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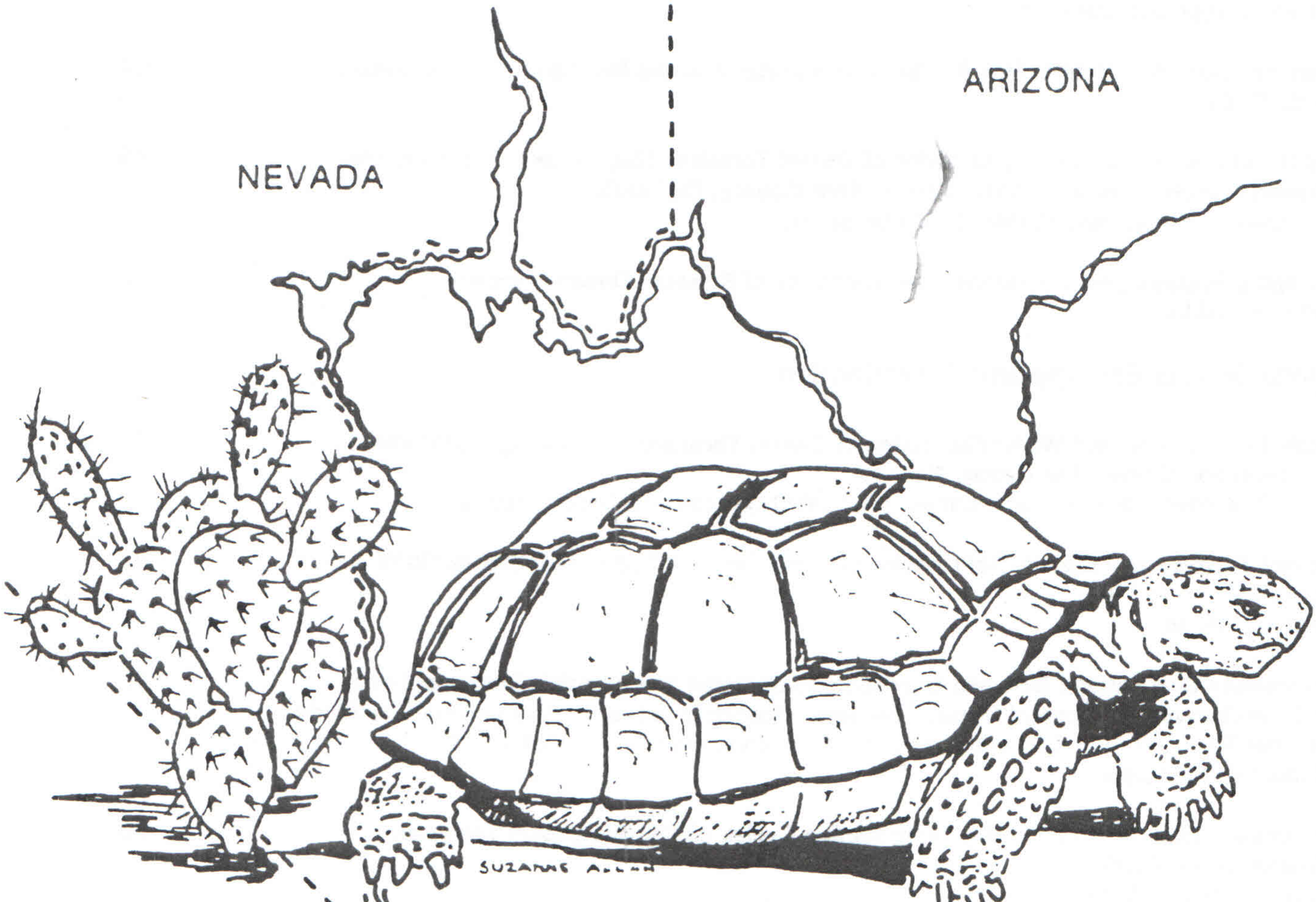

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Observations on the Feeding Behavior of Desert Tortoises (*Gopherus agassizii*) at the Desert Tortoise Research Natural Area, Kern County, California

W. Bryan Jennings and Clifford L. Fontenot, Jr.

Abstract. Data on the feeding habits and food preferences of two adult desert tortoises (*Gopherus agassizii*) were collected during May and June 1991 at the Desert Tortoise Research Natural Area in Kern County, California. One adult female and one male tortoise were observed for a total of 24 days, during which time they took 8,612 bites from 757 individual annual plants (21 species) and 3,483 bites from 171 individual herbaceous perennial plants (5 species). Both tortoises were highly selective feeders that largely favored relatively rare plant species. Moreover, several of these uncommon species (e.g., *Astragalus layneae*) were restricted to the margins of small (< 2 m wide) washes. Tortoises spent a considerable amount of time foraging along small washes and were successful at locating these uncommon species. Native composites (e.g., *Lygodesmia exigua* and *Stephanomeria parryi*) and native legumes (e.g., *Astragalus layneae*, *A. didymocarpus*, and *Lotus humistratus*) seemed to be important plant groups in tortoise diet (28% bites/19% plants and 27% bites/22% plants respectively). Further, native plant species were consumed more frequently than non-natives (88% bites/70% plants vs. 12% bites/30% plants respectively).

INTRODUCTION

Desert tortoise (*Gopherus agassizii*) populations have, over the past few decades, been rapidly declining (Berry 1984). Factors that have been implicated in this on-going decline include: chronic respiratory diseases (i.e., Upper Respiratory Tract Disease Syndrome); illegal collecting; raven predation on juveniles; and habitat loss and alteration (Luckenbach 1982; Bureau of Land Management 1988). Upper Respiratory Tract Disease Syndrome has been particularly devastating to tortoise populations at the Desert Tortoise Research Natural Area in eastern Kern County, California (Avery and Berry 1991; Jacobson et al. 1991). Although indirect evidence suggests that disease-carrying domesticated desert tortoises released into the wild are responsible for this outbreak, research shows that a dietary link to the susceptibility of diseases may exist (Jacobson et al. 1991). For many decades, the plant communities in the western Mojave Desert have been altered by human-related activities such as livestock grazing (Berry 1978) and off-road vehicle use (BLM 1988). Invasions by introduced plants following livestock grazing in the arid southwestern United States are well documented (D'Antonio and Vitousek 1992). These unnatural habitat disturbances have resulted in the rampant spread of mediterranean exotics such as filaree (*Erodium cicutarium*), split-grasses (*Schismus* spp.), brome grasses (*Bromus* spp.), and native weeds such as fiddleneck (*Amsinckia tessellata*) (Robbins et al. 1951). Succession in desert plant communities by mediterranean annuals has also been documented in other desert regions containing declining tortoise populations (Esque et al. 1990 and 1991). If tortoises depend upon certain native plant species to maintain their proper health, and these particular species

become either reduced in abundance or competively excluded by invasive species of inferior dietary quality, then tortoise populations may become more susceptible to diseases (Jacobson et al. 1991).

In 1991, the Bureau of Land Management sponsored a preliminary study of tortoise food habits at the Desert Tortoise Research Natural Area. The purpose of the project was to identify which plant species tortoises feed upon, determine if they are selective feeders, and observe their feeding habits.

METHODS

The study site was located within sections 1, 11, and 12 of Township 31 S, Range 38 E at the Desert Tortoise Research Natural Area in Kern County, California. At an elevational range of 850-915 m, the vegetational community was generally dominated by creosote bush (*Larrea tridentata*), burro-bush (*Ambrosia dumosa*) and goldenhead (*Acamptopappus sphaerocephalus*). An adult male (279 mm CL at the midline) and female (238 mm CL at the midline) desert tortoise were observed for a total of 24 days between 3 May and 14 June 1991. These particular animals were selected because they were part of an on-going health and disease profile study. The tortoises were located early in the day, using radio-telemetry equipment, when they were about to emerge from their respective cover sites (burrow, shrub, etc.) for daily activity.

Once a tortoise emerged from its cover site, it was then followed at distances of 4-8 m. This distance was determined to be effective at minimizing disturbance to the tortoises caused by our presence, yet close enough to clearly observe feeding habits and behavior. When a tortoise was observed feeding, the following data were recorded: (1) species of plant; (2) number of bites; (3) condition of the plant e.g., whether it was succulent (containing water) or dry (containing no water).

When the tortoise retreated to cover at midday and at the end of the day, 15 X 50 cm rectangular quadrats were positioned lengthwise at intervals along feeding routes. Quadrat sites were selected either randomly or placed in front of a spot where a plant was fed upon. We used 102 quadrats for the feeding routes of the female tortoise and 127 quadrats were used for the male. The plants within each quadrat were then identified to species, counted, and determined to be either succulent or dry. Nomenclature for plant species follows Munz (1974).

To determine if tortoises are selective feeders, the frequency of occurence for each plant species along tortoise feeding routes was compared to the frequency of occurence in tortoise diet using a R x C test of independence (Sokol and Rohlf, 1981).

RESULTS

Female Tortoise. - Once the female tortoise emerged in the morning, she would typically warm up in the sun for a short time (ca. 10-30 minutes), then start feeding. Her feeding patterns were often repeated. She would emerge from a cover site and head nearly straight for her next cover site while feeding along the way on selected plants. While traveling, she would move her head from side to side apparently scanning ahead for potential food plants. Although she seemed to select plants by visually cueing in on them, she would occasionally

sniff individual plants before either choosing to feed upon or continue foraging.

The female tortoise fed upon 11 species of annual and 2 species of perennial plants taking 4,697 bites from 306 individual plants (Table 1). The three most-eaten species of plants were: *Lygodesmia exigua*, 2,069 bites (44.0%); *Astragalus layneae*, 1,011 bites (21.5%); and *A. didymocarpus*, 870 bites (18.5%). Moreover, the female tortoise never passed any of the aforementioned species without consuming the entire plant. Of the 306 plants sampled by the female tortoise, 291 (95.1%) were succulent while the remaining 15 (4.9%) were dry (Table 1).

A comparison of the relative abundance of succulent annuals along the feeding routes of the female tortoise with diet reveals that she was a very selective feeder ($x^2 = 465.1$, d.f. = 15, P = 0.0001; Table 2 and Fig. 1). Nearly 40% of her diet consisted of plants that were not detected in the vegetation samples (Fig. 1). Personal observations confirm that her favorite plants are locally uncommon. Although, these plant species grow in restricted areas, hence, tortoises are able locate them.

The female tortoise spent a considerable amount of time traveling and foraging along "small" (< 2 m wide) washes. Many of her more-preferred plants grew almost exclusively in or along these same washes (e.g., *Astragalus layneae, Camissonia boothii, Mentzelia eremophila,* and *Cryptantha circumcissa*). Moreover, all seven of her burrows (permanent and pallet burrows) were located within 3 m of a small wash. She tended to avoid the wide washes (> 2 m wide) and would only occasionally cross them.

Male Tortoise. - The male tortoise exhibited feeding patterns similar to those of the female tortoise. He would emerge from a cover site and warm up for ca. 10-30 minutes, then he would initiate feeding activity. The male characteristically moved his head from side to side and seemed to locate food items by sight. Occasionally, he would sniff a plant or the ground. As was the case for the female tortoise, his feeding routes extended between consecutive cover sites. He would feed on selected plants while heading directly for his next cover site.

The male tortoise fed upon 20 species of annuals and 5 species of perennial plants taking 7398 bites from 622 individual plants (Table 3). The five most-eaten species of plants were: *Erodium cicutarium*, 1,442 bites (19.5%); *Astragalus layneae*, 1,281 bites (17.3%); *Mentzelia eremophila*, 1,253 bites (16.9%); *Stephanomeria parryi*, 939 bites (12.7%); *Chorizanthe brevicornu*, 882 bites (11.9%). Like the female, the male tortoise never passed some species without consuming the entire plant (e.g., *Astragalus layneae; A. didymocarpus; Mentzelia eremophila; Lygodesmia exigua; Glyptopleura marginata; Camissonia boothii;* and *Stephanomeria parryi*). Of the 622 plants sampled by the male tortoise, 601 (96.6%) were succulent while the remaining 21 (3.4%) were dry (Table 3).

The male tortoise was also a highly selective feeder ($x^2 = 139.5$, d.f. = 8, P = 0.0001; Table 4 and Fig. 2). Moreover, several of the plant species which were in the diet were not represented in the vegetation samples (Figure 2). The male tortoise also spent a considerable amount of time traveling and foraging in and along small washes. Several species in the diet grew exclusively along the margins of small washes (e.g., *Astragalus layneae, Stephanomeria parryi*, and *Camissonia boothii*).

Both tortoises consumed many of the same species of plants. For example, both tortoises fed almost exclusively on plants which grew in exposed areas such as the intershrub spaces and along washes. Moreover, plants in which the tortoises usually ate the entire plant included: *Mentzelia eremophila, Lygodesmia exigua, Astragalus layneae*, and *Stephanomeria parryi*. The male tortoise tended to eat the seeds and leaves of *Erodium cicutarium* and would

Table 1. Number of bites of annual and perennial plant species taken by the adult female tortoise between 3 May and 11 June 1991 at the Desert Tortoise Research Natural Area, Kern County, California.

	Plant Species	# Bites	% Bites	# Plants	% Plants
	Lygodesmia exigua	2069	44.05	111	36.27
**	*Astragalus layneae*	1011	21.52	55	17.97
	Astragalus didymocarpus	766	16.31	60	19.61
	Cryptantha circumcissa	307	6.54	33	10.78
	Camissonia boothii	129	2.75	12	3.92
*	*Astragalus didymocarpus*	104	2.21	13	4.25
	Malacothrix coulteri	85	1.81	1	0.33
	Mentzelia eremophila	70	1.49	5	1.63
	Erodium cicutarium	48	1.02	7	2.29
**	*Mirabilis bigelovii*	46	0.98	2	0.65
	Calycoseris parryi	31	0.66	3	0.98
	Glyptopleura marginata	20	0.43	1	0.33
*	*Mentzelia eremophila*	4	0.09	1	0.33
*	*Amsinckia tessellata*	4	0.09	1	0.33
	Choizanthe brevicornu	3	0.06	1	0.33
	Totals	4697	100.00	306	100.00

* Plant in a "dry" state
** Herbaceous perennial

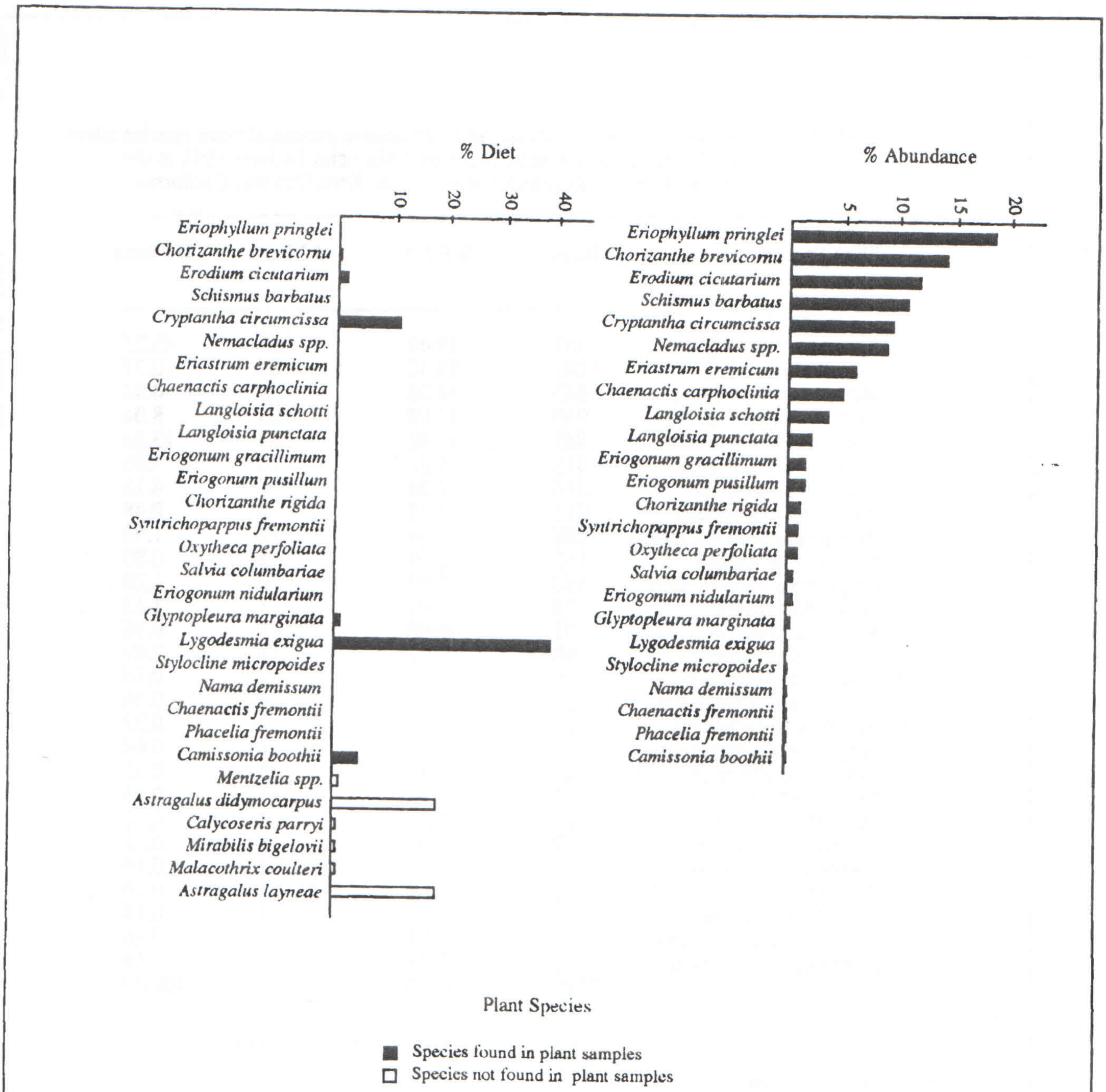

Figure 1. Comparison of relative abundance of plants along the feeding routes of the female tortoise (top graph) with the relative contribution of those plant species to the diet of the female tortoise (bottom graph).

Table 2. A comparison of the availability of succulent annual plants along the feeding routes with diet of the female tortoise.

Plant species	% Abundance	% Diet
Eriophyllum pringlei	17.94	0.00
Chorizanthe brevicornu	13.93	0.69
Erodium cicutarium	11.83	2.41
Schismus barbatus	10.69	0.00
Cryptantha circumcissa	9.54	11.34
Nemacladus spp.	8.97	0.00
Eriastrum eremicum	5.92	0.00
Chaenactis carphoclinia	4.96	0.00
Langloisia schotti	3.44	0.00
Langloisia punctata	2.29	0.00
Eriogonum gracillimum	1.91	0.00
Eriogonum pusillum	1.91	0.00
Chorizanthe rigida	1.34	0.00
Syntrichopappus fremontii	1.15	0.00
Oxytheca perfoliata	1.15	0.00
Salvia columbariae	0.57	0.00
Eriogonum nidularium	0.57	0.00
Glyptopleura marginata	0.38	1.37
Lygodesmia exigua	0.38	38.14
Stylocline micropoides	0.38	0.00
Nama demissum	0.19	0.00
Chaenactis fremontii	0.19	0.00
Phacelia fremontii	0.19	0.00
Camissonia boothii	0.19	4.47
Totals	100.00	58.42

Table 3. Number of bites of annual and herbaceous perennial plant species taken by the adult male tortoise between 3 May and 14 June 1991 at the Desert Tortoise Research Natural Area, Kern County, California.

	Plant Species	# Bites	% Bites	# Plants	% Plants
	Erodium cicutarium	1442	19.49	269	43.25
**	*Astragalus layneae*	1281	17.32	67	10.77
	Mentzelia eremophila	1042	14.08	31	4.98
**	*Stephanomeria parryi*	939	12.69	50	8.04
	Chorizanthe brevicornu	882	11.92	83	13.34
	Amsinckia tessellata	415	5.61	24	3.86
	Camissonia boothii	314	4.24	26	4.18
*	*Mentzelia eremophila*	211	2.85	3	0.48
**	*Euphorbia albomarginata*	188	2.54	12	1.93
	Lygodesmia exigua	142	1.92	5	0.80
	Cryptantha circumcissa	138	1.87	8	1.29
	Lotus humistratus	73	0.99	7	1.13
	Salvia carduacea	71	0.96	1	0.16
*	*Oxytheca perfoliata*	68	0.92	13	2.09
*	*Amsinckia tessellata*	49	0.66	1	0.16
	Chaenactis carphoclinia	30	0.41	4	0.64
*	*Pectocarya recurvata*	29	0.39	2	0.32
	Glyptopleura marginata	24	0.32	4	0.64
	Astragalus didymocarpus	21	0.28	2	0.32
	Nama demissum	12	0.16	1	0.16
**	*Mirabilis bigelovii*	11	0.15	2	0.32
**	*Lomatium mohavense*	7	0.09	2	0.32
	Pectocarya recurvata	3	0.04	1	0.16
*	*Thelypodium lasiophyllum*	2	0.03	1	0.16
	Eriogonum pusillum	2	0.03	1	0.16
*	*Lasthenia chrysostoma*	1	0.01	1	0.16
	Phacelia tanacetifolia	1	0.01	1	0.16
	Totals	7398	100.00	622	100.00

* Plant in a "dry" state
** Herbaceous perennial

Figure 2. Comparison of relative abundance of plants along the feeding routes of the male tortoise (top graph) with the relative contribution of those plant species to the diet of the male tortoise (bottom graph).

Table 4. A comparison of the availability of succulent annual and perennial plants along the feeding routes with diet of the male tortoise.

	Plant species	% Abundance	% Diet
	Erodium cicutarium	56.16	43.95
	Amsinckia tessellata	12.89	3.92
	Chorizanthe brevicornu	8.31	13.40
	Eriogonum pusillum	5.16	0.16
	Eriophyllum pringlei	4.58	0.00
	Eriastrum eremicum	2.87	0.00
	Cryptantha circumcissa	2.29	1.31
	Oxytheca perfoliata	2.29	2.12
	Eriogonum gracillimum	1.15	0.00
	Camissonia boothii	0.86	4.25
	Eriogonum nidularium	0.86	0.00
*	*Euphorbia albomarginata*	0.57	1.96
	Langloisia schotti	0.57	0.00
	Linanthus parryae	0.29	0.00
*	*Mirabilis bigelovii*	0.29	0.33
	Mentzelia spp.	0.29	5.07
	Stylocline micropoides	0.29	0.00
*	*Astragalus layneae*	0.29	10.95
	Totals	100.00	88.42

* Herbaceous perennial

rarely take more than 10 bites on a single plant. Curiously, both tortoises tended to decapitate *Camissonia boothii*, discard the inflorescence, and only consume the mid-section of the stem and leaves.

DISCUSSION

In February and March of 1992, the western Mojave Desert was deluged with precipitation. The excessive rains resulted in mass germination of annual plants and flowering of perennial species. Although climatic data are unavailable, winter storms and cold temperatures prevailed throughout February and March, so that tortoise activity did not begin until early April (pers. obs). Tortoises were active from early April to late June; thus, our observations , which were made between early May - mid June, roughly represented the latter half of the spring activity season. Unlike the eastern Mojave and Sonoran Deserts, the western Mojave Desert lacks a summer rainfall component, thus tortoise foraging activities are probably restricted to the spring months.

Although the female tortoise fed on 13 species of plants, 84% of her bites were taken from only 3 species (*Lygodesmia exigua, Astragalus layneae,* and *A. didymocarpus*). As preferred foods became dry, both tortoises switched to other species which were coming into flower. For example, from mid-April to the end of May, the annual legume, *Astragalus didymocarpus*, was in flower, during which time, the female tortoise fed largely upon this species. By June, *A. didymocarpus* were in a dried state, consequently, the female switched her preference to an annual composite, *Lygodesmia exigua*, which was beginning to flower. During the first half of June, the female fed almost exclusively on this species, however, if the female ever encountered an *Astagalus layneae, Calycoseris parryi, Mentzelia eremophila*, or *Mirabilis bigelovii*, she would opportunistically feed upon them. The aforementioned species are uncommon and all have patchy distributions throughout the area.

Although the male tortoise fed on 25 species of plants, nearly 80% of his bites were from only 5 species (*Erodium cicutarium, Astragalus layneae, Mentzelia eremophila, Stephanomeria parryi* and *Chorizanthe brevicornu*). The male also seemed to adjust his preferences as the season progressed. During the month of May while most annuals were still in flower, the male fed chiefly on native annuals (e.g., *Mentzelia eremophila* and *Chorizanthe brevicornu*) and native herbaceous perennials (e.g., *Stephanomeria parryi* and *Astragalus layneae*). By June, the exotic annual, *Erodium cicutarium*, was one of the few annuals that were still in a succulent state, consequently, it was frequently eaten by the male tortoise during this time.

The comparison between plant abundance and tortoise diet was conservative for two reasons. First, only the intershrub space was sampled, thus, plants growing in other microhabitats (e.g., shade of shrubs) were not represented in the samples. And second, several of the uncommon preferred species, tended to have clumped distributions, hence, by sampling the feeding routes, certain uncommon species were counted, whereas, if the habitat were sampled in a completely random manner, they probably would not have been detected.

The results obtained from this study suggest that tortoises are selective feeders. This is consistent with the findings of other studies on desert tortoise foraging ecology (Burge and Bradley 1976; Turner and Berry 1984; Turner et al. 1987; Avery 1992; Esque 1992). Further, many of the most-preferred species (e.g., *Astragalus* spp. and *Stephanomeria parryi*) were

the same species which were favored by tortoises at the Desert Tortoise Research Natural Area in the spring of 1973 (K. H. Berry, pers. comm.).

Similarities and differences became apparent between the female and male tortoises with regard to foraging behavior and food choices. Both tortoises seemed to prefer succulent forage over dried forage, native species over exotics, plants which grew in exposed areas rather than under or against shrubs, and both had similar strategies for locating uncommon plants (e.g., travel along small washes). The primary differences between the two tortoises concerned food choices. The disparity between their diets might be ascribed more to the availability of certain species of plants within the home range of a tortoise rather than individual tastes. For example, the annual plant community within the home range of the female tortoise was relatively devoid of weeds and exotics and thus contained a high diversity of native annuals. In contrast, the home range of the male tortoise was largely dominated by *Amsinckia tessellata* (a weedy native) and *Erodium cicutarium* (a non-native weed); the only areas where a diversity of native annuals could be found were in the washes. Hence, nearly all of the plants consumed by the male tortoise, other than *Erodium cicutarium* and *Chorizanthe brevicornu*, were found in the washes. Indeed, the majority of bites taken by the male tortoise were from the exotic, *Erodium cicutarium*. However, it is worth considering a couple of factors which may have had an influence on the diet selection of the male tortoise. First, as already mentioned above, qualitative differences in the annual plant communities existed among the home ranges of both tortoises. And second, both tortoises preferred plants in a succulent state over dried plants. By the end of May, many of the preferred native plants were drying out except for *Erodium*. At this time, the male tortoise began to feed heavily on this species. However, if the male tortoise ever encountered a preferred native species such as *Astragalus layneae*, that was in a succulent state, he would invariably consume the plant in entirety. Thus, it is possible that the male tortoise fed upon a large amount of *Erodium* simply because of the paucity of preferred native species within his home range.

To establish whether these similarities and differences are real, future studies will require larger sample sizes including immatures and juveniles. Furthermore, data should be collected over a period of many years so that foraging behavior could be studied in wet and dry years.

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