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Foraging Ecology of the Bolson Tortoise (*Gopherus flavomarginatus*) in the Northern and Southern Chihuahuan Desert.

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Abstract

I studied the foraging ecology of captive and wild populations of Bolson Tortoises (*Gopherus flavomarginatus*) in Engle, New Mexico (northern Chihuahuan Desert) and Durango, Mexico (Southern Chihuahuan Desert). I conducted direct foraging observations and scat analysis on the captive population in 2009-2010 and scat analysis on the wild population in 2010. Direct foraging observations indicate these tortoises consume mainly grass species with tobosa (*Pleuraphis mutica*) being dominant followed by blue grama (*Bouteloua gracilis*) and purple threeawn (*Aristida purpurea*). There was no difference in the percentage of grass consumed among tortoises by year or season. However, differences were detected in the percent consumption of grass species by year and sex but not season. Consumption of tobosa was higher in 2009; blue grama increased in diets in 2010 with increasing basal cover of the species. Males had a broader diet, attributed to their larger home range size, feeding more equally on the three dominant grass species while females fed primarily on tobosa. Direct foraging observations indicated forbs were more important in tortoise diets in the dry season where as scat analysis indicated forbs were represented in diets in both seasons; this suggests differences in individual diets and that while generally in agreement, both methods may present biases.

Microhistological analysis comparing diet between the northern and southern Chihuahuan Desert tortoises indicates substantial overlap in diet between the two locations for this one year of data collection, with a similar percentage of grass at both locations. Tobosa was the dominant grass at each site; however, tortoise diets in Durango, Mexico had a higher component of tobosa with less representation of other perennial grass species. Overlap in diet between the two populations suggests the available forage at the northern Chihuahuan Desert site would support populations of wild Bolson Tortoise.

Key words: Bolson Tortoise; Chihuahuan Desert; Food preference, *Gopherus flavomarginatus* ,

Microhistology, Nutrition tobosa

Resumen

Estudié la preferencia en la dieta de una población en cautiverio de Tortugas del Bolsón (*Gopherus flavomarginatus*) en Engle, Nuevo México (el norte del desierto Chihuahuense). Realicé observaciones directas y análisis de excreta en la población en cautiverio en 2009-2010 y los análisis de excretas en la población silvestre en el 2010. Las observaciones directas indican que estas tortugas consumen principalmente especies de pastos, siendo toboso (*Pleauraphis mutica*) la especie dominante, seguido por navajita azul (*Bouteloua gracilis*) y tres barbas purpura (*Aristida purpurea*) en ambos años. No hubo diferencia en los porcentajes de pasto que consumieron las tortugas por año o por estación. Sin embargo, fueron detectadas diferencias en los porcentajes en el consumo de especies de pastos por año y por sexo pero no por estación. El consumo de toboso fue más alto en el 2009; la navajita azul incremento en las dietas en el 2010 con un aumento en la cobertura basal de las especies. Los machos tuvieron una dieta más amplia, atribuida a que su ámbito hogareño es mayor, alimentándose en cantidades similares de las tres especies de pastos dominantes mientras que las hembras se alimentaron principalmente de toboso. Las observaciones directas indicaron que las herbáceas fueron más importantes en las dietas de las tortugas en la estación seca mientras que el análisis de excretas indicó que las herbáceas fueron representadas en ambas estaciones; esto sugiere que hay diferencias entre dietas individuales y que mientras generalmente los resultados concuerdan, ambos métodos presentan errores. El análisis microhistológico que compara la dieta entre el desierto chihuahuense del norte y sur indica que hay un traslape sustancial en la dieta entre ambas localidades. El toboso fue el pasto dominante en cada sitio; sin embargo, las dietas en Durango, México tuvieron un alto componente de toboso con una representación de otras especies de pastos perennes. El traslape en la dieta entre dos poblaciones sugiere que el forrajeo disponible en el norte del desierto Chihuahuense podría sostener poblaciones silvestres de tortugas del Bolson.

Palabras clave: Tortuga del Bolson; Desierto Chihuahuense; Preferencia alimenticia, *Gopherus flavomarginatus* , Microhistología, Nutrición, toboso.

Knowledge of diet and nutritional condition are essential for the conservation and management of endangered species, and for the maintenance of captive breeding programs. This information can be especially challenging to obtain for reptiles with slow metabolic rates and short periods of annual activity. The Bolson Tortoise (*Gopherus flavomarginatus*), an endangered species endemic to the Chihuahuan Desert, is an excellent example. This tortoise is well adapted to arid environments. In late September-early October, when temperatures cool and plants enter dormancy, tortoises reduce their metabolism and hibernate, emerging in March-April as plants turn green and nutritional quality increases (Morafka et al., 1981). Their main period of activity is restricted to a four month period each year, June-September. Little is known about the ecology, including dietary preferences and nutritional needs, of this tortoise, yet this is important for the successful establishment of new wild and captive populations.

The Bolson Tortoise was only formally described 53 years ago (Legler, 1959), which in part, explains the paucity of information on its ecology. It eluded detection due to its small population size and isolated location in the enclosed basin of the Bolson de Mapimi in north central Mexico (Lemos-Espinal and Smith, 2007). Based on fossil records, it is known that this species was formerly widely distributed across the Chihuahuan Desert in the late Pleistocene ranging from southern New Mexico and Arizona to the edges of the Transverse Volcanic ranges of southern Mexico (Auffenberg, 1976). Population declines and extirpation throughout its historic range are attributed to anthropogenic activities including agriculture, overharvest, and livestock production (Aguirre-León, 1995). This tortoise is a long-lived species thought to reach 100 years in the wild (Lemos-Espinal and Smith, 2007). The Bolson Tortoise becomes sexually mature at 15-20 years of age, however, survival to maturity is low, and in some areas there appears to be little or no juvenile recruitment (Adest and Aguirre-León, 1995; Lemos-Espinal and Smith, 2007).

Nutrition plays a critical role in animal survival and condition. However, this is difficult to evaluate for reptiles in general, and particularly the Bolson Tortoise due to its small isolated population and the secretive nature of this species (Lemos-Espinal and Smith, 2007). Quality of an individual's diet can be evaluated directly by examining food choice and linking this to repeated measures of the animal's health, although repeated captures of individuals is often not possible or considered invasive. Indirect studies often include an examination of food choice and avoidance (MacDonald and Mushinsky, 1988; Oftedal et al., 2002; Mushinksy et al., 2003). Desert (*Gopherus agassizii*) and Gopher Tortoises (*Gopherus polyphemus*) have both been found to avoid the most common plants in their foraging areas exhibiting a selection for more nutritious forb species (Oftedal et al.,2002; Mushinsky et al., 2003). In a naturally vegetated enclosure, juvenile Desert Tortoises selected plants rich in water, protein and potassium excretion potential (PEP index) content, but not lower in potassium as anticipated (Oftedal et al., 2002). Many desert plants have a high potassium content, which in excess has been found to cause health problems to tortoises because they lack salt glands necessary to excrete potassium (Oftedal et al., 2002). Juvenile tortoises also selected for plant parts, foraging more on leaves that have higher water, protein and PEP content and low potassium content compared to other uneaten parts of plants. Forbs are an important food item for juveniles to consume as they are richer in minerals necessary for shell development and bone density (MacDonald and Mushinsky, 1988; Adest et al., 1989; Oftedal et al., 2002; Mushinsky et al., 2003).

In 2006, 25 adult Bolson Tortoises were relocated from the Audubon Appleton-Whittell Research Ranch in Arizona to naturally vegetated enclosures on the Turner Armendaris Ranch in southcentral New Mexico. The Armendaris Ranch was selected due to its location within the historic range of the tortoise and its potential as a release site for the establishment of a new wild population. In 2009 research was initiated to better understand dietary and nutritional selection of the Bolson Tortoise in the northern Chihuahuan Desert, and to compare the diet of this captive population with wild tortoises in the southern Chihuahuan Desert of Durango, Mexico. Prior to the establishment of a new wild population, it is important to evaluate if these individuals can adapt to the small but potentially significant climatic and vegetation differences between the southern and northern Chihuahuan Desert.

In this study, I examine the dietary habits of captive and wild Bolson Tortoises through direct foraging observations by season and sex and by microhistological analysis of fresh tortoise scat. I hypothesize that tortoises will forage selectively due to the different nutritional values of plants and plant parts encountered. I also hypothesize that tortoise diet will vary by season (dry vs. monsoon) and by gender due to plant availability and nutritional content. Specifically, I predict that: 1) tortoises will forage selectively, choosing plants rich in fiber, protein, phosphorus and calcium in comparison to availability within plots. Important plants should include tobosa (*Pleuraphis mutica)*, blue grama (*Bouteloua gracilis)*, Wright's globemallow (*Sphaeralcea wrightii*), and Fendler's bladderpod (*Lesquerella fendleri*) which should be abundant on plots and rich in protein content; 2) tortoise diet will vary between the dry and monsoon seasons with a higher forb component during the wet season; and 3) tortoise diets will have higher plant diversity in the southern Chihuahuan Desert due to higher in plant diversity in the south as a result of different climatic conditions (García-Arévalo, 2002).

Materials and Methods

Study Sites.-Research took place in two study locations. The northern Chihuahuan Desert site was located at the Armendaris Ranch, in Engle, New Mexico (33° 17' 57.7'' N latitude, 106° 59' 35.2'' W longitude) with data collection in the summers of 2009 and 2010. The southern Chihuahuan Desert site was located at rancho San Ignacio at the Mapimi Biosphere Reserve (26° 37' 55.9''N latitude, 103° 46' 34.2'' W longitude) in Durango, Mexico in July 2010. Research on the Armendaris Ranch was conducted in two naturally vegetated enclosures approximately 3.5 ha each that were established in 2007 and populated with Bolson Tortoises at a density of 3.4 tortoise per ha. This density is similar to sites with high Bolson Tortoise densities in the wild (Aguirre et al., 1984). The sex ratio is 6 males and 6 females in each enclosure. Common grass species in enclosures includes tobosa (*Pleuraphis mutica*), blue grama (*Bouteloua gracilis*), burrograss (*Scleropogon brevifolius*), fluffgrass (*Dasyochloa pulchella*) and purple threeawn (*Aristida purpurea*). Dominant shrubs and forbs include honey mesquite (*Prosopis glandulosa*), creosote bush (*Larrea tridentata*), fourwing saltbush (*Atriplex canescens*), Fendler's bladderpod (*Lesquerella fendlerii*), hairyseed bahia (*Bahia absinthifolia*), Wright's globemallow (*Sphaeralcea wrightii*), woolly tidestromia (*Tidestromia lanuginosa*) *and* desert holly (*Acourtia nana*) (Table 1). Average annual precipitation at this site (2001-2010) is 176.8 mm (NOAA 2010) and mostly comes in the form of monsoonal summer rains in mid July – mid September (Figure 1). Elevation ranges from 1400-1463m. All tortoises are adults (*n* = 24), and are sexed and marked with individual tags. I conducted research in the southern Chihuahuan Desert (Durango, Mexico) at the Mapimi Biosphere Reserve, with an elevation that ranges from 1150 to 1480 m and an annual average precipitation (1979-1984) of 264.2 mm (Cornet, 1988). Dominant plants at the study site include tobosa (*P. mutica),* blue grama *(B. gracilis),* matted grama *(Bouteloua simplex),* feather fingergrass *(Chloris virgata), fluffgrass (Dasyochloa pulchella),* honey mesquite *(P. glandulosa),* globemallow (*Sphaeralcea angustifolia),* leatherwood *(Jatropha dioica),* goosefoot *(Chenopodium* spp.), creosote bush (*Larrea tridentata),* broom snakeweed (*Gutierrezia sarothrae)* and prickly pear (*Opuntia* spp.) (Table 2). Research at the Mapimi Biosphere Reserve in Durango, Mexico was restricted to July 2010 and involved the daily collection of fresh scat and dominant plant samples to determine diet of wild tortoises and examine nutritional content of common plant species.

Foraging Observations.-Observations on foraging Bolson Tortoises were divided into two seasons, the dry season (May 15th-June 30th) and the wet season (July 1st-August 15th). Foraging observations were conducted during times of peak tortoise activity, 0800-1200 and 1500-1800 hours (Oftedal et al., 2002). Each morning I choose at random which enclosure to survey for each period that day. Stationary observation towers of 3.6 m in height were used to locate actively foraging tortoises with the help of a pair of binoculars. Tortoises had either a number or letter glued to their scutes. When a foraging tortoise was spotted, it was approached on ground at a distance of 50-120 m to not disturb its foraging behavior. The focal individual was followed until the foraging activity ceased. As each focal animal was tracked, impacted plants were marked with pin flags as the tortoise moved ahead. If more than one foraging tortoise was located, I selected the tortoise with less foraging data collected. When the focal tortoise completed its foraging activity, the foraging trail was re-traced. All data was collected on foraged and non-foraged plants by placing a 50 cm (approximate length of a tortoise carapace) circular quadrat at each foraging location that was marked with pin flags making sure the foraged plant was in the center of the circular plot. Data was recorded on plant species and the basal cover based on ocular estimates of all foraged and non-foraged plant species within the circular quadrat. A nearby non-foraged area was quantified by choosing a random direction and recording the plant species and basal area of all plants in the circular sampling plot 1m from each foraging location. The data from these random plots was used to calculate basal cover and species composition to determine the available plants within the enclosures. When possible, I recorded the plant part(s) that the tortoise consumed (stems, leaf, fruit, or flower); however, this was not always possible due to tall vegetation obstructing the view.

Microhistology.-Tortoise diet was also examined through microhistological analysis of fresh scat collected daily along foraging trails in Engle, New Mexico and Mapimi Biosphere Reserve in Durango, Mexico. In New Mexico tortoise enclosures were walked daily and fresh scat samples collected. Scat samples were placed in individual paper bags, with the tortoise number or letter, date and location. In Durango, Mexico, two volunteers searched for Bolson Tortoise colonies and collected fresh scat and plant samples. At this location, it was not possible to link fresh scat with individual tortoises; however I assumed each individual scat analyzed represented a different individual, based on associated burrows and distance between collection locations (minimum of 100 m). Sex and age of those individuals was unknown. To identify plant species in tortoise scat, dominant plant samples of foraged and non-foraged plants were collected at each location to create a reference slide collection for the microhistological analysis (Johnson et al., 1983). All reference plants and tortoise scats were oven dried at 50°C for three days (Sparks and Malecheck, 1968). To prepare the slides, individual plant samples and tortoise scats were grounded in a Wiley mill with a 2 mm sieve screen to obtain same size fragments (Peña and Habib, 1980). To prepare the reference collection, 1 g of plant sample was placed in 20 ml of commercial bleach to clear pigments from the fragments and to make the different anatomical features easier to view under the microscope (Johnson et al., 1983). The plant sample was later spread uniformly in a 70X20 mm glass slide with 20X40 mm cover slip (Johnson et al., 1983). To prepare scat slides, I added 1g of sample to 20 ml of commercial bleach to remove pigments (Johnson et al., 1983) and then spread it evenly in a 70X20 mm glass slide with 20X40 mm cover slip (Johnson et al., 1983). For each scat sample I made 5 slides or replicas to record the presence of each plant species (Sparks and Malecheck, 1968; Johnson et al., 1983). I used plastic mounting medium to make the reference slides and the scat slides permanent (Johnson et al., 1983). To determine plant species frequency in the microhistological analysis, I systematically examined 20 microscope fields at a total magnification of 400X (40X objective, 10X eyepiece) for each slide and recorded the presence of each species (Peña and Habib, 1980). Plant species were identified in the samples by epidermal characters and these were used to indicate the presence or absence of a species (Sparks and Malecheck, 1968).

Nutritional Analysis.-I examined the nutrient content (protein, fiber, sodium, phosphorous, potassium and calcium content) of common plants (and plant parts) foraged and avoided by Bolson Tortoise. I collected 50 g of plant samples from 6 plant species during the dry (May 15th-June 30th) and wet (July 1st-August 15th) seasons on both years to compare nutrient content between these two periods. Plants were separated into the various parts that were eaten (leaves, flowers, stem). In the field, plants were placed in sealed plastic bags on ice in insulated coolers, and then frozen at -20°C until analysis. Thawed samples were dried to a constant weight at 55°C in a forced convection oven and ground to pass through a screen (2 mm mesh) in a Wiley food mill (Oftedal et al., 2002). Plant samples were analyzed for protein and fiber at the Animal Nutrition Laboratory at New Mexico State University. Analysis of the mineral content (sodium, phosphorous, potassium and calcium) of the plant samples was done by SDK laboratories in Kansas.

Statistical Analyses.-A two-way analysis of variance (ANOVA) was used to examine percent grass consumed in direct observations of foraging Bolson Tortoises by year and season. A student's t test was used to examine percent grass consumed by sex. Chi Square Contingency Tables were used to examine the consumption of the three dominant grasses by year and season and to examine the consumption of plant parts (stems vs. leaves) by year and season. To determine if male and female tortoises were feeding on plants in relation to availability or were being selective, I used Johnson's rank preference index (Johnson, 1980), which orders food items in a ranking order from most preferred to least preferred based on use vs. availability. This analysis was done by sex to determine if adult male and female tortoises were selecting plant species differently. For each year and season, I attempted to represent each foraging individual within the sexes equally by including no more than the mean number of foraging observations for that period in the dataset. When I had more observations than the mean for a particular tortoise, I randomly selected which foraging observations to include. Analysis was conducted using the statistical software PREFER v5.1 to perform all calculations (Pankratz, 1994). By using the multiple comparison procedure of Waller and Duncan (1969), PREFER compares components and tests the hypothesis that all components are equally preferred. All plant species with percentages less than 5 % in tortoise diets were excluded from the analysis (Mendez-Gonzalez, 2010).

For the microhistological analysis, I determined the frequency of each plant fragment in each scat sample to estimate frequency of occurrence of each plant species. To obtain the frequency (F) of each plant fragment in each scat sample I used the following formula:

$$F\ (\%) = \frac{\text{No. of fields were X species was present}}{\text{Total No. of fields examined}} \times 100$$

The total number of examined fields were obtained by multiplying the number of replicas made per sample (5 replicas), times the number of fields observed under the microscope (20 microscope fields) in each slide (Valero and Durant, 2001). A student's t test was used to compare results from direct foraging observations with microhistological analysis of tortoise scat in the northern Chihuahuan Desert. Student's t tests were also used to compare the percent composition (grass, forb, tobosa and blue grama) of tortoise scats in the northern and southern Chihuahuan Desert. These statistical analyses were completed using SYSTAT 11.0 (2005).

Results

Foraging Observations and Food Choice.-During the spring and summer of 2009 and 2010, foraging data was collected on 19 tortoises for a total of 599 foraging observations. Tortoises initiated activity in May but foraging was sporadic until late June. Over the two years of this study, tortoises were observed foraging on 28 plant species, including 10 monocots and 18 dicots. Tobosa was the most common plant in enclosures followed by blue grama. In general tortoises consumed substantially more grasses than forbs; forbs comprised only 34 of 599 foraging observations (6%). Of the 34 observed foraging bites on forbs, 27 of these took place in 2010. There was no difference in the percentage of grass consumed among tortoises by year or season ($F = 0.584$, df = 37 $P = 0.740$). There was also no difference in percent consumption of grass by sex ($t = -1.197$, df = 36 $P = 0.239$) but the sample size was too small to compare this between seasons and years. Looking at the three dominant grasses only (tobosa, blue grama, and purple three awn) differences were detected in the consumption of grasses by year ($\chi^2 = 67.4$, df = 2, $P < 0.001$) and sex ($\chi^2 = 7.36$, df = 2, $P = 0.025$) but not season ($\chi^2 = 0.690$, df = 2, $P = 0.708$). There was approximately 3 times more tobosa consumed in 2009 compared blue grama and purple three awn, whereas in 2010 the percentage of blue grama in diets increased with twice as much tobosa consumed compared to blue grama and no purple threeawn. Interestingly, males consumed more of all three grass species compared to females who fed predominantly on tobosa. In terms of plant parts consumed, tortoises fed predominantly on stems and leaves. There was a year effect in relation to consumption of plant parts ($\chi^2 = 39.5$, df = 1, $P < 0.001$) , in year one, tortoises consumed significantly more stems than leaves whereas in year two the consumption of leaves and stems was similar. There was no difference in consumption of leaves and stems between the sexes ($\chi^2 = 0.33$, df = 1, $P = 0.57$).

Grasses, especially tobosa, were the most common plants in tortoise diets; however, plant species were not consumed in relation to availability. In both years grasses were predominantly preferred over forbs; however forbs were an important component of tortoise diets. Tobosa, in addition to being the most common plant in diets based on direct foraging observations, was the most preferred plant species for females during 2009. In the dry season of that year, female tortoises exhibited a significant preference for tobosa over other grass and forb species, and showed more variety in food selection, adding more forbs to their diet (Table 4). In the wet season, female preference for tobosa was not significantly different from consumption of purple three awn. Few forbs were detected in female diets in the wet seasons. Forbs were also an important component of male diets during the dry seasons of both years, and similar to females, males were observed consuming fewer forbs during the wet season (Table 4). In 2010, with the exception of males in the dry season, tortoises consistently preferred grasses over forbs. Interestingly, in this year, tortoises preferred other grass species over tobosa, with preferences varying by sex and season (Table 4). Important forb species over the two years of this study included, *Iva dealbata*, and *Tidestroemia lanuginosa* and the flowers of the cactus *Cylindropuntia imbricata*. Forb consumption was highest in the dry season with females having a greater diversity of forbs in diets in 2009 and males in 2010.

Microhistology of tortoise scat –I analyzed 36 scats from 20 tortoises from the captive population in New Mexico by season and year, and 12 scats from the wild population in Mexico for the wet season in 2010. Tortoise diets in New Mexico analyzed by scat detected a minimum of 13 plant species, with 7 monocots and 6 dicots. The most common fragments belonged to the family Poaceae (Table 5). In the 2009 dry season (n = 8), the most common fragments in tortoise scats included *P. mutica* and *B. gracilis* followed by *Aristida purpurea* and *Scleropogon brevifolius*. Similar results were observed in the wet season (n = 9) of the same year although there was an observed increase in consumption of *B. gracilis* and a decrease in *A. purpurea* and *Scleropogon brevifolius*. In 2010 *P. mutica* and *B. gracilis* were again the dominant plants in tortoise scats again followed by *A. purpurea* and *S. brevifolius*, but their consumption appeared more variable. Forb fragments rarely were found in the samples, (< 4%) with the exception of the wet season in 2009 when forb abundance, particularly *L. fendleri,* increased, accounting for 9.5% of the total fragments identified (Table 5). No differences were detected in the percent grass, forb, tobosa or blue grama in tortoise scats by year or season ($P > 0.05$) in New Mexico. When comparing results from direct foraging observations with the microhistology of tortoise scat, there was no difference detected in the percent composition of grass, forb or blue grama using the two methods ($P > 0.05$), however significantly more tobosa was observed in tortoise diets through the direct foraging observations compared to the microhistological analysis of tortoise scat ($t = -4.68$, $df = 27$, $P < 0.001$).

Interestingly, for the wild population on the Mapimi Biosphere Reserve in Durango Mexico, results of the microhistological analysis were similar to New Mexico samples in that the most common epidermal fragments belonged to the Poaceae family (Table 6). Grass epidermal fragments from the Mexico samples accounted for 77% of the total fragments identified (Table 6). Plant fragments from *P. mutica* accounted for 40% of epidermal fragments found in the microscope fields. Forb fragments rarely were found in the samples, (< 4%). No differences were detected in the percent grass or forb in the diets of Bolson Tortoises from the northern and southern Chihuahuan Desert ($P > 0.05$) using microhistology. However according to this technique, tortoises in the northern Chihuauan Desert consumed significantly less tobosa (t = -4.68, df = 27, $P < 0.001$) and significantly more blue grama (t = 4.60, df = 27, $P < 0.001$). In the scat samples from Mapimi, prickly pear fruit seeds (*Opuntia* sp. were found as well as *Prosopis* sp. seeds) (no epidermal fragments of prickly pear pads were found in the microscope fields). These plants were not found in the New Mexico samples but flowers from other cactus species were found in tortoise diets in New Mexico.

Discussion

Direct observations on foraging Bolson Tortoises in New Mexico indicates that although tortoises consumed a variety of plant species, their diet lacked diversity with tortoises consuming mainly two species of grass, tobosa and blue grama. These were also the most common plants in tortoise enclosures. This indicates that Bolson Tortoises eat what is available to them; however I found they also forage opportunistically taking advantage of forb species when available. This is similar to studies on the wild population in Mexico, where Lieberman and Morafka (1988) suggest that tobosa in Bolson Tortoise diets reflects availability and not preference. The location of wild colonies of Bolson Tortoises in Mexico has been linked to the presence and density of tobosa, however, colony centers are often found in areas of mixed grasses adjacent to tobosa grasslands (Lieberman and Morafka, 1988). I found Bolson Tortoises foraged primarily on tobosa but increased their consumption of blue grama in 2010 with increasing basal cover of this species. Interestingly, males foraged on a greater diversity of grass species while females primarily consumed tobosa. This is likely related to the larger home range size of males during the summer, when the mating season peaks (Aguirre et al., 1984). Other studies have not compared diet between sexes.

Bolson Tortoise diets differed between years and seasons based on direct foraging observations, however the pattern was not as straightforward as predicted. Grasses were generally preferred over forbs. Interestingly, foraging observations suggested forbs are more important in the dry compared to the wet season. I originally predicted greater importance of forbs in tortoise diets during the wet season due to increased germination during this period. Females in the 2009 dry season consumed a diversity of forbs, with two species ranked second and fourth in terms of diet preference. The selection of forb species during this period may be related to the consumption of important nutrients for egg development. Although mating peaks in July and August, female Bolson Tortoises store sperm over winter and lay eggs the following year during May and June (González-Trápaga et al., 2000; Lemos-Espinal and Smith, 2007). Adult Bolson Tortoises do not lay eggs each year (Lemos-Espinal and Smith, 2007), and this may contribute to variability in nutrient requirements and plant selection among individuals. Interestingly, forbs were also more important in male diets during the dry season, in part, related to large home range sizes during the mating season, which typically starts in mid to late spring (Martínez-Cárdenas, 2006). In addition, dominant grasses had substantially lower protein content in the dry compared to wet season, so tortoises may lack important nutrients during this period and preferentially select forbs when available.

Obtaining sufficient nutrients for dietary requirements is an important component of food choice for tortoises in general. Forbs contain essential nutrients for tortoises but in desert environments also tend to be high in potassium content which can be toxic for tortoises because they lack salt glands necessary to excrete potassium (Oftedal et al., 2002). In California, Desert Tortoises avoid plants that are high in potassium content (Oftedal et al., 2002). High potassium content may be one of the reasons that forbs, although seasonally important, comprised a relatively small component of tortoise diets in this study. Tortoises may consume enough forbs to obtain their required nutrients and minerals but no more. This would explain higher consumption of forbs during the dry season when forbs should be less abundant but consumption of forbs would be biologically more meaningful. Grass species have low nutrient content when dormant and both females and males needed important nutrients for egg laying and mating during this period (González-Trápaga et al., 2000).

Bolson Tortoises are central place foragers with activity centers directly related to the distribution of their burrows (Aguirre et al., 1984), as a result, they often revisit previously foraged areas. This tendency to revisit previously foraged areas, likely contributed to tortoises consuming more stems than leaves in 2009. The drier conditions that year may have resulted in little regrowth forcing tortoises to consume more stems. When conditions were wetter in 2010, tortoises consumed equal amounts of stems and leaves, while still remaining in the vicinity of their burrows. Desert Tortoises were observed to prefer leaves over other plant parts due to the higher water and protein but lower potassium content (Oftedal et al., 2002), and when possible Bolson Tortoises would likely do the same. Frequent clipping of plants in general, (Whicker and Detling, 1988) and specifically tobosa (Canfield, 1939) promotes regrowth, and new vegetative shoots have been documented to have higher nutrient content then unclipped vegetation (Whicker and Detling, 1988). Therefore, the central place foraging strategy, in addition to allowing tortoises to stay close to burrows to defend those sites and for protection from predators, also may increase nutritional benefits by increasing foraging activity in previously grazed areas as nutrient content of regrowth may be greater than ungrazed plants. This is not something I examined but would be interesting for future studies to investigate.

Microhistological analysis has been widely employed to examine diets of herbivores and is especially useful to obtain data on hard to observe species or individuals (Rogers-Wydeven and Dahlgren, 1982; MacDonald and Muskinsky, 1988; Rouag et al., 2008; Lightfoot et al, 2010). I found this technique useful for the Bolson Tortoise, especially the wild population in Durango, Mexico that is shy and difficult to track using direct foraging observations. A comparison of the two techniques (i.e. scat analysis vs. direct foraging observations) for New Mexico tortoises both identify grasses as being the dominant component of Bolson Tortoise diets. However, the two methods differ in the percentages of grass species and forbs in diets. Direct foraging observations suggest a much higher content of tobosa compared to blue grama than detected through microhistogical analysis. Both methods detect an increase in consumption of blue grama in 2010, which coincides with the increase in blue grama cover that year, however, the microhistological approach estimates a higher percentage of blue grama in tortoise diets. The scat analysis also indicates a substantially higher content of forbs in tortoise diets compared to direct observations and contrary to foraging observations, forb content in tortoise scats increases in the wet season, as originally predicted. These differences, in part, can be attributed to differences in diets of individual tortoises (fewer individuals were included in the microhistological analysis) and the small sample size of scats analyzed. However, this contradiction also indicates that direct foraging observations may sometimes fail to detect foraging bites of small forbs hidden amongst the dominant grasses. The direct foraging observations likely underestimated the amount of forbs consumed by tortoises, especially in the wet season.

Diets of wild Bolson Tortoises in the southern Chihuahuan Desert (Durango, Mexico) were similar to tortoises in semi-wild enclosures in the northern Chihuahuan Desert (New Mexico) in that tortoises in both populations consume similar amounts of grass and forbs, with tobosa and blue grama being the dominant plants consumed in both populations. The data does not support the prediction that tortoise diets in the southern compared to northern Chihuahuan Desert would be more diverse. While I was somewhat surprised by this result, tobosa was the most common plant at both locations and comprised the majority of plant fragments in tortoise scats. Forbs comprised a small, but potentially significant, component of epidermal fragments in scat samples at both locations. It appears that tortoises forage on forbs opportunistically, but may only consume plants with high potassium content when deficient in other nutrients. Forb species were different in the northern and southern Chihuahuan Desert sites and I was unable to identify the two important forb species in scat samples from Mexico. Items found in tortoise scats in Durango, Mexico that were not detected in New Mexico included *Opuntia* sp. seeds from fruits, *Prosopis glandulosa* seeds, grit and insects. Few prickly pear and honey mesquite plants were present in the enclosures and I never observed tortoises feeding on plant parts or seeds of these species although I did observe tortoises feeding on flowers of the cactus *Cylindropuntia imbricata*. Prickly pear may offer an important water source for wild tortoises and has been documented to be important for other reptiles (Highfield, 1997). The value of mesquite seeds were unclear as these seeds were found undigested in tortoise scats. Grit and invertebrates are common in scats of other tortoise species and may provide additional nutrients and grit may aid in digestion (Woodbury and Hardy, 1948).

Conclusions- Diets of Bolson Tortoise are less diverse than other tortoise species with tobosa and blue grama being the dominant plants consumed at both locations. Direct foraging observations indicate males in New Mexico consume a greater diversity of grass species than females, likely related to their larger home range sizes. Foraging observations suggest forbs are more important in diets in the northern Chihuahuan Desert during the dry compared to wet season, possibly related to lack of essential nutrients prior to the onset of summer rains. However scat analysis suggests forbs may be more important in the wet season than detected through direct observations, indicating an importance of forbs during both seasons. The two techniques, direct foraging observations and scat analysis, both provided useful information on tortoise diets and also identified limitations. Direct foraging observations allow for the collection of a large amount of data on individuals that are easy to observe (i.e. captive population) but consumption of forbs within stands of grass may be difficult to detect. Comparisons with scat analysis led me to speculate that forb consumption was likely underestimated (especially after summer green up) using this technique. The microhistology technique identifies frequency of plant fragments in tortoise scats. This technique is tedious and labor intensive. Therefore it is difficult to process a large sample size of scats and I was only able to examine a portion of scats collected. I found substantial variation in individual diets; therefore, the smaller sample size used in this technique may not represent the overall population. This may also lead to inconsistencies with direct foraging observations. However, the wild population of the Bolson Tortoise is extremely shy and difficult to observe (Bury et al. 1988). By employing this technique, I was able to obtain some of the only information available on the diets of the wild population of this recently described species, allowing for a direct comparison with diets of a captive population at a potential release site.

Management Implications- Substantial overlap was observed in the diets of Bolson Tortoises from the northern (New Mexico) and southern (Durango, Mexico) Chihuahuan Deserts. This information is encouraging related to the proposed establishment of a wild population in the historic part of the tortoises range in southern New Mexico. The presence of prickly pear seeds from cactus fruits in the wild population suggests that this may be an important component of tortoise diets that should be available in pre-release enclosures and at release locations for re-introduced tortoises. The greatest threat to the re-establishment of Bolson Tortoise in its historic northern Chihuahuan Desert range is global climate change. A warmer climate poses a major threat to this species across its range where sex of hatchlings is temperature driven (Lemos-Espinal and Smith, 2007). In addition, global climate change models predict the northern Chihuahuan Desert will become drier and experience increased shrub encroachment (Gao and Reynolds, 2003; Asner and Heidebrecht, 2005; Seager et al., 2007). If true, this will limit the amount and quality of forage available at northern locations.

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FIGURE 1. Precipitation data from the Armendaris Ranch, Engle New Mexico for the years 2009 and 2010 and the 45 year rainfall averages from nearby Truth or Consequences, NM.

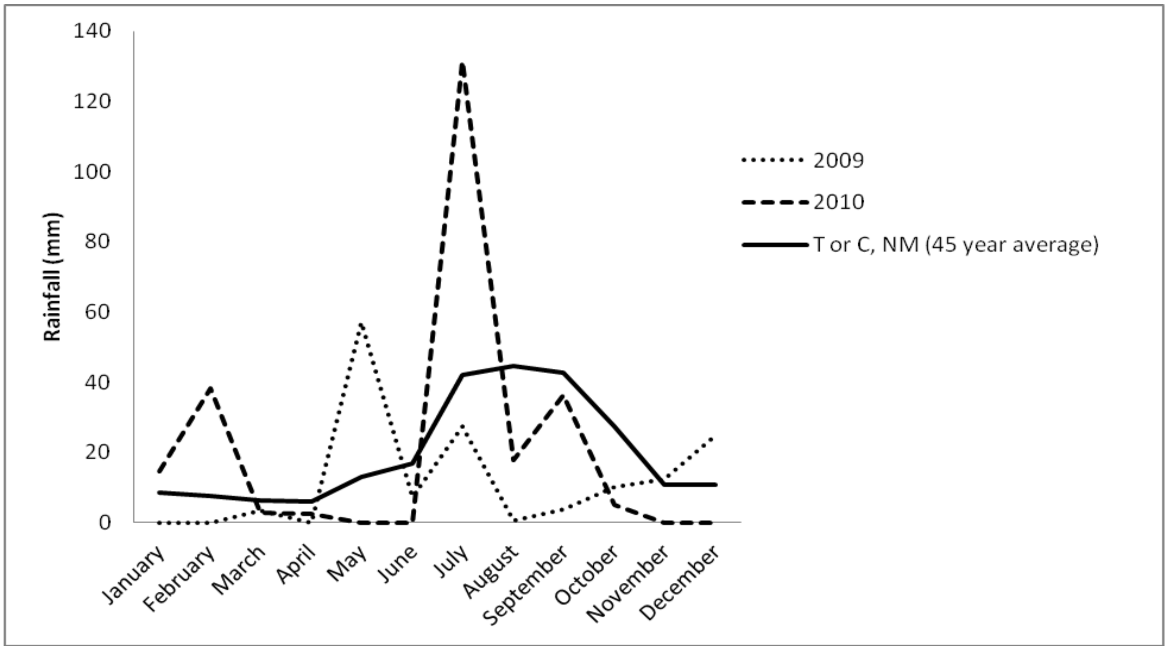

TABLE 1. Plants documented growing inside Bolson Tortoise enclosures at the northern Chihuahuan Desert site in Engle, NM. Foraged plants are indicated with an asterisk (*).

Family	Species	Common name
Poaceae	*Aristida purpurea**	Purple threeawn
	Bouteloua curtipendula	Sideoats grama
	*Bouteloua eriopoda**	Black grama
	*Bouteloua gracilis**	Blue grama
	*Dasyochloa pulchella**	Fluff grass
	*Eragrostis lehmanniana**	Lehmann lovegrass
	*Muhlenbergia arenacea**	Ear muhly
	*Panicum obtusum**	Vine mesquite
	Panicum virgatum	Switchgrass
	*Pleuraphis mutica**	Tobosa
	*Scleropogon brevifolius**	Burrograss
	*Sporobolus airoides**	Alkali sacaton
Amaranthaceae	*Tidestromia lanuginosa**	Woolly tidestromia
Agavaceae	*Yucca elata*	Soaptree yucca
Asteraceae	*Aster subulatus**	Baby aster
	*Acourtia nana**	Desert holly
	*Bahia absinthifolia**	Hairyseed bahía
	*Berlandiera lyrata**	Chocolate daisy
	*Gaillardia pulchella**	Indian blanket
	Gutierrezia sarothrae	Broom snakeweed
	*Iva dealbata**	Woolly marshelder
	*Machaeranthera tanacetifolia**	Tanseyleaf tansyaster
	Psilostrophe cooperi	Paper flower
	Thymophylla acerosa	Dogweed
	Zinnia grandiflora	Prairie zinnia
Brassicaceae	*Lesquerella fendleri**	Fendler's bladderpod
Cactaceae	*Cylindropuntia imbricata**	Tree cholla
	Opuntia sp.	Prickly pear cactus
Chenopodiaceae	*Chenopodium album*	Lambsquarters
	*Salsola kali**	Russian thistle
Ephedraceae	*Ephedra trifurca*	Mormon tea
Euphorbiaceae	*Euphorbia albomarginata*	Rattlesnake weed
Fabaceae	*Astragalus mollissimus*	Woolly locoweed
	Hoffmannseggia glauca*	Hog potato

	Prosopis glandulosa	Honey mesquite
	Senna bauhinioides	Twinleaf senna
Hydrophyllaceae	*Nama hispidum**	Purple mat
Linaceae	*Linum* lewisii*	Blue flax
Malvaceae	*Sphaeralcea angustifolia**	Fendler globemallow
	Sphaeralcea wrightii	Wright's globe mallow
Nyctaginaceae	*Selinocarpus lanceolatus*	Gypsum moonpod
Onagraceae	*Gaura coccinea**	Scarlet gaura
	Calylophus hartwegii	Hartweg's sundrops
Plantaginaceae	*Plantago purshii**	Woolly plantain
Polygonaceae	*Erigonum rotundifolium*	Roundleaf buckwheat
Solanaceae	*Solanum elaeagnifolium*	Silverleaf nightshade
Verbenaceae	*Glandularia wrightii**	Verbena

TABLE 2. Plant samples collected at the southern site at the Mapimi Biosphere Reserve, Durango, Mexico in the month of July 2010 to prepare reference slides.

Family	Species	Common name
Asteraceae	*Aster subulatus*	Baby aster
	Acourtia nana	Desert holly
	Bahia absinthifolia	Hairyseed bahía
	Gutierrezia sarothrae	Broom snakeweed
Cactaceae	*Opuntia* olivacea	Prickly pear cactus
	Peniocereus maculatus	Peniocereus
Caesalpiniaceae	*Hoffmanseggia glauca*	Hogpotato
Chenopodiaceae	*Chenopodium* sp.	Goosefoot
Euphorbiaceae	*Jatropha dioica*	Leatherstem
Malvaceae	*Sphaeralcea angustifolia*	Fendler globemallow
Poaceae	*Aristida* sp.	Three awn
	Bouteloua gracilis	Blue grama
	Bouteloua simplex	Matted grama
	Choris virgata	Showy windmillgrass
	Dasyochloa pulchella	Fluffgrass
	Pleuraphis mutica	Tobosa
	Scleropogon brevifolius	Burrograss
Solanaceae	*Solanum elaeagnifolium*	Silverleaf nightshade

TABLE 3. Basal cover percentages (BC%) and species composition (SC) at the northern Chihuahuan Desert site, Engle, NM by seasons (Dry season=DS, wet season=WS) for the years 2009 and 2010. Blank spaces indicate that species was not present in plots.

Plants at enclosures	BC% 2009 DS	SC 2009 DS	BC% 2009 WS	SC 2009 WS	BC% 2010 DS	SC 2010 DS	BC% 2010 WS	SC 2010 WS
Grasses								
Pleuraphis mutica	7.4	63.8	7.3	57.9	6.4	32.6	5.7	29.2
Bouteloa gracilis	2.0	17.5	2.5	20.2	4.2	21.2	4.1	20.9
Aristida purpurea	1.7	14.4	2.0	16.2	1.0	5.3	3.4	17.5
Scleropogon brevifolius					3.2	16.3		
Muhlenbergia arenacea	0.2	1.4	0	0.2	0.3	1.7	0.1	0.7
Sporobolus airoides	0.2	1.4	0.3	2.3	1.6	7.9		
Dasyochloa pulchella				0.2	1.0	5.1	0	0.1
Forbs								
Plantago purshii					0.1	0.4	0.1	0.3
Sphaeralcea wrightii					0.1	0.6	3.4	17.3
Lesquerella fendleri					0.9	4.6	0.4	2.1
Tidestromia lanuginosa					0.6	3.1	0.3	1.3
Hoffmanseggia glauca			0	0	0.1	0.6	0	0.2
Acourtia nana	0.1	0.6						
Gaura coccinea							0.1	0.5
Bahia absthintifolia							0.9	4.4
Cripthantha crasisepala							0.2	0.8
Salsola kali							3.3	1.7
Phacelia crenulata					0.1	0.3		
Iva dalbata	0.1	1.0						
Cactus								
Cylindropuntia imbricata	0.2	1.4			0	0.2	0.6	3.0

TABLE 4. Comparison of plant species foraged by the tortoises at the northern Chihuahuan Desert site, Engle, NM, during the dry season (May 15th-June 15th) and the wet season (July 1st- August 15th) of 2010 using Johnson's rank preference index (ranking). A blank space means that the plant species was not present in the foraging trail.

	2009				2010			
	Dry Season Ranking		Wet Season Ranking		Dry Season Ranking		Wet Season Ranking	
Foraged plants	Females[I] (n=16)	Males[II] (n=10)	Females[III] (n=46)	Males[IV] (n=57)	Females[V] (n=12)	Males[VI] (n=21)	Females[VIII] (n=24)	Males[VIII] (n=11)
GRASSES								
Pleuraphis mutica	1^{a}	4^{c}	1^{a}	3^{a}	2^{a}	9^{e}	2^{b}	2^{a}
Bouteloua gracilis	3^{b}	3^{b}	3^{b}	4^{b}	1^{a}		3^{b}	1^{a}
Aristida purpurea	5^{d}		2^{a}	6^{d}		1^{a}	4^{b}	
Muhlenbergia arenacea				1^{a}			1^{a}	
Sporobolus airoides		2^{a}						
Dasyochloa pulchella						4^{a}		
Scleropogon brevifolius				2^{a}	3^{b}	5^{a}		
CACTUS								
C. imbricata (flower)		1^{a}				3^{a}		
FORBS								
Salsola kali				5^{c}				
Iva dealbata	2^{b}							

Plantago purshii	8^{h}		8^{d}	
Acourtia nana	4^{c}			
Hoffmanseggia glauca	6^{e}		6^{b}	
Lesquerella fendleri	7^{g}		7^{c}	
Gaura coccinea				5^{b}
Salsola kali				
Tidestromia lanuginosa		4^{c}	2^{a}	

$^{I}F_{4,12} = 1.32, W=2.73$

$^{II}F_{3,7}=1.12, W=2.75$

$^{III}F_{2,44} =1.00, W=2.44$

$^{IV}F_{5,52} =2.89, W=2.24$

$^{V}F_{3,9} =0.19, W=2.89$

$^{VI}F_{8,13} =1.21, W=2.97$

$^{VII}F_{4,20} =1.31, W=2.69$

$^{VIII}F_{1,10}=1.00, W=2.42$

TABLE 5. Plant composition in tortoise scats at the northern Chihuahuan Desert site, Engle, NM, USA by season (dry season: May 15th-June 30th) and wet season (July 1st- August 15th) and year (2009 and 2010). Dashed lines (---) indicate that species did not appear in sample.

	2009		2010	
	Dry Season	Wet Season	Dry Season	Wet Season
Epidermal fragments	**Plant Composition % (n=8)**	**Plant Composition % (n=9)**	**Plant Composition % (n=9)**	**Plant Composition % (n=10)**
Grasses				
Pleuraphis mutica	16.35	17.43	20.66	20.03
Bouteloua gracilis	17.41	24.77	19.86	20.97
Aristida purpurea	9.11	2.64	4.37	2.81
Scleropogon brevifolius	9.03	2.87	6.38	7.35
Muhlenbergia arenacea	2.11	1.03	1.67	0.3
Sporobolus airoides	5.12	1.83	3.76	0.4
Dasyochloa pulchella	----	0.34	0.48	----
Unknown grass tissue	27.01	22.36	25.08	22.94
Cactus				
Cylindropuntia imbricata (flower)	----	1.03	0.43	0.2
Forbs				
Plantago purshii	----	1.26	0.71	2.58
Sphaeralcea wrightii	1.22	3.21	2.05	0.99
Lesquerella fendleri	3.17	9.52	5.81	3.08
Tidestromia lanuginosa	----	1.15	0.52	3.57

Hoffmanseggia glauca	1.05	2.98	1.86	0
Unknown forb tissue	7.56	7.11	7.38	13.7

TABLE 6. Plant composition in tortoise scats collected at the southern Chihuahuan Desert site, Mapimi Biosphere Reserve, Durango, Mexico in July 2010.

Epidermal fragments	**Plant Composition % (n=12)**
Grasses	
Pleuraphis mutica	41.34
Bouteloua gracilis	0.30
Bouteloua sp.	0.75
Aristida sp.	3.13
Scleropogon brevifolius	11.04
Unknown grass tissue	20.45
Cacti	
Opuntia sp.	0.30
Forbs	
Forb 1	1.04
Forb 2	10.90
Unknown forb tissue	10.75

TABLE 7. Nutritional content of plant samples by plant part (L=leaf, S=stem, F=flower and W=whole plant) and season for the year 2009 at the northern Chihuahuan Desert site, Engle, NM.

		2009									
		Dry season (%)					Wet season (%)				
Species	Part	Protein	Fiber	Calcium	Phosphorus	Potassium	Protein	Fiber	Calcium	Phosphorus	Potassium
Grasses											
Pleuraphis mutica	L	>.01	85.6	0.53	0.15	2.35	14.3	65.1	-	-	-
	S	2.1	77.6	0.34	0.07	0.41	20.2	84.4	0.22	>.01	0.31
Bouteloua gracilis	L	0.3	-	0.36	0.04	0.22	-	71.7	0.33	0.2	1.38
Forbs											
B. absinthifolia	L	94.5	-	-	-	-	-	21.0	2.30	0.21	3.60
	F	95.6	-	-	-	-	-	32.4	0.96	0.06	2.37
G. sarothrae	W	8.5	42.1	1.05	0.14	2.28	-	-	-	-	-
Nama hispidum	W	-	-	-	-	-	8.3	49.1	1.94	0.15	1.72

TABLE 8. Nutritional content of plant samples by plant part and season for the year 2010 at the northern Chihuahuan Desert site, Engle, NM.

		2010									
		Dry season (%)					Wet season (%)				
Species	Part	Protein	Fiber	Calcium	Phosphorus	Potassium	Protein	Fiber	Calcium	Phosphorus	Potassium
Grasses											
P. mutica	Leaf	6.6	68	0.72	0.1	1.31	14.7	67.3	0.64	0.12	1.03
	Stem	2.8	79.2	0.4	0.07	0.99	7.1	74.8	0.28	0.15	1.6
	Flower	5.6	78.7	0.3	0.18	1.2	9.3	73	0.3	0.2	1.16
B. gracilis	Leaf	-	73.3	0.47	0.12	0.91	-	-	-	-	-
	Stem	-	84.3	0.2	0.02	0.14	4.6	-	0.2	0.12	1.31
D. pulchella	Whole plant	6.2	69.8	0.93	0.11	0.77	-	-	-	-	-
Forbs											
B. absinthifolia	Leaf	18.7	25.8	2.47	0.14	2.59	20.9	25.7	2.57	0.2	3.28
	Stem	6.2	57.8	0.59	0.1	2.26	5.1	64	0.74	0.12	2.9
T. lanuginosa	Whole plant	17.2	28.5	1.85	0.22	4.49	4.7	60	0.88	0.14	3.31

TABLE 9. Nutritional content of plant samples by plant part collected at the southern Chihuahuan Desert site, Durango, MX in July 2010.

Family	Species	Part	Protein	Calcium	Phosphorus	Potassium
Poaceae	*Bouteloua simplex*	W	22	0.56	0.32	0.38
	Pleuraphis mutica	L	7.6	0.65	0.19	1.23
		S	17.4	0.29	0.09	0.61
		F	26.6	0.27	0.3	1.39
	Scleropogon brevifolius	W	23.2	0.57	0.14	1.25
Cactaceae	*Opuntia olivacea*	W	14.3	1.52	0.09	1.83
Caesalpiniaceae	*Hoffmanseggia glauca*	W	18.9	1.2	0.54	1.98
Chenopodiaceae	*Chenopodium* sp.	W	12.7	1.97	0.22	2.71
Euphorbiaceae	*Jatropha dioica*	W	21.9	0.82	0.25	2.98
Malvaceae	*Sphaeralcea angustifolia*	W	10.3	3.0	0.35	2.66