring and 392 times in summer (Table 10). We identified approximately 20 food plants in our observations of tortoises foraging (Table 11).

Tort. #	1996	1997		1998		1999	
	Summer	Spring	Summer	Spring	Summer	Spring	Summer
1		9	13	14	10	13	18
3	8	15	6	15	9	14	
14					16	12	14
17				14	8	14	7
25	13	14	14	11	15		
29		13	14	14	11	11	6
46		15	17	10	17	12	18
51		9	17	11	18	8	
55		10	16	10	12		
56				16	16	8	17
57		9	14	7	12	1	14
58		16	16	12	15	10	17
61		16	14	12			
63		15	14	17	12	12	18
65		10	11	14	12	4	17
66				7	13	8	13
67				13			
68				10	12	13	18
71							20
73						11	16
77				15	16		
80				16			
81				10	16	11	15
Mean		12.6	13.8	12.4	13.3	10.1	15.2
(SD)		2.94	3.01	2.87	2.89	3.59	4.00

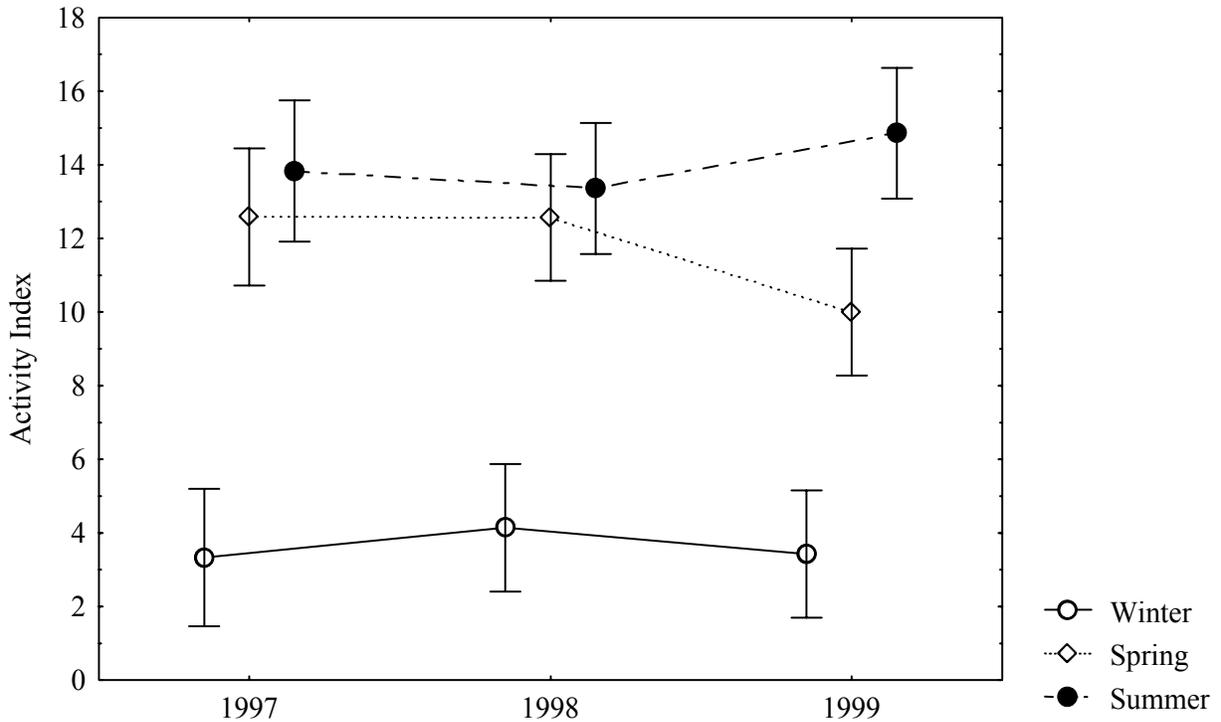


Figure 14. Mean seasonal activity indices (± 1 SD) for female desert tortoises at Sugarloaf, 1997-99.

Table 10. Frequency of behavioral observations of desert tortoises by month. Behaviors are coded as follows: 1 = courtship/mating; 2 = drinking; 3 = digging; 4 = walking; 5 = foraging; 6 = beak stained.

Behavior	J	F	M	A	M	J	J	A	S	O	N	D
1								1		1		
2		1		2				1	1			
3				1			1	1		1		
4			7	17	10	9	26	21	21	5	4	
5		1	6	15	11	4	10	10	23	3	2	
6		10	96	151	105	62	76	95	140	81	5	

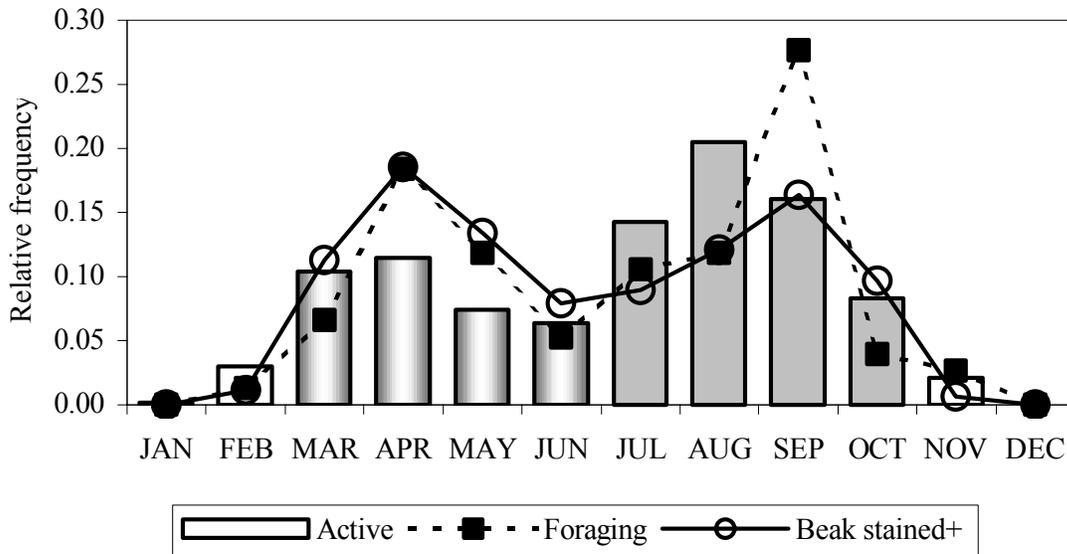


Figure 15. Relative monthly activity, foraging observations, and evidence of foraging for female desert tortoises at Sugarloaf, all years combined. “Active” includes all tortoises found outside a shelter each month, “Foraging” includes all observations of tortoises actively eating, and “Beak stained+” includes all foraging observations plus observations of tortoises with plant parts in their beaks and beaks stained with vegetative material. Winter is indicated by open bars, spring by banded bars, and summer by gray bars.

Table 11. Plant species observed to be eaten by desert tortoises at Sugarloaf. Asterisks indicate non-native species.		
<u>Trees and shrubs</u>	<u>Grasses</u>	<u>Spring annuals</u>
<i>Calliandra eriophylla</i>	<i>Bouteloua</i> sp.	<i>Cryptantha</i> sp.
<i>Eriogonum fasciculatum</i>	* <i>Bromus rubens</i>	* <i>Erodium cicutarium</i>
<i>Krameria</i> sp.	* <i>Schismus barbatus</i>	<i>Lepidium lasiocarpum</i>
<u>Subshrubs and woody vines</u>	dry/green grass, grass shoots	<i>Lupinus sparsiflorus</i>
<i>Janusia gracilis</i>	<u>Succulents</u>	<i>Plantago insularis</i>
<i>Lotus rigidus</i> , sp.	<i>Opuntia engelmannii</i> , dry flower	<u>Other</u>
<i>Sphaeralcea ambigua</i>	<u>Herbaceous perennials</u>	<i>Euphorbia</i> sp.
<i>Viguiera deltoidea</i>	<i>Avena filiformis</i>	

HIBERNATION

Hibernation parameters were highly variable (Table 12). Tortoises began hibernation in early to mid November on average, but the range included dates as early as 6 October 1998 and as late as 28 January 1998. Hibernation typically ended in mid March, but tortoises ended hibernation as

early as 4 February (1998) and as late as 24 June (1999). Mean hibernation durations ranged from 111-133 days, with individual durations ranging from 36 days (1997-98) to 262 days (1998-99).

Hibernaculum characteristics were even more variable than the temporal measures (Table 13). Mean female hibernaculum depths ranged from 94.6 to 114.3 cm over the 3 years of the study. Several tortoises hibernated in pallets with little cover other than shrubby overstory (coded as 0 depth in Table 13). The deepest hibernacula exceeded 350 cm. Tortoises hibernated on slopes of all aspects each year. Mean orientation was only significantly different from uniform in 1998-99 ($z_{15} = 6.46, P < 0.001$; Table 13), but the combined X^2 test revealed a significant southerly angle overall ($X^2 > 20, P < 0.003$). Hibernaculum depth was uncorrelated with slope aspect ($U_{32} = 0.93, P > 0.10$).

Tort. #	1996-97			1997-98			1998-99		
	Onset	End	Dur.	Onset	End	Dur.	Onset	End	Dur.
1	23 Oct	24 Apr	184	26 Nov	4 Mar	99	29 Oct	17 Feb	112
3	23 Oct	6 Mar	135	26 Nov	4 Mar	99	4 Nov	24 Feb	100
14							18 Nov	24 Mar	127
17					11 Mar		12 Nov	24 Feb	105
25	13 Nov	6 Mar	114	12 Nov	17 Apr	157	18 Nov	16 Apr	150
29	29 Oct	6 Mar	129	19 Nov	4 Mar	106	29 Oct	24 Mar	147
46	23 Oct	13 Feb	87	26 Nov	18 Mar	113	24 Nov	17 Mar	114
51	29 Oct	17 Apr	158	29 Oct	17 Apr	171	4 Nov	16 Apr	164
55	29 Oct	29 Mar	143	26 Nov	17 Apr	143			
56				2 Dec	4 Mar	93	4 Nov	22 Apr	170
57	29 Oct	15 May	180	29 Oct	17 Apr	158	6 Oct	24 Jun	262
58	23 Oct	6 Mar	135	19 Nov	11 Mar	113	18 Nov	24 Mar	121
61	30 Dec	6 Mar	61	26 Nov	18 Mar	113			
63				6 Nov	25 Feb	112	18 Nov	24 Feb	99
65				12 Nov	25 Feb	106	9 Dec	13 May	156
66							4 Nov	24 Feb	113
67				12 Nov	18 Mar	114			
68				19 Nov	18 Feb	92	16 Dec	17 Feb	64
73							12 Nov	24 Feb	105
77				26 Nov	4 Feb	65	12 Nov	24 Feb	105
80				28 Jan	4 Mar	36			
81							12 Nov	7 Apr	147
26m		6 Feb							
49m	5 Dec	6 Mar	92						
76m				2 Dec	11 Mar	100			
Mean	3 Nov	22 Mar	133	22 Nov	14 Mar	111	12 Nov	23 Mar	131
SD	20.9	28.6	38.3	20.0	21.4	33.3	15.7	34.5	42.6

Table 13. Hibernaculum depth (cm) and aspect (deg), winter activity index (WAI), and # winter shelters (#WS) for tortoises at Sugarloaf. When tortoises used >1 hibernaculum, depth and aspect refers to that shelter used the longest. Underlined values between years indicate that the same hibernaculum was used each year. + indicates minimum depth measurable. Aspect is uncorrected for declination; mean aspects with * are significant at $P < 0.05$. WAI and #WS include data throughout the entire winter (November – February). Means include females only.

Tort. #	1996-97				1997-98				1998-99			
	Depth	Aspect	WAI	#WS	Depth	Aspect	WAI	#WS	Depth	Aspect	WAI	#WS
1	200+	278	0	1	17	322	2	3	50	---	5	2
3	<u>70</u>	<u>180</u>	4	1	350+	180	2	2	<u>70</u>	<u>180</u>	4	3
14									0	206	2	3
17					55	180			115	250	1	2
25	19	280	2	3	30	146	3	2	25	148	1	2
29	<u>47</u>	<u>240</u>	7	1	<u>47</u>	<u>240</u>	7	3	200+	240	6	1
46	165	230	6	5	80+	196	3	3	90+	---	3	3
51	<u>70±</u>	<u>40</u>	3	3	<u>70±</u>	<u>40</u>	0	1	0	160	1	1
55	---	160	1	1	0	230	3	4				
56					0	302	4	5	50	220	0	1
57	<u>200±</u>	<u>290</u>	0	1	<u>200±</u>	<u>290</u>	2	3	350+	180	6	1
58	80	80	10	1	<u>200±</u>	<u>290</u>	2	3	<u>200±</u>	<u>290</u>	2	2
61	0	---	7	7	67	346	2	3				
63					60	179	9	1	46	204	4	2
65					<u>180</u>	<u>135</u>	2	2	<u>180</u>	<u>135</u>	4	4
66									163+	224	1	1
67					100	7	5	4				
68					<u>200±</u>	<u>230</u>	11	4	<u>200±</u>	<u>230</u>	11	5
73									---	---	2	2
77					---	248	8	7	---	200		
80					0	270	9	8				
81									90	32	1	2
26m	48	170	9	6								
49m	0	330	5	5								
76m					0	225	---	5				
Mean	94.6	210	4.0	2.4	97.4	205	4.4	3.4	114.3	246*	3.2	2.2
SD, s	75.44	66.3	3.40	2.12	96.63	63.9	3.22	1.87	94.68	47.5	2.74	1.13

Finally, winter activity was also highly variable (Table 13). Winter activity indices ranged from 0-11, with annual means of 3.2-4.4. The number of winter shelters (including burrows, pallets, boulder piles, etc.) used by each tortoise ranged from 1-8, with means of 2.2-3.4.

ANOVA indicated that hibernation onset and hibernaculum depth were inversely related to each other relative to hibernation duration ($F_{1,32} = 8.28, P = 0.007$; Fig. 16). Tortoises that began hibernation earlier tended to have longer hibernation durations, while tortoises in deeper hibernacula also tended to hibernate longer. Tortoises hibernating on easterly-facing slopes

tended to hibernate longer than those on westerly-facing slopes ($F_{1,32} = 6.28, P = 0.017$; Fig. 17), but hibernation duration was not related to north/south-facing slopes ($F_{1,32} = 0.72, P = 0.401$) or year ($F_{2,32} = 1.19, P = 0.317$). The interaction illustrated in Figure 16 is a result of a significant negative relationship between hibernation onset and hibernaculum depth, but this relationship was influenced by 2-3 extreme observations ($F_{1,34} = 5.13, P = 0.030$; Fig. 18); hibernaculum depth was unrelated to year ($F_{2,34} = 0.84, P = 0.439$) or aspect ($F_{1,34} < 1.53, P > 0.225$). Mean hibernation duration was nearly significantly correlated with winter rainfall ($r = -0.9948, P = 0.065$), even though this preliminary test was only based on 3 seasons. WAI was unrelated to year ($F_{2,33} = 1.93, P = 0.162$) or depth ($F_{1,33} = 0.94, P = 0.340$), but tortoises hibernating on southerly-facing slopes were significantly more active than those on north-facing slopes ($F_{1,33} = 13.08, P = 0.001$; Fig. 19). WAI was positively correlated with the number of shelters used each winter ($F_{1,32} = 12.68, P = 0.001$). Hibernation duration and number of winter shelters were also negatively correlated ($r = -0.592, P = 0.000$; Fig. 20).

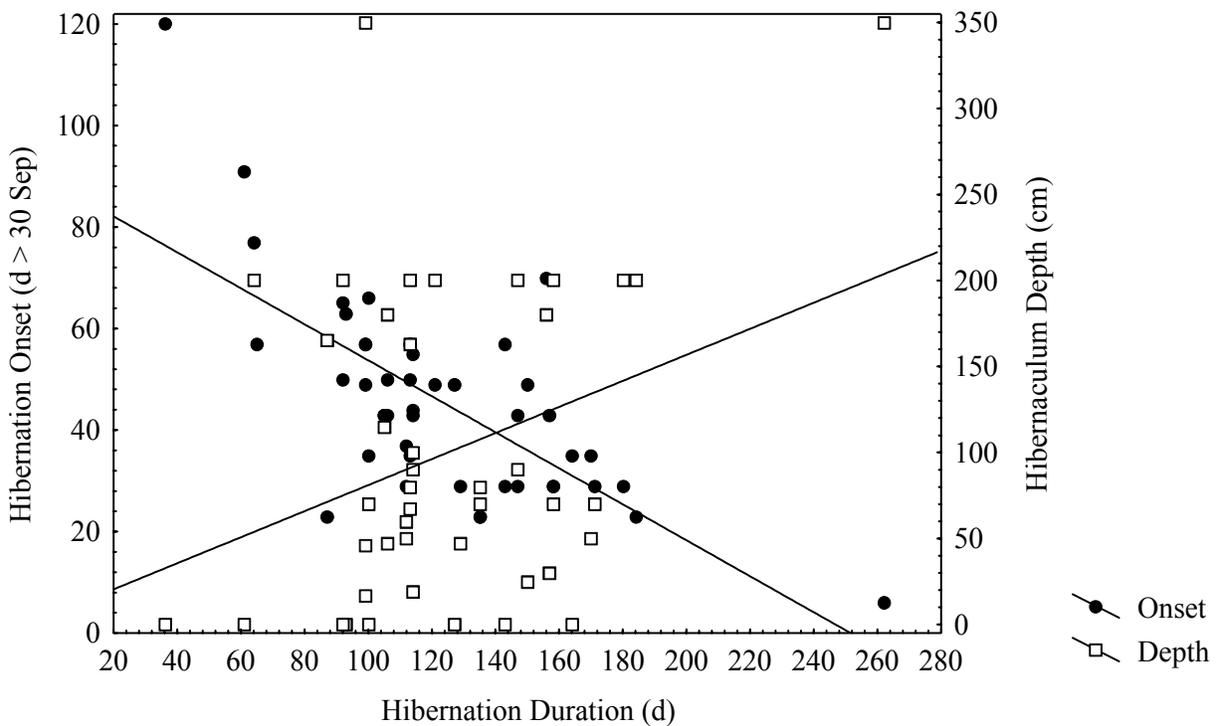


Figure 16. Hibernation onset and hibernaculum depth vs hibernation duration for female desert tortoises at Sugarloaf, 1996-99.

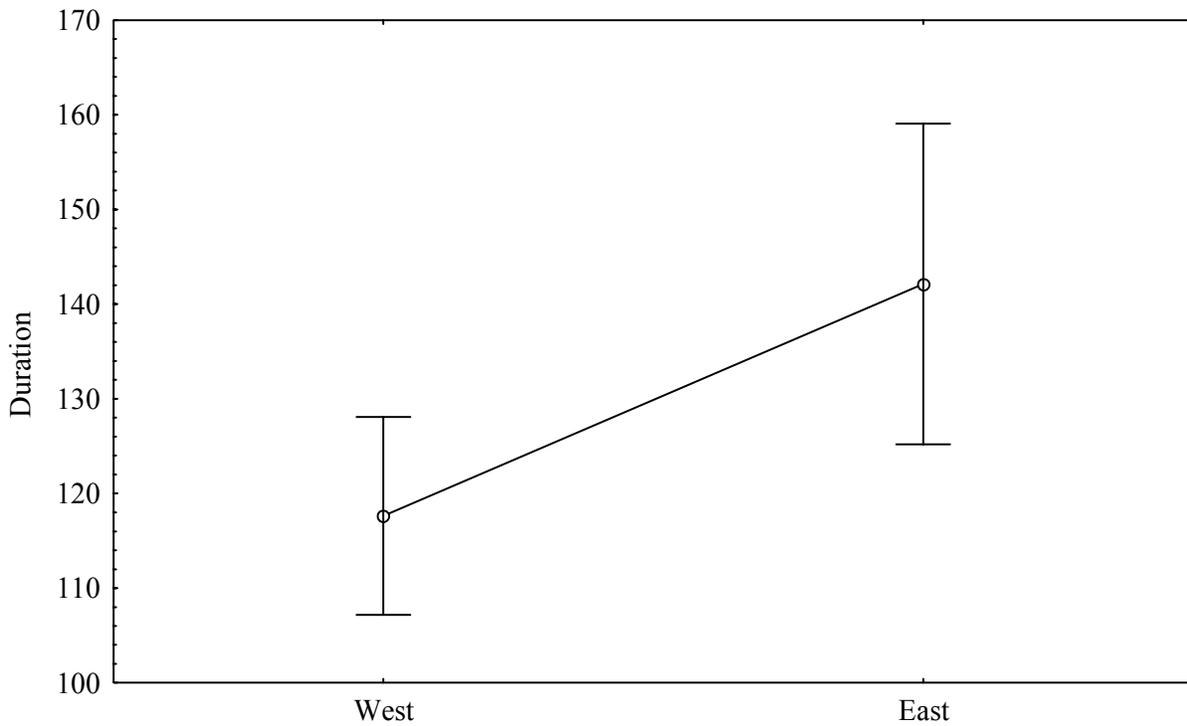


Figure 17. Hibernation duration (days; means and standard errors) relative to west- or east-facing slopes for female desert tortoises at Sugarloaf, 1996-99.

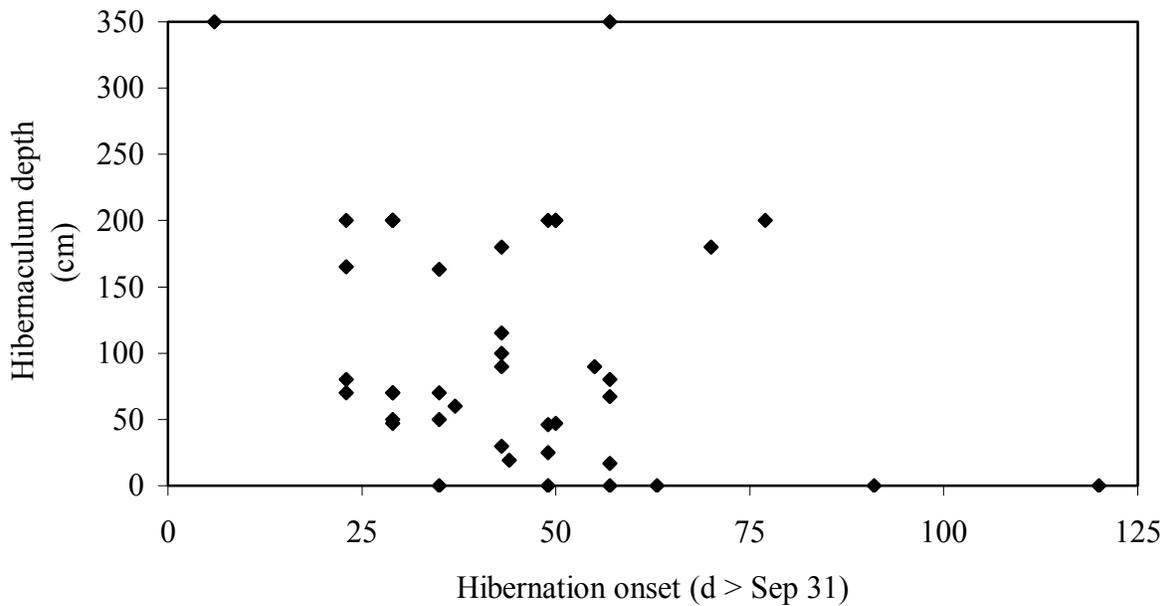


Figure 18. Hibernaculum depth vs hibernation onset for female desert tortoises at Sugarloaf, 1996-99.

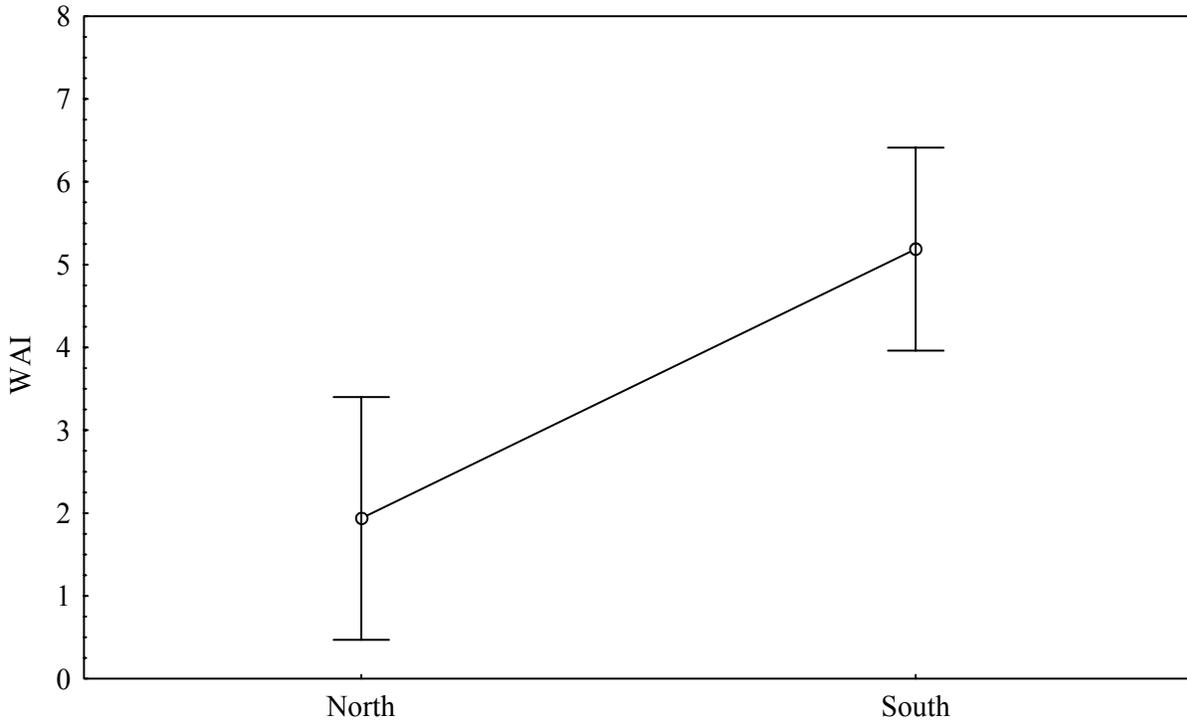


Figure 19. Winter activity index (WAI; means and standard errors) vs hibernaculum slope orientation for female tortoises at Sugarloaf, 1996-99.

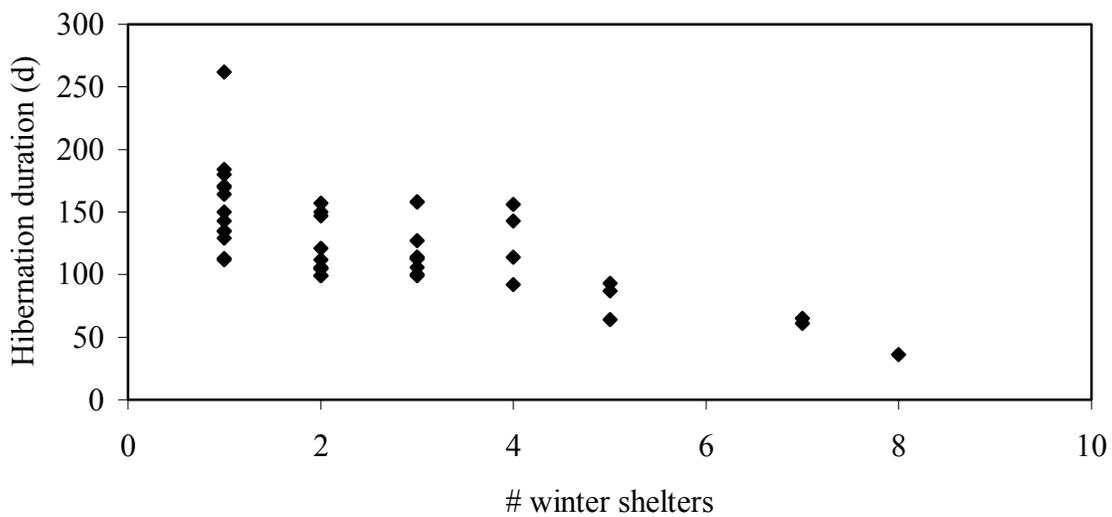


Figure 20. Hibernation duration vs the number of winter shelters used by female desert tortoises at Sugarloaf, 1996-99.

HOME RANGE

MCP home range areas were variable between individuals, both within years and overall (Tables 14 and 15). Home range area was not correlated with sample size for females for all years combined ($P = 0.597$) or within individual years ($P \geq 0.062$), but small samples overall for males resulted in a trend of more locations resulting in larger home ranges ($r = 0.629$, $P = 0.038$). Most tortoises occupied relatively small and distinct areas during the study. For example, all but 1 tortoise monitored at least 2 years (that is, $n > 100$) had home ranges ≤ 22 ha, and tortoise #1 had a cumulative home range of only 2.0 ha (Table 14; Fig. 21). Overall female home ranges averaged 73.2 ha (± 225.69), but a mean of 10.9 (± 15.09) results from the exclusion of 2 anomalous females (#14 and #55) that made extraordinary movements (Table 14). Average annual home ranges varied from 3.4 to 6.3 ha, excluding the 2 anomalous tortoises (Table 14), and range areas overlapped both spatially and temporally between individual tortoises (Fig. 22). Although there appeared to be a negative correlation between annual rainfall and female home range area, this effect was not statistically significant with only 4 annual data points ($r = -0.796$, $P = 0.204$) and did not change when tortoises #14 and 55 were excluded ($P = 0.941$).

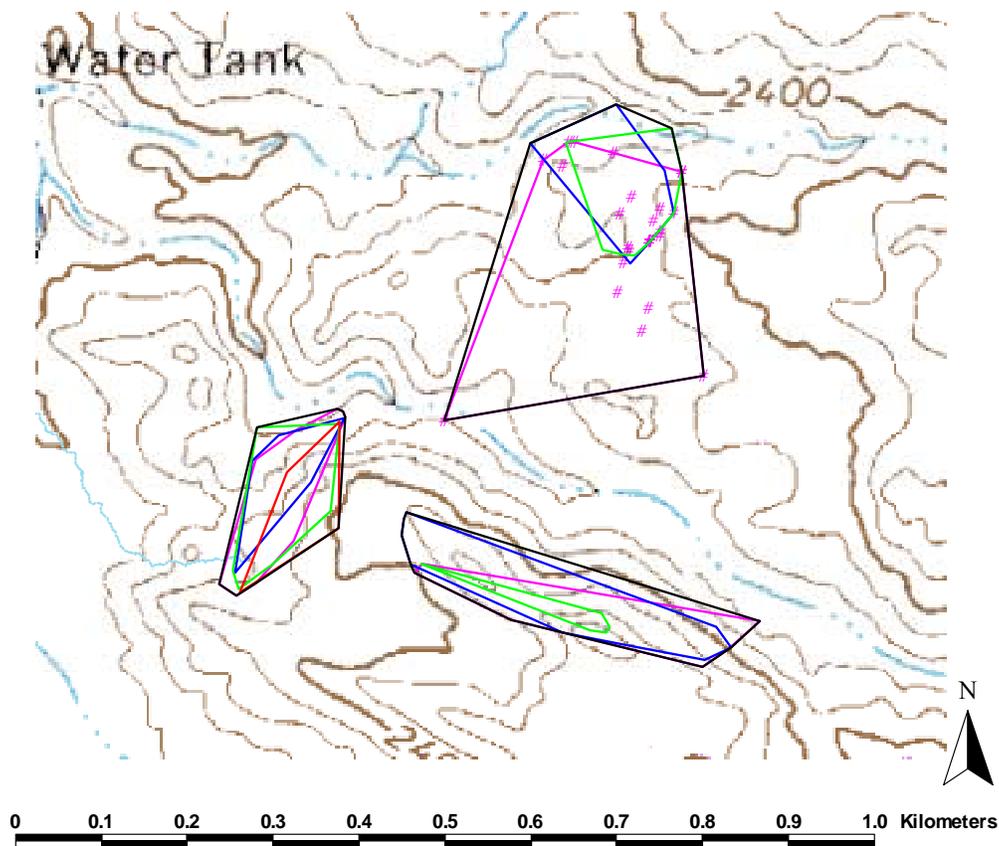


Figure 21. Minimum convex polygon (MCP) home range areas for representative tortoises at Sugarloaf (clockwise from top: #68, #56, #1). Outer polygons represent overall home range areas, and each inner polygon represents a different year. 1999 weekly points are plotted for #68.

Table 14. Minimum Convex Polygon home range areas (ha) for female desert tortoises at Sugarloaf, 1996-99. Asterisk indicates means excluding tortoises #14 and 55.										
Tort. #	All locations		1996		1997		1998		1999	
	Area	n	Area	n	Area	n	Area	n	Area	n
1	2.0	179	1.0	24	1.5	51	0.9	50	1.4	54
3	4.9	174	1.6	37	3.9	51	3.1	54	0.8	32
14	991.1	87					127.5	37	485.4	48
17	6.5	106					4.9	51	2.1	54
25	4.9	156	1.3	32	1.7	51	4.3	53	0.5	20
29	6.1	172	1.1	15	5.4	52	1.1	51	1.2	54
46	13.8	181	9.3	24	3.7	52	3.0	52	6.4	53
51	6.3	150	1.4	19	2.8	52	4.6	52	1.2	27
55	649.9	106	7.3	19	441.2	49	34.2	38		
56	3.0	112			0.3	11	2.3	50	1.8	51
57	6.3	176	0.7	18	4.1	50	2.1	51	1.4	57
58	4.9	169	2.3	20	2.7	50	2.9	53	2.0	46
61	22.0	109	14.8	19	9.9	49	4.2	33		
63	12.6	150			5.0	43	5.0	53	12.1	54
65	8.1	151			4.4	41	3.7	53	8.1	57
66	2.7	93					2.1	41	2.3	51
67	8.0	54			3.2	16	6.1	38		
68	7.4	134			1.4	28	1.6	49	6.4	57
69	51.7	26							51.7	25
71	7.2	38							7.2	33
72	1.6	16							1.6	16
73	1.5	92					0.7	39	1.4	52
77	63.0	69			0.3	11	63.0	50		
80	7.5	60					5.5	37	6.0	16
81	9.2	89					5.4	38	4.8	51
86	1.3	37							1.2	36
Mean	73.2	111.0	4.1	22.7	30.7	41.1	13.1	46.5	27.6	42.9
SD	225.69	52.33	4.79	6.86	109.49	15.39	29.18	7.09	102.81	14.43
Mean*	10.9	112.2	3.7	23.1	3.4	40.5	6.3	47.4	5.8	42.6
SD	15.09	54.31	4.94	7.15	2.41	15.77	13.44	6.79	10.96	14.74

Table 15. Minimum Convex Polygon home range areas (ha) for male and juvenile (j) desert tortoises at Sugarloaf, 1996-99. Means are for males only.

Tort. #	All locations		1996		1997		1998	
	Area	n	Area	n	Area	n	Area	n
9	3.9	9						
26	1.8	31						
44	1.5	7						
45-j	0.4	5						
47	1.7	12						
48	0.4	6						
49	96.3	38	28.4	20	24.1	18		
52	0.3	4						
54	0.9	9						
60	1.6	6						
62	2.1	11						
76	22.0	47			1.3	12	22.0	35
Mean	12.0	16.4						
SD	28.62	14.94						

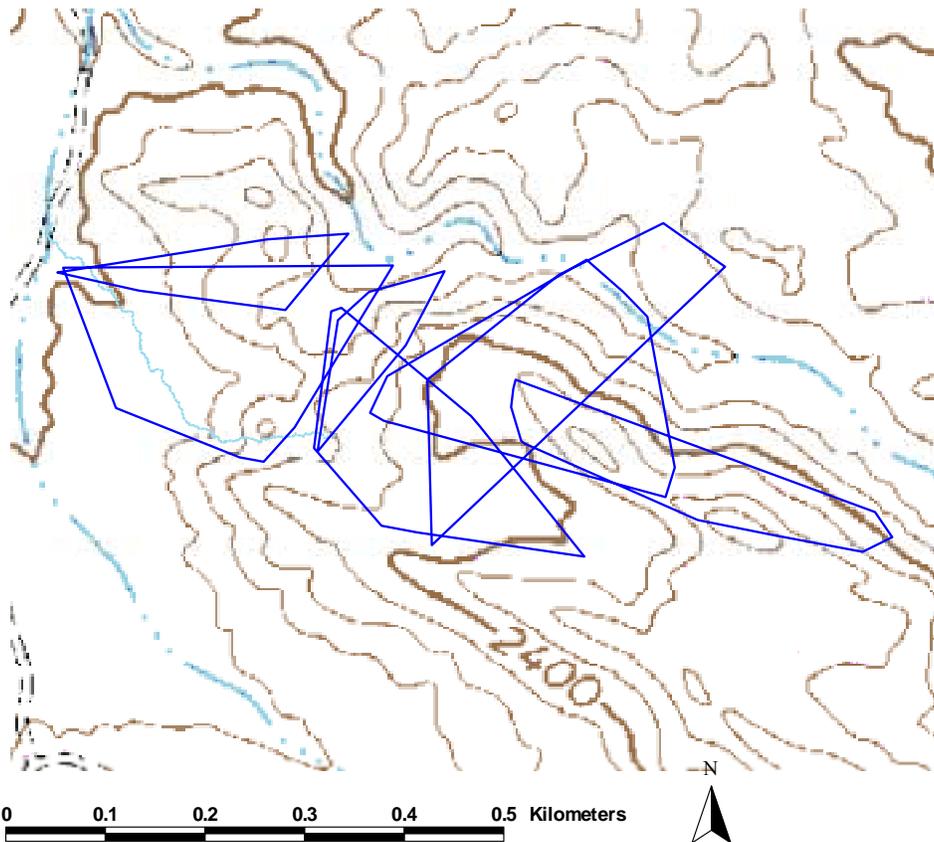


Figure 22. 1998 MCP home range polygons for Sugarloaf desert tortoises #1, 3, 25, 29, 56, 61, and 65.

Some tortoises used relatively small areas each year but made marked movements outside their “normal” ranges each year. For example, female #17 generally occupied the same ridge in 1998 and 1999 but moved to the north in 1998 and to the south in 1999 to nest (Fig. 23). Another tortoise (female #69) did not appear to occupy a clearly-defined home range in 1999 (Fig. 24); she was very active after receiving her transmitter, moving over 1 km before returning to the general area of her original capture. Finally, 2 tortoises (females #14 and 55) made dramatically long-range movements, spanning up to 7 km in total (Figs. 25-26). In October 1997, female #55 began a circuitous route of about 5 km across a braided floodplain and along a ridge of atypical tortoise habitat (that is, completely lacking large rocks or boulders); she finally hibernated in more typical, rocky habitat and occupied an area of 34.2 ha in 1998 before her transmitter failed (Fig. 25). Female #14 moved approximately 3 km to the northwest in late summer 1998, hibernated, then moved about 4.5 km west in 1999 before hibernating again (Fig. 26).

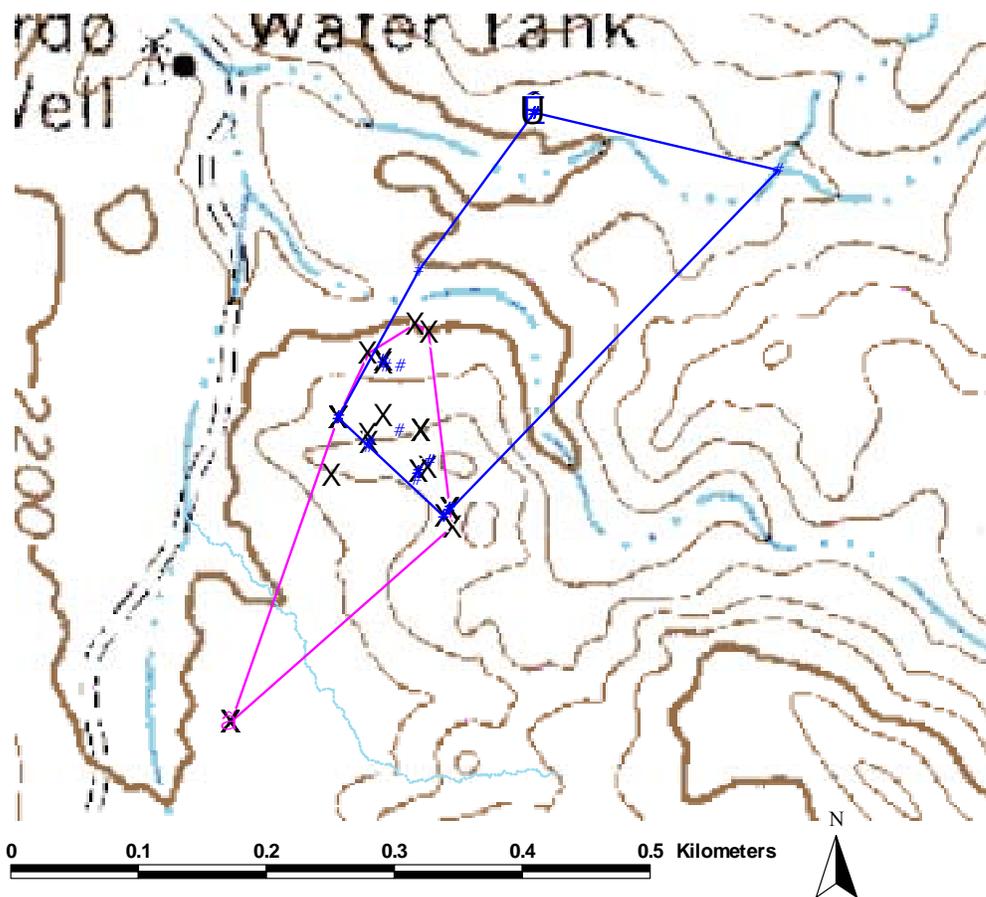


Figure 23. Tortoise #17's home range polygons for 1998 (solid circles) and 1999 (open circles). The northern-most and southern-most locations (starred) are nest sites in 1998 and 1999, respectively.

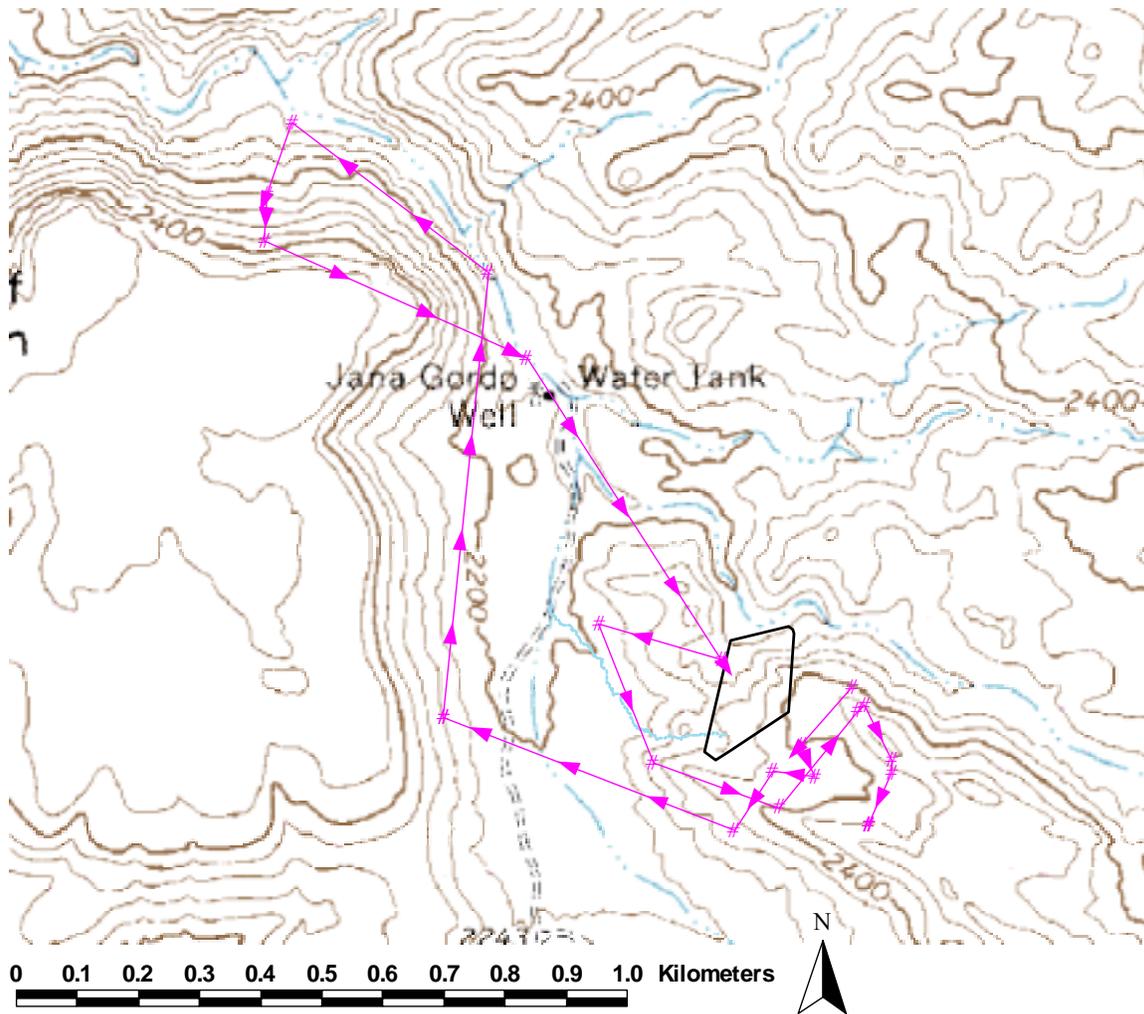


Figure 24. Tortoise #69's weekly movements during 1999. The polygon represents tortoise #1's total home range area, for reference.

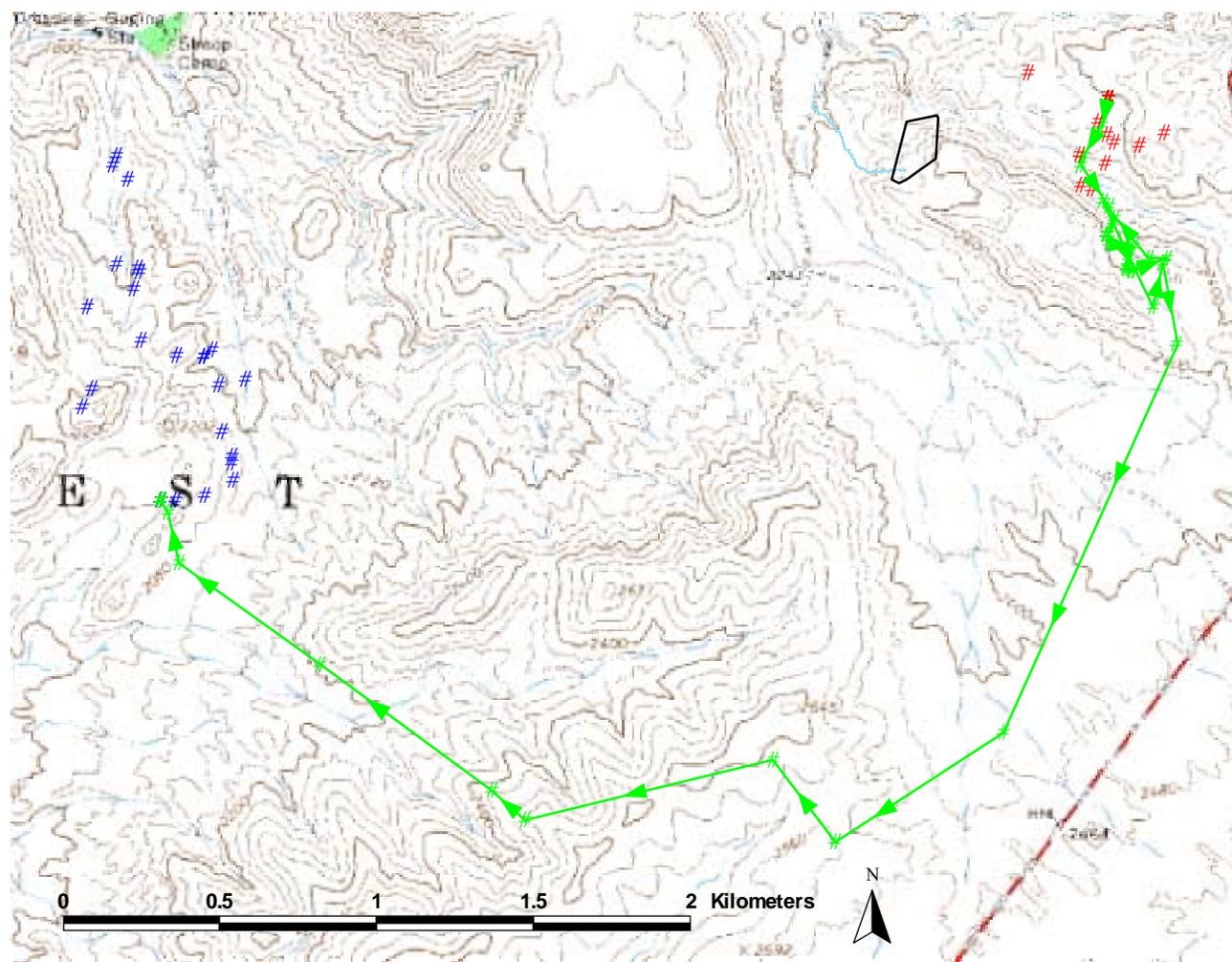


Figure 25. Tortoise #55's annual movements. 1997 weekly movements are connected by the line. 1997 locations broadly overlap 1996 locations until the long-distance movement in October 1997. The polygon represents tortoise #1's total home range area, for reference.

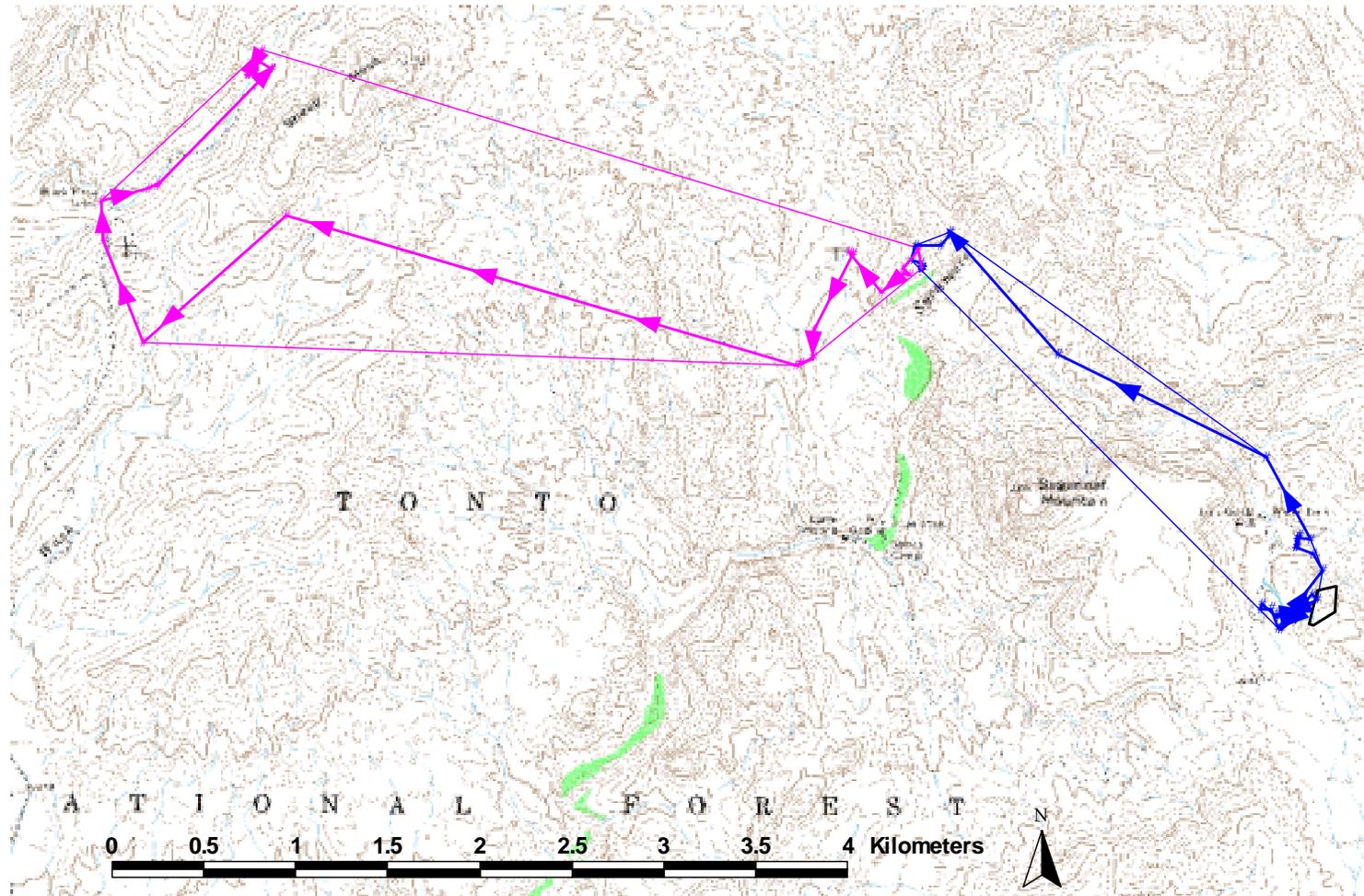


Figure 26. Desert tortoise #14's annual MCP home range areas and paths for 1998 (right) and 1999 (left).

BURROW USE

Telemetered female tortoises used as few as 3 and as many as 20 burrows each year. Annual averages ranged from 8.3 to 11.7, and cumulative totals reached as many as 34 individual burrows used during a 3.5-year period (Table 16). Overall, the number of burrows we found a tortoise to use increased with the number of observations ($r = 0.893$, $P = 0.000$; Fig. 27); within years, this was only true for 1998 ($r = 0.596$, $P = 0.012$). Tortoises also re-used many burrows from prior years, sometimes over intervals >1 year (Table 16; Fig. 28). As many as 80% of burrows used by a tortoise in a given year were used by the same tortoise in a prior year (Table 16), and these proportions tend to increase overall with the length of time each tortoise is monitored (Fig. 28).

Burrow use varied seasonally ($F_{6,127} = 21.92$, $P = 0.000$) but not by year ($F_{3,127} = 2.08$, $P = 0.106$) (Table 17). Burrow use did not differ within winters or summers (all $P = 1.000$) or between any spring and summer ($P > 0.280$). The only difference within springs occurred between the 1997 and 1999 seasons ($P = 0.007$). All inter-seasonal comparisons with winter were different ($P < 0.020$) except between winter 1996 and spring 1999 ($P = 0.074$); this is likely an artifact of 2 relatively active tortoises in winter 1996 and 1 relatively inactive tortoise in spring 1999 (Table 17). Tortoises only used an average of 1.3 to 1.8 burrows during winter (overall mean = 1.6 ± 1.02) but used 4.3 to 7.0 in spring (overall mean = 5.4 ± 2.51) and 5.1-6.1 in summer (overall mean = 5.7 ± 2.14) (Table 17). Correlations of burrow use within seasons across years revealed that tortoises used fewer burrows during wetter summers than drier summers ($r = -0.994$, $P = 0.006$), but there was no correlation between spring or winter burrow use and seasonal rainfall ($P \geq 0.497$) (Fig. 29).

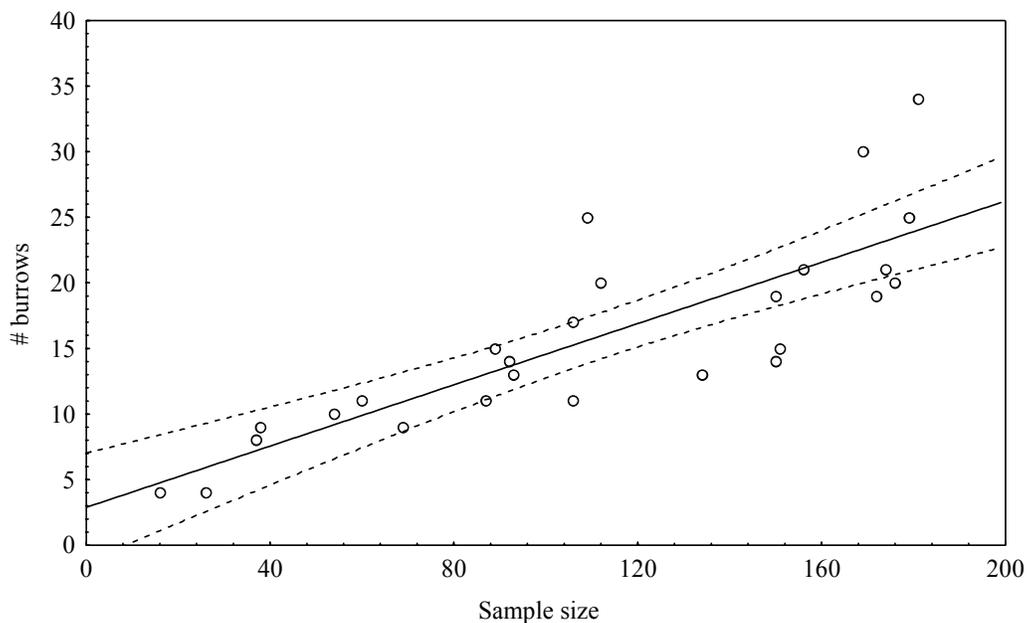


Figure 27. Numbers of burrows used by female desert tortoises vs sample size at Sugarloaf from 1996 to 1999 . Dashed lines represent 95% confidence limits.

Table 16. Annual and cumulative frequencies of burrows used by desert tortoises at Sugarloaf, 1996-99. Annual values reported for tortoises telemetered at least from May-December each year. Parentheses contain numbers of burrows (and proportions) used in a prior year.

Tort. #	1996	1997	1998	1999	Total
1		12 (1, 8%)	11 (5, 45%)	13 (9, 69%)	25
3	10	14 (7, 50%)	12 (8, 67%)	--- (6)	21
14			7	3 (0)	11
17			12 (1, 8%)	11 (6, 55%)	17
25	11	14 (9, 64%)	13 (8, 62%)	--- (2)	21
29		13 (2, 15%)	11 (8, 73%)	8 (6, 75%)	19
46		20 (6, 30%)	17 (8, 47%)	14 (11, 79%)	34
51		10 (3, 30%)	9 (2, 22%)	--- (3)	19
55		4 (1, 25%)	3 (0)		11
56			11	11 (3, 27%)	20
57		10 (2, 20%)	11 (6, 55%)	4 (3, 75%)	20
58		15 (2, 13%)	6 (3, 50%)	--- (2)	30
61		9	--- (1)	--- (1)	25
63		9	10 (8, 80%)	9 (7, 78%)	14
65		10	11 (7, 64%)	7 (5, 71%)	15
66			9	7 (3, 43%)	13
67			--- (2)		10
68			7 (3, 43%)	7 (4, 57%)	13
69					4
71				--- (1)	9
72					4
73				9 (4, 44%)	14
77			9	--- (1)	9
80				--- (1)	11
81				5 (3, 60%)	15
86					8
Mean (SD)	10.5 (0.71)	11.7 (3.98)	9.9 (3.13)	8.3 (3.33)	---
<i>Males, juvenile:</i>					
9			(1)	(1)	4
26		(2)	(1)		9
44		(1)			3
45-j					2
47					7
48					3
49					0
52					1
54		(1)		(1)	7
60					3
62					2
76			(1)		9

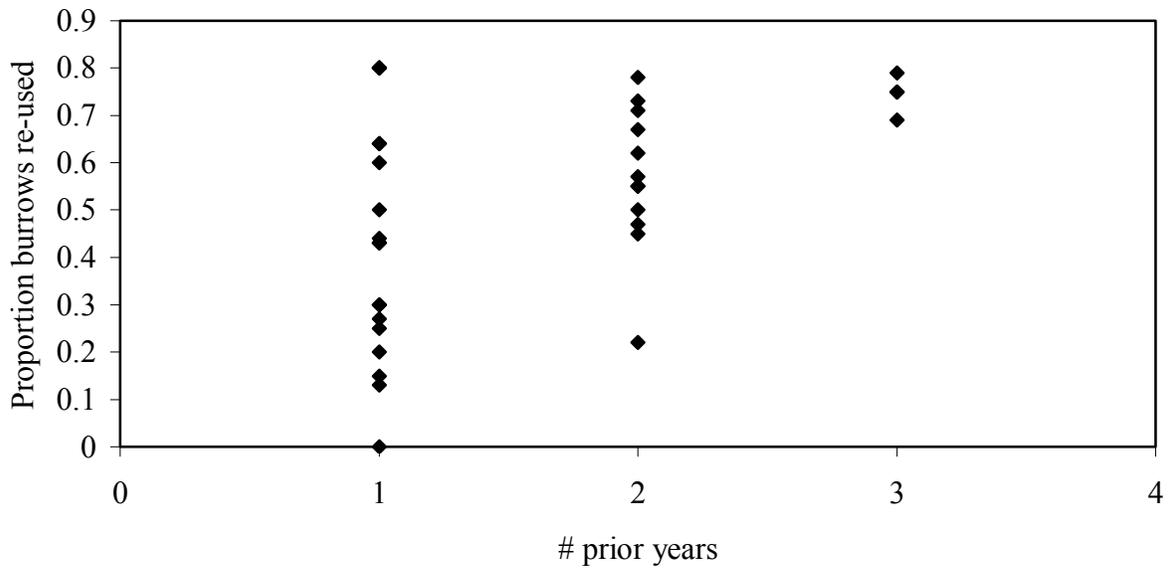


Figure 28. Proportions of burrows re-used in successive years of monitoring telemetered desert tortoises at Sugarloaf, 1996-99. “# prior years” refers to the number of years a given tortoise had been monitored when found in each burrow.

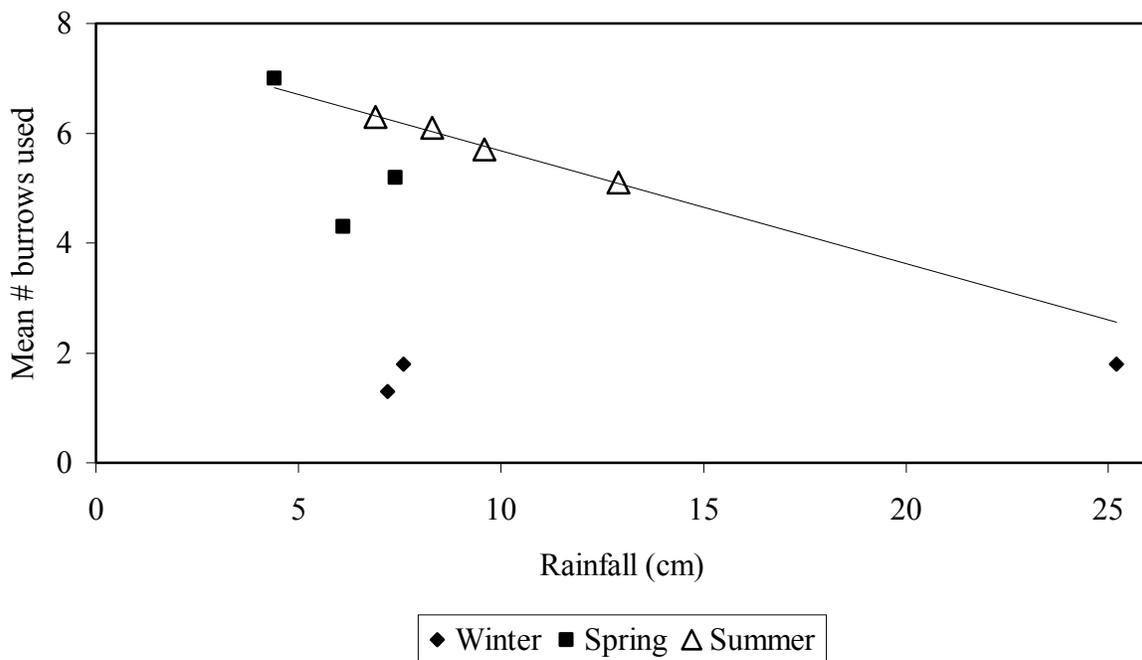


Figure 29. Mean number of burrows used each season by desert tortoises at Sugarloaf vs seasonal rainfall, 1996-99.

Table 17. Numbers of burrows used by desert tortoises at Sugarloaf, 1996-99.										
Tort. #	1996		1997			1998			1999	
	Su	W	Sp	Su	W	Sp	Su	W	Sp	Su
1	5	0	7	5	2	8	5	2	6	7
3	6	1	10	3	2	7	6	1	5	
14							4	0	2	2
17						8	6	2	8	4
25	5	3	7	8	2	6	8	1		
29		1	9	9	1	6	7	1	5	4
46	9	4	9	11	3	7	9	3	9	8
51		2	6	8	1	7	3	0	3	
55		1	3	1	0	0				
56					0	3	7	1	3	8
57		1	9	5	3	6	7	1	1	4
58		1	9	6	3	3	3	2	6	
61		4	4	5	2	4				
63				7	1	6	4	2	7	4
65			7	6	2	7	3	2	3	6
66							9	1	5	4
67					3	5				
68				5	2	2	6	2	2	6
71										5
73							5	1	2	7
77							2	1		
80						6				
81							8	1	2	3
86										5
26-m			4							
76-m					2	3				
Mean	6.3	1.8	7.0	6.1	1.8	5.2	5.7	1.3	4.3	5.1
SD	1.89	1.40	2.34	2.60	0.98	2.24	2.17	0.77	2.41	1.81
Mean (SD)	Spring: 5.4 (2.51)			Summer: 5.7 (2.14)			Winter: 1.6 (1.02)			

DISCUSSION

Similar to our results, tortoises at the Tortolita Mountains were less active in spring; in fact, 10 years of mark-recapture surveys resulted in only 14% of all tortoise observations (primarily females) occurring in spring (Martin 1995). Even though activity levels are lower overall during spring than summer, female tortoises at Sugarloaf appear to spend relatively more of their active time foraging in spring than in summer. Summer activity is relatively high at Sugarloaf, regardless of the amount of summer rain (at least within the observed amount of variation), while activity in spring and winter increases with increasing rainfall. Frequent spring foraging when

conditions are favorable may be required to obtain the energy necessary to produce eggs for the upcoming reproductive season (Chapter 3). Reproductive females may spend less time foraging in summer due to nest searching, nest building, and nest defense requirements. The specific forage plants we observed at Sugarloaf have all been reported in Sonoran desert tortoise diets except *Viguera deltoidea* (Hansen and others 1976; Vaughan 1984; Van Devender and Schwalbe 1999; Dickinson, unpubl. data [see Arizona Interagency Desert Tortoise Team 1996]).

Interestingly, our opportunistic observations suggest that male activity patterns essentially follow those of females. This is somewhat surprising, because other studies have shown that males typically leave hibernation later and are less active in spring than females (Vaughan 1984; Bailey 1992; Martin 1995). More work with males needs to be done at Sugarloaf to determine if this pattern is real or an artifact of opportunistic sampling. Likewise, additional attention paid to juvenile activity will lead to important information on growth rates and survival.

Hibernation characteristics were extremely variable, both within and between years. Hibernation durations ranged from just over 1 month to almost 9 months, tortoises used hibernacula on all aspects, and hibernaculum depths ranged from approximately 0 in shallow pallets below shrubs to >4 m deep below a massive rock outcrop. Onset of hibernation has been variable in other studies as well, ranging from late September through mid-December (Vaughan 1984; Bailey and others 1995; Martin 1995). Some of the population-level variation probably results from variation in seasonal temperature (Averill-Murray and others, *in press*). As noted above, previous studies have shown male tortoises to terminate hibernation later than females, but they may be quite variable as well, ranging from late February to mid-August (mean = 28 April) for males and late February to mid-May (mean = 22 March) for females (Vaughan 1984; Bailey and others 1995; Martin 1995).

We observed tortoise activity during all months of winter. Possible reasons suggested for winter activity of desert tortoises include 1) thermoregulation by ill or injured tortoises to elevate their body temperatures for an infection-fighting immune response, or 2) basking to dry out and reduce fungal growth on the shell (Averill-Murray and others, *in press*). Some individual tortoises at Sugarloaf basked relatively frequently during our study (as indicated by WAI), but the above explanations do not seem to fit our observations. We saw no obvious signs of ill health or fungal growth prior to or during hibernation, and there was a general pattern of higher winter activity on southwest-facing slopes than others (Fig. 19). Much of the winter activity at Sugarloaf involved tortoises moving between shelters. The significance and underlying reasons for such behavior are unclear.

Female tortoises at other Sonoran Desert sites tend to hibernate in shallower hibernacula than males (Lowe 1990; Bailey and others 1995; Martin 1995). For example, in a combined analysis of 3 Sonoran Desert sites, 15% of males (n = 20) hibernated in burrows <0.5 m deep, while 47.6% of females (n = 21) used burrows <0.5 m deep (Martin 1995). By selecting shallow hibernacula, which warm faster than deeper ones in the spring, female tortoises may be able to readily respond to warm spring temperatures and emerge in time to forage and obtain energy for

egg production (Averill-Murray and others, *in press*). If this hypothesis is true, then we would expect a correlation between hibernaculum depth or hibernation end dates and egg production among individual female tortoises at Sugarloaf.

High variability in both egg production (Chapter 3) and hibernation characteristics precluded an effective analysis of relationships between these variables with the current data, but additional work currently being conducted may shed more light on the question. In particular, additional investigation into the significant relationships we observed between hibernation onset and duration, hibernaculum depth and aspect, and winter activity relative to females that subsequently produce eggs and those that don't is warranted.

Annual home range areas ranged from 0.3 to 485.4 ha (Table 14). Caution must be used in interpreting large MCP areas, however, as indicated by Figures 25 and 26. Tortoise #14 actually occupied very little of each of the annual home range polygons during her extensive movements (Fig. 26). The tortoises' activities and how they used (or did not use) the habitat within the polygons are more biologically relevant than artificially inflated MCP estimates (see below). Excluding tortoises #14 and #55, average annual home range areas were similar to those reported by Murray and others (1995) from Sugarloaf in 1993, as were overall home ranges from 1996-99 compared to 1992-93. Sugarloaf tortoises had a mean home range area of 4.1 ha in 1993 and 12.6 ha overall. The mean for 1992 was 9.2 ha. Estimates from 1992-93 were adjusted with Jennrich and Turner's (1969) correction factor, so they are slightly inflated relative to those reported in the current study. However, 1992 was the wettest summer (22.1 cm) we have worked at Sugarloaf, and the larger estimate for that year may reflect a response to exceptionally lush environmental conditions.

Adult desert tortoises appear to be quite familiar with their home range areas. Although the number of burrows used by tortoises increases with the number of observations, many burrows are used repeatedly over the years, especially as hibernacula or nest sites (Vaughan 1984; Bailey 1992; Martin 1995). Intuitively, we expected the result that tortoises use fewer burrows in winter than spring or summer, as activity declines for hibernation. The fact that tortoises used fewer burrows in wetter than drier summers probably resulted from increased activity and less time spent inside shelter.

Three individuals were monitored during both the 1992-93 and 1996-99 studies: #1, 14, and 17. Tortoise #1 has occupied the same 2-3 ha area during the 6 years we have observed her (Fig. 21). Tortoise #17 occupied the same general area in 1992-93 and 1998-99 and has made similar nesting movements (Fig. 23). In 1992 tortoise #17 moved about 0.75 km to the north, where she apparently nested, before returning in mid-September. On the other hand, in 1992-93 tortoise #14 occupied a discrete area of about 5 ha, broadly overlapping that of tortoise #17. Since this area is near our base camp, we spent a considerable amount of time unsuccessfully searching specifically for tortoise #14 in 1996-97. We finally found her in this area in 1998 before she began her 3-km movement late that summer (Fig. 26).

Tortoise #12 made a relatively long-distance movement of about 1 km in late summer 1992 and occupied an area that did not overlap her previous range in 1993; she appeared to be moving back toward her 1992 range when the study concluded in summer 1993 (Murray and others 1995). This observation leads to the question of whether longer movements such as those of tortoises #14 and 55 are temporary and if those tortoises will eventually return to their original capture areas. Tortoise #55's transmitter failed in 1998, but we are currently still monitoring tortoise #14.

Even though most home range estimates from ≤ 4 years in the current study are similar to approximately 2-year estimates reported in other studies in the Sonoran Desert (adjusted means for females range from 2.6 to 23.3 ha; Averill-Murray and others, *in press*), long-distance movements hold important management implications. Such movements may be interpreted as random wanderings (perhaps as in Fig. 24), infrequent travels to known sources of biological needs (for example, Fig. 23), explorations, or they may be adaptations for genetic interchange with neighboring populations or for dispersal to other suitable areas (perhaps as in Figs. 25-26) (Vaughan 1984). Construction and development projects, such as canals, roads, housing, and agriculture, could form barriers or sources of mortality for individual tortoises that attempt to make such a movement. This may be true even if the project only occurs adjacent to or between apparently suitable desert tortoise habitat, as in intermountain valleys generally unoccupied by tortoises in the Sonoran Desert. For example, tortoise #55 spent over 1 month in habitat we would not have considered likely for finding tortoises during her 5-km movement in 1997. Long-term studies are required to determine how often this type of movement occurs, what factors influence them, whether they represent temporary excursions or permanent relocations, and what population-level effects result from habitat fragmentation, whether within or between populations.

CHAPTER 5
CONCLUSION

SYNTHESIS

Surveys of monitoring plots within the Sonoran Desert population of desert tortoises have been conducted since 1987. To date, 24 Sonoran population plots have been surveyed (18 at least twice each; Table 1). These surveys and other ecological research provide a solid baseline from which to begin drawing inferences about tortoise demographics, population regulation, and trends in abundance.

Tortoise densities within local populations vary widely within the Sonoran Desert, ranging from 15 to more than 100 adults per square mile (Table 1), with density apparently related to habitat features providing burrow sites (Fig. 5). Typically, tortoise populations benefit from adult survival rates >90% and only slightly lower for large juveniles (Table 3). Although nest predation appeared to be high at Sugarloaf, survival rates of hatchlings and small juveniles remain unknown but presumed low. Disease has not recently impacted Sonoran populations, as it has in the Mojave Desert; URTD appears to be rare to non-existent in most Sonoran Desert populations. Cutaneous dyskeratosis does occur in virtually every population studied so far, but we have observed no detrimental effects to individuals or populations. Notable human-related impacts to tortoise populations include predation by feral dogs on the Bonanza Wash and East Bajada plots, a large number of burrows trampled by cattle on the East Bajada plot, tortoises trapped in a mining pit at the Granite Hills plot, development occurring adjacent to the Hualapai Foothills plot, and a shot tortoise and a painted tortoise on the West Silverbells plot (Appendix). Only 1 documented population crash has occurred in the Sonoran Desert in Arizona during the last 13 years, at the Maricopa Mountains from just before 1987 through about 1990, possibly as a result of drought.

Female tortoises at Sugarloaf laid a single clutch of eggs near the onset of each summer rainy season (Table 5). Not all females reproduced every year, with the proportion reproducing correlated with winter and spring rainfall and, presumably, subsequent plant production. The smallest female observed to lay eggs in the Sonoran Desert has been 220 mm MCL (at Sugarloaf and the Maricopa Mountains [Wirt and Holm 1997]). Ages of these tortoises were not measured directly, but comparison of growth curves (Fig. 4) indicates that they reach this size in 10-20 years. More precise age at maturity estimates are not yet possible, because insufficient data on growth, which varies geographically, exist for these populations.

The effects of geographic differences in growth and body size on reproductive output between tortoise populations in the Sonoran Desert are unclear based on the available data. Minimum reproductive size each year at Sugarloaf was negatively correlated with winter rainfall. Mean clutch size ranged from 3.8 to 5.7 eggs (Table 5) and was not related to female body size or rainfall. Mean egg width was not related to year or clutch size, but large females laid larger eggs than small females (Fig. 10). The lack of a correlation between clutch size and female body size

indicates that large-tortoise populations in the northwestern Sonoran Desert may not lay more eggs/female on average than in small-tortoise populations, but large-tortoise populations might produce larger hatchlings. Relatively large tortoises in the northwestern Sonoran Desert might also be able to store more nutrient reserves and reproduce under drier conditions than smaller tortoises in more mesic parts of the distribution.

Sonoran desert tortoises may be active throughout the year. Peak activity occurs during the summer monsoon season (Figs. 12-13; Tables 8-9), but relative spring and winter activity increases with increasing rainfall during those seasons (Fig. 11). Spring foraging appears to be important (Fig. 15), especially for female tortoises, since their ovarian follicles mature during spring. Male tortoises also appear to be more active during spring, at least at Sugarloaf, than previously thought. Tortoise activity is usually concentrated within a fairly specific home range area (Tables 14-15; Fig. 21). Adult tortoises are very familiar with their areas, repeatedly using the same burrows over the years, especially as hibernacula or nest sites (Table 16; Fig. 28). However, some individuals may make relatively long-distance movements outside their “normal” home ranges (Figs. 23-26). Some of these movements are obviously temporary excursions to specific resource sites, such as nesting burrows (Fig. 23). Others are more difficult to explain at present, but some may represent dispersal movements (Fig. 25-26).

How the naturally disjunct and sometimes low-density tortoise populations in the Sonoran Desert persist remains poorly understood. Life history traits of turtles, including delayed sexual maturity and iteroparous reproduction of desert tortoises, require high adult survival and relatively high (average) juvenile survival to maintain viable populations. High variability in existing data and important data gaps (for example, juvenile growth and survival) preclude effective population viability analysis, at present, of the Sugarloaf population, for which the most complete information is available. However, long-distance movements observed at Sugarloaf suggest a potential meta-population relationship between local populations. Tortoises dispersing from rocky upland habitats may represent occasional cross-valley immigration and result in genetic interchange. Effects of variation in juvenile survival may be apparent in size class distributions showing clumps or gaps in the juvenile size class; particular cohorts exposed to a series of particularly wet or dry years probably experience different survival rates. A large cohort of young tortoises that experiences a relatively wet and productive environment and high survival may provide the stock for dispersal between populations as they approach sexual maturity in addition to the replacement of aging adults within the local population (for example, Morafka 1994).

MANAGEMENT RECOMMENDATIONS

Given the information currently available, desert tortoise populations appear to be stable within the Sonoran Desert in Arizona. However, existing trend data are currently insufficient to draw secure conclusions about population trajectories, especially with increasing urban growth and habitat fragmentation. The unknown significance of currently low incidence of URTD symptoms but high incidence of cutaneous dyskeratosis within tortoise populations poses another concern;

apparently healthy populations in the Mojave Desert have suffered dramatic declines in the presence of these diseases (FWS 1994; Berry 1997). Continued and more efficient monitoring across the range is essential to better quantify population trends. Individual and cooperative efforts by land and wildlife management agencies must continue to ensure that sufficient habitat area and quality remain for the survival of tortoise populations. Finally, additional research should be conducted to answer questions about population dynamics, habitat impacts (especially fire and invasion of exotic grasses), and disease, so managers can better direct their conservation efforts (AIDTT 1996). Specific management recommendations are listed below.

- *Continue state-wide monitoring of desert tortoise populations using the revised protocol of Averill-Murray (2000) to estimate trends in abundance. Evaluate the effectiveness of this protocol and revise as necessary.

- *Continue gathering life history data from Sugarloaf to better understand and quantify temporal variability of reproductive output. Increased emphasis should be placed on monitoring juvenile tortoises, so growth and survival may be estimated for this size class. Use these data to conduct population viability analyses of local populations. Life history research should be replicated at additional Sonoran Desert sites to gain a better understanding of spatial variability.

- *Conduct studies of tortoise energy budgets to determine when and how females allocate energy to reproduction. Determine limitations to annual reproduction in Sonoran desert tortoises.

- *Continue long-term monitoring of individual tortoises with radio telemetry to better understand home range and habitat use, especially related to long-distance movements. Increased emphasis should be placed on monitoring adult male and juvenile tortoises to supplement data on adult females.

- *Determine the genetic relationships between adjacent local tortoise populations and estimate rates of genetic interchange. Apply this information to a meta-population viability analysis. In the meantime, maintain open space as potential corridors of dispersal between local populations.

- *Determine the prevalence of URTD within apparently symptomatic tortoises on the long-term monitoring plots.

- *Determine the cause of cutaneous dyskeratosis and potential effects to individuals and populations.

- *Implement additional management options listed in AIDTT (1996).

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APPENDIX: INDIVIDUAL MONITORING PLOT SUMMARIES

The following accounts summarize survey results for each desert tortoise monitoring plot conducted under the *Partnerships for Wildlife* project, as well as plots funded by the U.S. Bureau of Land Management (BLM) during and prior to the duration of this project. Other plots funded and surveyed outside this project (including the Mazatzal Mountains, Organ Pipe Cactus National Monument, Rincon Mountains, Sand Tank Mountains, and Tucson Mountains plots) are not included here.

Each plot account follows the same format, beginning with the plot name followed by citations for the original plot reports in parentheses. Each account then begins with a physical description of the plot, including size, topography, elevation ranges, geology, biome, and human impacts. The next section, coverage history, describes the number of days the plot was surveyed and over what time period each survey occurred.

Three final sections list observed sex ratios (enumerated as males:females), health observations, and anomalous scute numbering observations during each survey of the plot. Health inspections were directed toward upper respiratory tract disease (URTD) and cutaneous dyskeratosis. URTD is often characterized by a serous nasal discharge, swollen eyes, and listless behavior (Jacobson and others 1991), so records of these symptoms may be of particular note. Field workers also noted cases of tortoises with whistles or wheezes in their breath; these observations may be the result of nasal congestion but could also result from other foreign materials (for example, dirt or plant parts) in the nares. Affected areas of cutaneous dyskeratosis usually occur on the plastron, less often on the carapace or forelimbs, and are usually white-gray, have a flaky appearance, and appear to commence at seams between scutes (Jacobson and others 1994). Tortoises with anomalous numbers of scutes were those that had greater than or fewer than the normal number of carapace (5 vertebrals, 4 costals each side, 11 marginals each side, 1 nuchal, 1 pygal) or plastron (paired gulars, humerals, pectorals, abdominals, femorals, anals) scutes.

Numbers of tortoises marked, density estimates, and numbers of carcasses found on each plot are summarized in Table 1. Table A-1 lists plants observed as forage at each of the plots. This list represents opportunistic foraging observations and is intended as simply a species list to complement other studies of tortoise diet. Diversity observed within and among plots is influenced by search effort as much as differences between plots.

<u>Table A-1. Desert tortoise forage species observed on monitoring plots, 1990-99.</u>		
<u>Arrastra Mountains:</u> <i>Digitaria</i> sp. <i>Fagonnia californica</i> <i>Janusia gracilis</i>	<u>Granite Hills (cont.):</u> <i>Cercidium microphyllum</i> <i>Cryptantha nevadensis</i> <i>Ditaxis lanceolata</i> <i>Euphorbia polycarpa</i> <i>Euphorbia (Chamaesyce)</i> sp. <i>Lepidium lasiocarpum</i> <i>Lotus</i> sp. <i>Lupinus sparsiflorus</i> <i>Lycium berlandieri</i> <i>Opuntia engelmannii</i> <i>Opuntia</i> sp. <i>Phacelia</i> sp. <i>Schismus barbatus</i> <i>Sphaeralcea ambigua</i> <i>Vulpia octoflora</i>	<u>Little Shipp Wash (cont.):</u> <i>Bouteloua curtipendula</i> <i>Bouteloua</i> sp. <i>Calliandra eriophylla</i> <i>Cryptantha</i> sp. <i>Descuriana pinnata</i> <i>Ditaxis lanceolata</i> <i>Evolvulus alsinoides</i> <i>Janusia gracilis</i> <i>Opuntia engelmannii</i> <i>Opuntia phaeacantha</i> <i>Opuntia</i> sp. <i>Pleuraphis rigida</i>
<u>Bonanza Wash:</u> <i>Bouteloua curtipendula</i> <i>Bromus madritensis</i> <i>Janusia gracilis</i> <i>Pleuraphis rigida</i>	<u>East Bajada (Mojave Desert):</u> <i>Amsinckia</i> sp. <i>Astragalus nutallianus</i> <i>Bouteloua barbatus</i> <i>Bromus madritensis</i> <i>Erioneuron pulchellum</i> <i>Lepidium lasiocarpum</i> <i>Lotus humistratus</i> <i>Plantago ovata</i>	<u>Maricopa Mountains:</u> <i>Boerhaavia wrightii</i> <i>Euphorbia</i> sp. <i>Janusia gracilis</i> desert bedstraw
<u>Eagletail Mountains:</u> <i>Allionia imbricata</i> <i>Ambrosia dumosa</i> <i>Argthamnia lanceolata</i> <i>Aristida adscensionis</i> <i>Boerhaavia wrightii</i> <i>Bouteloua aristidoides</i> <i>Bouteloua barbatus</i> <i>Brassica tornefortii</i> <i>Bromus madritensis</i> <i>Ditaxis lanceolata</i> <i>Marina parryi</i> <i>Plantago insularis</i> <i>Plantago ovata</i> <i>Pleuraphis rigida</i> <i>Tidestroma lanuginosa</i>	<u>Harcuvar Mountains:</u> <i>Bouteloua barbatus</i> <i>Bromus madritensis</i> <i>Ditaxis lanceolata</i> <i>Hibiscus coulteri</i> <i>Janusia gracilis</i> <i>Lupinus sparsiflorus</i> <i>Muhlenbergia porteri</i> <i>Plantago insularis</i> <i>Pleuraphis rigida</i> <i>Vulpia octoflora</i>	<u>New Water Mountains:</u> <i>Plantago insularis</i>
	<u>Harquahala Mountains:</u> <i>Aristida purpurea</i> <i>Ditaxis lanceolata</i>	<u>San Pedro Valley:</u> <i>Allionia incarnata</i> <i>Erioneuron pulchellum</i> <i>Janusia gracilis</i> <i>Lupinus</i> sp. <i>Panicum arizonicum</i>
<u>Granite Hills:</u> <i>Ambrosia deltoidea</i> <i>Amsinckia</i> sp. <i>Aristida adscensionis</i> <i>Aristida</i> sp. <i>Bouteloua</i> sp. <i>Bromus madritensis</i>	<u>Hualapai Foothills:</u> <i>Bouteloua aristidoides</i> <i>Bromus madritensis</i>	<u>Tortilla Mountains:</u> <i>Aristida adscensionis</i>
	<u>Little Shipp Wash:</u> <i>Aristida purpurea</i> <i>Aristida</i> sp. <i>Ayenia compacta</i> <i>Boerhaavia wrightii</i> <i>Bouteloua aristidoides</i> <i>Bouteloua barbatus</i>	<u>West Silverbell Mountains:</u> <i>Aristida adscensionis</i> <i>Chamaesyce capitellata</i> <i>Chamaesyce setiloba</i> <i>Ditaxis lanceolata</i> <i>Janusia gracilis</i> <i>Muhlenbergia porteri</i> <i>Selaginella arizonica</i>
		<u>Wickenburg Mountains:</u> <i>Opuntia</i> sp.

ARRASTRA MOUNTAINS (Wirt 1988; Woodman and others 1998)

Description

The 2.7 sq. km (1.06 sq. mi) Arrastra Mountain study plot is located near the north end of the Poachie Mountain Range in southeastern Mohave County. The northern boundary of the Arrastra Mountain Wilderness abuts the southern boundary of the plot. There is a multi-peaked ridge that extends across the north half of the plot. Many arroyos come off of this main ridge. The southern portion of the plot, below the main ridgeline, is composed of lower hills. Elevations on the plot range from 910 m (2980 ft) in the southwest corner to 1130 m (3708 ft) in the center of the main ridge. Geologically, the plot is primarily granitic, with some outcrops of basalt and quartz. The slopes of the westernmost peak are covered in boulders, but the number of boulders decreases further east. Vegetation is dominated by the Arizona Upland subdivision of the Sonoran Desert, but there are influences of both Interior Chaparral and Mohave Desertscrub.

Human influences include cattle grazing, burro use, vehicular traffic, mining, and hunting. Cattle are grazed on the plot, and cattle sign was seen throughout the plot except in small, inaccessible areas. Distribution of burro sign was similar. There is a primitive road that crosses the southern portion of the plot. This road receives light use. Mining claim markers were scattered throughout the plot, but there was no sign of recent mining. Some hunting occurs on plot as evidenced by spent shell casings, but it is probably light. Garbage on the plot is light.

Coverage history

Wirt (1988) conducted the first survey of the Arrastra Mountains plot in 1987. This survey included 60 person-days over 57 calendar days. Nineteen days were spent searching in the spring, from 1 April to 30 May. The remainder of the survey was conducted from 18 August to 28 October. The original plot was composed of only section 10. In October 1987, six 0.01 sq. mi (0.03 sq. km) cells in section 9 were added to the plot due to the low number of captures on the original plot. In 1997, 35 person-days (27 calendar days) from 5 September to 10 October were spent surveying.

Sex ratio

Sex ratios for adult tortoises did not differ statistically from the expected 1:1 in 1987 (6 males, 9 females) or 1997 (5 males, 8 females).

Health

Health information was not collected in 1987. All tortoises appeared healthy during the 1997 surveys. Cutaneous dyskeratosis was noted on 1 individual (7%).

Scute numbering anomalies

Scute numbering anomalies were not documented in 1987. In 1997, 6 tortoises (43%) had anomalous numbers of scutes.

BONANZA WASH (Woodman and others 1993, 1998)

Description

The 2.6 sq. km (1 sq. mi) Bonanza study plot is located on the western edge of central Yavapai County. Elevations range from 960 m (3120 ft) in the northeast corner to 1077 m (3500 ft) in the central part of the plot. With the exception of 1 small wash that drains to the west, the majority of the plot drains from south to north into Bonanza Wash, which crosses the northeast corner of the plot. The northern portion of the plot is composed primarily of a gently rising grade bisected by incised washes. There are a few scattered rock piles in this area. Three large hills dominate the southern half; slopes are steeper, and the incised washes are deeper. There are generally more rock outcrops in this area, and shelter site potential is higher. The plot is mostly granitic. Soils are poorly developed, especially on south-facing slopes and in the northern portion. The highly variable vegetation combines elements of Arizona Upland, desert grassland, and interior chaparral with both Mojave and Sonoran desert influences.

Human impacts to the plot have been minimal. Cattle grazing is permitted on the plot but has been very light. There are several roads that receive little use. Mining has occurred both on and near the plot. Hunters have been seen on the plot but hunting seems to be light, based on the small number of shotgun shells found. In 1992 a domestic dog was observed attacking an adult tortoise, and several tortoises were observed extensive gnaw marks. Feral dogs were not noted in 1997.

Coverage history

The 1992 survey, conducted between 2 September and 17 October, was the first 60-day survey conducted on the plot. The plot was situated based on results of transects done in the spring of 1992. In 1997, a 35 person-day study was conducted between 4 September and 28 September.

Sex ratio

Sex ratios for adult tortoises did not differ from the expected 1:1 in either 1992 (8 males, 6 females) or 1997 (6 males, 4 females).

Health

In 1992, almost all tortoises (94%) were in good health. One large male had a slight wheeze on 1 of his 3 captures. Seven tortoises (5 males, 2 females; 41%) had cutaneous dyskeratosis lesions; only 1 had extensive lesions. In 1997, 1 tortoise (8%) showed symptoms of URTD. This immature animal had been captured in 1992 and was normal at that time. Five tortoises (38%) had cutaneous dyskeratosis, including 2 that were symptomatic in 1992.

Scute numbering anomalies

Three tortoises in both 1992 (18%) and 1997 (23%) exhibited scute-numbering anomalies. In 1992, 1 tortoise was found with a deformed carapace that could have been congenital or traumatic.

EAGLETAIL MOUNTAINS (Shields and Woodman 1987; Shields and others 1990; Hart and others 1992; Woodman and others 1993, 1994, 1995, 1999)

Description

The 2.6 sq. km (1 sq. mi) Eagletail Mountains study plot is located near the south end of the Eagletail Mountains in Maricopa County. Elevations on the plot range from 450 m (1476 ft) to 700 m (2296 ft). The plot is almost entirely bisected by a large ridge that runs from the southeast to northwest. Cliffs from 20 to 100 m (66-328 ft) high are present along both sides of the ridge. These cliffs are highest along the northeast face and provide a great deal of afternoon shade. In addition to the main ridgeline, there is a shallow basin in the northeastern part of the plot and a southwest-facing bowl in the southwest corner. Primary tortoise habitat on the plot is along the main ridge and in the southwest bowl. There are several incised washes draining the northeast face. Geologically the plot is volcanic, consisting of rhyolite and welded tuff. Many of the rocks are worn smooth, and covered with a dark desert varnish. The mineral makeup of the rocks, combined with the desert varnish, give them a dark color. This contributes to high surface temperatures. Vegetation is a combination of Lower Colorado River Valley and Arizona Upland subdivisions of the Sonoran Desert.

The primary human impact on the plot is grazing. Cattle were not seen on the plot in 1990, but cattle sign was present. Cattle were not grazed in 1991 or 1992. Between November and April 1994 and 1997, 380 head of cattle were grazed on the allotment that includes the Eagletails plot. Fieldworkers in both 1994 and 1998 noted cattle sign throughout the plot. Cattle grazed the slopes, but concentrated in the creosote flats in the northeast corner of the plot. The plot is within the Eagletail Mountains Wilderness, designated in November 1990. The only road on the plot, which used to exit the plot in the northwest corner, is now closed at the wilderness boundary (on the eastern plot boundary). Trash on the plot was light. A few shotgun shells were seen, but hunting use is probably minimal.

Coverage history

Population monitoring surveys were conducted in 1987, annually from 1990 to 1994, and again in 1999. The 1987 survey was a 52 person-day effort conducted over 36 calendar days from 9 August to 27 September. The 1990 survey was a 61 person-day effort conducted over 48 calendar days from 13 August to 29 October. In 1991, a 36 person-day survey was conducted over 47 calendar days from 17 August to 3 October. The 1992 through 1994 surveys were each 36 person-day surveys, but starting and ending dates differed slightly. The 1992 survey was conducted over 31 calendar days from 3 September to 8 October. In 1993, fieldworkers spent 28 calendar days from 9 August to 9 September. The 1994 survey took 32 calendar days from 17 August to 1 October. The 1999 survey covered 35 person-days over 28 calendar days from 9 August to 23 September.

Sex ratio

Observed sex ratios for adult tortoises did not differ from the expected 1:1 in either 1987 (11:19), 1992 (10:12), 1993 (10:12), 1994 (10:15), or 1998 (14:17). Sex ratios were significantly different from 1:1 in both 1990 (8:21) and 1991 (9:17).

Health

Almost all tortoises appeared healthy during plot surveys but tortoise health was not documented during the 1987 survey. In 1994, one female tortoise (2%) was excreting copious amounts of exudate from her right naris and a small amount from her left. This tortoise was relocated 4 times in 1998 and appeared healthy. Cutaneous dyskeratosis was noted on 5 tortoises (16%) in 1990, 1 (3%) in 1993, 4 (9%) in 1994, and 5 (13%) in 1998.

Scute numbering anomalies

Four (10%) tortoises were recorded with scute numbering anomalies in 1987, 4 (12%) in 1990, 4 (11%) in 1991, 5 (17%) in 1992, 11 (31%) in 1993, 11 (23%) in 1994, and 15 (38%) in 1998.

EAST BAJADA (SWCA, Inc. 1990; Woodman and others 1994, 1998)

Description

The 2.6 sq. km (1 sq. mi) East Bajada study plot is located on the lower, eastern slopes of the Black Mountains in central Mohave County. Plot terrain is characterized as either upper bajada or foothills. The foothills are an east-northeast facing slope of the Black Mountains, transitioning into an east-southeast facing bajada. Elevations range from 693 m (2287 ft) in the southeast quarter to 812 m (2681 ft) on a peak in the southwest quarter. The plot is bisected by a large wash that crosses the plot from northwest to southeast. This main wash divides the plot, bajada to the northeast and foothills to the southwest. Three smaller washes drain other parts of the plot. Most of the washes on plot have cut banks with caliche caves. Geologically, the bajada is covered with basalt and rhyolite boulders. The foothills area is mostly rhyolite, either solid, in outcrops, broken alluvium, or as bedrock covered with basalt boulders. Vegetation is primarily characteristic of Mohave Desertscrub.

Human impacts to the plot include vehicular access, grazing, past mining, feral dogs, and use by burros. The study plot is located in a designated wilderness area. There is 1 road that passes through the plot that is open to vehicles. This road was well utilized by the grazing lessee, hunters, and recreationists. Several other roads have been closed at the wilderness boundary. Cattle have been grazed on the plot, and there is a stock tank located in grid cell 95. Cattle grazing was not documented during either the 1990 or 1993 surveys. In 1997, cattle were seen throughout the survey and the area around the stock tank showed signs of heavy, recent use. There were cattle trails leading away from the tank, and there was dung throughout the plot. Fieldworkers documented 187 burrows that they felt were trampled by cattle. This assumption is supported by cattle dung, tracks, and trails in the vicinity of many of the collapsed burrows. Four very old mining test pits are on the plot. A pack of feral dogs was seen on the plot several times during the 1993 survey. Burros or their recent sign have been documented on the plot during each

survey. In 1997, burros were seen 3 times, usually west of the plot. In these areas, plants were noticeably cropped and soil disturbed. Trash was common along the main road. Smaller amounts of trash were also found scattered around the plot.

Coverage history

In 1990, SWCA personnel spent 86 person-days over 45 calendar days between 29 August and 26 October. This survey included 4 coverages of the plot. In 1993, 60 person-days over 45 calendar days (31 July to 7 October) were spent surveying the plot. The 1997 survey was a 60 person-day effort conducted over 48 calendar days between 13 August and 9 October.

Sex ratio

Reported sex ratios were 21:12 in 1990, 29:14 in 1993, and 20:23 in 1997. Of these ratios, only that in 1993 was statistically different from 1:1. Examination of data from all 3 years revealed that 2 additional tortoises should have been coded as females in 1990 (1 male and 1 unsexed tortoise), changing the actual observed sex ratio to 20:14. In 1993 one female was incorrectly coded as male, and several adults were apparently not included in the reported sex ratio. The actual sex ratio for 1993 was 29:18, which is not statistically different from 1:1 ($P > 0.10$). Still, males outnumbered females in both years, but females outnumbered males in 1997. Eight new females were captured in 1997, compared to only 3 new males; all these tortoises were ≥ 200 mm MCL, and only 4 (2 males and 2 females) were < 220 mm.

Health

In 1990, 8 tortoises (18%) with URTD symptoms were observed. None of these had nasal exudate. In 1993, 2 tortoises (4%), both vigorous males, were noted with multiple symptoms of URTD including nasal exudate. Nasal exudate was documented in 2 tortoises (4%) in 1997 as well, including one of the tortoises that had exudate in 1993. Surveyors did not look for symptoms of cutaneous dyskeratosis in 1990. In 1993, 13 tortoises (28%) had pronounced widespread lesions, while 28 (62%) had lesions in 1997.

Scute numbering anomalies

Morphological anomalies were not documented in 1990. Seven (14%) tortoises had scute numbering anomalies described in 1993, and 13 (29%) were recorded in 1997.

GRANITE HILLS (Shields and others 1990; Hart and others 1992; Woodman and others 1993, 1994, 1995, 1999)

Description

The 2.6 sq. km (1 sq. mi) Granite Hills plot is located near the northeast end of the Picacho Mountains in Pinal County. This plot is rectangular, with a 1.1 sq. km (0.42 sq. mi) northern section and a 1.6 sq. km (0.60 sq. mi) southern section. The southern section is dominated by a steep, boulder covered ridge ("main ridge"). Along the base of the main ridge steep slopes give way to an alluvial bajada. The northern section has more variable topography. There are 2 conspicuous features: peak 2252, a volcano shaped hill; and a pegmatite ridge crested with

massive quartz outcrops. The remainder of the northern section is mostly open, rolling hills. Elevations on the plot range from 600 m (1830 ft) in the extreme northeast corner to the high point on the main ridge at 702 m (2305 ft). Geologically the plot is primarily composed of granite, porphyry, and quartz. All drainages on the plot lead to Brady Wash, a large wash that flows parallel to the eastern boundary. Vegetation is typical of the Arizona Upland subdivision of the Sonoran Desert.

Most human impacts to the plot are related to past mining activity. Assessment scrapes and pits are located along all roads and on the bajada. There are 3 large troughs in the northern section. In 1990, 3 tortoises were found in a 1-m deep, vertical walled pit. They were rehydrated by plot workers. One escaped, the other 2 were released into a known shelter. One of these 2 was found dead 2 weeks later. Cattle are grazed on the plot as evidenced by dung and trails, but they are seldom seen. The entire plot is surrounded by a loop of roads. Only the road that crosses to the south receives any substantial use. Most use is by hunters or people associated with a ranch to the west. Trash was common near mining areas, otherwise it was scattered lightly throughout the plot. Native Americans used this area in the past. Pottery fragments, morteros, flaking waste, and the remains of a stone shelter on the main ridge were noted.

Coverage history

Schwartzmann studied the Granite Hills area from 1975 to 1979. His radio telemetry study of tortoise home ranges and movement patterns concentrated on the low hills in the northern part of the plot. Population monitoring surveys were conducted annually from 1990 to 1994. The 1990 survey was a 66 person-day effort conducted over 46 calendar days from 21 August to 28 October. The 1991-1994 and 1998 surveys were each 60 person-day surveys, but starting and ending dates differed slightly. The 1991 survey was conducted over 46 calendar days from 20 August to 17 October. In 1992, fieldworkers spent 45 calendar days from 1 September to 21 October. The 1993 survey took 45 calendar days from 2 August to 10 October. The 1994 effort was conducted over 45 calendar days from 6 August to 6 October. The 1998 survey took 47 calendar days from 15 August to 5 October.

Sex ratio

Observed sex ratios for adult tortoises did not differ from the expected 1:1 in either 1990 (16:15), 1991 (20:29), 1992 (21:24), 1993 (26:29), 1994 (29:31), or 1998 (16:20).

Health

All tortoises encountered during each year have been healthy. One tortoise (2%) in 1998 was noted with swollen eyes. Cutaneous dyskeratosis has been noted each year. In 1990, 2 tortoises (4%) were described as having "hyperkeratosis". In 1994, fieldworkers reviewed slides from previous years looking for evidence of cutaneous dyskeratosis. Slides for 1991 and 1992 revealed 4 tortoises with shell lesions (6% and 5%, respectively). In 1993 only 1 tortoise (1%) was noted as having lesions. In 1994 there were 23 cases (21%), and there were 13 (23%) in 1998.

Scute numbering anomalies

In 1990, 6 tortoises (12%) were noted with scute numbering anomalies. Nineteen (27%) animals had numbering anomalies in 1991, 18 (24%) in 1992, 15 (16%) in 1993, 27 (25%) in 1994, and 13 (20%) in 1998.

HARCUVAR MOUNTAINS (Woodman and Shields 1988; Woodman and others 1994, 1998)

Description

The 2.6 sq. km (1 sq. mi) Harcuvar Mountains plot is located at the eastern end of the Harcuvar Mountains near the southwest corner of Yavapai County. Elevations range from 750 m (2460 ft) on the central-eastern edge to 1045 m (3450 ft) along the west edge of the plot. The dominant topographic feature of the plot is peak 3415, located just north of the center of the plot. Four ridges extend from this peak. There are also 4 major washes on the plot. The first bisects the plot from the southwest corner to the center of the eastern border. The second begins just north of the southwest corner, curves through the plot, then exits at the northwest corner. A third flows off the east side of peak 3415 and exits the plot near the northeast corner. One other wash barely crosses the southeast corner. Geologically, the plot is mostly fine-grained granite with outcrops of gabbro. Vegetation on the plot combines elements of both the Arizona Upland and Lower Colorado subdivisions of the Sonoran Desert.

Human use of the plot is light. Cattle are grazed on the plot, but cattle sign was limited to ridges and shallow sloped hillsides. There is 1 road on the plot. It enters the plot along the east edge and continues for only about 0.5 km, ending at an old campsite. No vehicles were seen on the road in either 1993 or 1997. In 1988, one group of hunters drove up scouting for deer. Hunting appears to be light, as few spent shells were noted. The plot has been mined in the past. About 10 claims have been found, the most recent dated 1970. There are several scrapes and pits on the plot, and mining trash was also noted in several locations.

Coverage history

In 1988, 68 person-days over 49 calendar days were spent surveying the plot from 6 August to 25 October. The 1993 survey consisted of 64 person-days over 49 calendar days from 25 July to 4 October. The 1997 survey was a 60 person-day effort conducted over 49 calendar days from 9 August to 5 October.

Sex ratio

Observed sex ratios for adult tortoises did not differ from the expected 1:1 in either 1988 (32 males, 22 females) or 1997 (27 males, 23 females). The 1993 ratio was significantly different from 1:1 (29 males, 15 females).

Health

All tortoises appeared vigorous and healthy. Symptoms of URTD were not noted during any survey. Cutaneous dyskeratosis was not noted during the 1988 survey. It was noted on 7 tortoises

(15%) in 1993. Five of these animals were recaptured in 1997 and showed no signs of the disease. Only 1 tortoise (2%) was noted with cutaneous dyskeratosis in 1997.

Scute numbering anomalies

Anomalous numbers of scutes were documented on 19 tortoises (32%) in 1988. In both 1993 and 1997, 10 tortoises (20% and 18%, respectively) were noted with anomalous numbers of scutes.

HARQUAHALA MOUNTAINS (Holm 1989; Woodman and others 1995)

Description

The 1.6-km by 2.4-km (1 mile by 1.5 miles) Harquahala plot is located near the eastern end of the Harquahala Mountains in Maricopa County. The Harquahala Range is bordered to the north by U.S. Highway 60; to the south lies the Harquahala Plain. Elevations on the plot range from 780 m (2560 ft) in Brown's Canyon to the high point of the plot at 1036 m (3399 ft). Topography is complex, with several ridge systems occurring on the plot. The plot is divided into north and south portions by 2 major wash systems. Seven washes drain the northern portion, while 5 drain the southern portion. Geologically, the Harquahala plot is mostly granitic, with many intrusive bands of dark colored gneiss. These bands, often exposed for hundreds of meters, tend to erode faster than the surrounding granite, thus forming natural routes through the rough terrain. Vegetation is composed of elements from both the Arizona Upland and Lower Colorado subdivisions of the Sonoran Desert. Approximately 7% of the plot, mostly 2 north-facing ridges, burned in 1993. Catclaw acacia was the only perennial to survive; grasses and forbs were dominant in these areas.

Human impacts to the plot are minimal. There was evidence of cattle grazing, hunting, Native Americans, and mining. There is 1 road that cuts through the northeast corner of the plot. Trash was mostly found along this road or at 2 established campsites. Small amounts of trash were scattered throughout the plot, mostly shotgun shells and food and beverage containers.

Coverage history

The Harquahala Mountains study plot was first surveyed in 1988. This BLM survey consisted of 67 person days conducted over 47 calendar days from August 17 to November 3. In 1994, 60.5 person days were spent over 47 calendar days from August 15 to October 5.

Sex ratio

The sex ratio did not differ from 1:1 in either 1988 or 1994. Seven males and 9 females were caught in each year.

Health

Holm (1989) did not mention any health observations, but based on photographs from the 1988 survey, 6 tortoises (29%) had cutaneous dyskeratosis. Five of these 6 were recaptured in 1994, and all still had lesions. In 1994, 12 tortoises (63%) had lesions. Otherwise, tortoises on this plot seem healthy.

Scute numbering anomalies

No scute numbering anomalies were documented in 1988. In 1994, 4 tortoises (21%) were noted with anomalous scutes.

HUALAPAI FOOTHILLS (Hart and others 1992; Woodman and others 1997)

Description

The 2.6 sq. km (1 sq. mi) Hualapai Foothills plot is among the scattered isolated foothills in the southwestern edge of the Hualapai Mountain Range, approximately 60 km (37 mi) south of Kingman and 25 km (15.5 mi) west of Wikieup. The plot is dominated by a large, isolated, granitic hill 1149 m (3767 ft) high. This peak is nearly centered on the plot. Three distinct ridges radiate from this peak, and many smaller ridges descend from these. Three major washes also flow from this peak and are the major drainages for the plot. Vegetation on the plot is a combination of several biomes, Great Basin Conifer Woodland, Mohave Desertscrub, and Sonoran Desertscrub. The majority of the plot occurs within the pinyon-juniper series of Great Basin Conifer Woodland but is nearly ecotonal with the joshuatree series. On certain hillsides there are influences from the creosotebush crucifixion-thorn series and the paloverde cacti-mixed scrub series of the Arizona Upland subdivision of the Sonoran Desert.

Human impacts to the plot are moderate. Signs of old mining activity (claim posts, scrapes, and cairns) were scattered throughout the plot, but there was no evidence of recent mining in either 1991 or 1996. Cattle grazing occurs on the plot. Cattle droppings are found throughout the plot except on the steepest slopes. Areas under large trees in washes were noted as heavily impacted in 1996. Alamo Road, a light duty dirt road, runs northwest-southeast 0.8 km (0.5 mi) west of the southwest corner of the plot. A seldom-used jeep trail extends east-northeast from Alamo Road, through the northwest portion of the plot, and ends at an abandoned corral. Hunting is common on the plot based on the number of spent shotgun shells noted. Trash in low abundance was found along the jeep trail and in the main wash downstream from the jeep trail.

Increased urban development has begun to occur adjacent to the plot since it was last surveyed. In 1999 approximately 60,000 acres (24,000 ha) of BLM land, primarily in Dutch Flat south of the Hualapai Mountains, were exchanged for approximately 70,000 acres (28,000 ha) of private land in the Hualapai Mountains and southern Dutch Flat area (BLM 1999). The private lands are slated to be sold in 40-acre (16-ha) parcels with some 160-acre (65-ha) parcels (BLM 1998). Private lands abut the plot boundaries on 2.5 sides.

Coverage history

In 1991 a 60-day survey was conducted between 6 September and 8 November. In 1996 the 60-day plot coverage occurred between 14 August and 9 October.

Sex ratio

Sex ratios for adult tortoises did not differ from the expected 1:1 in either 1991 (19 males, 13 females) or 1996 (21 males, 13 females).

Health

Almost all tortoises were in good health. In 1991, 2 tortoises (5%) were noted with dry whistles in their breath. Three tortoises (8%) had whistles or a rasp in their breath in 1996. In 1996, 5 tortoises (14%) had cutaneous dyskeratosis lesions. Cutaneous dyskeratosis was not documented in 1991, but review of slides showed that 3 tortoises (8%) had lesions in 1991.

Scute numbering anomalies

In 1991, 19 tortoises (50%) were noted with scute anomalies. Eighteen tortoises (44%) had anomalies in 1996.

LITTLE SHIPP WASH (Schneider 1981; Shields and others 1990; Hart and others 1992; Woodman and others 1993, 1994, 1995, 1999)

Description

The 2.6 sq. km (1 sq. mi) Little Shipp Wash plot is located in west central Yavapai County. Elevations range from 800 m (2624 ft) to 967 m (3172 ft). The northwestern corner of the plot features a large hill with 2 peaks (peaks 3172 and 3125). These 2 peaks have a broad summit plateau and steep slopes to the north, south, and east. The southwestern third of the plot is composed of 2 ridges separated by a deep wash. The eastern edge of the plot is dominated by peak 2997, an isolated, bouldery hill rising approximately 250 m (820 ft) above the surrounding terrain. The plot is mostly granitic, with some sedimentary shale in the southeast corner and in the central region. Vegetation on the plot combines both the Arizona Upland and Interior Chaparral subdivisions of the Sonoran Desert.

Human impacts to the plot are primarily from grazing, vehicular access, and hunting. Cattle have been documented on the plot during each survey. There are several wet areas on the plot, including 1 spring. These areas were heavily used by cattle as were the flats and gently sloping hills. Cattle dung and trails are found throughout the plot. The plot is 1.6 km (1.0 mi) north of State Highway 96. A good condition dirt road borders the plot to the south and east. One spur off this road borders the southern plot boundary, ending in the southwest corner. Another spur runs through the northwest corner of the plot. There are many old campsites along these roads. Most vehicular traffic was related to ranch operations, but there were also hunters and target shooters on the roads. Trash is lightly scattered all over the plot, consisting mostly of spent ammunition and beverage containers.

Coverage history

Schneider (1981) spent 40 days on the plot from late February through June 1980. His study area was slightly different than the current plot boundaries, and his study was oriented towards tortoise movements. Sixty-person-day surveys have been done from 1990 to 1994 and in 1998.

The 1990 survey lasted 48 calendar days from 13 August to 29 October. The 1991 effort took 50 calendar days from 19 August to 31 October. The 1992 survey was conducted over 45 calendar days from 3 September to 18 October. In 1993, 45 calendar days were spent from 9 August to 3 October. The 1994 survey took 45 calendar days from 9 August to 5 October. The 1998 survey lasted 50 calendar days, from 11 August to 11 October.

Sex ratio

Schneider (1981) did not calculate a sex ratio for his study. Observed sex ratios for adult tortoises did not differ from the expected 1:1 in 1991 (30:37), 1992 (38:42), 1993 (36:47), 1994 (27:34), or 1998 (18:30). The 1990 ratio was significantly different from 1:1 (26 males, 42 females).

Health

Health information was not recorded during Schneider's 1980 survey. Overall, tortoises on the plot appear to be healthy. One tortoise (1%) was reported with slightly swollen eyelids in 1991, 1 (1%) with nasal exudate in 1992, 1 (1%) with a wet naris in 1994, and 2 (3%) with puffy eyes in 1998. Various breathing abnormalities were noted every year: 16 (19%) in 1990, 16 (20%) in 1991, 9 (10%) in 1992, 15 (15%) in 1993, 11 (14%) in 1994, and 3 (5%) in 1998.

Cutaneous dyskeratosis was noted in each year from 1990 to 1994. In 1990, 19 animals (23%) were noted with "hyperkeratosis". In 1991, 20 tortoises (24%) were observed with lesions. There were 16 tortoises (18%) in 1992, 30 (29%) in 1993, 24 (31%) in 1994, and 22 (38%) in 1998 with cutaneous dyskeratosis lesions.

Scute numbering anomalies

In 1990, 26 tortoises (30%) were noted with scute numbering anomalies. Twenty-one animals (25%) had numbering anomalies in 1991, 31 (34%) in 1992, 32 (29%) in 1993, 19 (24%) in 1994, and 18 (27%) in 1998.

MARICOPA MOUNTAINS (Wirt 1988; Shields and others 1990; Hart and others 1992)

Description

The 2.6 sq. km (1 sq. mi) Maricopa Mountains plot is located in the central part of the Maricopa Mountains in Maricopa County. Elevations range from 525 m (1719 ft) in the northeast corner to 820 m (2690 ft) on a peak in the southeast corner. The northeast corner is primarily bajada with many braided washes. There is a main ridge that runs from the southeast corner to the north-central part of the plot. Southwest of the main ridge is an area of lower peaks and a large bowl. There are 2 major washes on the plot. One wash in the northwest quarter drains almost directly north. The second wash is composed of 2 forks that drain the west-southwest side of the main ridge. This wash exits the plot in the southwest corner. Geologically the plot is primarily granitic. Vegetation is characteristic of the Arizona Upland subdivision of the Sonoran Desert.

Human impacts to the plot are light. Most use is by hunters and OHV's. The plot has been grazed, but cattle sign was limited to the northeast corner and northern boundary. In November of 1990, the North Maricopa Mountains Wilderness area was designated. The study plot falls within the wilderness boundary. The road leading to the plot is closed at the wilderness boundary. Human impacts to the plot have decreased since designation due to lack of easy access.

Coverage history

Wirt (1987) spent 17 field days on the plot during April and May, then another 43 days from 8 August to 14 November. The 1990 survey was a 60 person-day effort conducted over 43 calendar days from 5 August to 25 October. In 1992 fieldworkers conducted a special search for dead or diseased tortoises. Twenty-four person-days were spent searching 4 outlying areas and the plot itself.

Sex ratio

Sex ratios for adult tortoises did not differ from the expected 1:1 in either 1987 (33 males, 23 females) or 1990 (7 males, 6 females). A sex ratio was not calculated in 1991.

Health

All live tortoises appeared healthy during all surveys, although plot workers in 1990 characterized them as "noticeably less feisty" than those on other plots. One 1990 tortoise (6%) was described as having a possible case of cutaneous dyskeratosis.

Scute numbering anomalies

In 1987, 13 tortoises (23%) were noted with anomalous numbers of scutes. The 1990 survey found 4 (22%) with numbering anomalies. Scute numbering anomalies were not noted in the 1991 survey.

NEW WATER MOUNTAINS (Shields and Woodman 1988; Woodman and others 2000)

Description

The 2.6 sq. km (1 sq. mi) New Water Mountains plot is located near the center of the New Water Mountain Range. The crest of the New Waters bisects the plot in the southern half of the plot. The plot lies primarily north of the crest of the range, however the southwest corner is south of the crest. Elevations range from 457 m (1500 ft) on the northern boundary to 792 m (2600 ft) along the crest of the mountains.

The New Waters drop precipitously immediately north of the crest before the slope declines into a series of terrace-like cliffs until the mountains flatten out. Many small, deeply incised washes drain the steep slopes of the New Waters. On the north side, the small washes converge into 3 broad, shallow washes. The mid-slope region consists of deeply incised washes interspersed with ridges, terraces (generally the tops of hills), and steep, but passable slopes. The lower slopes consist of fewer but broader and less deeply incised washes, shallow slopes, and several prominent hills. Between the hills and washes there is some desert pavement. The flats north of

the mountains consist of 3 broad washes interspersed with desert pavement. The southwest corner of the plot consists of several washes interspersed with steep hills.

The New Water Mountains are primarily volcanic, with many areas of basalt, tuff, and rhyolite. The basalt and tuff tend to be primarily on the lower slopes, and the upper and middle slopes are generally composed of rhyolite. The largest boulders and best soil formation tend to be in the areas of basalt and tuff. Although there are small outcrops of rock and boulders, the rhyolite tended to be broken into pebbles or small cobble. There is very little or no soil development in the rhyolite and very little potential for digging burrows. Vegetation in the New Waters is a combination of Colorado Desert and Arizona Upland subdivisions of the Sonoran Desert. The 2 communities are separated primarily by topography.

Human impacts to the plot appear to be light. There are several mining claims dated 1959. Roads to the claims and assessment scrapes are evident, but it appears that mining activity ceased shortly after it began. The roads on the plot were not used in either 1988 or 1999. Cattle use of the plot is also light. Cattle droppings were noted as infrequent in 1988. The 1999 fieldworkers noted only a few old, gray droppings. Hunters probably use the plot, but trash, including spent shells, was light.

Coverage history

From 6 August to 26 October 1988, 46 person days over 34 calendar days were spent searching for tortoises on the New Water Mountains study plot. The 1999 plot coverage of 35 person days over 29 calendar days occurred between 26 August and 25 September.

Sex ratio

The observed sex ratio for adult tortoises did not differ from the expected 1:1 in either 1988 (7 males, 8 females) or 1999 (8 males, 9 females).

Health

Tortoise health was not documented in 1988. In 1999, 1 tortoise (5%) was noted with symptoms of cutaneous dyskeratosis.

Scute numbering anomalies

Four tortoises (24%) with scute numbering anomalies were noted in 1988. In 1999, 3 tortoises (14%) were noted with numbering anomalies.

SAN PEDRO VALLEY (Hart and others 1992; Woodman and others 1996)

Description

The 2.6 sq. km (1 sq. mi) San Pedro Valley plot is located in the southeast corner of Pinal County. It is southwest of the Galiuro Mountains and northeast of the San Pedro River. The plot occurs in a broad river valley and covers only a portion of many square miles of contiguous similar habitat. This is unlike most tortoise plots in Arizona, which are on steep, isolated desert

mountains. Elevations range from about 825 m (2680 ft) on the west edge of the plot to 948 m (3080 ft) near the northeast corner. The plot is characterized by many arroyos with steep, rocky slopes, tall soil cliffs (some >20 m [65.6 ft] high), and some level to rolling gravel covered areas. Three major washes cross the plot. Geologically, the plot is composed primarily of granitic bedrock, lakebed sediments, undifferentiated silt and gravel, and alluvium. There are very few large boulders for tortoises to burrow under. Tortoises find shelter in naturally formed cavities under the terraced gravel or in natural or excavated cavities in silt, diatomite, or diatomaceous marl layers found throughout the plot. Vegetation on the plot is ecotonal between the Arizona Upland subdivision of the Sonoran Desert and semi-desert grassland.

Primary human impacts observed include mining, smelting, grazing, power transmission lines, roads, and recreational use (hunting, OHV's). Five mining claims cover the entire plot, and there are others on adjacent BLM land. A small diatomaceous earth mine is located approximately 1 km (0.6 mi) west of the plot. There have also been explorations of diatomaceous earth deposits within 400 m (1312 ft) of the plot. The copper smelter at San Manuel is approximately 10 km (6.2 mi) west of the plot. Smoke often lingered on the plot during surveys, and dust from tailings was present during windy conditions. Cattle droppings have been found throughout the plot. Cattle trails and bedding areas were also observed. There is 1 power line with an access road and 3 other roads on the plot. Road use ranged from light to practically non-existent. Litter was common but not abundant, most often near the roads; windblown trash was scattered throughout the plot.

Coverage history

BLM personnel searched for tortoises in the general area during the summers of 1988 and 1989 (Schnell and Drobka 1988; Duncan 1989). Of the 9 tortoises captured, 1 was captured within the plot boundary, and 1 was very close to the boundary. The first standard survey of the plot was conducted in 1991. This was a standard 60 person-day survey conducted over 45 calendar days from 31 August to 28 October. BLM land adjacent to the plot was the site of a radio-telemetry study (Bailey 1992; Bailey and others 1995). Twenty-two tortoises were marked, including one captured by the BLM in 1988. None of these animals were captured on the plot during the 1991 survey. In 1995, 60 person days (45 calendar days) were spent surveying the plot between 7 August and 5 October. Two tortoises marked during the telemetry study were observed. One was captured on plot, and 1 was seen just off the plot.

Sex ratio

Sex ratios for adult tortoises did not differ from the expected 1:1 in either 1991 (16 males, 18 females) or 1995 (48 males, 36 females).

Health

All tortoises seem to be in good health on this plot. The only slight anomalies include 2 tortoises (5%) with slight whistles in the breath in 1991 and 4 (6%) in 1995; 1 tortoise was found with some moisture on its left naris in 1995. One of the tortoises that had a slight whistle during

exhalation in 1991 was found recently dead in 1995. Only 3 tortoises (3%) had symptoms somewhat similar to cutaneous dyskeratosis in 1995.

Scute Numbering Anomalies

In 1991, 11 tortoises (24%) had 1 or more scute numbering anomalies. In 1995, 36 tortoises (39%) were noted with anomalies.

SANTAN MOUNTAINS (SWCA 1990, 1992)

Description

The Santan Mountains plot is located within the Santan Mountains Regional Park, south of the town of Chandler Heights in Pinal County. The original plot (1990) was 2.6 sq. km (1 sq. mi), but after an initial survey revealed no tortoise sign in the southern portion of the plot, 2 additional areas were added to the northeast and northwest. The reconfigured plot was 3.1 sq. km (1.2 sq. mi). In 1991, areas were added to the western and northern sides of the 1990 plot, and some areas from the eastern and southern sides were eliminated. The 1991 plot was approximately 2.7 sq. km (1.04 sq. mi) and included about 67% of the 1990 plot. Both plot configurations included the same key topographic features, dominated by the rocky east-west ridge of Goldmine Mountain. This ridge divided the 1990 plot into north and south and formed the southern boundary of the 1991 plot. A north-south ridge separates the 2 major drainage systems which originate on the plot. The southwest corner of both plot configurations was the most complex portion, containing several hills, low ridges, and minor drainages. Elevation ranges from 488 m (1600 ft) in the north to 731 m (2400 ft) along the east-west ridge.

Human impacts to the plot have until recently been centered on mining. There are several mine shafts and mining roads on the plot. Development has increased to the north of the plot since the plot surveys. The population is no more isolated as a result of this, but human use of Goldmine Mountain has probably increased. Trash, shotgun shells, and other debris were common on the plot in a 1996 visit (pers. obs.). One tortoise in 1990 was found on its back with a fresh bullet wound to the plastron.

Coverage history

In 1990, 63.4 person days over 37 calendar days were spent surveying the plot between August 29 and October 24. The 1991 survey covered 96 person days over 48 calendar days from August 13 to October 28.

Sex Ratio

Observed sex ratios for adult tortoises did not differ from the expected 1:1 ($P > 0.10$) in either 1990 (4 males, 3 females) or 1991 (10 males, 16 females).

Health

Tortoises on the plot appeared to be in good health in both 1990 and 1991. Only one tortoise showed signs of URTD. This animal had raspy breathing and swollen eyes when first captured,

but on subsequent capture it only had raspy breathing.

Scute numbering anomalies

In 1990, 1 tortoise (12%) was noted with scute numbering anomalies. In 1992, 9 tortoises (31%) with numbering anomalies were noted, including the animal described in 1990.

TORTILLA MOUNTAINS (Woodman and others 1993, 1997)

Description

The 2.6 sq. km (1 sq. mi) Tortilla Mountains study plot is located in the northwestern portion of the Tortilla Mountains, Pinal County. Elevations range from 656 m (2000 ft) in the west-central part of the plot to >853 m (>2240 ft) on 2 peaks in the east-central portion of the plot. Geologically, the plot is primarily granitic, with exposed granite capping the 3 tallest peaks. Large granitic boulders are found along the upper to middle slopes. Lower elevation slopes and ridges often have granitic outcrops. The plot is bisected east-west by a major wash. There is 1 large hill north of this wash. Most tortoise habitat is south of this wash, an area characterized by 4 large hills connected by a ridgeline in the form of an inverted "U". This area is bisected by 1 incised wash that drains to the south. Vegetation on the plot is typical of the Arizona Upland subdivision.

Primary human impacts to the plot are from mining and grazing. More than 30 claim posts were noted along with 21 assessment scrapes (typically associated with copper-bearing outcrops). These were scattered throughout the plot. Cattle grazing occurs on the plot. Cattle dung and trails were found throughout the plot except on the steepest slopes. Most of the saddles on the plot were heavily impacted, with areas devoid of vegetation and covered with dung. There were no cattle seen in 1996, and none of the cattle sign appeared to be recent. Hunting is minimal but does occur, as evidenced by spent shell casings. Litter is uncommon. Most was old and associated with past mining activities. There are 5 roads on the plot. The main access road cuts across the northwest corner of the plot. This road receives regular use. The other roads get very light use, usually during hunting season.

Coverage history

In 1992 a 60 person-day survey was conducted over 46 calendar days between 2 September and 21 October. In 1996 a 60 person-day survey (45 calendar days) was conducted between 11 August and 9 October.

Sex ratio

The observed sex ratio for adult tortoises did not differ from the expected 1:1 in either 1992 (20 males, 29 females) or 1996 (26 males, 34 females).

Health

All tortoises appeared healthy during both surveys. In 1992, 3 tortoises (6%) with cutaneous dyskeratosis were noted. In 1996 there were 7 tortoises (10%) documented with cutaneous

dyskeratosis, including 3 that were asymptomatic in 1992. One tortoise (1%) in 1996 had slightly puffy eyes.

Scute numbering anomalies

In 1992, 12 tortoises (23%) had scute numbering anomalies. Twelve different tortoises (17%) had numbering anomalies in 1996.

WEST SILVERBELL MOUNTAINS (Hart and others 1992; Woodman and others 1996)

Description

The 2.6 sq. km (1 sq. mi) West Silverbell Mountains plot is comprised of the eastern half of an isolated granitic ridge at the western edge of the West Silverbell Mountains in Pima County. A northwest to southeast ridge divides the plot into 2 primary sections, a southwest half with complex, steep, bouldery slopes and a northeast half characterized by more open cover. There are 3 main washes and several smaller washes with cave shelters. Elevations range from 600 m (1950 ft) to 945 m (3100 ft). Exfoliated granitic soil, rocks, and boulders cover the majority of the plot. There are solid granitic outcrops on the higher points. There are also sandy alluvial wash deposits in the northeast corner and along the southern boundary. Vegetation on the plot is typical of the paloverde-cacti-mixed scrub series of the Arizona Upland subdivision.

There is very little evidence (shells, tracks, or trash) of human impacts on the plot. It appears that most use is for hunting. In 1995 field workers found a tortoise that had been shot and one with a painted carapace, however.

Coverage history

The West Silverbell plot has been surveyed twice, in 1991 and 1995. Both were 60-day surveys. The 1991 survey was conducted over 46 calendar days from 5 September to 30 October. In 1995 the survey was conducted over 50 calendar days from 3 August to 7 October.

Sex ratio

In 1991 the adult sex ratio was significantly different from 1:1 (20 males, 39 females), but the ratio was not significant in 1995 (35 males, 40 females).

Health

Only 1 tortoise with primary symptoms of URTD has been found on this plot. In 1995, 1 tortoise (1%) had puffy eyes on 1 occasion but not on 2 previous captures. In addition, 1 tortoise was considered "somewhat light in weight" in 1991. An adult male tortoise was noted as being lethargic on 4 August 1995; this tortoise was found dead on 24 August, with a large bladder stone in his body cavity. Seven tortoises (8%) had symptoms of cutaneous dyskeratosis in 1995.

Scute Numbering Anomalies

In 1991, 21 tortoises (33%) had 1 or more scute numbering anomalies. In 1995, 30 tortoises (33%) were noted with anomalies.

WICKENBURG MOUNTAINS (Hart and others 1992)

Description

The 2.6 sq. km (1 sq. mi) Wickenburg Mountains plot is located at the eastern end of the Wickenburg Mountains in Yavapai County. Trilby Wash bisects the plot from north to south. Approximately 2/3 of the plot is east of Trilby Wash. Terrain rises steeply to either side of Trilby Wash, with the highest points of the plot along the eastern plot boundary. Elevations range from 890 m (2920 ft) in the south to 1230 m (4035 ft) on the ridges along the east boundary. The west faces of these ridges are drained by several deeply incised washes that flow into Trilby Wash. The diverse vegetation on the plot is primarily paloverde-cacti-mixed scrub series of the Arizona Upland subdivision of the Sonoran Desert.

Current or past human impacts to the plot have included mining, vehicular travel, grazing, and hunting/shooting. Traffic was fairly common in Trilby Wash (usually 1 miner with a nearby claim). There was no current mining on the plot, but 1 butte on the plot had been the site of extensive mining in the past. On top of this butte, there were several concrete pads, shafts, assorted debris, and at least 1 well. Rock cairns, claim stakes, and test holes were found throughout the plot. Spent shotgun shells, probably from quail hunters, are scattered throughout the plot. There were also 2 areas of concentrated trash that included engine blocks and carpeting. Cattle grazing occurs throughout the plot. Manure and trails were everywhere except the steepest slopes. Saddles on the plot had denuded areas where cattle assembled. Feral burros were common.

Coverage history

The 1991 survey of the Wickenburg Mountains has been the only survey of the plot. The 60 person-day survey was conducted between 4 September and 29 October.

Sex ratio

The observed sex ratio for adult tortoises did not differ from the expected 1:1 (10 males, 5 females).

Health

All tortoises appeared healthy. One animal (7%) had a slight whistle during exhalation in 1991.

Scute numbering anomalies

Six tortoises (40%) had anomalous scute numbers. In addition, 1 female was "hinged" along the seam between her abdominal and femoral scutes.