Sonoran Desert Tortoise (*Gopherus morafkai*)
Growth and Juvenile Habitat Selection
at a Long-term Study Site in Central Arizona, USA

by

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ABSTRACT

Biological diversity is threatened by increasing anthropogenic modification of natural environments and increasing demands on natural resources. Sonoran desert tortoises (*Gopherus morafkai*) currently have Candidate status under the Endangered Species Act (ESA) based on health and habitat threats. To ensure this animal persists in the midst of multiple threats requires an understanding of the life history and ecology of each population. I looked at one physiological and one behavioral aspect of a population of tortoises at the Sugarloaf Mountain (SL) study site in central Arizona, USA. I used 21 years of capture-recapture records to estimate growth parameters of the entire population. I investigated habitat selection of juvenile tortoises by selecting 117 locations of 11 tortoises that had been tracked by radio-telemetry one to three times weekly for two years, selecting locations from both summer active season and during winter hibernation. I compared 22 microhabitat variables of tortoise locations to random SL locations to determine habitat use and availability. Male tortoises at SL reach a greater asymptotic length than females, and males and females appear to grow at the same rate. Juvenile tortoises at the SL site use steep rocky hillsides with high proportions of sand and annual vegetation, few succulents, and enclosed shelters in summer. They use enclosed shelters on steep slopes for winter hibernation. An understanding of these features can allow managers to quantify Sonoran desert tortoise habitat needs and life history characteristics and to understand the impact of land use policies.

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Biological diversity is threatened by increasing anthropogenic modification of natural environments and increasing demands on natural resources. These activities are degrading, fragmenting, and often destroying or significantly altering habitats that support a wide range of taxa (AGFD 2012; IUCN 2000; Germaine and Wakeling 2001). Species conservation relies on the identification and protection of essential features that make up habitat for a species (Noss et al. 1997). Conservation biologists have an important role in understanding the impacts of anthropogenic and environmental change on habitat, and to make recommendations to managers and policy makers on how to protect habitat for species conservation (Spencer and Janzen 2010).

Within North America, the Sonoran desert tortoise (*Gopherus marafkai*) is a species of conservation concern and is endemic to Arizona and northern Mexico (Germano 1994; Murphy et al. 2011). Sonoran desert tortoises use specific habitat consisting of rocky boulders on steep slopes, incised washes in bajadas (Grandmaison et al. 2010; Murphy et al. 2011), and Sinaloan thorn scrub and deciduous woodland (Germano 1994*a*). The inaccessibility and complexity of this terrain, to some extent, limits the direct impact of traditional means of habitat destruction such as urbanization, agriculture, cattle grazing, military activities, or high-impact recreational activities such as off-road vehicles (Howland and Rorabaugh 2002). However, significant threats to tortoises and their habitat do exist. Roads, canals, and highly populated intermountain valleys fragment habitat and effectively create barriers to movement that may genetically isolate populations (Howland and Rorabaugh 2002; Edwards et al. 2004). The introduction of nonnative invasive plants (Esque, et al. 2002) may replace native plant diversity. These introduced species often do not contain the same nutritional value as native plants and can increase the frequency of fire (Howland and Rorabaugh 2002). In addition to drastically altering the landscape and habitat, fire can cause direct tortoise mortality for individuals in the open or in shallow or exposed burrows (Esque, et al. 2002). Road mortality impacts populations by removing individuals and reducing the effective population size (Howland and Rorabaugh 2002). Based on these health and habitat threats, Sonoran desert tortoises were listed as a closed season species in Arizona in 1989 (AGFD 2010), and a Species of Greatest Conservation Need (AGFD 2012) by the Arizona Game and Fish Department (AGFD). They also gained Candidate status under the Endangered Species Act (ESA) in 2010 (USFWS 2010).

Until recently, desert tortoises were considered a single species (*G. agassizii*) with distinct populations on either side of the Colorado River. In 2011, these populations were split into two species based on genetic, morphological, physiological, and ecological differences. The Mohave desert tortoise (*G. agassizii*) occupies parts of southeastern California, northwestern Arizona, southern Nevada, and southwestern Utah in the Mohave, Sonoran, and Great Basin deserts north and west of the Colorado River. The Sonoran desert tortoise (*Gopherus marafkai*) occupies areas of southwestern Arizona and northwestern Mexico in the Sonoran desert, south and east of the Colorado River (Murphy et al. 2011).

Much of what is known about desert tortoises is from research on the Mohave desert tortoise (*G. agassizii*) listed as Threatened under the ESA in 1980 (USFWS 1980). Although there are fewer studies on Sonoran desert tortoises than Mohave desert tortoises, there are even fewer studies of juvenile size desert tortoises and none of more than a few years duration (Averill-Murray et al. 2002*a*; Van Devender 2002). Desert tortoises of both species are considered juveniles if they have a mid-line carapace length (MCL) measurement of less than 180 mm (Germano 1994; Berry and Christopher 2001; Averill-Murray and Averill-Murray 2005). This is the size at which many individuals attain reproductive maturity and morphological characteristics indicative of sex begin to be discernible (Germano 1994*b).*

Juvenile Sonoran desert tortoises are considered one of the least-studied groups in the Sonoran desert (Germano 1994*a*) and are infrequently the focus of biological studies because of their cryptic nature, low survivability (Morafka 1994; Wilson et al. 1999), and the resource investment required to study a slow-growing and long-lived animal in a complex habitat (Heppell 1998).

Sonoran desert tortoises are infrequently encountered more than once as juveniles, contributing to the lack of studies addressing age and growth rate of desert tortoise wild populations (Zylstra et al. 2012; Averill-Murray et al. 2002*a*). Age estimation is further hampered by the lack of morphological or physiological characters to indicate age. However, age structures, growth rates, and habitat preferences are key demographic features. An understanding of these features can allow managers to quantify Sonoran desert tortoise habitat needs and life history characteristics and to understand the impact of land use policies (Medica et al. 1975). To properly quantify the habitat needs and life history characteristics of this unique desert dweller, individual populations must be monitored and documented and information made available to conservation managers. Germano et al. (2002) wrote: “conservation plans for desert tortoises must include an understanding of the normal rates of growth of free-ranging tortoises and of the ecological, behavioral and nutritional requirements of both juveniles and adults.”

This study focused on two areas of Sonoran desert tortoise biology where information is lacking: growth rates of juveniles and adults and habitat selection by juveniles. The goals of this research were to determine size-based age classes and asymptotic sizes for each sex, to quantify available habitat at the Sugarloaf Mountain (SL) study site, and to determine juvenile tortoise habitat selection. To address my first objective, I fit growth curves to recaptured tortoises to:

1. Determine the asymptotic lengths of male and female tortoises
2. Determine the growth rates of male and female tortoises

To address my second objective, I used location information of juvenile tortoises to:

1. Determine whether juvenile tortoises exhibited habitat selection during the summer
2. Determine whether juvenile tortoises exhibited habitat selection when choosing a winter hibernation location
3. Compare summer habitat selection and winter hibernation habitat selection
4. Create a predictive model to identify suitable juvenile desert tortoise habitat at the SL site

STUDY SITE

Sugarloaf Mountain is located in the Mazatzal Mountains, within the Tonto National Forest, and is 22 km northeast of the city of Fountain Hills, Arizona (Figure 1). Tortoises are found throughout the area, but an approximately 66-ha area (approximately 2 km east-southeast of Sugarloaf Mountain) has a large number of individuals (181) and has been studied since 1991.

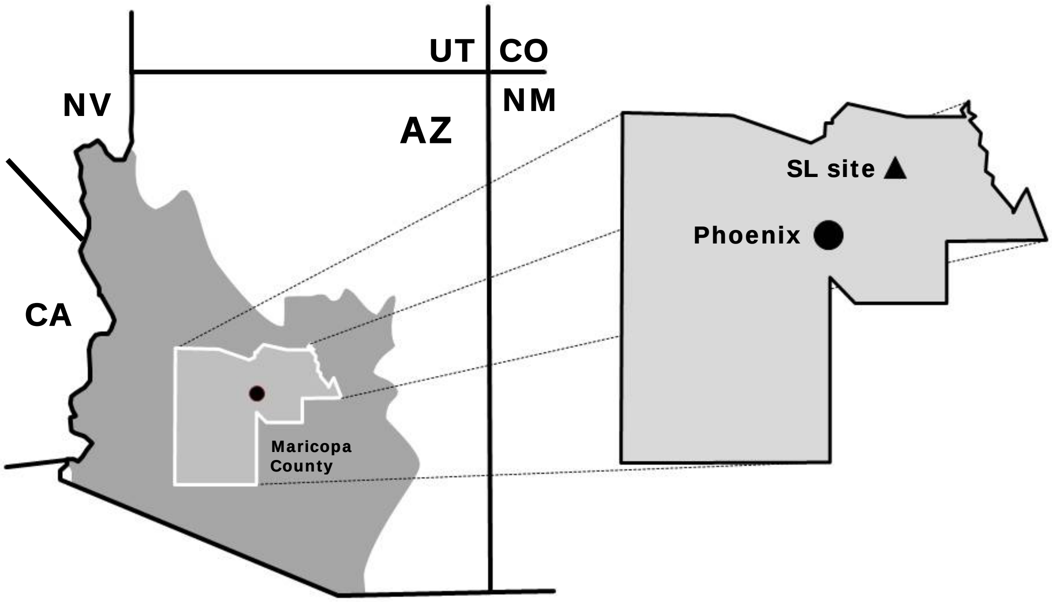


Figure 1. Location map of the Sugarloaf Mountain Sonoran desert tortoise (*Gopherus morafkai*) study site in the Mazatzal Mountains, Tonto National Forest, Maricopa County, Arizona, USA. The dark shading on the map indicates *G. morafkai* range within the state of Arizona.

The study site (Figure 2) is best described as the Arizona Upland Desertscrub subdivision of the Sonoran Desertscrub biotic community (Brown 1994) and is characterized by low rocky hills with large boulders and ridges, steep slopes, and bajadas and bisected by a dry sandy wash. Geologically, the site consists of Precambrian granite rocks, with occasional deposits of white quartz and red conglomerates, Olivine and Andesitic basalts, and fine to coarse alluvium (Skotnicki 1992). Much of the eroding granitic bedrock crumbles easily, and pea-sided remnants occur throughout the site. Annual precipitation is 11.01–13.70 in (The Flood Control District of Maricopa County 2012), which falls as rain during the winter and summer months with periods of drought in between. The timing of winter precipitation is highly variable but is typically characterized by widespread slow and steady light rainfall that may last for days to a week or more. Summer monsoon thunderstorms, consisting of localized heavy rains, usually occurs between mid-June and late September each year (Dinchak and Hill 1981).

Figure 2. Representative landscape at the Sugarloaf Mountain Sonoran desert tortoise (*Gopherus morafkai*) study site in central Arizona, USA. Habitat is typical of the Arizona Upland Desertscrub subdivision of the Sonoran Desertscrub biotic community and is characterized by low rocky hills and dry sandy washes. (*photo: A. K. Owens*)

Summer precipitation is an important source of water for the desert-adapted plants at the site. Tortoise activity fits within these patterns of temperatures, precipitation, and plant growth with most activity occurring during summer monsoons when annual vegetation is abundant and free water is readily available (Oftedal 2002; Van Devender 2002).

Woody perennial plants and succulents are common throughout the site except in extensive areas of exposed rock and in boulder piles (Appendix A). Annual vegetation is prevalent and is in the form of small wildflowers and grasses that were not identified to species as part of this study. Nonnative, invasive red brome (*Bromus rubens*) is prevalent throughout the site.

The AGFD has been collecting tortoise habitat and population data at the SL site since 1991, amassing over 10,000 radio-telemetry and capture-recapture encounter records for 181 individuals of all age classes. The quantity and quality of the records allow growth rate modeling by providing a large sample of initial capture and recapture measurements over a long duration. A current, ongoing study at the site uses radio-telemetry to track the movements of juvenile tortoises and has produced over 1,000 records since April 2010 (Arizona Game and Fish Department, unpublished data). The juvenile telemetry study is the first of its kind in Arizona and provides a unique set of location records from which to measure habitat use.

METHODS

Sampling Design—Growth

To determine asymptotic lengths and growth rates of tortoises, I used published mathematical models to fit growth curves to tortoise MCL measurements. AGFD personnel obtained tortoise measurements during visual encounter and telemetry surveys at the SL site from 12 September 1999 to 28 August 2012. I compared these measurements to published lengths and growth rates from other *G. agassizii* and *G. morafkai* populations.

Vertebrate animal growth curves are a mathematical relationship between time and an animal's size (Fabens 1965). Reptile growth has been calculated using weight (Richards 1959; Schoener and Schoener 1978) and length (Turner et al. 1987; Frazer et al. 1990; Germano 1994; Lovich et al. 2011). Climatic changes that alter the availability of food and water can affect tortoise weight and length. Compared to weight, length is likely to show less variation based on the condition of the animal (Schoener and Schoener 1978), and therefore was the preferred measurement for this study.

Some reptiles, including desert tortoises, display indeterminate growth (Heatwole 1976; Germano 1992; Kozlowski 1996; Vitt and Caldwell 2009). Although tortoise growth slows as an individual ages (Patterson and Brattstrom 1972), individuals may continue to increase their body size throughout their life (Heatwole 1976) as long as there are sufficient resources and appropriate environmental conditions (i.e., temperature is especially important for ectothermic animals). Original work by Ludwig von Bertalanffy (1957) presented a growth function for animals based on the allometric relationship between an animal's metabolic rate and body condition. The growth function models the rapid growth of juveniles, slower growth in adulthood, and the negligible growth of older animals as they near an assumed asymptotic size.

Frazer et al. (1990) summarized the von Bertalanffy equation by calling it a "known-age method" because it includes a variable (*b)* that is related to the size of an animal at birth and has the following equation:

$$L_t = a\left(1 - be^{-kt}\right) \tag{1.1}$$

where L_t is the length at age t, a is the asymptotic size, b is the size at birth, e is the base of the natural logarithm, and k is the intrinsic growth rate for a given species. Von Bertalanffy's equations have been rearranged and modified since original publication but are the basis of many modern growth studies. The most commonly used forms of the von Bertalanffy equations are by Richards (1959) and by Fabens (1965). Fabens rearranged the von Bertalanffy equation to get a non-linear interval version (Schoener and Schoener 1978; Murray and Klug 1996):

$$L_r = a - \left(a - L_c\right)e^{-kd} \tag{1.2}$$

where L_r is length at some recapture point, L_c is length at initial capture, d is the duration between the date of L_c and the date of L_r (in years), and all other variables are defined as for equation 1.1. Fabens' rearrangements removed the need to know the size of an animal at a particular age and, instead, allows a curve to be properly plotted using estimates of intrinsic rate of growth (k) and asymptotic size (a; Frazer et al. 1990). Fabens also published equations for estimating *a* and *k* independently. Models using Fabens no-known-age method have been compared to models developed using known-age techniques and have been found to be reliable estimates of the parameters that produced the curves (Frazer et al. 1990).

Three steps were used to determine growth rates of SL desert tortoises in this study. First, I determined the most effective method for developing growth curves; second, I produced growth curves; and, finally, I compared the curves for males and females.

Determining the method used.— Previous studies have used capture-recapture techniques to gather size data of male and female desert tortoises (See: Patterson and Brattstrom 1972; Medica et al. 1975; Turner et al. 1987; Averill-Murray et al. 2002*a*; Lovich et al. 2011) and produce growth curves for specific populations. An extensive literature review yielded thousands of studies that developed growth curves for many taxonomic classes including reptiles, fish, and mammals. Specifically for tortoises, Murray and Klug (1996) used non-linear regression analysis and Richards (1959) equation modified by Bradley et al. (1984) and the capture-recapture interval equation of Schoener and Schoener (1978) to develop growth curves that depict both growth rate and age at different sizes for three *G. morafkai* populations in Arizona. Lovich et al. (2011) analyzed growth of *G. agassizii* in southern California using Fabens (1965) equation and produced curves with the von Bertalanffy equation.

Germano (1994*a*) compared growth among four species of tortoises in North America using Richards (1959) method and deemed it superior to other models as it showed the least amount of bias in its estimate of the growth function and allowed the data to determine the shape of the growth curve. Schoener and Schoener (1978) used three models to describe growth in *Anolis* lizards. They found von Bertalanffy to be the superior choice when using “unfixed” data (i.e., lengths reported exactly as measured). They also used “fixed” data, zeroing out any negative growth, assuming negative measures were an error rather than a reflection of the animal’s true size.

Lindeman (1997) compared 11 methods for producing growth curves and found von Bertalanffy to be the “most satisfactory descriptor of turtle growth” for aquatic turtles but lists one study in which it was found to be less accurate for terrestrial turtles. However, Andrews (1982) stated that the von Bertalanffy model is suitable for the growth patterns of large, long-lived reptiles. Lindeman reaffirmed his 1997 use of the von Bertalanffy model during a review of three different models during which he conducted a study with Emydid turtles using the von Bertalanffy model as his primary analysis tool (Lindeman 1999).

I used Fabens’ equations to estimate the variables a and k, an equation published by Frazer et al. (1990) to obtain an estimate of b, and the von Bertalanffy equation in a non-linear regression to produce the curves following the basic procedure used by Frazer et al. (1990) and Lovich et al. (2011).

Producing the curves.— I selected capture records for 109 (60.2%) of the 181 tortoises (n = 53 females, 35 males, and 21 juveniles of unknown sex) from both the long-term and telemetry survey records that had at least two capture records with MCL measures at each capture. For 100 of the 109 tortoises that had more than two capture records with MCL measurements, I used the oldest capture MCL and the most recent recapture MCL in the analysis to provide the longest possible duration between measurements.

The time between the oldest capture and the most recent capture for 22 animals (10 adults and 12 juveniles) was less than one year. Eight of these animals were initially captured and most recently captured in the same year, but 14 were initially captured just prior to hibernation and recaptured at some point soon after exiting hibernation the following year. These 14 animals were initially a concern with regard to biasing the data toward slower growth if the measurements were before and after a single hibernation period when no growth would be anticipated (Bogert 1937; Medica et al. 1975). However, 11 of the 14 showed positive growth, three showed no growth, and none had negative growth. Since Lindeman (1997) saw no difference in growth analysis when comparing seasonal growth with season-long measures, I included all measures for all animals in the analyses.

Sexually dimorphic growth is not apparent in Sonoran desert tortoises until approximately age 20, which is beyond the age at which tortoises reach sexual maturity and can be accurately sexed (approx. 16 years; Germano 1994). Therefore, I included juveniles of unknown sex in the analysis for both sexes to establish the lower size range (Murray and Klug 1996; Lindeman 1999; Germano et al. 2002; Lovich et al. 2011).

I calculated the estimate of *k*, the intrinsic growth rate (Frazer et al. 1990; Murray and Klug 1996), also called the rate of proportional growth of an animal (Fabens 1965), using Fabens' (1965) equation:

$$k = \frac{\left(\sum r_i s_i - n\sum r_i s_i\right)}{\left(n\sum s_i^{\,2} - \sum r_i \sum s_i\right)} \qquad (1.3)$$

Where r_i and s_i are functions of *k* and are determined by the following equations:

$$r_i = \frac{y_i - x_i}{d_i} \text{ and } s_i = \frac{x_i - y_i}{2}$$

where *n* is the sample size, y_i is the most recent capture MCL in millimeters, x_i is the initial capture MCL in millimeters, and d_i is the duration between oldest and most recent captures in years. Of the 109 tortoises selected, 17 (15.7%) had a recapture value that was less than initial capture value (minimum: 0.19%, maximum: 2.96%), indicating either an error in measurement or natural shrinkage. Shrinkage has been reported by Loehr et al. (2007) in a study of an African tortoise species. In that study, shrinkage of 4% of the carapace length was considered normal due to health and climatic conditions. Because none of the animals in the current study had shrinkage greater than 4%, I followed Schoener and Schoener (1978) and ran the analysis on the MCLs as measured.

Using the estimate of *k*, I solved for the variable *a*, the asymptotic size of a tortoise, using Fabens (1965) equation:

$$a = \frac{\sum s_i \sum r_i s_i - \sum r_i \sum s_i^{\,2}}{n\sum r_i s_i - \sum r_i \sum s_i} \qquad (1.4)$$

With the estimates of *a* and *k*, the only unknown parameter in the von Bertalanffy equation was *b*, the size of an animal at birth. I used the recapture information for one tortoise (#902) captured in the early Spring of 2010 with an obvious umbilical scar indicating it had recently hatched, and recaptured 2.3 years later. Before calculating *b* using a single tortoise to define the growth of an entire population, I performed a t-test to see if the initial MCL of tortoise #902 was different than the average MCL of all tortoises at the SL site that were considered hatchlings. I solved for *b* using two different methods. First, the Frazer et al. (1990) equation:

$$b = e^{k}\left(1 - \frac{h}{a}\right) \tag{1.5}$$

where *h* is the MCL at some known age, and then the Fabens (1965) equation:

$$b = \frac{\sum p_i(a - x_i)}{\sum p_i^{2}} \tag{1.6}$$

where p_i is a relationship between the known age of a tortoise and the calculated growth rate of the population (*k*, see equation 1.3):

$$p_i = e^{-kt_i}$$

With all variables estimated, and using the recapture MCL for each tortoise, I found the corresponding age of each tortoise by solving for *t* in the original von Bertalanffy equation (1.1) as follows:

$$t = \frac{-1}{k\left(\ln(a - L_t) - (\ln b - \ln a)\right)} \tag{1.7}$$

The variable *t* represents the age of the animal and is the x-axis value when plotting the data. The y-axis value is the recapture length for each individual. I produced a scatter plot for each sex and fit a curve based on a 3-

parameter logarithmic function using SigmaPlot Version 11.0, (SYSTAT Software Inc., Chicago, Illinois, USA).

Data analysis—comparing the curves.— I used SigmaPlot software to calculate a 95% confidence interval for male and female curves. If curves for each sex were not statistically different, data points for both sexes and juveniles (*n* = 109) would be pooled to create a single curve to describe the population.

Sampling Design—Habitat

Locating and relocating tortoises.— The juvenile tortoise telemetry study was initiated by AGFD personnel in April 2010 and conducted with the assistance of volunteers performing visual encounter surveys. When a juvenile tortoise was found, AGFD personnel attached a radio transmitter to its carapace, and tracked it one to three times weekly during the active season and at least twice each month during the winter (Figure 3). Between 7 April 2011, and 31 December 2011, a total of 11 juvenile tortoises were affixed with transmitters and tracked a total of 929 times in 404 unique locations. The maximum size of a desert tortoise considered to be a juvenile at the SL site is based on multiple comparative studies of both the Sonoran and Mohave species (Germano 1994*b*; Berry and Christopher 2001; Averill-Murray and Averill-Murray 2005).

Figure 3. Radio transmitter equipped juvenile Sonoran desert tortoises (*Gopherus morafkai*) at the Sugarloaf Mountain study site in central Arizona, USA (left #863, right #900). Transmitters are attached to the carapace first costal scute with epoxy. (*photos: A. Bridges*)

Selecting locations to measure habitat.— To determine if tortoises were selecting specific habitat features, I compared habitat characteristics tortoises were using to habitat broadly available at the site. To quantify habitat use, I selected locations from the tracking records during the months of little or no activity (winter: December 2010 – February 2011 and December 2011) and during the months of greatest activity (summer: July – September 2011). The number of tracking events and the number of unique locations tortoises were found by season and by tortoise are summarized in Table 1.

Table 1. Three hundred and ninety-two radio-telemetry tracking events resulted in 246 unique locations and 23 revisited locations for the 11 juvenile Sonoran desert tortoises (*Gopherus morafkai*) tracked at the Sugarloaf Mountain study site in central Arizona, USA between December 2010 and December 2011. Revisited locations are shelters in which a tortoise was found during multiple non-consecutive tracking events. Eight of the 11 tortoises revisited one to four shelters from two to five times each.

	Summer			Winter	
Tortoise number	Number of trackings	Unique locations	Revisited locations	Number of trackings	Unique locations
900	35	20	4	13	1
630	32	25	3	13	1
679	34	20	3	13	2
910	35	21	4	13	2
641	35	23	3	13	1
950	29	29	0	2	1
975	30	22	3	2	1
863	30	25	2	3	1
920	26	21	1	2	1
930	18	18	0	2	1
960	10	9	0	2	1
Totals	314	233	23	78	13

I determined that 10 summer locations per tortoise would create a large enough sample for comparison and that it was a reasonable number of locations to visit. I selected these locations from the 314 total summer locations using the following criteria:

1. Revisited locations. Locations where a tortoise was found multiple non-consecutive times (found at a location, found in a different location, and then found in the first location again). I felt it was important to prioritize all revisited locations as multiple visits may imply selection of preferred habitat.

2. Locations where a tortoise had only been found once, and locations where inactive tortoises had been found in the same location multiple consecutive times.

3. Because the ranges of several tortoises overlapped and there was the possibility of multiple tortoises using the same shelter, I compared the

locations of each tortoise to ensure all locations were unique, and I didn't measure the same location more than once.

All tortoises had 10 or more unique locations except for one individual. Tortoise #960 was captured late in the 2011 season and was tracked in 6 sites before it went into a hibernation burrow.

Although there were 78 different winter trackings, nine tortoises did not move, using one shelter each the entire winter season, and two tortoises moved once, using two different shelters each. I used the nine shelters and randomly selected one of the two shelters for each of the other two tortoises to create a total of 11 locations representing winter habitat. Therefore, the total number of locations investigated in this study was summer locations (10 tortoises x 10 locations + 1 tortoise x 6 locations) plus winter locations (11 tortoises x 1 location each) for a total of 117 tortoise locations. I also chose an equal number of random locations (117) for a total of $n = 234$ different locations.

I defined the habitat analysis area using a geographic information system (GIS) program, specifically ArcGIS (Environmental Systems Research Institute, Inc., Redlands, CA, USA), from the 929 telemetry locations. I used the distribution of these locations to create a polygon layer that defined the extent of recorded tortoise activity. After determining that the average cross sectional length of the individual tortoise's area of activity was 150 m (100% minimum convex polygon), I expanded the habitat analysis by an additional 150 m buffer. I generated 150 random locations within the extents of the buffered polygon. I used Microsoft Excel software (Microsoft Corporation, Redmond, WA, USA) to randomly select 117 of the 150 generated coordinates to represent available habitat (hereafter referred to as random locations).

Establishing habitat plots.— I used a handheld Garmin™ GPS unit to navigate to the coordinates of each location. As part of the AGFD study, any shelter where a tortoise was located and appeared to be of a permanent nature was marked with a small numbered aluminum tag affixed to a structural element near the shelter entrance. For tortoise locations associated with marked shelters, I navigated to, and centered the plot on that shelter. For tortoise locations not associated with a marked shelter, and for random sites, I inserted a flag in the ground at the location coordinates and searched within a 2-m radius for available shelters. If one or more shelters were within 2 m of the flag, the nearest shelter to the flag became the center of the plot; otherwise, the flag became the center of the plot and habitat variables were measured as if a tortoise had been found in the open at that spot.

Because the original tracking and my measurements were separated temporally, I inspected each plot to see if there was evidence of an environmental disturbance (fire, flood, rock slide, etc.) that may have altered either the vegetation or substrate composition.

Plot dimensions and transect design were based on a similar study on the Florence Military Reservation (FMR) in south-central Arizona (Grandmaison et al. 2010) and consisted of three 15-m transects to create a habitat plot. I generated 234 random numbers between 1 and 360 and randomly associated one of these numbers with each location to serve as a base transect azimuth. This base transect was centered on the coordinates of the tortoise or random location with the second and third transect azimuths offset by 60 and 120 degrees. The three 15-m long transects created a virtual circular-shaped plot of 15-m diameter and an area of 177-m^2 (Figure 4). Due to the complexity of the terrain at the site, measuring tapes used to establish each transect were sometimes suspended, but were kept as straight and parallel to the ground as possible. It was also impractical to center all three tape measures exactly in the same spot; therefore, a tolerance of ± 20 cm was used (Figure 5).

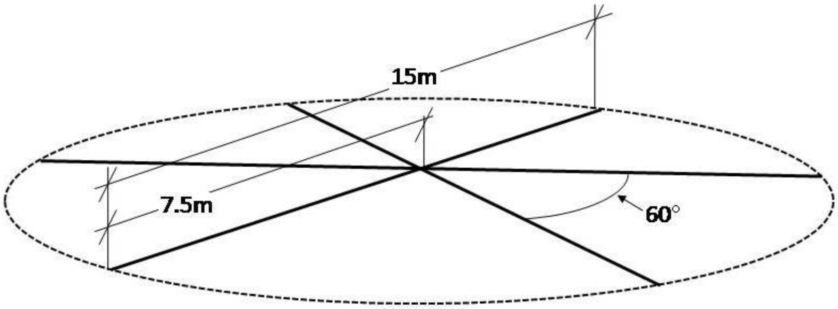


Figure 4. Diagram of plots used to measure habitat characteristics at 117 juvenile Sonoran desert tortoise (*Gopherus morafkai*) locations and 117 random locations at the Sugarloaf Mountain study site in central Arizona, USA. Three 15-m long transects, centered on a known tortoise shelter or the coordinates of a random location and separated by 60 degrees, create a 177-m^2 circular plot from which all habitat variables are measured.

Figure 5. Typical center of a 177-m^2 plot used to measure habitat characteristics at 117 juvenile Sonoran desert tortoise (*Gopherus morafkai*) locations at the Sugarloaf Mountain study site in central Arizona, USA. This plot is centered on a burrow (located under the large rock) and shows the alignment and spacing of the tapes with a ± 20 cm tolerance. The 7.5-m point on the tape is marked by colored adhesive tape for easy alignment. (*photo: A. Bridges*)

Measuring habitat variables.— I measured 13 variables in each plot and along each transect using line- and point-intercept techniques (Table 2; Appendix B). Nine of the variables have been used by other researchers to describe microhabitat used by Sonoran desert tortoises and the other four variables: rock proximity, rock structure, woody richness, and succulent richness are unique to this study and were added to quantify site features that had the potential to be important based on personal observation of juvenile tortoise behavior at the site.

Of all the habitat variables quantified, only annual vegetation had the potential to differ between the time of the original tortoise tracking and the time I revisited and measured the plot. To decrease variability, I measured plots during a time with mild temperatures and no measurable precipitation (20 February to 14

April 2012), so the quantity and health of existing annual vegetation did not change during measurement, providing consistent measurements in all plots.

Table 2. Habitat variables measured at 234 locations at the Sugarloaf Mountain study site in central Arizona, USA. Point measures were taken at the shelter or coordinates that formed the center of the plot. Transect measures were counted along each of the three 15 m transects. Plot measures were counts of shelters or plant species within the 177-m^2 plot. Where indicated in the notes, nine of these variables were used in similar studies in the region to measure habitat.

Variable	Measured	Description
Elevation[1,2]	point	Elevation of plot center in meters
Slope aspect[1,2,3]	point	Compass heading (°) perpendicular to slope
Slope grade[1,2]	point	Slope of the hill at the shelter or site
Shelter aspect[2,3]	point	If the plot is centered on a shelter, the compass heading (°) the shelter opening faces from the perspective of an exiting tortoise
Shelter type[2]	point	Classified as: rock shelter (R), pallet (P), all soil (S), burrow (B), Pack Rat midden (M), cave/crevice (C), or open (O)
Rock proximity	point	Proximity to nearest rock ≥ the size of an adult tortoise (0.3 m) recorded exactly, or > 7.5 m away from the shelter.
Rock structure	plot	Structure of rocks within the plot objectively classified as: none (NO), scattered (SC), stacked (ST), boulder pile (BP), bedrock (BR)
Ground cover[4]	transect	Proportion of ground cover classified as: bare ground (BG), litter (L), dead wood (DW), live vegetation (V), annual vegetation (VA), or rock (R) using point intercept measurement technique
Soil substrate[4]	transect	Proportion of soil substrate classified as: sand (S), fine gravel (FG), gravel (G), cobble (C), or boulder (B) based on particle size using point intercept measurement technique
Canopy cover[3,4]	transect	Mean proportion of usable (from the tortoise's perspective, above 40 cm) canopy cover using line intercept measurement technique
Shelter density[4]	plot	Number of available shelter sites within the plot
Woody Richness	plot	Number of woody (perennial) plant species within the plot
Succulent Richness	plot	Number of succulent plant species within the plot

[1] Zylstra and Steidl 2009

[2] AGFD, unpublished data

[3] Hazard and Morafka 2004

[4] Grandmaison, Ingraldi et al. 2010

Data analysis—Habitat

To determine juvenile desert tortoise habitat selection I compared plot measurements between summer and random, winter and random, and summer and winter locations using a Chi-square goodness of fit test (Zar 1999). I prepared data for analysis by subdividing all linear measures into increments using a frequency spread based on the minimum and maximum values (range). For example, the minimum elevation for all measured sites was 660 m and the maximum was 770 m and I subdivided the range into seven 10 m increments. I also set the number of increments for each variable to meet the assumptions of the Chi-square test in which no more than 20% of the responses could be less than five. The small winter sample size (*n* = 11) did not allow more than two increments per variable. If the Chi-square was significant at the 0.05 level, I performed a post-hoc (z-test of proportions) on each increment to determine which increment pairs had significant differences. A z-test resulting in a significant difference indicated "selection" when use was greater than availability, "avoidance" when use was lower than availability, and "used as available" when there was no significant difference at that increment.

Because slope aspect and shelter aspect were radial measurements, I used the program Oriana 4 (Kovach Computing Services, Anglesey, Wales, UK) to compare variables. I also used the program to calculate the mean radial angle for each season and performed a Rayleigh test to determine if angles differed from randomness (Batschelet 1981). I performed a Pearson Product Moment

Correlation test using Sigma Plot software to determine the direction of change between variables (Salkind 2004).

I used a Principle Component Analysis (PCA), SPSS (IBM Corporation, Armonk, New York, USA), to summarize and reduce habitat variables. I combined all tortoise and random habitat variables in the PCA and identified the number of components which described the most variation based on eigenvalues greater than one (Hair Jr. et al. 1998) and interpreted each component based on the correlation matrix.

Habitat Suitability Map.— I used ArcGIS to create a single image depicting the most likely places juvenile tortoises might be encountered at the SL site based on my analysis of habitat features that tortoises selected and avoided. I ran a PCA using only the variables that were identified as significant in the Chi-square analysis for the summer season, calculated a weighted value for each variable by multiplying the component value of each variable that contributed to either component 1 or component 2 by the value of the component score derived from the percent variance explained, and standardized the number on a 0 – 1 scale. When a variable was significant in more than one component, I summed the products of all the component scores to get a value for that variable. I scaled the increments within each component 1 and component 2 variable by dividing the percentage of use by the percentage of availability to create a Suitability Index (SI) number for each increment. Using those SI values, the selection or non-selection determination based on the z-test of proportions, and some judgment, I assigned each increment a number between 1 and 9. The number “1” indicated the least suitable habitat at the site as evidenced by tortoise avoidance, “5” indicated use was approximately the same as availability, and “9” indicated the most suitable habitat based on tortoise selection.

Using the Geostatistical Analyst extension in ArcGIS, I created raster images using the method of Universal Kriging, which interpolates a value in an unmeasured area based on the values of surrounding measured points (ESRI 2012), in my case, all summer sites. The raster image for shelter type was created using Thiessen polygons to identify an area of influence around a point (ESRI 2012). I used the scaled values to reclassify the raster images and to depict the scaled suitability of the site for each variable. I created the predictive habitat suitability map using a weighted overlay procedure, based on the summation of the cross products of the scaling values and the individual relative importance value of the significant trait. I then reclassified this map based on the minimum and maximum scaled values for all sites, reducing the nine increment scale to a five increment scale depicting the habitat as a range from most unsuitable to most suitable. I completed the map by adding contour lines and hydrologic information based on a National Elevation Database (NED) image (http://ned.usgs.gov; retrieved 16 Oct 2012).

I validated the model by plotting 50 additional tortoise locations on the suitability map. These locations were randomly selected from the same summer season and from the same tortoises, but had not been used to produce the model. I used a Chi-square goodness of fit test used to determine if the validation points differed from available habitat.

RESULTS

Growth

The initial capture MCL of tortoise #902 was not different than the average MCL of all hatchling tortoises at the SL site (t=3.132, *P*= 0.089), therefore I used its initial capture MCL to calculate the estimate of *b* (Equations 1.5 and 1.6). Male and female tortoises at the SL site varied both in adult size and rate of growth, but fell within the range of other tortoise populations (Table 3). The estimate of asymptotic size (*a*) was 277.7 mm for males and 262.1 mm for females. The intrinsic rate of growth estimate (*k*) was 0.058 for males and 0.061 for females (Table 3; Appendix C).

Male and female growth curves showed no difference based on the 95% confidence interval; therefore, I combined male and female tortoise recapture MCLs (n = 109) and created a single curve for the population at SL (Figure 6).

Table 3. Asymptotic sizes and growth rates for male and female Sonoran desert tortoises (*Gopherus morafkai*) and Mohave desert tortoises (*G. agassizii*). Size and growth rate parameters for the tortoise population at the Sugarloaf Mountain study site in central Arizona, USA were estimated using a derived equation based on the von Bertalanffy growth model.

Species	Males			Females		
Site (Desert)	*n*	*a* (mm)	*k*	*n*	*a* (mm)	*k*
G. morafkai						
Sugarloaf (No. Sonoran)	54	277.7	0.058	72	261.1	0.061
Little Shipp Wash (No. Sonoran)[1]		299	0.09		267	0.21
Eagletail Mtns. (No. Sonoran)[1]		288	0.14		268	0.28
Granite Hills (So. Sonoran.)[1]		244	0.22		243	0.15
Sinaloa (So. Sonoran)[2]	22	281.5	0.122	10	265	0.093
G. agassizii						
Western Mohave[2]	24	283	0.188	15	245.7	0.096
Eastern Mohave[2]	54	260	0.105	34	233.1	0.099
Mesa (Western Sonoran)[3]	30	311.5	0.054	21	263.5	0.019

[1] Murray and Klug 1996

[2] Germano 1994*a*

[3] Lovich et al. 2011

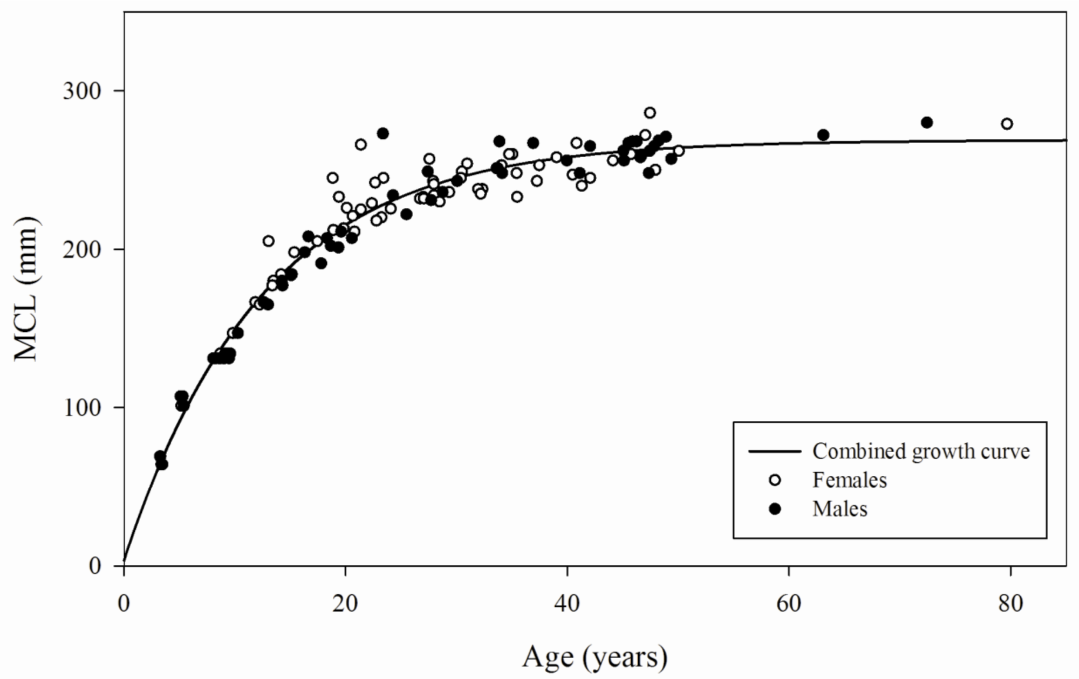


Figure 6. Estimated growth curve based on recapture lengths of 109 (35 males, 53 females, and 21 juveniles) Sonoran desert tortoises (*Gopherus morafkai*) at the Sugarloaf Mountain study site in central Arizona, USA. All mid-line carapace lengths were measured at initial capture and again at recapture. Unsexed juveniles were included in the sample of each sex to establish the lower range of sizes.

Habitat

Available habitat.— Juvenile tortoises showed habitat selection at the SL site both in summer and winter. Tortoises were found in locations with higher shelter densities, higher proportions of sand and annual vegetation, lower proportions of litter, and lower succulent richness, and were found closer to rocks than in random locations measured in available habitat (Table 4).

Six components described 70.5% of the total variation in habitat used by juvenile tortoises at SL (PCA; Table 5). The first two components (C1 and C2) described over 42% of the variation, and components 3 – 6 contributed less than 10% each to the overall variation.

Table 4. Mean (±SE) of non-categorical and non-radial variables used to describe habitat at 234 locations at the Sugarloaf Mountain study site in central Arizona, USA. Variables were measured in a 177-m^2 plot centered on coordinates where juvenile Sonoran desert tortoises (*Gopherus morafkai*) had been located during radio-telemetry events in summer (July – September 2011, *n* = 106) and in winter (December 2010 – February 2011 and December 2011, *n* = 11), and at an equal number of randomly generated coordinates (*n* = 117).

	Season		
Habitat Variable	Summer	Winter	Random
Elevation (m)	713.23 (1.75)	718.36 (6.3)	719.98 (2.27)
Slope grade (°)	19.80 (0.76)	24.57 (1.46)	16.64 (0.88)
Rock proximity (m)	0.37 (0.08)	0.10 (0.08)	0.81 (0.11)
Bare ground as ground cover (%)	14.4 (0.01)	17.2 (0.04)	20.7 (0.02)
Litter as ground cover (%)	16.6 (0.01)	16.5 (0.04)	33.5 (0.01)
Dead wood as ground cover (%)	1.2 (<0.01)	1.7 (0.01)	0.89 (<0.01)
Live vegetation as ground cover (%)	2.1 (<0.01)	1.7 (0.01)	1.1 (<0.01)
Annual vegetation as ground cover (%)	29.4 (0.02)	27.5 (0.05)	11.3 (0.01)
Rock as ground cover (%)	36.2 (0.02)	35.4 (0.06)	32.5 (0.02)
Sand as substrate (%)	29.4 (0.01)	25.4 (0.03)	19.9 (0.02)
Fine gravel as substrate (%)	18.6 (0.01)	22.9 (0.04)	28.9 (0.02)
Gravel as substrate (%)	10.5 (0.01)	12.5 (0.04)	16.1 (0.01)
Cobbles as substrate (%)	1.7 (<0.01)	2.1 (<0.01)	2.9 (<0.01)
Boulders as substrate (%)	39.7 (0.02)	37.1 (0.06)	32.2 (0.02)
Proportion of canopy cover (%)	38.7 (0.01)	36.4 (0.03)	35.0 (0.01)
Shelter density (shelters/ha)	0.18 (0.01)	0.19 (0.02)	0.13 (0.01)
Woody Richness (qty)	14.10 (0.27)	14.27 (0.90)	14.61 (0.37)
Succulent richness (qty)	1.23 (0.10)	1.82 (0.40)	2.26 (0.15)

Interpretation of components was based on the correlation matrix, where C1 is "Structure" and C2 is "Forage". Generally, plots with low C1 scores had high proportion of boulders and shelters. Plots with high C1 scores had high proportions of bare ground and gravel, fine gravel, and litter. Plots with high C2 scores had high proportions of sand and annual plants. Factor scores for C1 and C2 differed in tortoise plots compared to available habitat (Table 6).

Table 5. Correlation matrix from Principle Component Analysis with two components (C1 and C2) explaining variance in habitat at summer juvenile Sonoran desert tortoise (*Gopherus morafkai*) locations. Habitat was measured in a 177-m^2 plot centered on coordinates where tortoises had been located during radio-telemetry events (n = 117) and a set of randomly generated coordinates (n = 117) at the Sugarloaf Mountain study site in central Arizona, USA (total of 234 locations). Values in bold indicate variables that had a major influence component scores.

	PCA Components	
Habitat Variable	C1	C2
Boulders as ground cover (%)	**-0.916**	-0.318
Rock as substrate (%)	**-0.875**	-0.392
Fine gravel as substrate (%)	**0.804**	-0.158
Bare ground as ground cover (%)	**0.729**	-0.262
Shelter density (shelters/ha)	**-0.674**	-0.059
Litter as ground cover (%)	**0.619**	-0.174
Gravel as substrate (%)	**0.618**	-0.295
Rock proximity (m)	**0.588**	0.095
Succulent richness (qty)	**0.583**	-0.286
Sand as substrate (%)	0.062	**0.837**
Annual veg. as ground cover (%)	-0.114	**0.808**
Shelter type	-0.248	**0.540**
Slope grade (°)	-0.358	0.176
Elevation (m)	-0.320	-0.389
Woody species richness (qty)	0.152	-0.087
Proportion of canopy cover (%)	0.348	0.431
Cobbles as substrate (%)	0.217	-0.029
Woody veg. as ground cover (%)	-0.057	0.404
Dead wood as ground cover (%)	0.174	0.285
Eigenvalue	5.223	2.826
% variation explained	27.49	14.87
Cumulative % of variation explained		42.36

During the summer, tortoises selected habitats with high proportions of sand and annual vegetation, enclosed shelter types (C2 Forage), and a high proportion of boulders and high shelter density (C1 Structure; Figure 7). Random or available habitats showed greater variation in structure with lower proportions of sand and annual vegetation (Figure 4).

Table 6. Mean (±SE) of habitat characteristics from a Principal Components Analysis quantified within a 177-m^2 plot centered on the coordinates where juvenile Sonoran desert tortoises (*Gopherus morafkai*) were located using radio-telemetry in summer (July – September 2011, *n* = 106) and in winter (December 2010 – February 2011 and December 2011, *n* = 11) and at an equal number of randomly generated coordinates (*n* = 117) at the Sugarloaf Mountain study site in central Arizona, USA (total of 234 locations). Components 1 and 2 accounted for 42.4% of the total variation in habitat.

	Summer *n* = 106	Winter *n* = 11	Random *n* = 117
Structure (C_1)	-0.34 (0.07)	-0.31 (0.24)	0.34 (0.10)
Forage (C_2)	0.52 (0.10)	0.49 (0.26)	-0.52 (0.07)

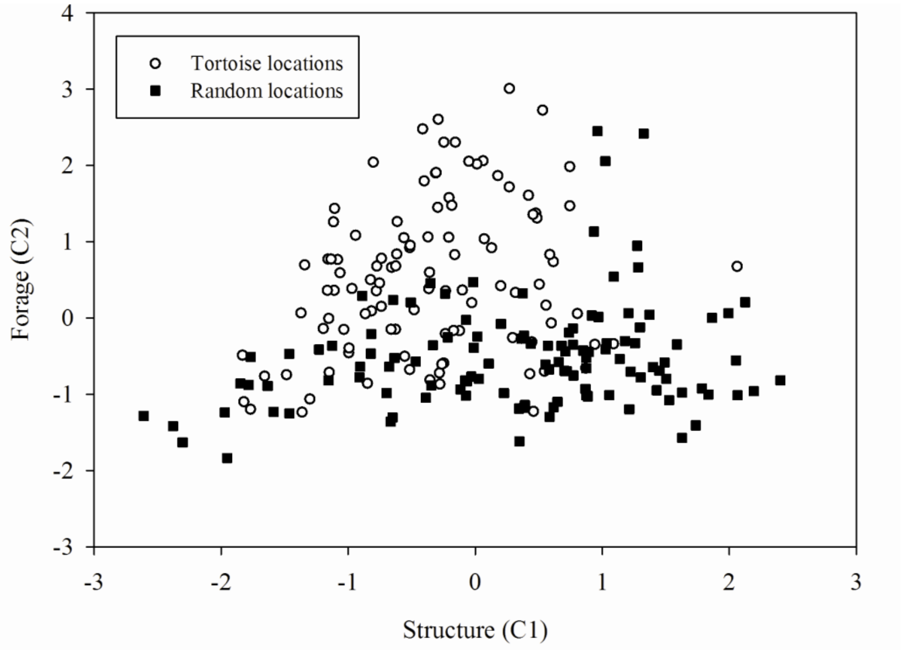
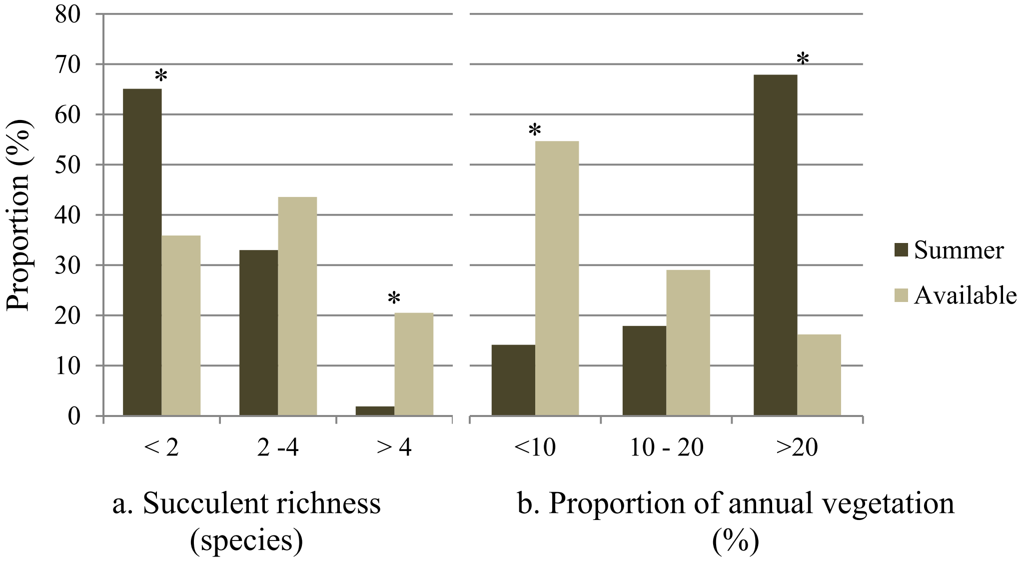


Figure 7. Principal Components Analysis habitat variables quantified within a 177-m^2 plot centered on the coordinates where juvenile Sonoran desert tortoises (*Gopherus morafkai*) had been located using radio-telemetry (*n* = 106) from July to September 2011 and at a set of random plots (*n* = 117) at the Sugarloaf Mountain study site in central Arizona, USA (total of 234 locations), as they relate to component 1 and component 2.

<u>Correlations between variables</u>.— Habitat variables showed both positive and negative correlations between pairs of measured variables (Appendix D).

Summer variables.— Tortoises showed selection for 10 of 20 non-radial variables in summer tortoise locations compared to available habitat (Chi-square analysis; Appendix E).

Canopy cover in all plots ranged from 2% to 100% (mean 37%). Generally, plots with low canopy cover had mostly rocky ground cover. One plot with high canopy cover (88%) was centered under the roots of a mature mesquite tree (*Prosopis* spp.). All plots had some woody species—the fewest species recorded was four and the most was 25 species. Most plant species were common throughout SL, with the exception of shrub live oak (*Quercus turbinella*), which was only found in 12 plots at the west end of the north face of the highest ridge. Neither the proportion of canopy cover nor woody richness was significant in summer analyses. Tortoises showed selection of two vegetation-related variables (Figure 8).



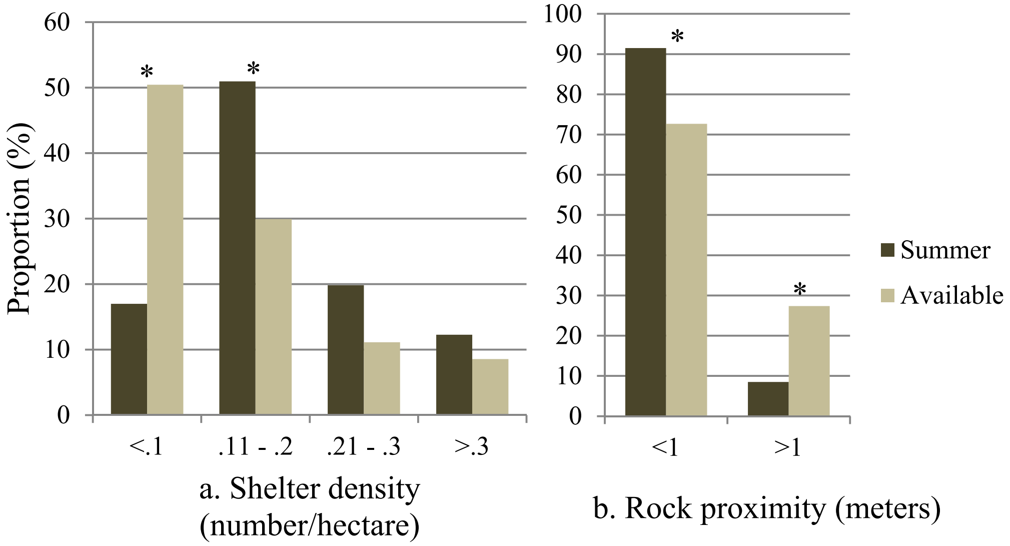
a. Succulent richness (species)

b. Proportion of annual vegetation (%)

Figure 8. Juvenile Sonoran desert tortoise (*Gopherus morafkai*) habitat selection in summer compared to available habitat at the Sugarloaf Mountain study site in central Arizona, USA. (a) Succulent richness is a count of the number of

succulent plant species within the plot. (b) Annual vegetation is a proportion of ground cover measured at 1 m increments on three 15-m transects. Asterisks indicate significance.

All summer and winter plots had at least one shelter (summer: minimum 1, maximum 23, average 10.1; winter: minimum 5, maximum 20, average 10.8) and tortoise selection was related to shelter density (Figure 9a). The quantity of shelters within the entire site ranged from no shelters in 13 (6%) random plots to one random plot that contained 43 potential shelters (mean density = 8.8 shelters). The plot with 43 shelters was in a large drainage filled with boulders piled on each other, creating voids under and between the stacked boulders. These boulder piles are a typical feature at the site and describe 26% of the 234 measured plots (Figure 2). Even when shelters were not found in a pile of rocks, they were generally associated with boulders: 91.5% of all shelters were within 1 m of a boulder (Figure 9b).



a. Shelter density (number/hectare)

b. Rock proximity (meters)

Figure 9. Juvenile Sonoran desert tortoise (*Gopherus morafkai*) habitat selection in summer compared to available habitat at the Sugarloaf Mountain study site in

central Arizona, USA. (a) Shelter density is a subjective count of the number of shelters judged usable to a juvenile tortoise based on size and approach and converted mathematically to shelters per hectare. (b) Rock proximity was the closest rock greater than 40 cm in any direction from the center of the habitat plot. Asterisks indicate significance.

Ground cover was generally a mix of rock and live vegetation. There were few areas of bare ground at the SL site. Only seven plots (3%) had more than 50% bare ground (maximum 79%, average 65%). This was contrasted by 94 plots (40%) that had between 0% and 10% bare ground (average 5%) reflecting the large proportion of ground cover at the site.

Soil substrate at the site was characterized by a mix of sand, two sizes of gravel, and boulders. Cobbles were present in 49% of plots; however, the average proportion of cobbles in those plots was low (1%). No plot had more than 19% cobbles. Most plots (96.6%) contained boulders and three plots were entirely composed of boulders (Figure 10a). Six plots located in a wash were composed mainly of sand and fine gravel with few boulders. The minimum proportion of sand in any plot was 0% but the maximum was 94% (Figure 10b).

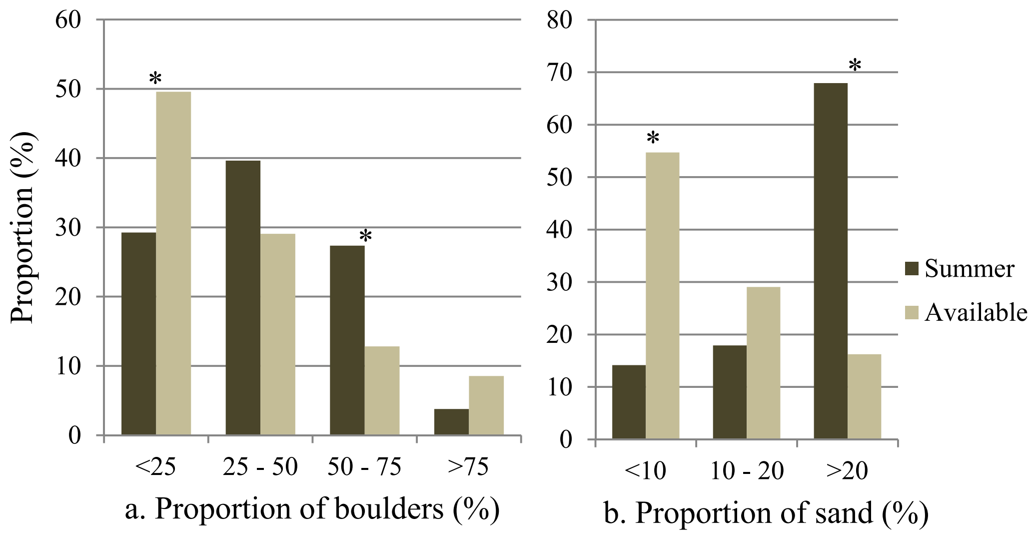


Figure 10. Juvenile Sonoran desert tortoise (*Gopherus morafkai*) habitat selection in summer compared to available habitat at the Sugarloaf Mountain study site in central Arizona, USA. Proportions of boulders (rocks > 25 cm) and sand (solid particle < 2 mm) are soil substrate and measured at 1 m increments on three 15-m transects. Asterisks indicate significance.

Most tortoises were found in several types of shelters more often than in the open. Fifty-four tortoise locations (46.2%) were in enclosed shelters (room-like, enclosed on all sides with a single entrance), 22 (18.8%) were in a shelter considered semi-open (exposed on one or more sides or the top) and 41 locations (35.0%) were in the open (Figure 11). Tortoises were also found at all elevations at the site (Figure 12).

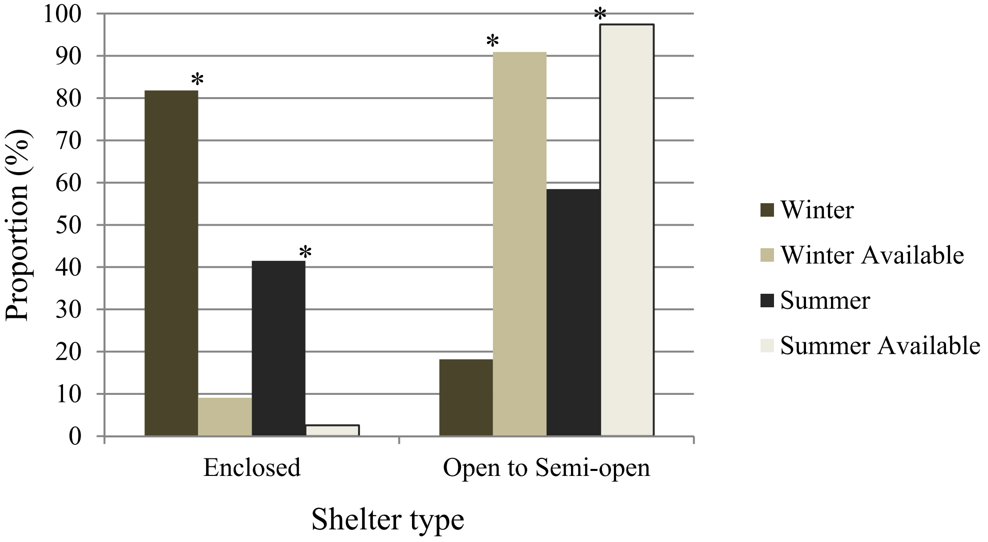


Figure 11. Juvenile Sonoran desert tortoise (*Gopherus morafkai*) habitat selection in summer and winter compared to available habitat at the Sugarloaf Mountain study site in central Arizona, USA. Enclosed shelters are room-like, enclosed on all sides with a single entrance. Open and semi-open shelters are exposed on one or more sides or the top. Asterisks indicate significance.

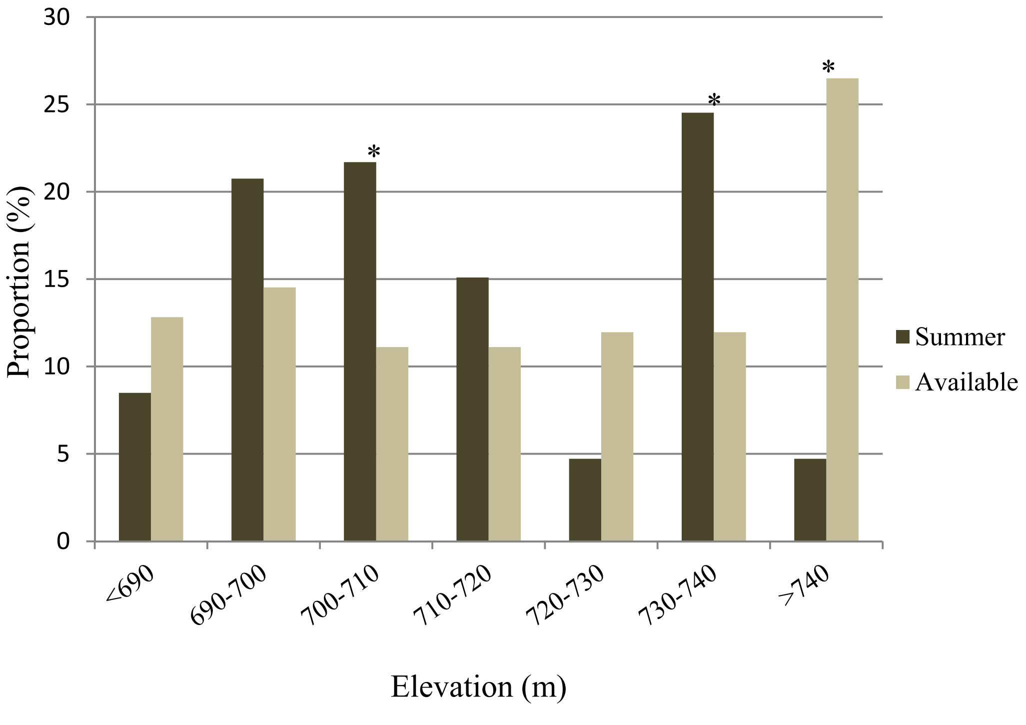


Figure 12. Juvenile Sonoran desert tortoise (*Gopherus morafkai*) habitat selection in summer compared to available habitat at the Sugarloaf Mountain study site in central Arizona, USA. The minimum elevation of any plot at the site was 665 m,

located in the large wash located north of the dominant ridgeline and highest point (768 m). Elevation change over the entire site is 103 m. Asterisks indicate significance.

Two of the significant summer variables did not show clear patterns of selection at one end of the scale or the other. The proportion of fine gravel as substrate showed selection between 11% and 20% and avoidance at > 40% with use as available where fine gravel is < 10% and between 21 – 40%. The proportion of gravel as substrate showed selection only at the < 10% increment and use as available at higher proportions (Appendix E).

Winter variables.— Tortoises showed selection for three of 20 non-radial variables in winter tortoise locations compared to available habitat (Chi-square analysis; Appendix F). Selection of shelter type was presented in Figure 11, and the proportion of ground cover classified as litter, and slope grade are represented by Figure 13.

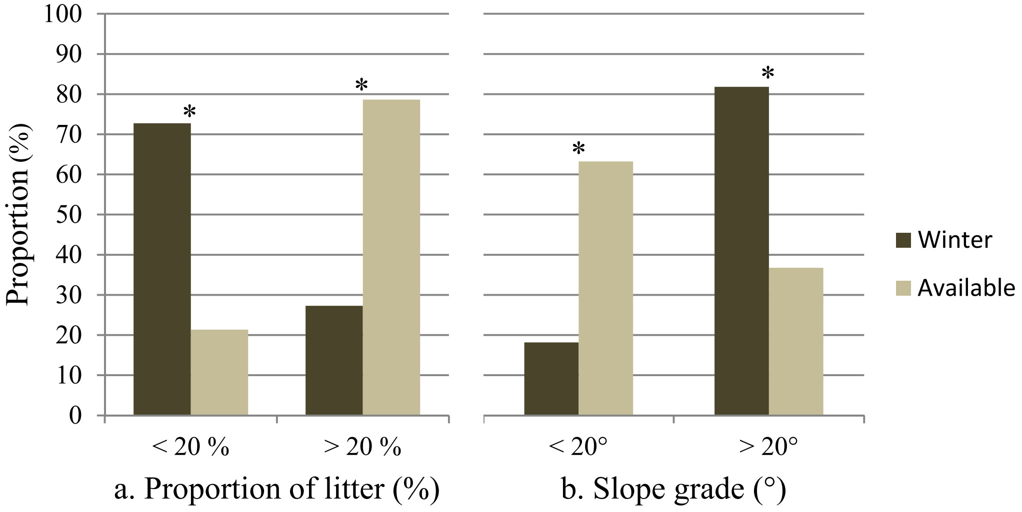
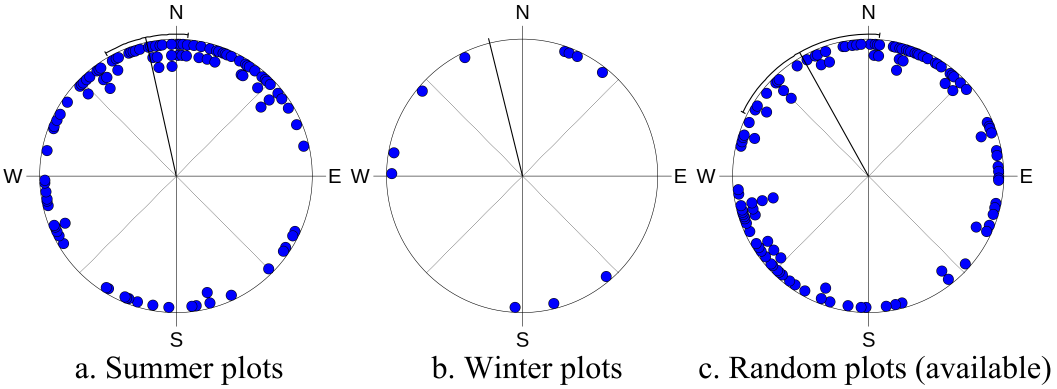


Figure 13. Juvenile Sonoran desert tortoise (*Gopherus morafkai*) habitat selection in winter compared to available habitat at the Sugarloaf Mountain study site in central Arizona, USA. (a) Litter is vegetative debris and non-woody plant

material or twigs with a diameter less than 1 cm. (b) Slope grade is the angle of the hillside containing a plot from horizontal. Asterisks indicate significance.

The flattest areas at the SL site ranged from a slope grade of 0.3 degrees – 6.3 degrees. The steepest measure at the center of any plot was 56 degrees with an average of 18.4 degrees. These measures are from the center of the plot, but there are many plots (especially near the tops of the two ridgelines) that included large boulders or rock outcrops with up to 90 degree slopes or overhangs. On average, summer plots had a slightly steeper slope grade than random plots (minimum = 2.3°, maximum = 36.7°, mean 19.8°, SE = 0.76°), and winter plots were less steep than random or summer plots (minimum = 2.0°, maximum = 27.7°, mean 16.6°, SE = 0.88°).

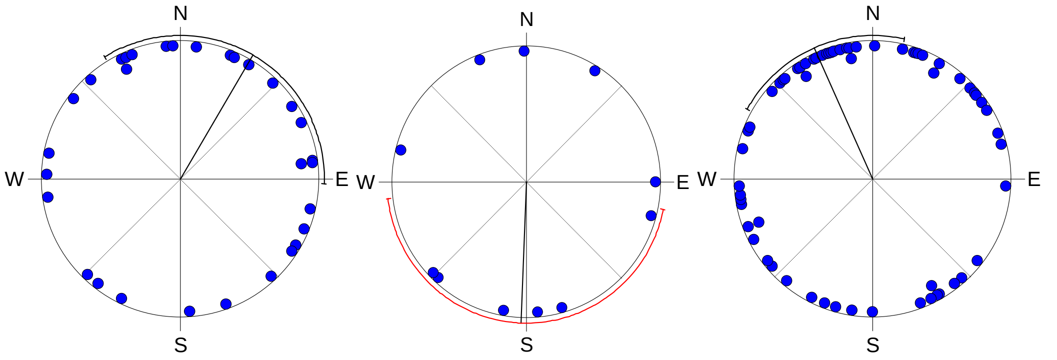
Summer and winter radial habitat variables.— Random locations on hillsides generally faced the northwest (mean angle 331°, SE 17°, $P = 0.005$) and were not randomly oriented. Tortoise locations on hillsides in summer were also not randomly oriented but faced north (mean angle 348°, SE 9°, $P < 0.001$). Tortoises selected slopes in the summer that were oriented to the north ($z = 2.140$, $P = 0.032$). In winter, plots with hibernating tortoises were randomly oriented with a mean angle of 346° ($P = 0.539$; Figure 14).



a. Summer plots b. Winter plots c. Random plots (available)

Figure 14. Slope aspect of habitat plots at the Sugarloaf Mountain study site in central Arizona, USA. (a) During summer, juvenile tortoises were found more often on hillsides oriented to the north, but this is not considered selection as the hillsides are oriented within the standard error of available hillsides. (b) During winter, tortoises were found on randomly oriented hillsides. (c) Aspect of available habitat was non-randomly oriented to the Northwest.

Shelter aspect for available habitat locations was randomly oriented (*n* = 31, mean angle 30°, SE 32°, *P* = 0.201). Shelters in summer plots were not randomly oriented but generally faced northwest (*n* = 63, mean angle 336°, SE 19°, *P* = 0.011). In summer, tortoises also avoided east-facing shelters (z = 4.515, *P* < 0.001). In winter, shelters with hibernating tortoises were randomly oriented (*n* = 11, mean angle 182°, *P* = 0.799). Although not statistically significant, the mean angle of winter shelters are the only mean angle (slope or burrow) located in the southern half of the compass card (Figure 15).



a. Summer plots b. Winter plots c. Random plots (available)

Figure 15. Shelter aspect of habitat plots at the Sugarloaf Mountain study site in central Arizona, USA. (a) Juvenile tortoises selected shelters oriented to the northwest in the summer. (b) Tortoises hibernated in randomly oriented shelters. (c) Shelters in available habitat were randomly oriented. Shelter aspect is the direction a tortoise would travel to exit the shelter, at the most likely entrance to the shelter.

<u>Habitat Suitability Map</u>.— Seven significant non-categorical variables (proportions of boulders, fine gravel, annual vegetation, shelter density, elevation, sand, and gravel) were used to define suitable habitat. The resulting image represents a range of suitable or unsuitable summer habitat based on habitat features selected for or avoided by juvenile tortoises (Table 7; Appendices E, F, and G). Plots of the 106 summer points found 36% in marginal habitat, 52% in suitable and most suitable habitat, and 12% in unsuitable habitat. The map accurately predicts juvenile tortoise selection (χ^2: 25.626, *P* <0.001)

Table 7. Correlation matrix from Principle Component Analysis with two components (C1 and C2) explaining variance in habitat at summer tortoise locations. Weighted values of significant (bold text) habitat variables on components were used to produce the habitat suitability map. Habitat was measured in a 177-m^2 plot centered on coordinates where juvenile Sonoran desert tortoises (*Gopherus morafkai*) had been located during 106 radio-telemetry events at the Sugarloaf Mountain study site in central Arizona, USA.

	PCA Components		
Habitat Variable	C1 (Structure)	C2 (Forage)	Weighted Value
Boulders as ground cover (%)	**-0.921**	-0.112	0.162
Fine gravel as substrate (%)	**0.680**	0.477	0.120
Annual veg. as ground cover (%)	**0.636**	**-0.565**	0.177
Shelter density (shelters/ha)	**-0.667**	-0.305	0.118
Elevation (m)	**-0.550**	0.324	0.128
Sand as substrate (%)	**0.583**	**-0.674**	0.180
Gravel as substrate (%)	0.206	**0.585**	0.115
Shelter type	-0.124	0.443	
Rock proximity (m)	0.404	0.402	
Succulent richness (qty)	0.240	0.303	
Eigenvalue	3.080	2.003	
% variation explained	30.805	20.034	
Cumulative % of variation explained		50.839	

DISCUSSION

Male tortoises at SL reach a greater asymptotic length than females, and males and females appear to grow at the same rate. During the summer activity period, tortoises at the SL site used steep rocky hillsides with a high proportion of sand and annual vegetation and few succulent species. They avoid areas of low shelter density and high succulent richness and used enclosed shelters close to boulders during summer, and enclosed shelters close to boulders on steep slopes for winter hibernation.

Wildlife research, especially in complex habitats, has the potential for error and bias. In this study, there are three potential sources of error. Tortoise lengths were measured by multiple AGFD biologists over two decades, telemetry locations may have been random encounters and not a reflection of habitat selection, and few winter locations were available for analysis.

However, by using a large number of growth measures recorded over long durations, and measuring a large number of habitat plots with consistency and accuracy make this a robust description of tortoise growth and habitat selection at SL. Winter data is presented knowing the results have the potential to vary as either the number of tortoises in the study increases or as multiple winter seasons are analyzed.

Growth

In this study, tortoise growth curves reflected high initial growth for each of the sexes followed by slower but seemingly continuous growth as asymptotic length was approached. This pattern is typical for most vertebrate animal species and follows the general pattern of larger males seen in seven sites in the Mohave and Sonoran deserts and in both species (Germano 1994*a*; Murray and Klug 1996; Lovich et al. 2011; Appendix C, figure 1). Desert tortoises grow most rapidly early in life, reaching approximately 45% of their maximum length (Murray and Klug 1996) before growth slows at approximately age 18-22 years (Germano 1994*a*). Juvenile tortoises are highly susceptible to predators (Germano et al. 2002), and rapid early growth contributes to higher juvenile survivorship (Averill-Murray et al. 2002*a*).

Male tortoises at SL grow to a larger asymptotic length than females. Sexual size dimorphism has also been found in studies of both species in the Sonoran and Mohave deserts which all report male tortoises larger than female tortoises (Germano 1994*a*; Murray and Klug 1996; Averill-Murray et al. 2002*a*; Lovich et al. 2011; Appendix C, figure 2). However, the factors controlling growth relative to different populations and species of tortoises are unknown (Germano 1994*a*). Different populations may therefore have population-specific maximum sizes, reinforcing the need to investigate the characteristics of each population separately and not generalize the findings of one population to others (Averill-Murray et al. 2002*a*).

Habitat

Desert tortoise literature is replete with studies documenting different habitat uses between the Mohave species and the Sonoran species (Murphy et al. 2011). The literature also shows habitat use varying between different tortoise populations within the Sonoran Desert. Murphy et al. (2011) report tortoises in the Mohave desert prefer valleys and alluvial fans whereas tortoises in the Sonoran desert predominately use slopes and rocky hillsides. Although much of the Sonoran desert tortoise population occupies mountain foothills and incised washes, Barrett (1990) and Riedle et al. (2008) found Sonoran desert tortoises occurring on bajadas and alluvial fans. Vegetation assemblages associated with different populations at each location also differ based on elevation and soil and moisture regimes.

Because tortoises need food, water, and shelter to survive and grow, and social interactions to reproduce, understanding how a habitat satisfies these requirements can describe mechanisms for habitat selection. The relationship between habitat selections and the basic needs of food and shelter at the SL site are described below.

Food.— Desert tortoises are obligate herbivores (Oftedal 2002) and graze daily during the active season (Jarchow et al. 2002) on a variety of trees, shrubs, woody vines, cacti, and herbaceous perennials, with grasses as the primary diet item (VanDevender et al. 2002). Consumption is limited temporally because tortoises hibernate from 100 to 200 days per year and daytime temperature extremes keep tortoises in shelters during hot, dry summers (Bailey et al. 1995). Tortoises may also adjust their activity patterns and home range sizes based on seasonally reduced forage biomass (Duda, Krzysik et al. 1999).

Juvenile tortoises at SL selected locations that support the growth of annual vegetation. For example, tortoises were found in areas where the substrate had a high proportion of sand. Annual vegetation and canopy cover are positively correlated with the proportion of sand, suggesting plants grow more frequently in sandy areas. A high proportion of sand is also important to female tortoises laying eggs in holes they dig themselves in soft soil under boulders (Jarchow et al. 2002) or in burrows (Averill-Murray et al. 2002*b*).

Three substrate or ground cover components were negatively correlated with annual vegetation: proportions of boulders, gravel and, fine gravel. Annual vegetation was less abundant in aggregates larger than sand. Succulent richness was also negatively correlated with annual vegetation. Unlike annual plants and most perennials, succulents thrive in areas of reduced moisture and prolonged drought. Therefore, high succulent richness signifies that more arid areas are less able to produce the types of forage materials that make up the bulk of a tortoise's diet. Although eight different succulent species were found in habitat plots, only four are generally used as forage by tortoises, and in the case of two species, only the fruits or young joints (Van Devender et al. 2002) which are highly seasonal and therefore a small proportion of total intake.

In a study from the Florence Military Reservation (FMR), AZ, an area of valley bottoms and alluvial fans, Grandmaison (2010) found canopy cover as the parameter of highest importance. In this same study and contrary to my findings, ground cover and soil composition were not correlated to habitat selection. Although canopy cover can be related to food sources, tortoises at the FMR used canopy cover and caliche burrows for shelter, whereas SL torts used boulders as shelter at a higher rate than they used plant cover for shelter, based on availability.

Shelter.— Tortoises are closely tied to shelters in both the Sonoran and Mohave deserts (Averill-Murray, et al. 2002*a*), using them for thermoregulation (Averill-Murray, et al. 2002*b*), courtship, nesting, predator avoidance, and to reduce evaporative water loss (Woodbury and Hardy 1948; Barrett and Humphrey 1986; Barrett 1990; Bailey et al. 1995; Lovich and Daniels 2000). Abundance and density of tortoises may be regulated by the number of shelter sites (Averill-Murray, et al. 2002*b*) with local populations highly correlated with shelter availability (Averill-Murray, et al. 2002*a*)and occupancy rates increasing with the number of shelter sites (Zylstra and Steidl 2009).

The geology, terrain, and vegetation at SL create the potential for high numbers of potential shelters. Although tortoises use a variety of different shelter types including cavities excavated in hillsides and flattened areas under trees and shrubs, the majority of shelters at SL were associated with rocks (67.9%). Tortoises at the SL site were also found most often in close proximity to rocks (< 1 m) in areas where boulders made up 50 – 75% of the site. Although 96.6% of available plots contained boulders, 100% of summer and winter plots contained boulders with 100% of winter hibernation shelters within 1 m of a boulder. Tortoises at SL also avoided areas of low shelter density, selected locations with a medium density, and used areas with high densities as available.

The size, shape, and depth of a shelter determines temperature and humidity (Averill-Murray et al. 2002*a*), with deeper, more enclosed shelters offering the greatest amount of thermal buffering. Tortoises at SL almost exclusively selected enclosed shelters in both summer and winter and avoided open or semi-open shelters in both seasons.

Tortoises at SL also selected locations on steep hillsides (slope gradient > 20°) in winter which is consistent with Zylstra and Steidl (2009) who found Sonoran tortoises in southern Arizona more likely to be associated with steep slopes. Burge (1980), in a study of 387 sites in western and southern Arizona found similar associations between tortoises and structure, finding 96% of tortoise sign on steep slopes with extensive rock outcrops and boulders.

Summer shelters selected by tortoises were orientated to the northwest. This aspect differs from the results of three other studies which found shelter aspect predominately to the south (Bailey et al. 1995; Lovich and Daniels 2000; Hazard and Morafka 2004). However, the selection of slope orientation reflects the mean orientation of the available habitat at SL. The topography of SL is dominated by two parallel ridges that bisect the site, northwest to southeast. These ridges create a predominance of northwest and southeast facing slopes.

Habitat suitability.—The suitability map appears to accurately reflect the habitat preferences of the juvenile tortoises at SL. However, during the analyzed period, one tortoise (#975) was tracked exclusively in unsuitable habitat and, as of this writing, has moved approximately 3 km to the north and is outside of the area modeled on the suitability map.

A winter suitability map was not created because there were only three significant winter variables (slope grade, proportion of litter, and shelter type), making the validity of a suitability map questionable. Also, a map to help locate juvenile tortoises in the winter would not be useful because tortoises are hibernating underground during winter and are unlikely to be located.

FUTURE RESEARCH

This study was based on 11 juvenile tortoises that measured 124 – 176 mm MCL at initial capture. As of this writing, two additional tortoises have been added to the study, and the larger (older) tortoises in the study will invariably begin to show morphological characteristics allowing determination of sex. Including information from these and from additional juvenile tortoises will inform our interpretation of habitat selection as it may differ between males and females and different age groups. The age structure of this population could be developed and compared to age structures of other populations to determine which age class(es) contribute(s) the most to population growth (Averill-Murray et al. 2002*b*; Berry and Nicholson 1984).

MANAGEMENT IMPLICATIONS

Human impacts on desert ecosystems will likely increase as the human population in the southwestern US continues to increase and desert-oriented recreation expands. Understanding the needs of wildlife and developing management plans with those needs in mind can preclude or minimize negative impacts and allow humans to coexist with other species, including tortoises. Specifically, the findings of this study can help managers:

- Understand the impacts to desert tortoise habitat in multiple use areas and as the result of habitat-altering actions such as urbanization
- Determine key habitat characteristics when maintaining or closing access to areas
- Understand regional population parameters for comprehensive species planning
- Focus future searches for juvenile tortoises at SL
- Estimate ages of tortoises based on measured sizes using a growth curve

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APPENDIX A

PLANTS FOUND AT THE SUGARLOAF MOUNTAIN STUDY SITE IN CENTRAL ARIZONA, USA

Family	Genus species	Common Name
	Trees	
Celastraceae	*Canotia holacantha*	Canotia
Fabaceae	*Acacia greggii*	Catclaw Acacia
	Parkinsonia spp.	Palo Verde
Fagaceae	*Quercus turbinella*	Shrub Live Oak
Leguminosae	*Prosopis* spp.	Mesquite
	Succulents	
Asparagaceae	*Yucca baccata*	Banana Yucca
Cactaceae	*Carnegiea gigantea*	Giant Saguaro
	Echinocereus engelmannii	Strawberry Hedgehog
	Ferocactus wislizenii	Barrel Cactus
	Opuntia sp.	Prickly Pear Cactus
	Opuntia acanthocarpa	Buckhorn Cholla
	Opuntia bigelovii	Teddy Bear Cholla
	Opuntia leptocaulis	Desert Christmas Cactus
	Mammillaria microcarpa	Pincushion Cactus
Fouquieriaceae	*Fouquieria splendens*	Ocotillo
	Woody species	
Asteraceae	*Ambrosia ambrosiodes*	Canyon Ragweed
	Ambrosia deltoidea	Triangle-leaf Bursage
	Brickellia coulteri	Coulter’s Brickellbush
	Dyssodia porophylloides	San Felipe Dogweed
	Encelia farinose	Brittlebush
	Ericameria cooperi	Turpentine Bush
	Guiterrezia sarothrae	Broom Snakeweed
	Isocoma acradenia	Alkalia Goldenbush
	Porophyllum gracile	Odora
	Stephanomeria parryi	Parry’s Wirelettuce
	Trixis californica	Trixis
	Viguiera deltoidea	Parish Goldeneye
Euphorbiaceae	*Argythamnia lanceolata*	Narrow-leaf Silverbush
	Bernardia incana	Hoary Myrtlecroton
Fabaceae	*Calliandra eriophylla*	Fairy Duster
	Cassia covesii	Desert Senna
	Lotus rigidus	Wiry Lotus

Family	Genus species	Common Name
	Marina perryi	Parry Dalea
Krameriaceae	*Krameriagrayi*	White Ratany
Lamiaceae	*Hyptis emoryi*	Desert Lavender
Leguminosae	*Acacia constricta*	White Thorn Acacia
Malpighiaceae	*Janusia californica*	Janusia
Malvaceae	*Abutilon palmeri*	Palmer's Abutilon
	Hibiscus coulteri	Desert Rose Mallow
	Sphaeralcea ambigua	Desert Globemallow
Nyctaginaceae	*Hesperonia aspera*	Desert Wishbone Bush
Polygonaceae	*Eriogonum fasciculatum*	Flat-top Buckwheat
Pteridaceae	*Pellaea truncate*	Spiny Cliff Brake
Rhamnaceae	*Ziziphus obtsifolia*	Gray Thorn
Rubiaceae	*Galium stellarum*	Starry Bedstraw
Rutaceae	*Thamnosma montana*	Turpentine Bush
Sapindaceae	*Dodonaea viscose*	Hopbush
Scrophulariaceae	*Keckiella antirrhinoides*	Yellow Bush Penstemon
Simmondsiaceae	*Simmondsia chinensis*	Jojoba
Solanaceae (Wolfberry)	*Lycium exsertum*	Arizona Desert Thorn
	Nicotiana obfusifolia	Desert Tobacco
Ulmaceae	*Celtis pallida*	Desert Hackberry
Verbenaceae	*Aloysia wrightii*	Wright's Beebrush
Zygophyllaceae	*Larrea tridentata*	Creosote Bush

APPENDIX B

HABITAT MEASURES PROTOCOL FOR THE SUGARLOAF MOUNTAIN STUDY SITE IN CENTRAL ARIZONA, USA

Measurement Methods

Line intercept. Used to measure the canopy cover variable. After establishing the three 15-m transects (all crossing at 7.5 m (± 20 cm) and spaced 60° apart), move along the length of each transect, recording where the edges of any shrub or tree at least 40 cm above the ground overhangs the transect line. Sum all the distances represented by coverage, divide by 45 (total length of all three transects), and multiply by 100 to get a percentage of cover for the plot.

Point intercept. Ground cover and soil substrate variables are measured at exact 1m increments along each transect (0 – 15 m), for a total of 16 measurements on each transect. After establishing the three 15 m transects (all crossing at 7.5 m (± 20 cm) and spaced 60° apart), use a pointed stick, placed on the ground at each meter interval, and record the category of variable the point of the stick touches.

Plot measures. The six ends of the three transect lines can be viewed as roughly establishing a circular plot of 15 m diameter. Plot measures are numerical counts of the variables of interest within the area of the plot or within the imaginary circle created by the ends of the transects.

Variables

Elevation: A direct reading of the elevation in meters from the GPS unit placed on or near the center of the plot.

Slope Aspect: The compass direction of the hillside. *Procedure*: Stand facing downhill (imagine the direction a ball would roll if the slope was actually a smooth surface with no obstructions) and orient your body in the same direction. Hold a magnetic compass at chest height, ensuring no metal objects are within 12 in of the compass, and read the heading (to the nearest degree) on the direction-of-travel arrow. The compass reading is converted to a categorical variable before analysis.

Slope Grade: The steepness of the hillside. *Procedure*: Find a place as close to the shelter or location as possible that approximates the slope and place a straight stick at least one meter long flush with the surface. Place the magnetic compass on the stick and, using the clinometer function, read the angle from the compass. Repeat twice more within 1 m of the shelter, recording each measure. The three measures are averaged to obtain the Slope Grade variable. The clinometer reading is converted to a categorical variable before analysis.

Shelter Aspect: The compass direction the shelter entrance faces. *Procedure*: Standing as close as practical to the shelter entrance (imagine a tortoise exiting the shelter) and orient your body in the same direction. Hold a magnetic compass at chest height, ensuring no metal objects are within 12 inches of the compass, and read the heading (to the nearest degree) on the direction-of-travel arrow. The compass reading is converted to a categorical variable based before analysis.

Shelter Type. Classified subjectively based on the configuration of rock and soil and the overall size of the opening:

- Burrow (B) = a shelter with rock top and soil bottom; sides could be either rock or soil
- Rock (R) = an open space or hollow under a rock, usually open on several sides, bottom could be either rock or soil
- All Soil (S) = a shelter with all sides soil
- Pallet (P) = a small flat spot where a tortoise has cleared the ground cover, usually level and often under the base of a shrub or other shade providing structure
- Midden (M) = a Pack Rat midden
- Cave/Crevice (C) = a shelter that is rock on top, sides, and bottom; a crevice is a crack in the rock, possibly open above
- Open = A location where there is no shelter

Rock Proximity: The distance in meters and decimeters from the center of the plot to the nearest rock greater than or equal to the size of an adult tortoise (0.3 m diameter). If the location is categorized as open, meaning there is no shelter associated with the location, measure the distance from the flagged center of the plot to the nearest two to three qualifying rocks within the error of the GPS unit. Rock proximity is the average of these measures.

Rock Structure: Classified subjectively as the distribution of rocks within the plot:

- Scattered (SC) = part of a group of surface rocks that are spread out within the plot
- Stacked (ST) = surface rocks are in a vertical pile
- Boulder Pile (BP) = large rocks jumbled in a heap, often in a low spot such as a ravine or draw
- Bedrock (BR) = the bottom of the rock disappears into the soil below it, rather than sitting on the soil as a boulder would
- None (NO) = no rocks ≥ size of adult tortoise (0.3 m) are in the plot

Ground Cover: Measured to determine the percentage of ground cover for the entire plot. *Procedure*: Using a straight stick, start at one end of each of the transects (0 m) and slowly walk along the tape measure, dangling the stick vertically above or next to the tape as appropriate and placing the stick in contact with the surface at each meter increment. Look at the exact spot the tip impacts the surface and record the material as categorized by the following groups:

- Bare Ground (BG) = exposed soil
- Litter (L) = vegetative debris and non-woody plant material or twigs with a diameter < 1cm
- Dead Wood (DW) = woody debris with diameter ≥ 1 cm

- Vegetation (V) = any living plant part at ground level
- Annual Vegetation (VA) = living annual vegetation
- Boulder (R) = aggregate ≥ 25 cm

Soil Substrate: Measured to determine the percentage of ground cover for the entire plot. *Procedure*: Measured at 0 m and at each 1 m increment along each transect exactly as ground cover was measured and categorized in the following groups by aggregate size:

- Sand (S) = < 2 mm
- Fine Gravel (FG) = 2 – 10 mm
- Gravel (G) = 1-6 cm
- Cobble (C) = 6 – 25 cm
- Boulder (B) = > 25 cm

Canopy Cover: Measured to determine the percentage of cover for the entire plot, specifically for any vegetation ≥ 40 cm tall that overhangs any transect and is available as overhead cover for a tortoise. The distance along each transect where qualifying cover starts and ends and the species are recorded. Although species is recorded and there is the potential for overlap between species, only the total line-distance is calculated for percent cover. *Procedure*: Using a straight stick marked at 40 cm, start at one end of each transect (0 m) and slowly walk along the tape measure, dangling the stick vertically above or next to the tape as appropriate until the stick impacts plant material, including overhead plant material. Place the tip of the stick on the surface and compare the height of the plant to the 40 cm mark on the stick. If the height of the plant is less than 40 cm, continue along the tape until that plant or the next plant is greater than 40 cm. As soon as the 40 cm minimum is met by any plant, record the place on the tape. Continue walking along the tape until the plant becomes less than 40 cm and record the place on the tape. The two measures should show the beginning and ending point to calculate the distance the plant extends over a transect at ≥ 40 cm. Record all plants individually, even when plants of the same species overlap.

Size of the boulder is measured by the amount visible. Neither the researcher nor the tortoise can determine the true size of a partially buried rock, so the measurement is the visible portion of any buried rock.

Shelter Density: A count of the number of shelters the researcher judged as usable to a juvenile tortoise based on size and approach (see Hazard and Morafka 2004) within the extents of the 177-m^2 plot. Convert to shelters per hectare using the following equation:

$$\text{shelter density/hectare} = (\pi r^2 / 10000)n$$

where r is the radius of the plot (7.5 m) and n is the number of shelters.

Woody Richness: The number of species of woody perennial plants within the area of the plot or within the imaginary circle created by the ends of the transects.

Succulent Richness: The number of species of woody perennial plants within the area of the plot or within the imaginary circle created by the ends of the transects.

APPENDIX C

ASYMPTOTIC LENGTHS AND INTRINSIC GROWTH RATES OF EIGHT DESERT TORTOISE POULATIONS IN THE SOUTHWESTERN UNITED STATES AND MEXICO

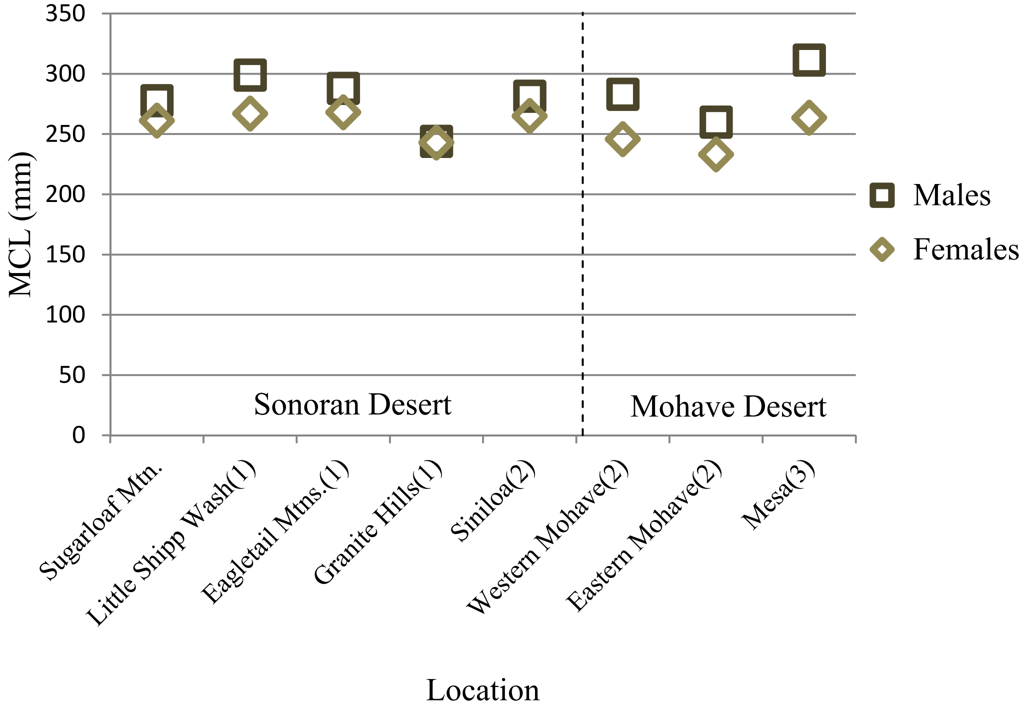


Figure 1. Asymptotic lengths of male and female Sonoran desert tortoises (*Gopherus morafkai*) at the Sugarloaf Mountain (SL) study site in central Arizona, USA compared to *G. morafkai* and *G. agassizii* from four sites in the Sonoran desert and three sites in the Mohave deserts. Values for sites other than SL are from: [1]Murray and Klug 1996, [2]Germano 1994*a*, and [3]Lovich et al. 2011.

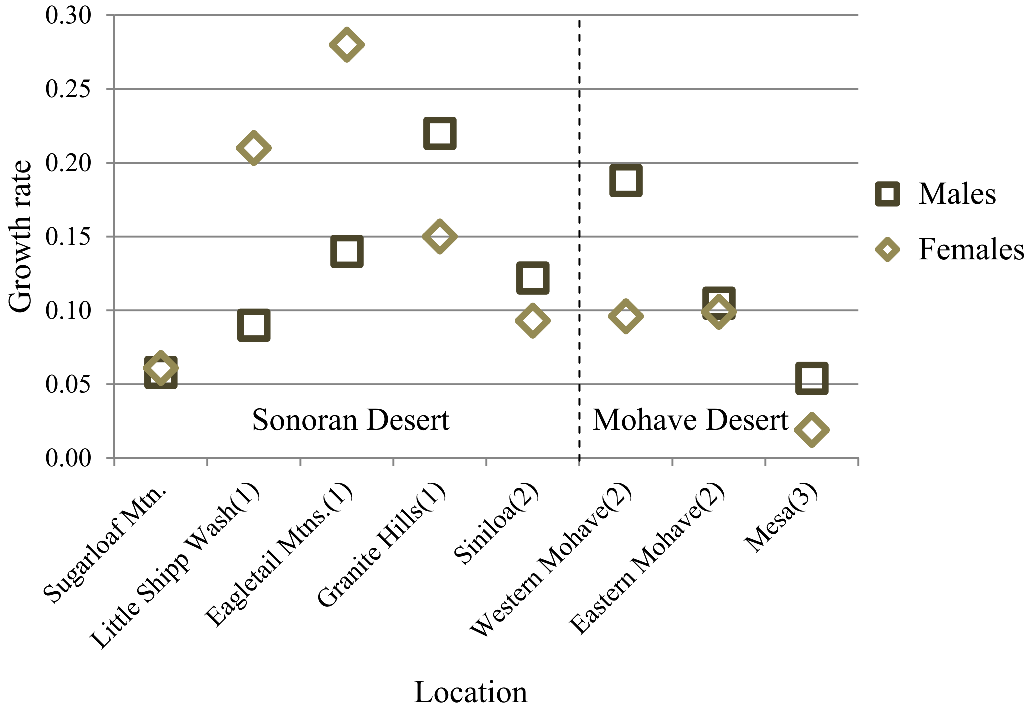


Figure 2. Intrinsic growth rates of male and female Sonoran desert tortoises (*Gopherus morafkai*) at the Sugarloaf Mountain (SL) study site in central Arizona, USA compared to *G. morafkai* and *G. agassizii* from four sites in the Sonoran desert and three sites in the Mohave deserts. Values for sites other than SL are from: [1]Murray and Klug 1996, [2]Germano 1994*a*, and [3]Lovich et al. 2011.

APPENDIX D

PEARSON COORELATION TEST RESULTS AT THE SUGARLOAF MOUNTAIN STUDY SITE IN CENTRAL ARIZONA, USA

Appendix D. Correlations between habitat variables in a 177 m^2 plot centered on coordinates where tortoises had been located during radio-telemetry events (*n* = 117) and a set of randomly generated coordinates (*n* = 117) at the Sugarloaf Mountain study site in central Arizona, USA (total of 234 locations). Correlation coefficients (CC) in bold text are significant at the 0.05 level. Pairs of variables with positive CC and *P* value <0.05 tend to increase together, pairs of variables with negative CC and *P* values <0.05 indicates one variable increases while the other variable decreases.

Variable	grade	elev	sheldens	propVA	propS	propFG	propG	propB	rockprox	sucrich	woodrich	propCC
Shelter type (sheltype)	**-0.349**	0.093	**-0.288**	**-0.330**	**-0.181**	**0.320**	**0.174**	**-0.181**	**0.381**	**0.250**	0.035	-0.073
	<0.001	0.157	<0.001	<0.001	0.006	<0.001	0.008	0.005	<0.001	<0.001	0.592	0.267
Slope grade (grade)		-0.079	**0.224**	**0.145**	-0.041	**-0.298**	-0.037	**0.219**	**-0.387**	**-0.208**	0.036	0.068
		0.228	<0.001	0.026	0.531	<0.001	0.575	<0.001	<0.001	0.001	0.587	0.303
Elevation (elev)			**0.14**	**-0.207**	-0.104	**-0.205**	**-0.190**	**0.351**	-0.097	-0.062	0.017	**-0.372**
			0.033	0.002	0.112	0.002	0.004	<0.001	0.141	0.346	0.801	<0.001
Shelter density (sheldens)				-0.008	-0.097	**-0.512**	**-0.292**	**0.584**	**-0.390**	**-0.428**	-0.013	-0.067
				0.907	0.139	<0.001	<0.001	<0.001	<0.001	<0.001	0.84	0.307
Proportion of annual vegetation (propVA) as ground cover					**0.619**	**-0.157**	**-0.227**	**-0.198**	-0.071	**-0.161**	-0.071	0.087
					<0.001	0.016	<0.001	0.002	0.281	0.014	0.278	0.187
Proportion of sand (props) as substrate						**-0.203**	**-0.367**	**-0.355**	**0.239**	**-0.207**	-0.066	**0.359**
						0.002	<0.001	<0.001	<0.001	0.002	0.318	<0.001
Proportion of fine gravel (propFG) as substrate							**0.352**	**-0.697**	**0.401**	**0.482**	0.084	0.094
							<0.001	<0.001	<0.001	<0.001	0.202	0.152
Proportion of gravel (propG) as substrate								**-0.520**	**0.176**	**0.422**	**0.201**	**0.151**
								<0.001	0.007	<0.001	0.002	0.021
Proportion of boulders (propB) as ground cover									**-0.506**	**-0.425**	-0.115	**-0.406**
									<0.001	<0.001	0.079	<0.001
Rock proximity (rockprox)										**0.201**	**-0.139**	**0.189**
										0.002	0.034	0.004
Succulent Richness (sucrich)											0.108	-0.055
											0.099	0.405
Woody perennial plant richness (woodrich)												**0.211**
												0.001

APPENDIX E

CHI-SQUARE AND Z-TEST RESULTS (SUMMER) AT THE SUGARLOAF MOUNTAIN STUDY SITE IN CENTRAL ARIZONA, USA

Appendix E. Chi-square analysis and z-test of proportions of microhabitat variables measured at juvenile Sonoran Desert Tortoise (*Gopherus morafkai*) during summer (July – September 2011) telemetry locations and random locations at the Sugarloaf Mountain study site in central Arizona, USA.

Variable	$\Sigma\chi^2$ (df)	Significant (*P*)	Classes	Tortoise Locations *n* = 106	Available Habitat *n* = 117	*Z* test
Slope grade	7.371(3)	0.061	< 10°	13.2%	25.6%	
			10.1°-20°	34.9%	37.6%	
			20.1°-30°	42.5%	29.9%	
			> 30°	9.4%	6.8%	
Shelter type	51.348(2)	< 0.001	Enclosed	41.51%	2.56%	2.378*
			Semi-open	18.87%	25.64%	1.050
			Open	39.62%	71.79%	4.704*
Elevation	31.404(6)	< 0.001	<690m	8.5%	12.8%	0.413
			690.1m – 700m	20.8%	14.5%	0.289
			700.1m – 710m	21.7%	11.1%	0.049*
			710.1m – 720m	15.1%	11.1%	0.492
			720.1m – 730m	4.7%	12.0%	0.087
			730.1m – 740m	24.5%	12.0%	0.024*
			>740m	4.7%	26.5%	<0.001*
Shelter Density	27.686(3)	< 0.001	< .1/ha	17.0%	50.4%	5.105*
			.11 - .2 /ha	50.9%	29.9%	3.065*
			.21 - .3 /ha	19.8%	11.1%	1.618
			> .3/ha	12.3%	8.5%	0.691
Proportion of Bare Ground	13.641(3)	0.003	<10 %	38.7%	28.2%	
			11 - 20 %	37.7%	24.8%	
			21 - 30 %	10.4%	23.9%	
			>30 %	13.2%	23.1%	
Proportion of Litter	76.054(4)	<0.001	<10 %	29.2%	6.0%	
			11 - 20 %	35.8%	15.4%	
			21 - 30 %	28.3%	17.9%	
			31 - 40 %	2.8%	23.9%	
			>40 %	3.8%	36.8%	
Proportion of Dead Wood		Not analyzed due to limited amount at summer sites.				
Proportion of Live Vegetation		Not analyzed due to limited amount at summer sites.				
Proportion of Annual Vegetation	68.849(5)	<0.001	<10 %	14.2%	54.7%	6.182*
			10 - 20 %	17.9%	29.1%	1.793
			>20 %	67.9%	16.2%	7.706*

Variable	$\Sigma\chi^2$ (df)	Significant (*P*)	Classes	Tortoise Locations *n* = 106	Available Habitat *n* = 117	*Z* test
Proportion of Rock	10.592(7)	0.157	<10 %	8.5%	15.4%	
			11 - 20 %	13.2%	17.9%	
			21 - 30 %	16.0%	22.2%	
			31 - 40 %	23.6%	12.8%	
			41 - 50 %	18.9%	12.0%	
			51 - 60 %	10.4%	7.7%	
			61 - 70 %	2.8%	5.1%	
			>70 %	6.6%	6.8%	
Proportion of Sand	33.624(4)	<0.001	<10 %	7.6%	23.9%	3.139*
			11 - 20 %	22.6%	34.2%	1.755
			21 - 30 %	22.6%	23.9%	0.069
			>30 %	47.2%	15.4%	5.003*
Proportion of Fine Gravel	30.347(4)	<0.001	<10 %	18.9%	13.7%	0.870
			11 - 20 %	41.5%	18.0%	3.719*
			21 - 30 %	25.5%	23.9%	0.111
			>30 %	14.2%	44.4%	4.781*
Proportion of Gravel	13.279(4)	0.010	<10 %	55.7%	32.5%	3.352*
			11 - 20 %	25.5%	35.0%	1.405
			21 - 30 %	12.3%	21.4%	1.627
			31 - 40 %	3.8%	8.5%	1.191
			>40 %	2.8%	2.6%	-0.292
Proportion of Cobbles	3.041(1)	0.081	<10 %	97.2%	90.6%	
			>10 %	2.8%	9.4%	
Proportion of Boulders	15.557(3)	0.001	<25 %	29.2%	49.6%	3.060*
			25 - 50 %	39.6%	29.1%	1.588
			50 - 75 %	27.4%	12.8%	2.459*
			>75 %	3.8%	8.5%	1.230
Proportion of Canopy Cover	7.658(5)	0.176	<10 %	0.9%	3.4%	
			11 - 20 %	7.5%	12.8%	
			21 - 30 %	25.5%	22.2%	
			31 - 40 %	26.4%	27.4%	
			41 - 50 %	12.3%	17.9%	
			>50 %	27.4%	16.2%	
Rock Proximity	16.014(2)	<0.001	<1 m	91.5%	72.6%	12.256*
			>1 m	8.5%	27.4%	7.145*
Rock Distribution	4.507(2)	0.105	1 = Scattered	78.3%	65.8%	
			2 = Grouped	20.8%	31.6%	
			3 = None	0.9%	2.6%	
Woody Species Richness	4.364(2)	0.113	< 10 species	11.3%	12.0%	
			10 - 20 species	59.4%	46.2%	
			> 20 species	29.2%	41.9%	
Succulent Species Richness	27.684(2)	<0.001	< 2 species	65.1%	35.9%	4.221*
			2 -4 species	33.0%	43.6%	1.482
			> 4 species	1.9%	20.5%	4.119*

*_Z_ test of proportions significant at the _P_< 0.05 level.

APPENDIX F

CHI-SQUARE AND Z-TEST RESULTS (WINTER) AT THE SUGARLOAF MOUNTAIN STUDY SITE IN CENTRAL ARIZONA, USA

Appendix F. Chi-square analysis of microhabitat variables measured at juvenile Sonoran Desert Tortoise (*Gopherus morafkai*) during winter (December 2010 – February 2011) telemetry locations and random locations at the Sugarloaf Mountain study site in central Arizona, USA. All variables were a comparison of two classes, therefore the Chi-square analysis reveals proportional relationships.

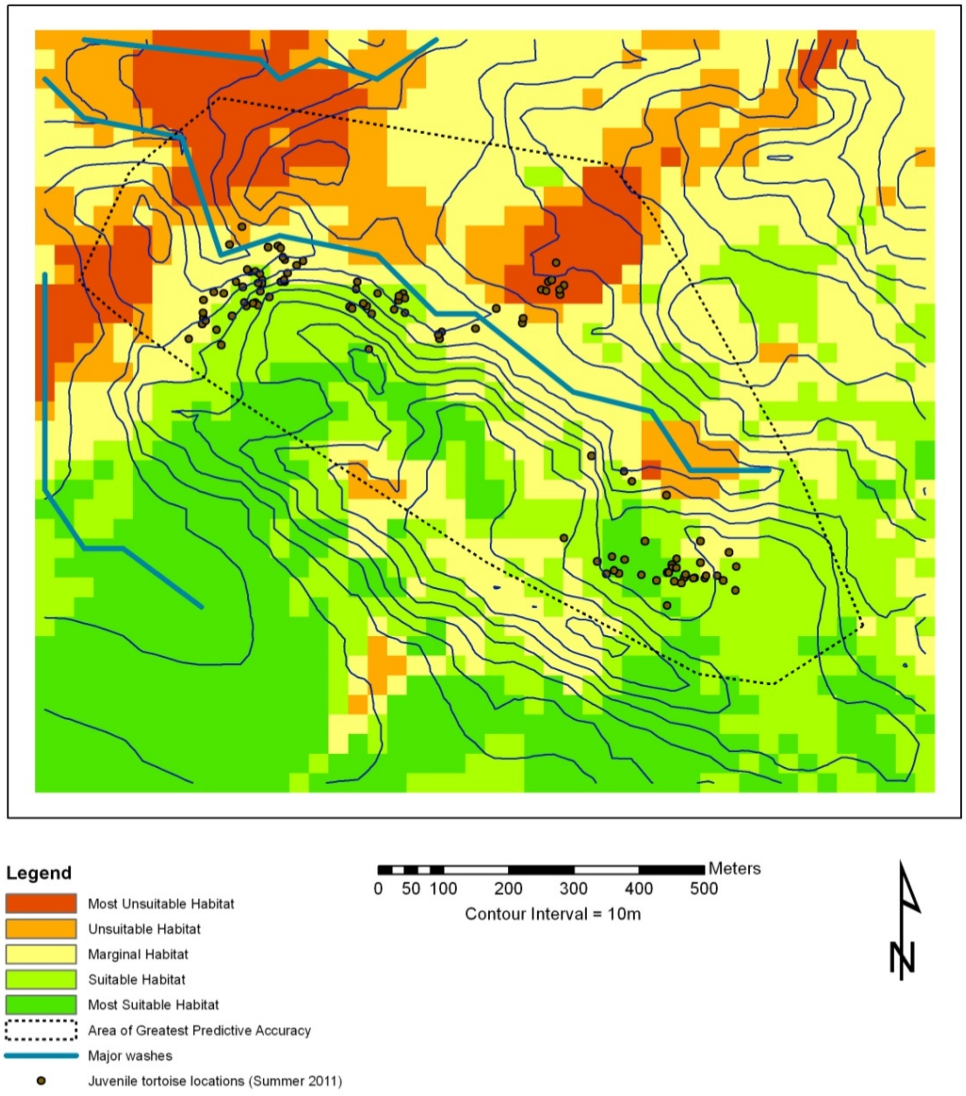
Variable	$\Sigma\chi^2$ (df)	Significant (*P*)	Classes	Tortoise Locations *n* = 11	Available Habitat *n* = 117**
Slope grade	6.701 (1)	0.010*	< 20° > 20°	18.18% 81.82%	63.25% 36.75%
Shelter type	NA (Fischer test of exact)	< 0.001*	Enclosed Partially enclosed	81.82% 18.18%	9.09% 90.91%
Elevation	0.003(1)	0.957	<710m >710m	45.45% 54.55%	49.57% 50.43%
Shelter Density	2.551(1)	0.110	< .2 /ha > .2 /ha	54.55% 45.45%	80.34% 19.66%
Proportion of Bare Ground	0.047(1)	0.828	< 20 % > 20 %	54.55% 45.45%	53.0% 47.0%
Proportion of Litter	11.307(1)	<0.001*	< 20 % > 20 %	72.73% 27.27%	21.4% 78.6%
Proportion of Dead Wood	Not analyzed. All values in one increment.		<10 %	100.0%	
Proportion of Live Vegetation	Not analyzed. All values in one increment.		<10 %	100.0%	
Proportion of Annual Vegetation	1.551(1)	0.213	<20 % >20 %	36.36% 63.64%	83.76% 16.24%
Proportion of Rock	0.358(1)	0.550	< 40 % > 40 %	54.55% 45.45%	68.4% 31.6%
Proportion of Sand	1.551(1)	0.213	< 20 % > 20 %	36.36% 63.64%	60.7% 39.3%
Proportion of Fine Gravel	0.611(1)	0.435	< 30 % > 30 %	72.73% 27.27%	55.6% 44.4%
Proportion of Gravel	0.289(1)	0.591	<10 % >10%	45.45% 54.55%	32.5% 67.5%

Variable	$\Sigma\chi^2$ (df)	Significant (P)	Classes	Tortoise Locations $n = 11$	Available Habitat $n = 117$**
Proportion of Cobbles	Not analyzed. All values in one increment.		<10 %	100.0%	
Proportion of Boulders	0.631(1)	0.427	< 30 %	36.36%	53.8%
			> 30 %	63.64%	46.2%
Proportion of Canopy Cover	0.035(1)	0.852	< 40 %	63.64%	65.8%
			> 40 %	36.36%	34.2%
Rock Proximity	Not analyzed. All values in one increment.		<1m	100.0%	
Rock Distribution	0.340(1)	0.560	None/Scattered	81.82%	68.4%
			Grouped	18.18%	31.6%
Woody Species Richness	0.001(1)	0.972	< 20 species	63.64%	58.1%
			> 20 species	36.36%	41.9%
Succulent Species Richness	2.206(1)	0.138	< 2 species	63.64%	35.9%
			> 2 species	36.36%	64.1%

*Chi-square significant at the $P < 0.05$ level.
**n=33 for shelter type as 33 of the 117 sampled sites were actual shelters. Since none of the 11 tortoises hibernated in the open, only shelters in the available area were compared by type.

APPENDIX G

JUVENILE SONORAN DESERT TORTOISE (*Gopherus marafkai*) HABITAT SUITABILITY MAP FOR THE SUGARLOAF MOUNTAIN STUDY SITE IN CENTRAL ARIZONA, USA


Legend
Most Unsuitable Habitat
Unsuitable Habitat
Marginal Habitat
Suitable Habitat
Most Suitable Habitat
Area of Greatest Predictive Accuracy
Major washes
Juvenile tortoise locations (Summer 2011)
Meters
0 50 100 200 300 400 500
Contour Interval = 10m
N