BURROW CHARACTERISTICS AND SOCIAL ELEMENTS OF CAPTIVE JUVENILE BOLSON TORTOISES (*GOPHERUS FLAVOMARGINATUS*) WITHIN A HEADSTART ENCLOSURE IN NEW MEXICO

BY

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ABSTRACT

BURROW CHARACTERISTICS AND SOCIAL ELEMENTS OF

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Knowledge of burrow use and social behaviors is essential for the management and conservation of juvenile tortoises. Twenty-three juvenile Bolson tortoises were observed within a headstart facility in south-central New Mexico during summer, 2010. Tortoises were housed within a 13 x 7.5 m outdoor enclosure under ambient conditions and provided 32 artificial burrows constructed at 45.0 cm in length, 15.0 % slope, and height of 10.0 cm. Eight burrow groups with four burrows (oriented north, south, east, and west) were used within each group. Tortoises freely roamed the area from 1 May through 20 September and were observed weekly for burrow selection, changes in burrow length, and monthly burrow microclimate. Changes in temperature, relative humidity, and precipitation were factors that contributed to differences in tortoise behavior. Of 160 opportunities within each orientation, tortoises occupied the north orientation most frequently (N = 90) and east orientation the least (N = 82). Burrow aggregation was most significant in the north direction (x^2 = 11.445, df = 3, P = 0.010). Tortoises used 2-13 different burrows and switched burrows 1-16 times. Artificial burrows were modified a mean 22.0 cm (range: -2.0-55.0 cm) with mean burrow length of 67.0 cm (range: 43.0-100.0 cm). Curving began at the end of each burrow tunneling left or right. There was no difference between curving direction by orientation (x^2 = 2.468, df = 6, P = 0.872). Total precipitation over the period was 175.3 mm, with highest mean relative humidity in August (61.8 %). June had the highest mean temperature (28.9 °C) and May had the lowest (20.7 °C). Temperature at maximum depth of burrows was not different between months May-September however relative humidity by orientation was different in all months except May ($F = 2.43$, $P = 0.008$). Curved burrows had lower mean temperatures (25.1 °C) and higher relative humidity (84.4 %) compared to non-curved burrows with mean temperatures (25.7 °C) and lower relative humidity (81.5 %) when ambient temperatures were higher. Weight gain and loss corresponded to rainfall. This project was developed to raise tortoises in a protective headstart enclosure with some artificiality while observing behaviors.

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INTRODUCTION

The Bolson tortoise *(Gopherus flavomarginatus)* is the largest tortoise in North America (Morafka, 1982). This endangered species inhabits an isolated range in north-central Mexico and its only wild population is restricted to a limited area in the Chihuahuan Desert which is a 50,000 km^2 area of the Bolson de Mapimi (Lemos-Espinal and Smith, 2007) (Fig. 1). Approximately 6,000 km^2 of this area is considered potential tortoise habitat; however, protected habitat is limited (Lemos-Espinal and Smith, 2007). Both natural and anthropogenic activities may have contributed to its population decline including development, soil disturbance, predation, and food consumption of both eggs and adult tortoises (Aguirre et al., 1997).

Historically, the Bolson tortoise had an extended geographic distribution in regions of the United States and northern Mexico. Fossil records indicate that this species had a broader range during the late Pleistocene era (10,000-13,000 years ago) occupying areas in the American Southwest from the southern Great Plains to Arizona (Morafka, 1988). Remains of the species have been found within Maravillas Canyon Cave in Texas (adjacent to Big Bend National Park, Texas), dating from approximately 11,500 years ago (Van Devender and Bradley, 1994). Morphological differences and fossil records proved the Bolson tortoise to be a separate species among the genus *Gopherus* (Auffenberg, 1976).

Legler (1959) was first to describe *G. flavomarginatus* as an extant species in 1959. Based on its small, remaining distribution, the U. S. Fish and Wildlife Service

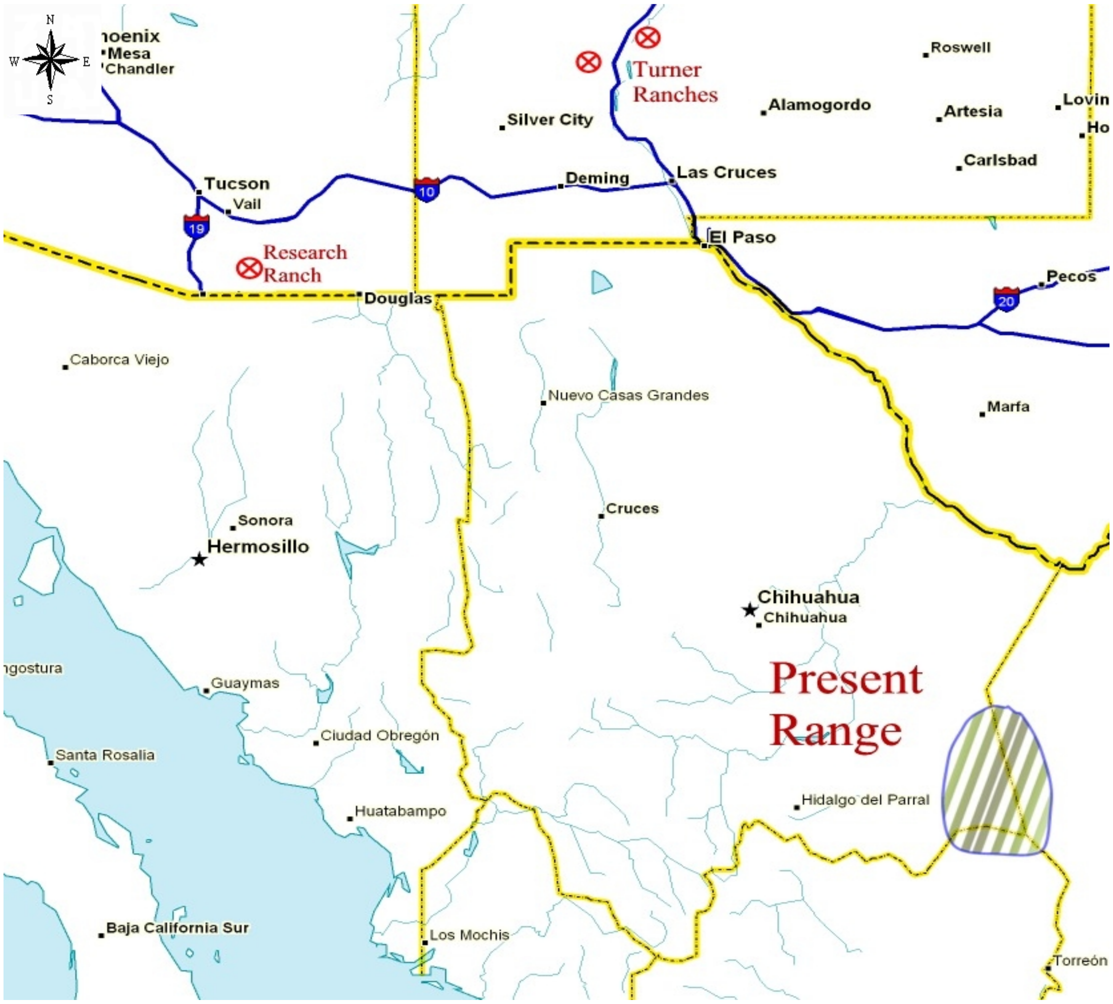

Fig. 1. Historical range of Bolson tortoises, approximately 700 km SSE of the study area (Truett and Phillips, 2009).

was petitioned in 1978 to list the Bolson tortoise as endangered under the Endangered Species Act of 1973 (Dodd, 1979; U.S. Fish and Wildlife Service, 1979). It was officially listed in 1978 and continues to have endangered status (Dodd, 1979). In addition, the Bolson tortoise is also protected under Mexican wildlife law (NOM-ECOL-059-2001) to establish a bi-national effort for its conservation (SEMARNAT, 2001). In 2006, the Turner Endangered Species Fund developed a long-term restoration project in New Mexico to raise both immature and adult tortoises in captivity until future release into the wild in areas where tortoises historically ranged (Truett and Phillips, 2009).

Most published information on Bolson tortoises has pertained to adults. Bolson tortoises are considered the largest North American tortoises with maximum carapace lengths reaching 371 mm (Legler, 1959). Adults experience delayed sexual maturity becoming reproductive between 15-20 years of age (Lemos-Espinal and Smith, 2007). Wild populations of adult tortoises have been observed having 1.4 clutches with 5.4 eggs annually (Adest et al., 1989a; Aguirre et al., 1997). In Mapimi, burrow densities are often greatest in sloping areas with relatively hard and compacted soils (Morafka et al., 1981). All age classes of Bolson tortoises change behavior based on seasonal climatic variation. Daily patterns of surface activity occur between May-September based on desert tortoise studies (Zimmerman et al., 1994). Activity level coincides with egg-laying and warm temperatures beginning in April through September. Most rainfall occurs during the summer months which promotes plant growth and provides tortoises with succulent forage (Adest et al., 1989b). Breeding season typically begins following summer monsoon rains (mid-

July to late August) and lasts until late October/early November (Morafka et al., 1981; Adest et al., 1989a). As temperatures cool, tortoises become inactive and enter hibernation inside burrows during the months of November through April (Morafka et al., 1981). However juvenile *G. agassizii* tortoises have been observed active during the winter months when ambient temperatures rose (Wilson et al., 1999).

Hatchlings (<1 year old) and juveniles (<8 years old) are the least documented stages of life for North American tortoises (Morafka, 1994). Young tortoises are rarely encountered in the field due to high mortality rates both pre and post-hatching, small size, and limited surface activity (Adest et al., 1989b; Morafka, 1994). Alford (1980) performed a study on *G. polyphemus* and estimated a first year mortality rate of 94%. Epperson and Heise (2003) found that the mortality rate for *G. polyphemus* was highest within the first 30 days of hatching. Lack of maternal care provided after nests are made, small body size, and shell softness are major contributors to heavy predation on young tortoises (Adest et al., 1989; Tom, 1994). Most information pertaining to immature tortoises is based on captive individuals (Adest et al., 1989b; Tom, 1994).

Captive management of juveniles is a formidable task; however, it gives opportunity for close observation and minimizes the risk of predation from threatening animals (Adest et al., 1989b) Bolson tortoises have continued to experience low wild population numbers from numerous causes. These include a limited wild range, low reproductive success, and increased mortality of hatchling and juvenile tortoises, making captive management and husbandry necessary to save populations from extirpation (Adest et al., 1989a).

Gopherus spp and other chelonians sometimes differ ecologically and behaviorally based on sex and age making it pertinent to document all stages of life (Pluto and Bellis, 1986; Tom, 1994). For example, Bolson tortoise hatchlings have greater demands for protein, calcium, and water needed for rapid growth when compared to adults (Esque and Peters, 1994; Morafka, 1994). Bolson tortoises within all age classes exhibit opportunistic and herbivorous diets, however hatchling and juveniles have greater metabolic rates and require more food compared to adult conspecifics (Morafka, 1994). Some plants that hatchlings and juveniles eat as natural forage with nutritional benefit include *Sphaeralcea angustifolia*, *Pleuraphis mutica*, *Bouteloua barbata*, *Solanum eleagnifolium*, and *Eragrostis spp* (Adest et al., 1989b). During the summer months, activity level is bimodal, with a peak of activity in the morning and then in the late afternoon (Nathan, 1979). Younger tortoises heat and cool faster and experience higher rates of water loss compared to larger adults (Morafka, 1994; Tom, 1994). One mechanism used to control extreme temperatures and evaporative water loss is the use of underground burrows, a commonality found within the genus *Gopherus* (McGinnis and Voigt, 1971; Bulova, 1997).

Bolson tortoises spend approximately 1% of the annual activity behavior above the surface and the remainder of the time inside dirt burrows (Adest et al., 1989a). Tortoises display fossorial behavior by using underground burrows as shelter, setting them apart from many other chelonians (Bramble, 1982). Burrows serve as a thermal refuge from daily and seasonal temperature fluctuations, provide protection from predators such as coyotes, badgers, falcons, and corvid birds, reduce evaporative water loss, and serve as a site for social interaction (McGinnis and Voigt, 1971;

Morafka, 1982; Bulova, 1997; Wilson et al., 2001). During the warm, active season, burrows provide the coolest temperatures during the day and the warmest temperatures at night (Douglass and Layne, 1978; Tom, 1994). In the cool inactive season, burrows are warmer in the day time. Adults' burrows are self-built with rounded tops and lengths up to 1.5 to 2.5 m (Morafka, 1981). In contrast, juveniles and hatchling tortoises often use rodent burrows opportunistically that are much shorter than adult burrows (Tom, 1994; Hazard and Morafka, 2004).

Young Bolson tortoises have been observed choosing and making burrows under vegetation such as cactus (*Opuntia rastrera*) and shrub grass (Tom, 1994). Digging behavior in hatchling tortoises starts shortly after emergence from the nest (Tom, 1994). Juveniles have been observed using more than one shelter and change burrows during the active season (Bulova, 1994; Tom, 1994). Seasonal climate difference contributes to burrow and social behavior as young tortoises are more active and travel further distances during the hot and rainy season (Tom, 1988).

Burrows are often the site of social interaction among individuals (Bulova, 1994). Bolson tortoises exhibit complex social structure, living in colonies from 3-100 individuals (Morafka, 1988). Adult Bolson tortoises typically occupy one burrow per tortoise except for minimal grouping during the mating season, however Aguirre et al. (1984) observed juvenile Bolson tortoises sharing burrows in a clumped distribution. Tortoise grouping may assist in regulation of burrow microclimate and may be attributed to tortoise relationships or changes in seasonal climate. Burrow grouping may be more prevalent during certain times of the active season.

Identifying these patterns could advance capture rates in the wild and determine the best time of the season to locate large densities of small tortoises.

Patterns may exist in the way juvenile Bolson tortoises orient their burrows. Juveniles may choose burrows based on directional orientation of the burrow entrance. Burrows provide different thermal characteristics that may be influenced by their orientation (McCoy et al., 1993). Tortoises may favor specific aspects over others due to thermal advantages that allow sunlight to shine directly inside burrows during the early mornings when tortoises emerge from their burrows (Morafka et al., 1981). Tortoises may also choose burrows that provide cooler temperatures when temperature extremes exist (Morafka et al., 1981). Research has been recorded on the compass orientation of adult gopher tortoises (*G. polyphemus*) and results showed a tendency for burrows to face the primary compass directions (north, south, east, west) rather than secondary directions (McCoy et al., 1993). Knowledge of burrow patterns can benefit the survival of juvenile tortoises in captivity by providing artificial burrows that fit the needs of the tortoise (Bulova, 1992). Searching for tortoises in the wild could be less arduous if tortoises choose specific burrows based on orientation. In addition, identifying burrow patterns may be used to estimate population densities in the wild (McCoy and Mushinsky, 1992; Bulova, 1994). No information however has been documented on juvenile Bolson tortoise burrow orientation and microclimate in either a wild or captive environment. Understanding both burrowing habits and microclimate that juveniles favor will be essential in determining the proper conditions for tortoises to grow and function properly during their most active time of the year (Bulova, 1994). In doing so, this project was developed to raise tortoises as natural as possible in a protective headstart enclosure with some artificiality, to observe behaviors while ensuring survival.

The objective of my research was 1) to identify patterns of burrow use and aggregation throughout the active season, 2) to identify burrow preference based on orientations facing north, south, east, and west, 3) to record modifications in burrow length, 4) to compare the changes in microclimate within burrows, and 5) to determine weight changes during the active season as they may relate to climate changes.

METHODS

Study Area

Field work was conducted on the Ladder Ranch located in Sierra County, New Mexico which is approximately 15 miles southwest of Truth or Consequences, New Mexico. An outdoor enclosure (20 x 7 m) was constructed of cinder blocks, adobe, mesh-screening, and a nylon-net canopy (Fig. 2). Within this enclosure, a 13 x 7.5 m section was designated for this study. Tortoises were separated by a 30 cm shade and hardware cloth barrier from the remainder of the enclosure. Shallow water dishes and *Cynodon dactylon* were carefully irrigated twice weekly prior to the monsoon season to following husbandry protocols.

The Chihuahuan Desert grassland study site had similar vegetation and elevation to the current wild population of Bolson tortoise in Mexico (Truett and Phillips, 2009). Soils in the enclosure contained well-drained sandy loam soils formed in gravely fine alluvium (Neher, 1984). Dominant native plants included *Acourtia nana, Bouteloua curtipendula, Gutierrezia sarothrae, Panicum obtusum, Pleuraphis mutica, Scleropogon brevifolius, Setaria leucopila,* and *Sphaeralcea angustifolia.* Non-native plants included *Buchloe dactyloides, Cynodon dactylon,* and *Salsola tragus.* Plants were not uniformly available in the enclosure (a list of all plant species can be found in Appendix A).

Tortoises and Study Design

Twenty-three juvenile Bolson tortoises (3-4 years old) were studied within the

Fig 2. Ladder Ranch, New Mexico headstart pen enclosure. Pen was predator-proofed with both native and non-native forage.

enclosure with a mean maximum carapace length (MCL) of 77.5 mm. Burrow characteristics and social behaviors were observed weekly from 1 May through 20

September, 2010. Sex of tortoises was not determined because no reliable methods exist for sexing immature tortoises (Adest et al., 1989b). Tortoises used in this study hatched from three separate locations; the Armendaris Ranch outside Truth or Consequences, NM, the Living Desert Zoo and Garden State Park in Carlsbad, NM, and the Appleton Ranch in Elgin, AZ. Tortoises hatched from either natural nests or artificial incubators. Differences in incubation versus tortoise behavior were not tested in this study due to small sample size. Each tortoise was previously labeled with an individual identification tag applied with a 2–part epoxy resin to the anterior carapace.

Thirty-two artificial burrows were constructed within the study site. At eight uniformly placed locations, four burrows were placed with entrances facing the major compass orientations (i.e., north, south, east, west) (Appendix B). Burrows faced inwards towards a center patch of grass (*Cynodon dactylon*) with a distance of 48 cm between burrows (Fig. 3). Initial burrow lengths were 45 cm with a 15 % slope, a burrow height of 10 cm, and width of 10-15 cm. Burrows were positioned in areas where vegetation did not obstruct entrances. Each burrow was labeled by a post with a burrow ID (1-32) and burrow orientation (N, S, E, W). Bermuda grass (*Cynodon dactylon*) was planted in the center of burrow groups for management purpose to provide sufficient green food for tortoises prior to monsoon season.

Fig 3. Section of four burrows with *Cynodon dactylon* placed in the center. Burrow orientations were determined by direction entrances were facing.

The 23 juveniles freely roamed the area beginning 1 May. Tortoises had 10 days to acclimate to their surroundings. Social behaviors were recorded for 20 weeks between 11 May and 20 September, 2010. Burrows were observed once a week for the presence of tortoises. Data collection began between 0700 and 0900 h while tortoises were inactive but accessible from the entrances. Data collection was completed between 0930 and 1130 h depending on the difficulty of tortoise removal and changes in climate throughout the summer. The entire process took approximately three hours to complete.

To test whether tortoises inhabited certain burrows equally, burrow was recorded as occupied or unoccupied and noted each individual tortoise within. Burrows were shallow enough to observe all inhabitants. Each tortoise was observed between 16 and 20 times during data collection. A burrow with the presence of one or more tortoise was considered an aggregated burrow. Aggregation within burrows was recorded by orientation.

Ambient air temperature and relative humidity data were collected using a HOBO ProV2 external temperature and relative humidity data logger that ran continuously at 1 h intervals during the period of the study. The data logger was placed 15 cm from the ground covered by a circular plastic protective shelter outside the tortoise enclosure. This height level was appropriate because it was similar to heights to which juvenile tortoises were exposed during activity. Precipitation data were collected monthly using an All Weather Rain Gauge Metric Model that was attached to the side of the tortoise enclosure.

Burrow Characteristics

Each week burrow length was recorded by using a 1.3 cm diameter flexible copper tube that measured the maximum length of each burrow which included the burrow curving. The tube was placed next to a meter stick and measured to the nearest 0.5 cm. Curving within burrows was recorded as left, right, or no curve. Tortoises were removed from each burrow, weighed, soaked in individual water dishes, and placed back to original locations after data were recorded. Individuals were soaked to follow the Turner Endangered Species Fund protocol for tortoise husbandry.

On the last week of each month, temperature and relative humidity were recorded at the maximum depth of each burrow to determine if microclimate changed during the active season. Data were collected using a four-channel HOBO micro station data logger (H21-002) each equipped with four temperature/humidity sensors and 2 m cables (S-THB-M002). Data were collected for 8 minutes inside each burrow. Each data logger measured microclimate inside four burrows at one time.

Tortoise Weight

During each weekly survey, tortoises were removed and weighed using a calibrated Cen-Tech Digital Pocket Scale with a maximum capacity of 500g. Weight gain was calculated by noting the difference between weekly weights. Greatest week of weight gain and weight loss were determined by examining weekly data throughout the active season.

Tortoise Activity

Combined epigean activities were recorded as a secondary element to this project. Most visits were between 0800-1200 h and during this time, tortoise activity was observed. Activity was considered any behavior that took place outside the burrow. Activity was related to ambient temperature and relative humidity. Anecdotal foraging data were collected by recording food that tortoises ate. Plants that tortoises foraged on are listed in Appendix A. Tortoise activity was compared to ambient temperature and relative humidity. Dominant forage was listed as plants that were eaten before and after monsoon season.

Statistical Analysis

A Chi-square test was used to test for a relationship in burrow occupancy and burrow aggregation by burrow compass orientation. Data were divided into four categories, one for each compass orientation (i.e., north, south, east, west). These categorical analyses were computed using the Frequency procedure of SAS. To test for significance, a p-value of 0.10 was used. For each tortoise during each week, number of shelters used and number of switches among different shelters were calculated.

Burrow orientation was a major item of interest in this study. Effects of burrow orientation on burrow length were examined by analysis of variance (ANOVA) for a completely randomized design. Burrow orientation influences on burrow temperature and relative humidity were subjected to split-plot ANOVA because repeated measures of these variables were obtained monthly. Burrow orientation was included in the main plot and tested using burrow within orientation as the error term. Effects of month and the burrow orientation by month interaction were included in the subplot and tested using the residual error. When a significant orientation by month interaction was detected, effects of orientation were examined within month and effects of month were examined within orientation. Analyses were computed using the general linear models procedure of SAS (SAS Inst. Inc., Cary, NC) and means were separated using the predicted difference method of SAS.

The effect of monsoon season (before and during/after) on burrow occupancy and burrow aggregation distribution on occupied burrows within each orientation were examined using a Chi square analysis. These categorical analyses were computed using the Frequency procedure of SAS.

Another major item of interest was whether burrow temperature and relative humidity were influenced by burrow curving (curving versus non-curving). These responses were evaluated by ANOVA using the split-plot analysis repeated across months previously described for burrow orientation effects on burrow temperature and relative humidity. The same sources of variation and testing terms were employed to examine effects of burrow curving.

In addition to examining normally distributed response variables (burrow temperature, humidity, length), a number of categorical responses were also evaluated. Effects of burrow orientation on burrow curving, occupancy, and aggregation were examined using Chi square analysis. These categorical analyses were computed using the Frequency procedure of SAS.

RESULTS

Burrow Occupancy and Aggregation

Thirty-two burrows were observed weekly during 20 weeks to check for the presence or absence of tortoises. For each week, 8 burrows were available for each compass orientation facing north, south, east, and west. Occupancy by orientation showed no significant difference in the beginning of the active season, however north and west burrows were occupied the most in the beginning of active season. After 20 July, occupancy within orientations began to vary and there was a significant difference on week 17 (x^2 = 6.603, df = 3, P = 0.086) with a preference towards east (Fig. 4; Appendix C). Week 12 was not significantly different (x^2 = 4.849, df = 3, P = 0.183), however there was a preference for west orientation. The north orientation was occupied the most (N = 90) and the east was used the least (N=82) (Fig. 5). Over the course of the study, tortoises used an average of 6.3 different burrows (SD = 2.6, range: 2-13) and switched burrows an average of 8.0 times (SD = 4.0, range: 1-16)

(Appendix D). Some tortoises were found in the same burrow at almost every observation, whereas other switched as many as 16 times.

Burrow aggregation was different during week 11 (x^2 = 10.193, df = 3, P = 0.017) (Fig. 6). During this week, the east had high burrow aggregation (Appendix E). When comparing aggregation and orientation across all months, there was a difference (x^2 = 4.010, df = 3, P = 0.260). For each orientation across all months, N=160 chances of burrows being occupied with more than 1 tortoise. The north

Fig. 4. Total number of occupied burrows by compass orientation during each week of study. Within each orientation, 8 burrows were available. Week 17 was different. *Indicates beginning of monsoon season. (P < 0.10)

Fig. 5. Total number of burrows occupied by Bolson tortoises within orientation during May-September, 2010. N = 160 chances for each orientation to be occupied.

Fig. 6. Total number of aggregated burrows by compass orientation during each week of study. Within each orientation, 8 burrows were available. Week 11 was different. *Indicates beginning of monsoon season. ($P < 0.10$)

orientation was nearly double in burrow aggregation when compared to other orientations with a significance of ($x^2 = 11.445$, df = 3, P = 0.010. The total and percentage of aggregated burrows included: north (34; 21.3%), south (17; 10.6%), east (19; 11.9%), and west (16; 10.0%) (Fig. 7).

Climate Data

Mean ambient temperature and relative humidity on each day of data collection were correlated with weekly burrow occupancy by orientation. After week 11 (20 July), temperature declined and relative humidity increased corresponding to an increase in number of burrows selected and occupied. During the sampling period, ambient daily mean temperatures averaged 26.2 °C and mean relative humidity averaged 40.5 %. Temperatures on sampling days ranged from 3.4-48.1 °C (Fig. 8A). Relative humidity on sampling days ranged from 3.8-100 % (Fig. 8B).

The highest mean ambient temperature was in June (28.9 °C) and lowest mean temperature was in May (20.7 °C) (Table 1). Highest temperatures occurred between 1400 and 1500 h and lowest temperatures occurred between 0400 and 0600 h. August had the highest mean relative humidity (61.8 %) and June had the lowest mean relative humidity (22.6 %). Overall, the highest relative humidity occurred after rainfall (100 %) and lowest relative humidity occurred between 1400 and 2100 h. Adest et al (1989a) found that the warmest month of June had a mean air temperature of 28.0 °C in Mapimi versus the 2010 June mean air temperatures at Ladder Ranch at 28.9 °C.

Fig. 7. Total number of burrows aggregated by Bolson tortoises within orientation during May-September, 2010. N = 160 chances for each orientation to be occupied.

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Fig. 8. Weekly burrow occupancy by compass orientation. A) Daily ambient mean, maximum, and minimum temperature (°C) during weekly surveys; B) Daily ambient mean, maximum, and minimum relative humidity (%) during weekly surveys. *Indicates beginning of monsoon season.

Table 1. Ambient temperature and relative humidity climate data during May-September, 2010. Data logger was 15 cm above ground in a shaded area. Rainfall contributed to high humidity.

	Ambient Temperature (°C)					Ambient Relative Humidity (%)			
Month	Mean	High	High Time	Low	Low Time	Mean	High	Low	Low Time
May	20.7	42.5	3PM	-3.7	5AM	26.3	100.0	3.1	5PM
June	28.9	51.5	3PM	9.1	5AM	22.6	100.0	1.7	9PM
July	26.7	47.8	3PM	11.8	5AM	59.6	100.0	5.4	4PM
August	25.3	45.3	3PM	10.4	6AM	61.8	100.0	19.5	2PM
September	23.6	44.2	2PM	8.5	4AM	49.4	100.0	9.7	3PM

Rainfall may have contributed to differences in social behavior. The research area received 175.3 mm of rainfall between May-September. Heavy rainfall began on 26 June and continued several times a week until 28 August. Limited rainfall continued into September with only 2 heavy bouts of rainfall, which is best described as a day with continuous rainfall. Rainfall occurred with convective thunderstorms during mid-afternoons and evenings. May was the driest month with 7.2 mm and July was the wettest month with 113.0 mm (Fig. 9). Annual rainfall in Mapimi was estimated at 271 mm with 60 % of rainfall occurring between June-September (Adest et al., 1989a).

Burrow occupancy was analyzed by comparing pre and -monsoon season by orientation and occupancy. The south orientation showed a difference in burrow occupancy before and during/after monsoon season on 26 June ($x^2 = 2.806$, df = 1, P = 0.094). All orientations had fewer occupied burrows prior to monsoon season (Fig. 10). Burrow aggregations were not statistically different within orientations of north ($x^2 = 0.199$, df = 1, P = 0.656), south ($x^2 = 0.319$, df = 1, P = 0.572), east ($x^2 = 0.111$, df = 1, P = 0.739), and west ($x^2 = 1.758$, df = 1, P = 0.185) before and during/after monsoon season. North, south, and west orientations decreased in burrow aggregations and east orientations increased with the onset of rainfall (Fig. 11).

Burrow Characteristics

Initial burrow length was 45 cm for each of the 32 burrows (Table 2). There were no differences between length and orientation ($F = 0.16$; $P = 0.921$). Mean

Fig. 9. 2010 active season monthly rainfall the Ladder Ranch
Total = 175.3 mm.

Fig. 10. Percent total number of burrows occupied by compass orientation before and after the onset of monsoon season on 26 June. *The south orientation showed a difference in occupancy. ($P < 0.10$)

Fig. 11. Percent total number of burrows aggregated by compass orientation before and after the onset of monsoon season on 26 June. There were no significant differences in aggregation within burrow orientation. ($P < 0.10$)

Table 2. Changes in burrow length related to orientation over a 20 week field study.

Burrow ID N=32	Orientation	Burrow Length (cm) Initial	Final	Difference	Mean by Orientation
1	North	45.0	53.0	8.0	67.8
5	North	45.0	60.0	15.0	67.8
9	North	45.0	96.0	51.0	67.8
13	North	45.0	56.0	11.0	67.8
17	North	45.0	61.0	16.0	67.8
21	North	45.0	86.0	41.0	67.8
25	North	45.0	79.0	34.0	67.8
29	North	45.0	51.0	6.0	67.8
2	South	45.0	92.0	47.0	66.9
6	South	45.0	59.5	14.5	66.9
10	South	45.0	63.0	18.0	66.9
14	South	45.0	77.0	32.0	66.9
18	South	45.0	56.5	11.5	66.9
22	South	45.0	43.0	-2.0	66.9
26	South	45.0	100.0	55.0	66.9
30	South	45.0	44.0	-1.0	66.9
3	East	45.0	93.0	48.0	69.6
7	East	45.0	60.0	15.0	69.6
11	East	45.0	75.0	30.0	69.6
15	East	45.0	81.0	36.0	69.6
19	East	45.0	57.0	12.0	69.6
23	East	45.0	47.0	2.0	69.6
27	East	45.0	58.0	13.0	69.6
31	East	45.0	86.0	41.0	69.6
4	West	45.0	89.5	44.5	63.8
8	West	45.0	58.0	13.0	63.8
12	West	45.0	58.0	13.0	63.8

16	West	45.0	67.0	22.0	63.8
20	West	45.0	63.0	18.0	63.8
24	West	45.0	46.0	1.0	63.8
28	West	45.0	71.5	26.5	63.8
32	West	45.0	57.5	12.5	63.8

burrow length for each orientation was north (67.8 cm, SD = 16.90), south (66.9 cm, SD = 21.05), east (69.6 cm, SD = 16.35), and west (63.8 cm, SD = 12.84). Mean change in burrow length was 22 cm (N= 32, SD = 16.33, range = -2.0-55.0 cm). One natural burrow was created within *Pleuraphis mutica* with a length of 16.5 cm. The east-facing natural burrow was shorter than the current artificial burrows and began curving at approximately 10 cm which suggests that tortoises may not require longer artificial burrows for proper shelter.

Burrow curving indicated the direction of tunneling at the back portion of burrows. There were no differences between left, right or no curving by orientation (x^2 = 2.468, df = 6, P = 0.872). Of 32 burrows, 13 curved left, 10 curved right, and 9 had no curves. North and east had the most left curves and west and south had the least amount of curves.

Curving within burrows changed the microclimate when comparing non-curving burrows however differences were not significant. Curving by month was different with temperature (F = 4.74, P = 0.002) and relative humidity (F = 5.96, P = 0.001). Burrow curving in May was different in temperature (F = 7.55, P = 0.010) and relative humidity (F = 4.97, P = 0.034). Within May, curving (24.0 °C) was cooler than non-curved (26.3 °C) and relative humidity was higher within curved burrows (67.9 %) compared to non-curved burrows (55.9 %) (Table 3). Curved burrows were 0.7-2.3 °C cooler in temperature and 1.2-12.0 % higher in relative humidity than non-curved burrows. Temperatures were similar in August and September when ambient temperatures began to cool, and relative humidity was

Table 3. Temperature and relative humidity were taken once at the end of each month at the maximum depth of each burrow between 0800-1200 h. Curved burrows differed in microclimate by month compared to non-curved burrows. ($P < 0.10$)

	Temperature (°C)					Relative Humidity (%)				
Month	Mean Burrow Curve	SE	Mean Burrow No Curve	SE	P-Value	Mean Burrow Curve	SE	Mean Burrow No Curve	SE	P-Value
May	**24.0***	0.647	**26.3***	0.535	**0.010**	**67.9***	4.129	**55.9***	3.415	**0.034**
June	26.5	0.485	27.2	0.428	0.285	81.3	1.907	80.1	1.682	0.621
July	**24.1***	0.273	**24.8***	0.273	**0.100**	93.2	1.261	91.4	1.261	0.321
August	25.8	0.173	25.6	0.209	0.407	93.7	0.958	92.9	1.159	0.601
September	25.0	0.177	24.7	0.282	0.460	86.1	1.340	87.2	2.23	0.698
Overall Mean	25.1		25.7			84.4		81.5		

*Indicates significant difference

similar in July and August during the monsoon season in both curved and non-curved burrows. Mean temperature for curved burrows across all months was lower (25.1 °C) however not significant compared to non-curved burrows (25.7 °C). Mean relative humidity for curved burrows across all months was higher (84.4 %) compared to non-curved burrows (81.5 %).

Maximum depth of 32 burrows was measured at the end of each month (May - September) to record temperature and relative humidity. There were no differences between orientation and temperature by month ($F = 0.79$, $P = 0.664$). Mean monthly burrow temperatures 25.6 °C (range: 21.7-31.3 °C) were cooler in May and decreased as burrows continued to be modified.

There were differences between orientation and relative humidity by month ($F = 2.43$, $P = 0.008$) (Fig. 12) (Appendix F). The north orientation had higher relative humidity compared to the west orientation with lower relative humidity. Relative humidity was different among sampling months. Orientation means were averaged across all months. Relative humidity was different in June ($F = 2.56$, $P = 0.075$), July ($F = 20.52$, $P = 0.001$), August ($F = 5.54$, $P = 0.004$), and September ($F = 3.19$, $P = 0.039$) (Table 4). The months of July and August had the highest mean relative humidity within all orientations. Relative humidity was higher inside burrows after rainfall and continued to maintain high levels of RH as ambient temperatures cooled. Mean monthly burrow relative humidity was 82.7 %.

Fig. 12. Temperature (°C) and relative humidity (%) at maximum depth of

burrows pooled together all months (May-September). Differences were found in relative humidity within orientation. Graph illustrates Appendix F. ($P < 0.10$)

Table 4. Relative humidity (%) at maximum depth of burrow taken at the end of each month. Data was collected at 8 minute intervals in the mornings between 0800-1000 h. Relative humidity was different among orientation by month. (P < 0.10)

	Burrow Orientation						
Month	North	South	East	West	SE	P-Value	F
May	69.0	65.1	53.4	55.6	5.346	0.142	1.96
June	84.3^{a}	75.8^{b}	79.7^{ab}	82.6^{a}	2.322	0.075	2.56
July	$\mathbf{95.2^{ac}}$	92.6^{a}	$\mathbf{95.9^{c}}$	85.5^{b}	1.049	0.050	20.52
August	94.6^{a}	$\mathbf{95.0^{a}}$	94.9^{a}	$\mathbf{89.1^{b}}$	1.217	0.004	5.54
September	82.8^{a}	91.6^{b}	86.8^{ab}	84.6^{a}	2.119	0.039	3.19

a, b, c, row values with different superscripts differ statistically (P < 0.10)
Bold text represents highest humidity within each orientation

Tortoise Weight

Weekly weights were recorded for 23 tortoises during 20 consecutive weeks (Appendix G). Week 8 (29 June), had the highest mean weight gain of 6.9 g. Week 17 (1 September), had the lowest mean weight gain of -4.1g.

Tortoise Activity

Most observations were between 0800-1200 h and infrequently during afternoon hours. Each observation pertained to one tortoise. Mean temperature of activity was 32.3 °C (N = 311, SD = 6.39, range: 20.5-43.5 °C). Mean relative humidity of activity was 34.0 % (N = 311, SD = 23.43, range: 3.8-100 %). Prior to monsoon season (26 June), tortoises were observed foraging on 12 different plant species, predominately on *Acourtia nana, Bahia absinthifolia, Cynodon dactylon, Pleuraphis mutica, Scleropogon brevifolius*, and *Sphaeralcea angustifolia* (Appendix A). After onset of monsoon season, tortoises foraged primarily on *Pleuraphis mutica* and *Sphaeralcea angustifolia*.

DISCUSSION

Bolson tortoise juveniles used burrows differently throughout the active season. The number of occupied burrows was reduced in the beginning (May-June) when ambient temperatures were high and relative humidity was low resulting in increased burrow aggregation. During this time, environmental conditions were dry due to lack of precipitation. North facing burrows were occupied the most out of all orientations and were consistently inhabited throughout the season. In southern Nevada, wild adult *G. agassizii* were observed with a trend of adult tortoise burrows facing north and northeast (Burge, 1978) and captive adult tortoises facing north, northeast, and south (Bulova, 1992). Bulova (1994) also found north facing burrows to be more common than other orientations when studying adult *G. agassizii* in Nevada. Morafka et al. (1981) found a trend in northeast facing adult Bolson tortoise burrow entrances in Mapimi and suggested that these burrows may provide a thermal advantage when compared to other orientations. One explanation for tortoise consistently occupying north facing burrows may be attributed to some tortoises establishing a permanent residency early on in the season when temperatures were warmer and north burrows were cooler. After rainfall began on 26 June, tortoise activity changed within burrows. As temperatures decreased and relative humidity increased, tortoises selected burrows within all orientations and frequently used them individually.

In a previous experiment within the Ladder Ranch enclosure in 2010, microclimate was measured at the burrow entrances within each orientation and found that south and east orientations were warmer and north and west orientations were cooler (McCann unpubl. data). In addition to north facing burrows, I found that west burrows were occupied more often in the beginning of the active season and east facing burrows were occupied more often at the end of the season.

One possible explanation for burrow choice in the west and north facing burrows in the beginning of the active season could be related to cooler burrows when temperatures were warmer providing less temperature extreme fluctuations. Sunlight penetrating within south and east facing burrows during hot ambient temperatures may rapidly increase the temperature inside the burrows, which may not only raise the tortoise's temperature to uncomfortable levels, but may also increase its rate of evaporative loss (J. L. Jarchow, pers. comm. 2010). East facing burrows were occupied more towards the end of the season when temperatures were cooler from both rainfall and seasonal changes in temperature. A thermal advantage may have provided a cooler microclimate within north and west facing burrows when ambient temperatures were hot and warmer burrow microclimate within east facing burrows when ambient temperatures cooled.

A second explanation for burrow choice may be related to tortoises selecting burrows in the afternoon and settling within them until the following morning. Tortoises may have chosen burrows that regulated body temperatures based on afternoon ambient temperature and simply remained inside burrows until the next day. During warmer ambient temperatures, tortoises may have settled in north and west burrows in the afternoon to reduce body heating. When temperatures lowered after monsoon season, a heat advantage may have been provided within east facing burrows that tortoises favored. Afternoon burrow selection was not tested in this study. However Bulova (1992) found *G. agassizii* in Nevada to choose burrows differently in the morning by observing limiting burrow selection to north, northeast, and south facing burrows and found tortoises to occupy all burrow orientations in the afternoon based on availability.

Tortoises resided the least in south facing burrows. However south orientations were occupied significantly more with the onset of rainfall compared to other orientations after monsoon rain suggesting that precipitation may have influenced burrow selection in the south burrow. Although this study did not observe south facing burrows to be occupied frequently, contrasting results were found with juvenile desert tortoises in the Mojave Desert to prefer west, south, southwest, and southeast facing burrows (Berry and Turner, 1986; Hazard and Morafka, 2002). Differences in burrow choice by location may be related to sloping and topographical differences in landscape (Morafka et al., 1981; McCoy et al., 1993). McCoy et al. (1993) found adult *G. polyphemus* to choose and create burrows based on slope of the landscape and preferred orientations in the primary compass direction (north, south, east, and west). Burrow choice within southeast and west orientations in the Mojave Desert may provide different thermal advantages when compared to New Mexico (Hazard and Morafka, 2004).

Of the 23 tortoises, all were found at least once to aggregate within a burrow during the active season. Bulova (1992) observed 83% of immature *G. agassizii* to aggregate within burrows when studying a captive population in Nevada. Burrow aggregation was often found in north facing burrows prior to the rain season when temperatures were higher and relative humidity was low. During the dry times, tortoises were more likely to be aggregated that after rainfall. North facing burrows may have provided a cooler microclimate compared to other orientations that prompted tortoises to group inside burrows. Tortoise aggregation may also correspond to higher humidity that could be accomplished with the presence of more than one tortoise. Affenberg (1969) suggested that the breathing of tortoises inside burrows adds moisture to the air, lowering evaporation rates thus benefiting the tortoise aggregations when humidity is decreased. At the end of the active season temperatures cooled and relative humidity was higher, east facing burrows had more aggregations than prior monsoon season. This was different from other orientations. Warmer temperatures within burrow entrances may have increased the desire to both occupy and aggregate east-facing burrows.

Some tortoises were consistently found within the same burrow whereas other tortoises were found in different burrows each week. The number of times a tortoise switched burrows was often greater than the number of burrows occupied by individuals because tortoises sometimes returned to a previously used burrow. Tom (1994) observed free-ranging hatching Bolson tortoises in Mapmi to occupy multiple burrows and pallets and switch up to 19 times during the rainy season. Bulova (1992, 1994) had similar findings when observing captive *G. agassizii* in Nevada. Bulova (1994) found gender differences when observing occupancy and aggregation however this is yet to be determined for juvenile Bolson tortoises. Burrow aggregation could be related to gender or social activity or assist in thermoregulation within burrows. However, gender activities are often non-existant or reduced in juvenile reptiles (Denardo, 2006). Another possibility for aggregation may be related to large densities of tortoises held in an enclosure which is a result of captive headstarting.

However, attempts were made to provide sufficient burrows to allow for individual use.

Tortoises modified their burrows throughout the summer months. Adest et al. (1989b) suggested that this allowed tortoises to withstand hot surface temperatures and to prepare for winter hibernation at the end of September. Daily fluctuation of ambient temperature and relative humidity were less extreme within burrows (Bulova, 2002; Shenbrot et al., 2002). As burrow lengths increase, temperatures at the back of the burrows become more stable providing tortoises with more suitable microclimate when temperature extremes were present, similar to the findings of Morafka (1982) and Tom (1994). Morafka et al. (1981) also found a positive correlation between adult burrow length and carapace length indicating that tortoises of greater size dig longer burrows. Juvenile *G. agassizii* have also been observed to occupy burrows that were related to tortoise sizes (Hazard and Morafka, 2004).

Most occupied burrows had curved pockets at the back of burrows. Curving burrows were associated with a difference in microclimate with cooler temperature and higher relative humidity when compared to non-curving burrows. The curved pockets may benefit tortoises by reducing air flow and providing tortoises with stable temperature and relative humidity. Curving may also absorb soil moisture that could reduce the amount of evaporative water loss for tortoises by reducing the amount of dry air from entering burrows. Curving may also serve as protection from predators trying to enter burrows and provide tortoises with an area that fits the tortoise body very snug for warmth and cooling.

Weight gains and losses were associated with precipitation. Precipitation provides the opportunity for direct hydration of water and also provides succulent plants for tortoises to forage on. Both water and plant consumption may have directly contributed to increased weight gain during rainfall. Juveniles gained the most weight with the onset of rain and lost the most weight at the end of the rainy season. Weight loss after rainfall may be associated with cooler temperatures in the fall. Cool temperatures prevent tortoises from body warming, thus decreasing metabolism and food intake. Zimmerman et al. (1994) found that tortoises, at this time, prepare for hibernation in burrows with cooler temperatures and higher humidity.

The early active season (May) had cooler temperatures which may have limited tortoise activity. Ambient temperature and relative humidity were recorded 15 cm off the ground and may have reflected heat off the soil thus true ambient temperatures were not completely accurate. Although temperatures were recorded as higher than true ambient, they represented the conditions (based on height) tortoises would forage at when exiting burrows. Adest et al. (1989a) found similar results with Bolson tortoises observed to be less active prior to the rain season. Activity levels invariably increase with the onset of rainfall changing tortoise behavior (Adest et al., 1989a). As temperatures warmed and rainfall began at the end of June, tortoises were more active. Adest et al. (1989a) suggested this was because of increased hydration and their ability to withstand hot temperatures. Tom (1994) found that with increased temperatures and lengthened surface activity tortoises traveled longer and selected burrows differently after rainfall. Changes in burrow occupancy and increased activity levels after rainfall may also be due to changes in seasonal variation (Tom, 1994).

All 23 tortoises were placed in the pen in 2009 and familiar with their surroundings. Bolson tortoises seem to use burrows predominantly rather than spending some nights on the surface in contrast to *G. agassizii* that often spend their nights on the surface (Bulova, 1994; Zimmerman et al., 1994). Many tortoises tossed soil behind them when entering burrows which has been noted with desert tortoises (Bulova, 2002). Tortoises often blocked the entrances of the burrows when other tortoises or researchers attempted to enter their burrows. One natural burrow was built within *Pleuraphis mutica* over the 20-week study. Two tortoises were found to infrequently occupy this burrow in the beginning of the season and were the smallest individuals among the cohorts. Adest et al. (1989b) suggests that small tortoises within groups may be subordinate and excluded from artificial burrows forcing them to create their own. Adest et al. (1989b) observed that smaller or weak individuals are intimidated by larger and more vigorous cohabitants and should be grouped by age, size, and relative strength for equal competition.

Tortoise activity was increased during and after rain events when temperatures were cooler, relative humidity was higher, and plants had more vigor, similar to a study on juvenile desert tortoises in southern Nevada by Nagy and Medica (1986). Hatchling and juvenile tortoises tend to forage during earlier times and cooler temperatures in the morning when compared to adults because their bodies heat faster due to high surface-to-volume ratio (Morafka, 1994). Thus smaller tortoises are able to become active at cooler temperatures when compared to adult tortoises (Naegle, 1976; Berry and Turner, 1986). Tortoises were not observed foraging at temperatures above 43.5 °C. This is near the lethal range (45.0 °C) for desert tortoises and (43.0-45.0 °C) for other *Gopherus* species (Hutchison et al., 1966; Rose, 1983; Adest et al., 1989a; Zimmerman et al., 1994).

Prior to monsoon season, tortoises fed widely on all available plants. After the rain, tortoises preferred the succulent plants of *Pleuraphis mutica* and *Sphaeralcea angustifolia*, mostly desiring the blades of the plants. Both plants are high in protein, carbohydrates, and moisture and serve as both dominant forage and primary habitat in Mapimi (Morafka et al., 1981; Adest et al., 1989b). Multiple tortoises were often found foraging on the same *Sphaeralcea angustifolia* for up to one hour.

MANAGEMENT IMPLICATIONS

Protective habitat for Bolson tortoises is limited in the wild. The conservation of this species is dependent on captive breeding and repatriation programs to protect young to ensure future population growth. Young tortoises can be raised by headstarting which is a program designed to care for tortoises during their beginning stages. Captive breeding offers close observation and data collected on animals that would be impossible to study in the wild (Nathan, 1979). Although advantageous, data collected may not represent accurate results that would be found in the wild. Captivity with juvenile Bolson tortoises included high densities of animals, excess available burrows, and supplemental food and water. Results were directed towards the management of juvenile Bolson tortoises that may assist in gaining knowledge of wild animals.

I found that tortoises occupied all directional orientations of burrows at different times of the active season. Tortoises preferred artificial burrows over building natural burrows which is similar to behaviors of wild young tortoises using pre-existing rodent burrows to conserve energy use. However, there were adequate artificial burrows available and tortoises were not lacking shelter. It is important that the number of available burrows is proportionate to the number of individuals to give tortoises ability to reduce overcrowding and spread of disease. Based on this study, tortoises selected west and north facing burrows and these areas might be preferred during the beginning of the active season (May-June) and east towards the end of the season (July-September). The least occupied orientation was the south facing which is important if space is limiting within a captive enclosure. Locating aggregation of tortoises in the wild would be most effective prior to monsoon season and concentrated in the north facing orientation if elevation and topography were similar to conditions in New Mexico.

One observed natural burrow was found shorter than the current modified artificial burrows. Burrow curving may be more important than burrow length because curving allows for thermoregulation and protection from solar radiation which is highest during the active season (Zimmerman et al., 1994). In captivity, artificial burrows can be designed shorter or impressions can be made into the soil for tortoises to modify and create their own natural burrows. At least one artificial burrow should be made for each tortoise if artificial burrows are made in captivity. It is important to provide some artificial burrows or modified natural burrows in captivity because young tortoises often use pre-existing burrows in the wild to reduce energy use.

Tortoises selected a wide variety of plants to forage on, however preference was refined to tobosa grass (*Pleuraphis mutica*) and narrowleaf globemallow (*Sphaeralcea angustifolia*) during and after monsoon season. Tobosa grass and narrowleaf globemallow plants should be made available to tortoises in captivity. These plants should be abundant in areas where tortoises will be released for both nutritional purposes and shelter location. Tall grasses are used as cover for natural burrows and also allow tortoises to create natural foraging trails that provide shading. Some plant species that are frequently selected and consumed in the wild may be rejected if plants are broken off; (Ashton and Ashton 2008) this was not the case however for *Sphaeralcea angustifolia* making it an excellent source of food for both captive and wild tortoises (Ashton and Ashton, 2008).

APPENDICES

APPENDIX A
LIST OF PLANTS IDENTIFIED IN THE TORTOISE ENCLOSURE AND OBSERVED FORAGING FOOD

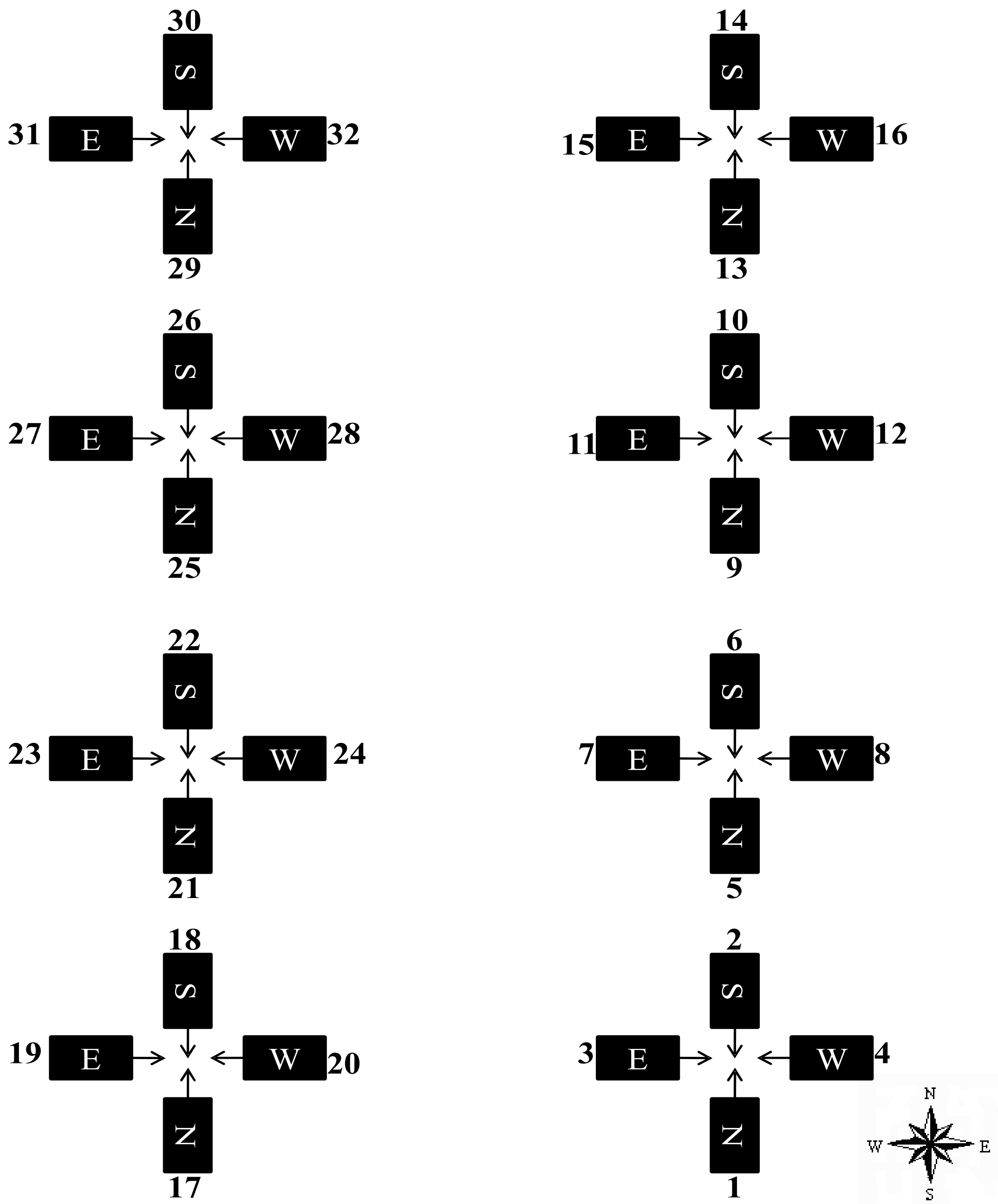
Scientific Name	Common Name
Achnatherum hymenoides	Indian Rice Grass
*Acourtia nana**	Dwarf Desert Holly
Amaranthus palmeri	Carelessweed
*Bahia absinthifolia**	Sageleaf Bahia
Bouteloua curtipendula	Sideoats Grama
Bouteloua gracilis	Blue Grama
Buchloe dactyloides *	Buffalograss
*Chamaesyce albomarginata**	Whitemargin Sandmat
Chenopodium incanum	Mealy Goosefoot
*Chaetopappa ericoides**	Baby Aster
*Cynodon dactylon**	Bermudagrass
Eragrostis pectinacea	Tufted Lovegrass
*Erigeron divergens**	Spreading Fleabane
Gaura coccinea	Scarlet gaura

Gutierrezia sarothrae	Broom Snakeweed
Hoffmannseggia glauca	Hog Potato
Larrea tridentata	Creosote
Panicum obtusum	Vine Mesquite
*Pleuraphis mutica**	Tobosagrass
*Psilostrophe tagetina**	Woolly Paperflower
Salsola tragus	Prickly Russian Thistle
*Scleropogon brevifolius**	Burrograss
*Setaria leucopila**	Plains Bristlegrass
Solanum elaeagnifolium	Silverleaf Nightshade
*Sphaeralcea angustifolia**	Narrowleaf Globemallow
Sporobolus airoides	Alkali Sacaton
Sporobolus contractus	Spike Dropseed
Thymophylla sp	Dogweed
Zinnia grandiflora	Wild Zinnia

*Indicates plants that tortoises were observed feeding on during the active season between May-September, 2010 within an outside captive enclosure in south-central New Mexico. Dominant foraging species included *Cynodon dactylon, Pleuraphis mutica, Scleropogon brevifolius,* and *Sphaeralcea angustifolia.*

APPENDIX B

EXPERIMENTAL DESIGN LAYOUT DURING SUMMER OF 2010 WITH 32 BURROW ENTRANCES FACING NORTH, SOUTH, EAST, AND WEST



APPENDIX C

TOTAL NUMBER OF BURROWS OCCUPIED WEEKLY BY ORIENTATION OVER A 20 WEEK FIELD STUDY

Burrow Orientation

Week	North N=8	South N=8	East N=8	West N=8	P-Value
1	4	3	4	4	0.945
2	4	4	4	5	0.945
3	5	3	4	4	0.801
4	4	4	4	5	0.945
5	3	4	3	4	0.917
6	4	3	3	4	0.917
7	4	3	3	4	0.917
8	4	4	3	4	0.945
9	5	3	4	3	0.710
10	5	3	4	5	0.710
11	5	2	4	6	0.222
12	5	6	3	7	0.183
13	5	6	5	4	0.785
14	7	5	4	5	0.452
15	4	5	4	5	0.917
16	5	5	5	5	1.000
17*	4	5	7	2	**0.086**
18	6	4	4	4	0.677
19	4	5	5	6	0.785
20	3	6	5	3	0.336
Total	**90**	**83**	**82**	**89**	

*Difference in orientation preference in the east during week 17. ($P < 0.10$)

APPENDIX D
TOTAL NUMBER OF BURROWS OCCUPIED AND BURROWS SWITCHED BY EACH INDIVIDUAL OVER A 20 WEEK FIELD STUDY

	Burrows	
Tort ID	Total No. Occupied	Total No. Switched
06-B2	10	15
06-MB1	6	7
06-MB4	7	9
06-MB5	8	8
07-5	6	9
07-6	13	16
07-7	3	2
07-A1	3	2
07-A2	6	9

07-CB1	7	10
07-CB2	6	8
07-CB3	5	7
07-CB4	7	11
07-JBT1	6	6
07-CB6	4	3
07-CB7	2	1
07-CB8	5	9
07-CB9	11	13
07-CB10	4	3
07-CB11	7	12
07-CB13	7	10
07-CB14	4	7
07-CB15	8	8
Mean	6.3	8.0
Range	2.0-13.0	1.0-16.0
SD	2.6	4.0

APPENDIX E
TOTAL NUMBER OF BURROWS AGGREGATED WEEKLY BY ORIENTATION OVER A 20 WEEK FIELD STUDY

Week	Burrow Orientation North N=8	South N=8	East N=8	West N=8	P-Value
1	0	1	1	2	0.513
2	1	0	1	1	0.776
3	2	1	1	2	0.845
4	2	0	0	2	0.206
5	2	1	1	1	0.871
6	3	2	1	0	0.251
7	3	2	1	0	0.251
8	3	1	1	1	0.482
9	2	1	1	1	0.871
10	1	1	1	3	0.482
11*	4	0	1	0	**0.017**
12	1	0	0	1	0.545
13	1	0	1	0	0.545

14	1	0	0	1	0.545
15	1	1	1	1	1.000
16	2	0	1	0	0.257
17	1	2	1	0	0.515
18	2	1	1	0	0.515
19	1	1	1	0	0.776
20	1	2	3	0	0.251
Total	**34**	**17**	**19**	**16**	

*Difference in burrow aggregation by orientation in the north during week 11. ($P < 0.10$)

APPENDIX F
RELATIVE HUMIDITY (%) AND TEMPERATURE (°C) TAKEN AT MAXIMUM DEPTH OF BURROWS AND POOLED ACROSS ALL MONTHS

Orientation	Temp (°C)	SE	P-Value	RH (%)	SE	P-Value
North	25.2	0.374	0.664	85.2	1.144	0.008
South	25.4	0.374	0.664	84.0	1.144	0.008
East	25.8	0.374	0.664	82.0	1.144	0.008
West	25.5	0.374	0.664	79.5	1.144	0.008

($P < 0.10$)

APPENDIX G

Weekly weights per tortoise during the active season in 2010. Highest week gain was on 29 June (6.9 g) and lowest was on 1 September (-4.1g).

TORT ID N=23	Date of Observation Juvenile Weekly Weights (grams)																			
	4/28	5/11	5/18	5/25	6/1	6/8	6/15	6/22	6/29*	7/6	7/13	7/20	7/29	8/3	8/12	8/18	8/24	9/1**	9/7	9/13	9/20
B2	165	165	171	171	189	186	186	183.2	186.2	191.0	191	193.3	192	198	186	190	194.0	186	195	204.3	197.6
MB1	160	161	174	171	180	185	178	179.9	192.0	192.3	195	196.2	205	210	215	213	211.6	213	212	207.8	208.5
MB4	118	123	132	135	135	132	143.3	142.6	146.4	142.1	148	150.7	157	152	155	157	159.5	157	159	155.9	160.7
MB5	167	172	182	184	187	194	195	198.0	206.2	214.1	219	215.2	223	230	241	245	237.5	234	232	244.2	233.0
07-5	98.8	.	119	123	128	107	129	123.5	135.4	137.8	141	143.8	148	143	135	.	152.8	146	150	155.7	147.4
07-6	113	93.4	90.9	96.6	98.4	95.6	96.8	100.3	106.1	105.6	110	108.0	114	116	121	125	122.6	121	119	125.8	119.2
07-7	88.8	.	98.8	96.6	97.6	96.2	99.7	103.8	107.8	105.1	110	110.3	118	120	127	128	124.9	118	126	125.4	120.7
07A1	73	76.2	74.5	77.1	80.4	78.6	81.1	83.4	84.7	85.0	85.6	88.2	93.3	92.5	97.2	102	97.5	93.9	94.3	94.9	93.5
07A2	97.9	111	114	113	115	114	117	118.7	127.6	126.3	126	120.7	.	130	117	.	134.9	140	137	135.3	138.6
07-CB1	67.1	65.2	63.6	62.9	65	59	63.6	64.5	64.9	66.4	69.6	70.4	74.5	74.5	79.2	82	82.4	79.3	79.6	80.7	80.5
07-CB2	101	.	111	111	117	111	.	117.8	135.3	134.8	132	139.4	142	145	124	154	150.7	142	154	153.4	150.0
07-CB3	90	91.6	98.3	95.8	102	100	102	105.0	111.5	115.4	118	119.7	122	122	124	127	126.5	124	122	123.6	123.8
07-CB4	126	132	132	140	134	140	138	136.4	148.8	147.2	149	148.6	155	157	153	155	160.4	155	160	162.4	160.1
07-JBT1	154	.	158	156	161	136	161	160.6	167.7	170.3	167	169.7	176	177	189	188	185.7	181	182	192.2	181.8
07-CB6	111	109	108	107	112	119	125	119.8	127.6	126.0	126	128.0	126	136	143	137	141.5	137	150	145.9	141.8
07-CB7	140	.	149	143	153	145	151	153.1	163.5	168.1	173	170.7	180	177	175	.	183.1	180	185	175.8	182.1
07-CB8	141	144	143	153	158	162	163	158.0	163.9	164.5	167	173.1	175	175	182	187	187.2	175	179	180.5	185.5
07-CB9	80.3	80	76.8	76.1	85.6	85.1	81.5	86.2	88.3	91.9	94.5	95.0	99.9	102	96.3	104	103.9	102	103	104.7	101.5
07-CB10	91	98.3	97.1	97.1	101	87.5	104	107.9	109.9	109.1	107	112.0	110	119	121	120	118.3	117	118	118.1	113.7
07-CB11	142	136	140	140	144	146	146	149.1	157.6	159.9	161	160.3	159	168	161	167	172.5	167	170	169.7	170.3
07-CB13	102	98.3	97.5	96.3	101	103	103	105.3	106.6	105.5	110	110.3	110	116	112	113	120.5	116	114	123.2	117.3
07-CB14	161	169	177	172	188	195	187	187.9	197.1	197.9	203	206.5	208	216	175	216	219.3	213	217	227.3	220.2
07-CB15	84.3	.	.	85.9	88.6	82.8	78.6	87.6	95.5	99.6	104	105.0	103	106	105	104	105.7	100	103	106.6	104.0
Mean weight change	0.0	2.9	4.0	-1.4	5.2	-2.7	4.3	0.6	**6.9**	1.1	2.1	1.3	4.3	2.0	-2.0	5.8	1.1	**-4.1**	2.7	2.3	-2.7

WEEKLY JUVENILE BOLSON TORTOISE WEIGHTS (GRAMS) DURING MAY-SEPTEMBER, 2010

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