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Selective Spring Foraging by Juvenile Desert Tortoises (*Gopherus agassizii*) in the Mojave Desert: Evidence of an Adaptive Nutritional Strategy

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ABSTRACT. – **Desert tortoises (*Gopherus agassizii*) are known to be selective while foraging, but the nutritional consequences have not been examined. Due to the burden of potassium excretion, which entails loss of water and/or nitrogen, we predicted that desert tortoises would select plants that were high in water, protein, and an index of potassium excretion potential (PEP index), but low in potassium. The foraging behavior of 15 juvenile tortoises was studied in relation to the nutrient composition of annual plants in a naturally vegetated enclosure at the Ft. Irwin National Training Center, San Bernardino Co., California. The study was conducted during an El Niño year, when large numbers of annual species germinated. The numbers of plants eaten, the numbers of bites taken, and the number of plants bypassed while foraging were recorded. The numbers of bites per foraging session differed not only among plant species but also among plant parts. On average, the plants tortoises ate were higher in water, protein, and PEP, but not lower in potassium, than the plants they bypassed while foraging. Part of this difference was due to the low consumption of split grass (*Schismus* spp.) which accounted for about 86% of the biomass along the foraging routes. If split grass was omitted from the comparison, the plants eaten by tortoises were higher in protein and PEP (but not in water) and lower in potassium than the plants bypassed. Tortoises were selective in the parts of plants eaten; leaves accounting for more than 70% of all bites. In four primary food species, the parts eaten were higher in water, protein, and PEP, and lower in potassium, than the uneaten parts of these species. As a consequence of this selectivity the ingested diet of tortoises (weighted by numbers of bites per part) had an average PEP index of 15, which was very different from the mean value of 1.4 (weighted by proportion of plant biomass) for all species encountered. We conclude that in a year of abundant plant germination juvenile tortoises are able to self-select a diet of high nutritional quality, but this depends on access to species with high PEP parts, such as brown-eyed primrose (*Camissonia claviformis*) and desert dandelion (*Malacothrix glabrata*). If habitat is to be managed for the recovery of threatened tortoise populations, it is important to consider the impact of livestock grazing and other uses not only on the overall biomass of food resources, but on the nutritional quality of those resources.**

KEY WORDS. – **Reptilia; Testudines; Testudinidae; *Gopherus agassizii*; tortoise; ecology; foraging; food plants; nutrition; protein; potassium; California; USA**

Desert tortoises (*Gopherus agassizii*) in the Mojave Desert must respond to extreme seasonal and annual variation in the biomass and diversity of annual plants that are their primary foods (Esque, 1994; Oftedal, 2002). Virtually no germination occurs in drought years, whereas 50–70 species of winter annuals may germinate and flower in years of high rainfall such as during the El Niño Southern Oscillation (ENSO) (Rundel and Gibson, 1996; Oftedal, 2002). As this tortoise may have evolved under considerably milder climactic conditions with less severe fluctuation (Morafka and Berry, 2002), its ability to cope with wide fluctuations in food supply may be limited.

It is known that tortoises respond to annual variation in food availability by altering the composition of their diets. In the northeastern Mojave Desert, Esque (1994) found that more species of plants were available, and were eaten by tortoises, in years of higher rainfall. However, species of relatively low abundance may contribute disproportionately to the diet. For example, in an ENSO spring, tortoises at the Desert Tortoise Research Natural Area (Kern Co., California) fed heavily on uncommon legumes (*Astragalus didymocarpus, Lotus humistratus*) and an evening primrose (*Camissonia boothii*), although about 75% of the more than 40 annual species were sampled (Jennings, 1993).

In the face of abundance and diversity, tortoises can clearly be selective, but does this reflect "nutritional wisdom," i.e. the selection of plants of high nutritional quality? Nutritional quality can be variously described, but is best defined with respect to nutrients that are limiting to the forager (Oftedal, 1991). As vertebrates, tortoises are presumed to require about 50 different nutrients, but those most likely to be limiting factors in the Mojave Desert are shortfalls of water, protein, phosphorus, sodium, and possibly copper or zinc, and excesses of potassium and calcium (Oftedal and Ullrey, unpubl. data).

The interactions among potassium, protein, and water in tortoise diets may be especially important. Desert plants typically contain high concentrations of potassium, which in excess is potentially toxic (Minnich, 1977; Oftedal, 2002). Tortoises lack salt glands and hence must excrete any excess via renal routes (Minnich, 1972, 1977; Bentley, 1976). Excretion of this electrolyte in fluid urine is wasteful of water since tortoise urine contains no more than about 165 mmol potassium even when tortoises are dehydrated or potassium-loaded (Nagy and Medica, 1986; Peterson, 1996; Oftedal, 2002). The alternative is to sequester urinary potassium into urate precipitates (Minnich, 1972). Captive studies have demonstrated that both the amounts of urates and their potassium concentration increase as dietary potassium increases (Oftedal et al., 1994). However, urate production entails a large loss of nitrogen as urates contain twice the nitrogen content (about 30%) of protein. Excretion of excess potassium involves a substantial cost to either water or nitrogen budgets.

A proposed index of food composition, the Potassium Excretion Potential (PEP) (Oftedal, 2002), accounts for both the amount of potassium in food and the excretory capacity derived from food water and protein. We hypothesized that juvenile tortoises should have a strong incentive to select foods low in potassium and/or high in water and nitrogen (as protein), and thus should select foods of high PEP content.

Captive desert tortoises offered choices between foods differing only in concentrations of potassium salts avoid potassium (Oftedal et al., 1995), as do meadow voles, *Microtus pennsylvanicus* (Mickelson and Christian, 1991). Yearling *Gopherus agassizii* grew faster in captivity on diets containing 20 and 30% protein than on a diet containing 10% protein (Oftedal, unpubl. data). Selection of foods high in protein is also thought to be important for growth of juvenile Bolson tortoises, *Gopherus flavomarginatus,* and slider turtles, *Trachemys scripta* (Adest et al., 1989; Avery et al., 1993). As juvenile desert tortoises gain mass predominantly in the spring (Nagy et al., 1997), selection of a high PEP diet may be especially important to nitrogen retention and protein deposition at that time.

A study was initiated to determine if juvenile tortoises are selective in feeding during late spring of an ENSO year, and if such selection is related to diet quality as measured by the PEP index. We predicted that selection would result in a diet higher in PEP index than that of the overall biomass of annuals that tortoises encounter while foraging. This study utilized the unique research facilities at the Fort Irwin Study Site (FISS) at which acclimated juvenile tortoises may be observed foraging in a naturally-vegetated, but predator-repelling, enclosure (Morafka et al., 1997).

METHODS

Site and Animals. — In April 1998 we monitored foraging behavior of 15 juvenile tortoises in a large (60 x 60 m) fenced enclosure (FISS 2) in an otherwise undisturbed area (35°09'N, 116°30'W) of the U.S Army's Fort Irwin National Training Center, about 58 km northeast of Barstow, San Bernardino, California. The vegetation at this site in the central Mojave Desert is dominated by creosote bush (*Larrea tridentata*) and white bursage (*Ambrosia dumosa*), but includes other shrubs and perennials such as wolfberry (*Lycium pallidum* var. *oligospermum*), mormon tea (*Ephedra* spp.), range ratany (*Krameria erecta*), big galleta grass (*Pleuraphis rigida*), and wishbone bush (*Mirabilis bigelovii* var. *retrorsa*). Rainfall measurements by an automated station at this site indicated precipitation of 14.7 cm from September 1997 through April 1998, including one rainfall event of 2.59 cm. In the Mojave Desert massive germination normally requires acute rainfall events of 2.5 cm or more (Beatley, 1974); rainfall

Table 1. Annual plants growing at Ft. Irwin Study Site (FISS), April–May 1998. * = in enclosure.

Species	Common Name
Asteraceae	
**Chaenactis carphoclinia*	Pebble pincushion
**Chaenactis fremontii*	Fremont pincushion
**Coreopsis bigelovii*	Bigelow tickseed
**Eriophyllum wallacei*	Yellow woolly-daisy
**Malacothrix glabrata*	Desert dandelion
**Rafinesquia neomexicana*	Desert chicory
Stylocline micropoides	Desert nest-straw
Boraginaceae	
**Amsinckia tesselata*	Fiddleneck
**Cryptantha angustifolia*	Creosote cryptantha
**Cryptantha circumscissa*	Cushion cryptantha
**Cryptantha dumetorum*	Flexuous cryptantha
Cryptantha maritima	Guadelupe cryptantha
**Cryptantha micrantha*	Redroot cryptantha
**Cryptantha nevadensis*	Nevada cryptantha
**Cryptantha pterocarya*	Wing-nut cryptantha
Pectocarya platycarpa	Broad-margined combseed
Pectocarya pencillata	Slender combseed
Brassicaceae	
**Caulanthus cooperi*	Cooper caulanthus
Dithryea californica	Spectacle pod
Guillenia lasiophylla	California mustard
**Lepidium lasiocarpum*	Modest peppergrass
**Streptanathella longirostris*	Longbeak
Caryophyllaceae	
**Achyronychia cooperi*	Frost-mat
Geraniaceae	
**Erodium cicutarium*	Red-stemmed filaree
Hydrophyllaceae	
Nama demissum	Purple mat
**Phacelia crenulata*	Notch-leaved phacelia
Loasaceae	
Mentzelia obscura	White-stemmed blazing star
Onagraceae	
**Camissonia boothii*	Woody bottle-washer
**Camissonia claviformis*	Brown-eyed primrose
**Oenothera primiveris*	Yellow evening primrose
Papaveraceae	
**Eschscholzia minutiflora*	Little gold poppy
Plantaginaceae	
**Plantago ovata*	Woolly plantain
Poaceae	
**Schismus barbatus, S. arabicus*	Split grass
Polemoniaceae	
**Gilia* sp.	Gilia
**Loeseliastrum mathewsii*	Desert calico
Polygonaceae	
**Chorizanthe brevicornu*	Brittle spineflower
**Eriogonum pusillum*	Low buckwheat
Eriogonum reniforme	Kidney-leaf buckwheat

in the FISS region averages about 10 cm over a rain year (July–June). The 1997–98 rainfall pattern, associated with an ENSO, permitted the germination of a wide variety of winter annuals ($n = 38$) in the immediate area (Table 1).

The enclosure, FISS 2, was populated by 16 juvenile tortoises that had lived there since April 1995; one animal was not observed in this study. These animals were 5–7 years of age and derived from clutches laid in a nearby enclosure by wild females (Morafka et al., 1997). The juveniles appeared free of signs of upper respiratory tract disease (URTD). URTD is a major cause of morbidity in some areas of the Mojave Desert (Jacobson et al., 1991), but the local tortoise population has had little exposure to the mycoplasma that causes URTD (E. Jacobson and I. Schoemaker, unpubl. ELISA data, 1994). All tortoises had access to about 77% of the enclosure; a drift fence partitioned off a 14 x 60 m strip on the south side of the enclosure. Tortoise density was 58 tortoises per hectare. All animals were weighed and measured on 15–22 March 1998. Tortoises averaged 124 g body mass (range 73–124 g) and had a mean midline carapace length of 81.0 mm, carapace width of 65.1 mm, maximum plastron length of 77.6 mm, and shell height of 37.1 mm.

Behavioral Observations. — Tortoise foraging was observed during a brief period (24 April – 1 May 1998) to minimize plant phenological variation during the study. Juvenile tortoises typically were active in the morning and in the late afternoon. Most observations were conducted between 0600–0900 hrs and 1400–1700 hrs (Pacific Standard Time), although on 26 April two animals were observed foraging during the middle of the day. Active juveniles located by visual scan were followed individually until they ceased biting at plants for at least 5 min, or until they entered a burrow. Once a foraging session was terminated, another foraging juvenile was located and followed, until all foraging activity had ceased. Different individuals were followed in sequential observation periods to increase sample size.

Tortoises were observed with binoculars at a distance of 1–6 m. The animals were accustomed to human presence and did not appear to pay attention to observers. The following data were recorded: time and location at the start and stop of foraging observations, the number and species of individual plants (other than split grass, *Schismus* spp.) that tortoises encountered within a distance of one carapace width on each side, the number and species of individual plants at which tortoises stopped to feed, and the numbers of bites made of each species and plant part. Only bites that appeared to be productive (i.e., animal observed to contact or pull on a plant, food seen in mouth, or swallowing motions seen) were counted as feeding bites. The speed of travel was estimated as 2.6 m per min (range 1.9–3.3) based on two individuals whose exact foraging paths were measured by tape measure for about 30 min each on the morning of 3 May.

Plant Sampling and Nutrient Analysis. — Plants were identified to species based on prior plant collections made in the Mojave Desert, as well as keys in Munz (1974) and the Jepson Manual (Hickman, 1993). Pressed voucher specimens are available at the Smithsonian National Zoological Park, Washington D.C.

Plant samples were collected in the immediate vicinity of the enclosure for nutritional analysis. A similar number of annual species ($n = 25$) were observed within 30 m east and west of the enclosure as in the enclosure ($n = 26$). Several additional uncommon species (Table 1) grew within a large wash to the north of the enclosure. As far as possible, plants were collected from the same microhabitat, at the same phenological stage, and of a similar size as plants observed growing within the enclosure. Plant samples were collected before (19–20 April), during (29–30 April), and after (4–5 May) the observation period.

Entire plants were collected by snipping off the root at ground level. Adhering sand and debris were removed. Depending on mass, 5 to 75 individual plants were collected per sample, and weighed to the nearest 0.01 g; the average mass of an individual plant was calculated as sample weight divided by number of plants per sample. In most cases duplicate samples were collected. At the second and third collections species upon which tortoises were observed to feed were separated into parts that were eaten (leaves, and sometimes inflorescences, immature fruit, or young stems) and the remainder that was not eaten. Plants were collected directly into plastic (ziplock) bags which were promptly sealed to avoid moisture loss. In the field these bags were placed on ice in insulated coolers. Samples were frozen at –20°C within 40 hrs of collection and kept frozen until analysis.

Thawed samples were dried to constant weight at 50°C in a forced convection oven and ground to pass through a screen (0.5 mm hole size) in a Wiley food mill. Subsamples weighing 8–10 mg were assayed in triplicate for nitrogen (N) in a CHN gas analyzer (Model 2400 Series II; Perkin Elmer Corp., Norwalk, CT) optimized to give equivalent results as Kjeldahl chemical analysis. Crude protein (CP) was calculated as N*6.25. Duplicate subsamples were digested in nitric acid in pressurized vessels in a microwave digestion system (Mars Series 5; CEM Corporation, Matthews, NC); temperature was ramped from ambient to 220°C in 15 min followed by 15 min at 220°C. This procedure gives comparable results as standard perchloric acid-nitric acid digestion at ambient pressure. Digested subsamples were diluted in a cesium chloride solution (final concentration 2000 ppm cesium) to prevent interferences and assayed for potassium (K) content by atomic absorption spectroscopy (Model Smith Hieftje 12; Thermo-Jarrell Ash Co., Franklin, MA) using an air-acetylene flame and detection at 766.5 nm. The Potassium Excretion Potential (PEP) index (g per kg dry matter [DM]) was calculated as follows:

$$\mathrm{PEP} = 6.5 * \text{water (g/g DM)} + 0.976 * \mathrm{CP\%} - 10 * \mathrm{K\%}$$

where CP and K are on a DM basis (Oftedal, 2002).

Biomass in and out of the Enclosure. — After the observational trial (on 5–12 May), the frequency and aboveground standing crop of annual plant species were measured at three sites: one site within the enclosure and two in the vicinity but outside the enclosure. A 100 m linear transect was established at each site; due to the limited dimensions of the enclosure (60 m width) the within-enclosure transect consisted of two parallel 50 m legs. Twenty-four paired 0.0929 m^2 plots were sampled at 8 m intervals along each transect. One plot was placed under a shrub (*Larrea*, *Ambrosia*, or *Lycium*) and one in the space between shrubs at one meter to the left or right of the centerline (determined by coin toss). Annual plants within each plot were counted (except split grass, which was too abundant to count), clipped off at ground level, oven-dried to constant weight and weighed to 0.01 g. Results were averaged across plots within or outside the enclosure and expressed as plants per m^2 or g/m^2.

Data Analysis. — Foraging sessions were considered to be comprised of three separate activities: 1. walking past plants (bypassing) without stopping to feed, 2. stopping at a plant to feed on it, and 3. taking bites of plants. The first was quantified by counting plants bypassed, the second by counting plants stopped at for foraging, and the third by counting the bites taken. While each of these is separate behaviors, they are not independent: 1 and 2 are mutually exclusive, while 2 is a necessary precursor to 3. Comparison of these activities is thus not informative. However, if tortoises treated all plant species the same, we would expect the pattern of rejection (bypassing), initial acceptance (stopping to feed) and ongoing foraging (taking bites) to be similar across species. We therefore compared the interactions between activity and plant species by factorial analysis of variance (ANOVA). Time of day (AM, PM) was also included as a factor. A second factorial ANOVA, using only the bite count data set, examined part eaten (leaves, flowers, fruit, stems), time of day, and plant species, and their interactions. Preliminary analyses indicated that size class of the juvenile tortoise had no significant effect, nor any significant interactions, in the above analyses, and therefore this factor was omitted.

The water, protein, potassium, and PEP concentrations of the ingested diet and of the plants bypassed were calculated for each tortoise based on 1. the numbers of individual plants eaten or bypassed, 2. the average fresh and dry masses of these plant species (as determined during nutritional analysis), and 3. the assayed nutrient values of the entire plants (except roots). The differences in nutrient concentrations between ingested plants and bypassed plants were tested by paired t-tests, using data for each animal ($n = 15$) as individual observations.

Eaten and uneaten parts were collected separately in some samples of the major food plants. The nutrient composition of the aggregate eaten portion and of the aggregate uneaten portion could be calculated for these samples and were compared by paired t-tests, using data for each paired plant sample ($n = 20$) as individual observations.

RESULTS

Plant Abundance and Biomass. — A total of 29 species of annuals were observed in the pen, representing 76% of the 38 species of annuals observed in the surrounding creosote-white bursage scrub (Table 1). Split grass (*Schismus barbatus*, including *S. arabicus*) was particularly dense, forming a carpet both between and under shrubs. Both inside and outside the pen, the most speciose families were the Asteraceae, Boraginaceae, and Brassicaceae. Prior to the onset of foraging observations (19–20 April), ten species of annual plants were ranked as common or abundant in the pen based on visual scanning (Table 2). In comparison, a transect survey of the dry biomass of annuals inside and outside the enclosure after foraging observation (5–12 May) did not include two species, desert dandelion (*Malacothrix glabrata*)

Table 2. Biomass (g/m^2) of annual plants between and under shrubs at FISS, May 1998.

Species	Inside Pen (T1) Between	Inside Pen (T1) Under	Outside Pen (T2-3) Between	Outside Pen (T2-3) Under	Average (T1-3)	% of Total Biomass
Schismus spp.[1]	41.66	46.39	18.63	47.54	36.73	71.66
Chaenactis fremontii	0.54	1.40	0.36	12.97	4.76	9.30
Malacothrix glabrata			0.15	7.75	2.64	5.14
Cryptantha angustifolia	2.30	0.10	3.24	1.26	1.90	3.70
Camissonia claviformis	0.38		0.57	2.82	1.19	2.33
Cryptantha dumetorum		3.14		1.38	0.98	1.92
Erodium cicutarium	0.85	0.12	0.06	1.96	0.83	1.63
Plantago ovata	0.68		1.94	0.19	0.82	1.61
Lepidium lasiocarpum			0.22	0.68	0.30	0.59
Cryptantha circumscissa			0.72	0.12	0.28	0.54
Eriogonum spp.[2]			0.56	0.01	0.19	0.37
Cryptantha micrantha	0.01		0.02	0.47	0.16	0.32
Cryptantha pterocarya			0.06	0.37	0.14	0.28
Chorizanthe brevicornu	0.10	0.57		0.01	0.12	0.23
Loeseliastrum matthewsii	0.05				0.01	0.02
Other spp.[3]		0.17	0.26	0.23	0.13	0.24
All species combined	46.56	51.89	26.79	77.76	51.26	

[1] Includes the species *Schismus barbatus* and *S. arabicus*. [2] Includes the species *Eriogonum pusillum* and *E. reniforme*. [3] Includes the following species: *Pectocarya platycarpa, P. pencillata, Caulanthus cooperi, Guillenia lasiophylla, Eriophyllum wallacei, Stylocline micropoides, Gilia* spp., and *Cryptantha maritima*.

Table 3. Plants encountered by tortoises foraging in FISS enclosure, 24 April – 1 May 1998.

Species[1]	Plants Encountered *n*	Percent all plants (%)	Plants dried *n*	Indiv. plant dry mass (g)	Species dry mass[2] (g)	Species as % of total dry mass (%)
Schismus spp.[3]	239400	98.06	315	0.18	42074	86.31
Cryptantha angustifolia	1741	0.71	140	0.56	967	1.98
Camissonia claviformis	1054	0.43	54	2.08	2197	4.51
Erodium cicutarium	688	0.28	98	1.91	1311	2.69
Chaenactis fremontii	596	0.24	58	3.02	1802	3.70
Plantago ovata	346	0.14	100	0.54	186	0.38
Malacothrix glabrata	104	0.043	20	1.24	69	0.14
Loeseliastrum matthewsii	82	0.034	128	0.27	23	0.05
Chorizanthe brevicornu	52	0.021	45	0.71	37	0.08
Lepidium lasiocarpum	26	0.011	66	0.87	23	0.05
Eriogonum inflatum	17	0.007	10	1.20	20	0.04
Camissonia boothii	10	0.004	20	1.67	17	0.03
Phacelia crenulata	4	0.002	23	3.64	15	0.03
Oenothera primiveris	3	0.001	2	1.06	3	0.01
Rafinesquia neomexicana	2	0.001	11	2.64	5	0.01
Other species[4]	4	0.001		—	—	
All species	244129				48749	

[1] Other annuals observed in pen but not in foraging path: *Achyronychia cooperi, Amsinckia tesselata, Caulanthus cooperi, Chaenactis carphoclinia, Coreopsis bigelovii, Cryptantha circumscissa, Cryptantha dumetorum, Cryptantha micrantha.* [2] Calculated as number of plants encountered x dry mass of individual plant. [3] Number of plants and species dry mass estimated from density of split grass in enclosure, as determined by biomass survey (Table 2) and area encompassed by foraging paths (1010 m^2). [4] Includes *Eriophyllum wallacei* ($n = 2$), *Eschscholzia minutiflora* and *Gilia* sp.

and modest peppergrass (*Lepidium lasiocarpum*), that had been common or abundant at the outset (Table 2). This may reflect plant loss due to senescence or tortoise foraging, as well as sampling error given the small size of the transect plots.

In the enclosure the annual biomass between and under shrubs was similar, but this was not apparent outside the enclosure (Table 2). The average biomass in the pen was similar to the overall average for all transects, 51.3 g/m^2. The species with greatest biomass both in and out of the pens, and both between and under shrubs, was split grass, *Schismus* spp. Seven other species each provided more than 0.5 g/m^2 on average (Table 2). Variation in biomass among the three transects (not shown) was believed to be due to sampling error and local heterogeneity of habitat, but was not evaluated statistically (Table 2).

All plants that foraging tortoises walked past or approached within one body width on each side, whether eaten or not, were classified as encountered. We estimated that during 33.2 hrs foraging, the tortoises encountered more than 240,000 plants, all but 4725 being split grass (Table 3). Although tortoises encountered 17 species in addition to

Table 4. Numbers of plants eaten (as % of plants encountered) and number of bites taken by juvenile tortoises.

Species[1]	Tortoises eating	Plants eaten *n*	Plants eaten %	Total bites	Bites/ plant	Plant parts eaten (bites)[2] Lv	St	Lv/St	Fl	Im fr	Fl/Im fr	Ped
Winter Annuals												
Camissonia claviformis	13	148	14.0	2348	15.9	**1989**	**248**	**64**	25	22		
Plantago ovata	10	120	34.7	1039	8.7	**539**			4	**466**		30
Erodium cicutarium	13	113	16.4	949	8.4	**676**	36		**45**	**192**		
Malacothrix glabrata	7	22	21.2	253	11.5	**143**		**84**	26			
Cryptantha angustifolia	9	42	2.4	245	5.8	**147**	8		**15**	**16**	**59**	
Schismus spp.	12	42	<0.1	112	2.7	3				**74**		35
Chaenactis fremontii	8	15	2.5	61	4.1	**52**	2		6	1		
Loeseliastrum matthewsii	4	8	9.8	24	3.0	**24**						
Oenothera primiveris	1	2	66.7	28	14.0	**28**						
Phacelia crenulata	1	1	25.0	7	7.0	**7**						
Chorizanthe brevicornu	1	1	1.9	3	3.0		3					
Lepidium lasiocarpum	1	1	3.8	1	1.0	1						
Eriophyllum wallacei	1	1	50.0	2	2.0	2						
Perennials[3]												
Eriogonum inflatum	1	1	5.9	**4**	4.0	4						
Pleuraphis rigida	1	1	1.4	3	3.0		3					
Mirabilis bigelovii	1	1	—	1	1.0	1						
All Plants	15	519		5080		3616	300	148	121	771	59	65

[1] See Table 1 for common names; tortoises were also observed to ingest a caterpillar of the white-lined sphinx moth, (*Hyles lineata*), a white grub (unknown taxon), and half of a cocoon; several bites were also taken of two tortoise feces and of an unknown stem. [2] Parts in bold collected for analysis (Table 7); Lv = leaves; St = stems; Lv/St = mixed leaves and stems; Fl = flowers; Im fr = immature fruit; Fl/Im fr = mixed flowers and immature fruit; Ped = peduncles. [3] Species: *E. inflatum* = desert trumpet, *P. rigida* = big galleta, *M. bigelovii* var. *retrorsa* = wishbone bush.

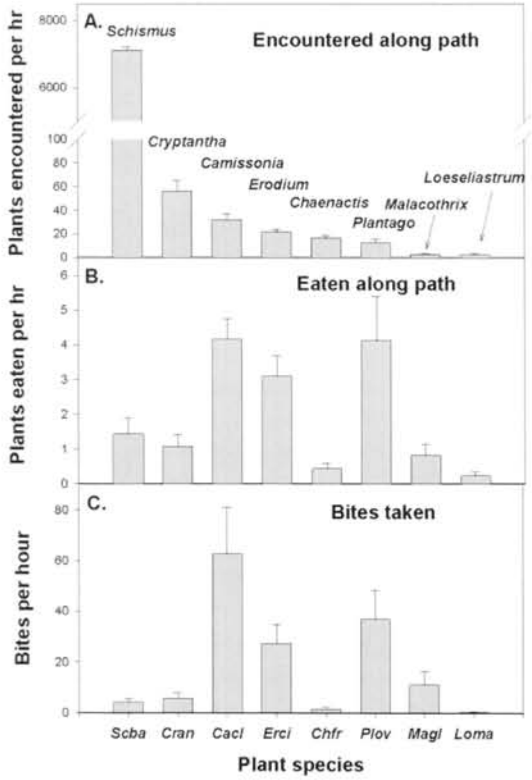

Figure 1. Foraging activity of juvenile desert tortoises with respect to the 8 most frequently encountered plant species along their foraging path. **A.** Number of plants encountered per hour observation time. Split grass (*Schismus* spp.) was estimated from biomass density and an estimate of the distance travelled by juveniles (see text), but other plants were counted as the plants were encountered to within one carapace width on each side by walking tortoises. **B.** Number of plants that tortoises stopped to eat per hour observation time. **C.** Number of feeding bites of each plant species taken per hour observation time. Error bars refer to s.e.m. for 48 individual foraging sessions. Species as follows: *Scba* = *Schismus barbatus* and *S. arabicus*; *Cran* = *Cryptantha angustifolia; Cacl* = *Camissonia claviformis; Erci* = *Erodium cicutarium; Chfr* = *Chaenactis fremontii; Plov* = *Plantago ovata; Magl* = *Malacothrix glabrata; Loma* = *Loeseliastrum matthewsii.*

split grass, only nine of these were represented by more than 20 plants (Table 3).

The total dry biomass of each species encountered can be estimated from the numbers of plants encountered and the average dry mass of each plant species. Nine species of annuals (other than split grass) represented more than 20 g dry matter (DM) on the collective foraging path (Table 3). As split grass was not counted, its biomass was determined from the average biomass of this species in the intershrub space of the pen (41.7 g/m^2) multiplied by the estimated distance traveled by all tortoises (5180 m) and the width of the foraging path ($3 * 0.065 = 0.195$ m). The collective foraging path encompassed 1040 m^2, 42.1 kg DM split grass and 6.7 kg DM of other plants (Table 3). Split grass constituted 86% of biomass on the foraging route (Table 3), as compared to 89% of biomass in the enclosure, based on the biomass survey (Table 2).

Plants Eaten by Juvenile Tortoises. — During 48 foraging sessions tortoises took 5080 bites of 522 plants of 16 species. On average, tortoises took 159 bites of 17 plants per hour, although the bite rate per hour varied from 49 to 301 among individuals. Individual tortoises were observed to feed on 3 to 9 plant species. Seven plant species were eaten by seven or more individual tortoises, desert calico (*Loeseliastrum matthewsii*) was eaten by four tortoises, while eight species were eaten by only one tortoise (Table 4). Other foods occasionally ingested included a caterpillar, an insect cocoon, an unidentified insect larva (white grub) and tortoise feces (8 bites); these were not included in the aggregate bite counts or in dietary evaluations.

The eight species that were encountered most frequently along the foraging routes (Fig. 1) were treated differently by foraging tortoises. The two most frequently encountered species, split grass and creosote cryptantha (*Cryptantha angustifolia*), were not the most frequently eaten nor the species of which most bites were taken (Fig. 1). Even if frequently encountered split grass (ca. 7100 plants per hour) is excluded, there was a highly significant interaction between activity type (bypassing plants, stopping to eat plants, and bites taken) and plant species (3-way ANOVA, $F = 9.98$, $df = 14, 1105$, $p < 0.0001$); however time of day (AM, PM) had no significant effect or interaction ($p > 0.20$ for all). Tortoises stopped frequently to feed at, and took many bites per hour of, *Camissonia claviformis, Erodium cicutarium,* and *Plantago ovata* (Fig. 1).

Tortoises took a particularly large number of bites (per plant eaten) of three species: *Camissonia claviformis*, *Oenothera primiveris*, and *Malacothrix glabrata* (Table 4). However, as only 3 plants of *Oenothera primiveris* were encountered (Table 3), it did not comprise much of the diet. The percentage use (plants eaten as a percent of plants encountered) varied among species. For example, tortoises ate only 0.02% of the estimated 240,000 plants of split grass encountered and 2–3% of *Cryptantha angustifolia* and *Chaenactis fremontii*, but ate 14–35% of *Plantago ovata*, *Malacothrix glabrata*, *Erodium cicutarium*, and *Camissonia claviformis* (Table 4).

Camissonia claviformis accounted for nearly half (46%) of all bites taken by juvenile tortoises. This reflected the large numbers of plants encountered, the relatively high percentage use, and the large number of bites taken per plant. Tortoises ate predominantly the leaves of this species, as they did for most species (Table 4). Factorial ANOVA revealed significant differences in numbers of bites among the eight primary species eaten ($F = 11.5$, $df = 7, 1472$, $p < 0.0001$) and among plant parts ($F = 23.1$, $df = 3, 1472$, $p < 0.0001$), as well as between these two factors ($F = 8.1$, $df = 21, 1472$, $p < .0001$). However, time of day (AM vs. PM) had no effect on bite counts nor any significant interactions ($p > 0.15$ for all). Bites of leaves represented 72% of all bites (Table 4); the only food plant for which leaves were rarely eaten was split grass. Immature fruit were important food parts for split grass and woolly plantain (*Plantago ovata*) (Table 4). Although flowers of a number of species were eaten, flowers did not comprise a large proportion of bites of any species.

We had the impression that tortoises avoided *Camissonia claviformis* plants from which most leaves

Table 5. The composition of plants encountered by foraging tortoises.

			Nutrient Composition of Plants							
			Water (% FWB)		Protein (% DMB)		Potassium (% DMB)		PEP (g/kg DM)	
Species	Stage[1]	*n*	x	se	x	se	x	se	x	se
Schismus spp.	mfr,sen	5	28.5	5.8	4.93	0.40	0.71	0.05	0.58	1.22
Cryptantha angustifolia	imfr, mfr	10	70.2	1.6	9.09	0.70	2.80	0.21	-3.21	0.91
Camissonia claviformis	imfr, mfr	7	74.9	0.5	9.41	0.55	1.55	0.10	13.33	1.39
Erodium cicutarium	imfr, mfr	7	64.2	1.3	9.53	0.58	1.73	0.11	4.66	1.18
Chaenactis fremontii	imfr, mfr	7	70.3	1.0	6.05	0.44	1.60	0.08	5.90	1.38
Plantago ovata	imfr	7	59.1	1.1	7.22	0.39	0.87	0.04	7.91	0.50
Malacothrix glabrata	imfr	3	76.6	1.0	7.31	0.58	2.37	0.22	4.89	3.44
Loeseliastrum matthewsii	bd,fl	7	68.7	0.6	5.38	0.47	1.41	0.14	5.71	0.82
Chorizanthe brevicornu	imfr, mfr	3	58.6	4.3	6.26	0.67	1.31	0.07	2.62	1.12
Lepidium lasiocarpum	imfr, mfr	4	49.4	2.9	10.75	0.22	1.11	0.05	5.92	1.29
Eriogonum inflatum	imfr	2	72.0	1.5	9.30	1.10	1.68	0.21	9.54	0.01
Camissonia boothii	imfr	7	70.5	0.7	7.24	0.17	1.29	0.02	9.88	0.55
Phacelia crenulata	imfr, mfr	3	70.4	0.9	7.52	0.82	1.93	0.04	3.60	0.84
Oenothera primiveris	imfr	1	72.6	—	5.74	—	2.37	—	4.89	—
Rafinesquia neomexicana	fl,imfr	2	75.6	1.1	7.24	0.32	2.46	0.18	2.69	0.19

[1] Stage refers to the most advanced reproductive parts: bd = flower bud, fl = flower, imfr = immature fruit, mfr = mature fruit, sen = beginning to senesce.

had been removed, although the amount of remaining leaf on plants that were bypassed was not routinely recorded. On 3 May, after observations ended, the annual plants in 8 random between-shrub plots were inspected. The only plants with evident feeding effects (clipped or missing leaves, stems or inflorescences) were *Camissonia claviformis* (82% of 33 plants) and *Plantago ovata* (18% of 33 plants); feeding effects were not evident in other species, including *Cryptantha angustifolia* (n = 30), *Erodium cicutarium* (n = 17) and *Chaenactis fremontii* (n = 9). Split grass was excluded from this assessment due to its abundance and low percentage use. The extent of feeding effect was subjectively ranked as light, moderate, or heavy. In *Plantago ovata* one plant each had heavy and moderate effects; four others had light effects. In *Camissonia claviformis* 25 of 27 (93%) affected plants had sustained heavy feeding effects, while the remaining two showed moderate effects.

Nutrient Composition of Tortoise Diets. — The annual plants encountered by foraging tortoises contained 29 to 77% water; on a dry matter basis (DMB) they varied from 5 to 11% crude protein, 0.7 to 2.8% potassium and –3 to 13 in the calculated Potassium Excretion Potential (PEP) index (Table 5).

Table 6. The nutrient composition of plant parts eaten by tortoises.

				Nutrient Composition of Plant Parts								
Species[1]	Part	Bites by Part[2]			Water (% FWB)		Protein (% DMB)		Potassium (% DMB)		PEP (g/kg DM)	
		n	(% total)	*n*	x	se	x	se	x	se	x	se
Camissonia claviformis	lvs	2021	41.84	5	77.3	0.8	11.72	0.75	1.37	0.15	19.9	2.5
	yng st	280	5.80	2	79.9	0.1	8.00	0.54	1.73	0.02	16.4	0.2
Plantago ovata	lv	539	11.16	2	67.1	0.8	8.95	0.69	0.89	0.06	13.1	2.9
	im fr	466	9.65	5	57.3	1.7	8.33	0.59	0.82	0.01	8.8	0.2
Erodium cicutarium	lv	676	14.00	2	68.0	1.8	14.35	0.75	1.51	0.04	12.8	1.5
	fl/im fr	237	4.91	3	69.2	3.1	13.46	0.52	1.61	0.04	12.0	2.6
Malacothrix glabrata	lv	227	3.83	1	81.5	—	5.94	—	1.13	—	23.2	—
Cryptantha angustifolia	lv	147	3.04	2	75.1	1.0	11.49	0.05	3.74	0.23	-6.6	1.3
	fl/im fr	90	1.86	3	75.6	1.1	14.05	0.54	3.90	1.47	-5.0	1.5
Schismus spp.	im fr	74	1.53	3	17.5	3.4	7.71	0.59	0.71	0.01	1.9	0.4
Chaenactis fremontii	lv	52	1.08	3	81.9	0.4	4.18	0.51	1.51	0.30	18.4	3.9
Loeseliastrum matthewsii	lv	24	0.50	3	73.0	0.5	8.04	0.39	2.03	0.04	5.1	0.6
Oenothera primiveris	lv	28	0.58	1	82.9	—	6.17	—	2.22	—	15.4	—
Phacelia crenulata	lv	7	0.14	1	72.8	—	7.78	—	1.70	—	8.0	—
Eriogonum inflatum	lv	4	0.08	2	73.8	0.6	9.53	1.19	1.74	0.20	10.3	0.3
All species		4872										
Average for ingested diet, weighted by bites					72.0		10.9		1.42		15.0	

[1] See Table 1 for common names and Table 5 for abbreviations for parts. [2] When bites were recorded for mixed parts (e.g., leaves and stems) half of the bites were assigned to each part for this analysis; percentage is calculated relative to the total bites for parts for which nutrient composition data are available (n = 4872).

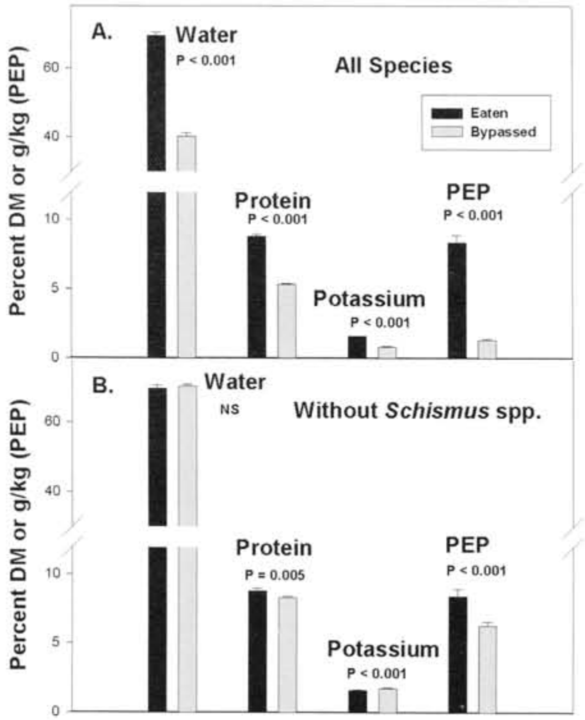

Figure 2. Comparison of the nutrient composition of eaten plants to those that were bypassed by foraging tortoises. Nutrient values were calculated for each tortoise ($n = 15$, all foraging sessions combined) based on numbers and masses of plants eaten or bypassed, as well as the nutrient composition of entire plants of each species (Table 5). The means for eaten and bypassed plants were compared by paired t-tests, using each tortoise as a replicate. Error bars indicate s.e.m.; those for potassium were too small (0.012–0.049) to be visible.

By combining these analytic data with the numbers of plants of each species encountered by each foraging tortoise, and the average wet and dry masses of plants of these species, it was possible to calculate the nutrient composition of the biomass encountered by each tortoise. The overall biomass was rather low in water (41%), protein (5.4% DMB), potassium (0.85% DMB) and PEP (1.4 g/kg DM), reflecting the very high proportion of biomass represented by split grass (Table 3) which at the time of this study was in a mature fruit-early senescent stage that was low in all of these constituents (Table 6).

As noted above, tortoises did not feed indiscriminately, but appeared to prefer to eat some species (Fig. 1). The nutrient concentrations in eaten and bypassed biomass could be calculated separately using data from Table 5. There was a large difference ($P < 0.001$) in each measured constituent between eaten and bypassed plants, with the eaten plants being higher in water, protein, potassium, and PEP (Fig. 2). This difference appeared to stem primarily from the avoidance of split grass which represented 86% of the encountered biomass (Table 3). However, if split grass was omitted from the comparison, there were still significant differences in protein, potassium, and PEP (but not in water) between the eaten and bypassed biomasses. The eaten plants were higher in protein and PEP, but lower in potassium, than the bypassed non-*Schismus* plants (Fig. 2).

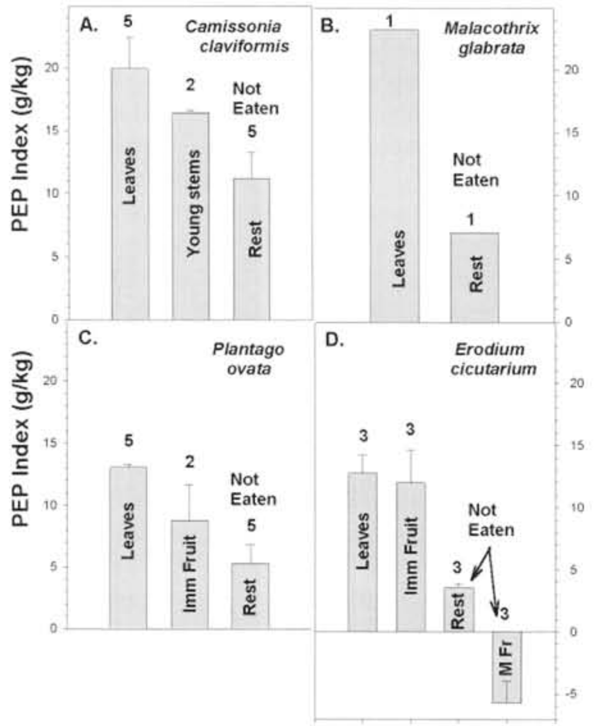

Figure 3. Comparison of the Potassium Excretion Potential (PEP index) among eaten and uneaten parts of the four most commonly eaten food plants: **A.** brown-eyed primrose (*Camissonia claviformis*), **B.** desert dandelion (*Malacothrix glabrata*), **C.** wooly plantain (*Plantago ovata*) and **D.** red-stemmed filaree (*Erodium cicutarium*). Note that eaten parts are to the left in each panel. Numbers of samples analyzed are indicated above each bar, and the error bars indicate s.e.m.

The above calculations were based on the nutrient composition of entire plants, but juvenile tortoises selected specific parts of species while foraging (Table 4). The nutrient composition of 15 eaten parts that we were able to collect in sufficient amount, representing 4872 bites (95.9% of all bites), are presented in Table 6. Although the eaten parts varied considerably in composition, a high proportion (9 of 15) had a PEP index greater than 10; by contrast, among encountered entire plants only one species was greater than 10 (Table 5). Particularly high PEP indices were found for the leaves of four eaten species: *Camissonia claviformis, Chaenactis fremontii, Malacothrix glabrata,* and *Oenothera primiveris. Camissonia claviformis* leaves accounted for 42% of all plant part bites. The aggregate diet, as estimated from the relative proportions of bites for each plant part, contained 72.0% water, 10.9% protein, 1.41% potassium, and 15.1 PEP (Table 6). By comparison to the calculated average for entire eaten plants (Fig. 2) the ingested parts were high in protein, low in potassium, and very high in PEP.

The nutritional consequences of selection of specific plant parts is illustrated in Fig. 3 in which specific eaten and uneaten parts of four species are compared. The aggregate portions representing what was eaten by tortoises for these 4 species (plus *Crypantha angustifolia* and *Schismus* spp.) were significantly higher in water ($p = 0.037$), protein ($p < 0.001$) and PEP ($p < 0.001$), and lower in potassium ($p = 0.027$), than the uneaten portions (paired t-tests; $n = 20$).

DISCUSSION

Diet Selectivity and Its Consequences. — In this study juvenile desert tortoises were clearly selective in their foraging: 1. they ate relatively little of the abundant split grass even though it constituted a great proportion of the biomass of annuals in the pen and along their foraging paths, 2. of the other species they regularly encountered, two (*Cryptantha angustifolia, Chaenactis fremontii*) were eaten infrequently (£ 2.5% of plants), 3. of the species eaten, one (*Camissonia claviformis*) accounted for nearly 50% of all bites even though it accounted for less than 5% of the biomass encountered, and 4. most bites were taken of leaves rather than of other plant parts (Tables 2, 3, 4, 6).

We had predicted, based on the need of Mojave Desert tortoises to expend water and nitrogen in disposing of excess potassium (Minnich, 1977; Nagy and Medica, 1986; Oftedal et al., 1994), that tortoises should select foods high in water and protein, but low in potassium, with the result that the ingested food would be high in the Potassium Excretion Potential (PEP) index (Oftedal, 2002). In fact, the ingested diet was higher in water, protein, and PEP, but not lower in potassium, than would be expected from the abundance, biomass, and nutrient composition of the species encountered. Much of the nutritional difference was attributable to avoidance of abundant split grass that had mature fruit and was beginning to senesce during this study. At this phenological stage split grass is low in water, protein, potassium, and PEP (Table 6; see also Barboza, 1995; Nagy et al., 1998). However, tortoises also exercised selectivity among the other species encountered. Among species other than split grass, the selected plants were higher in protein and PEP (but not in water), and lower in potassium than the plants bypassed (Fig. 2). Juvenile tortoises were also selective in choosing plant parts. The parts eaten were higher in water, protein, and PEP, and lower in potassium, than the uneaten portions of the same species (Fig. 3). This overall selectivity produced the remarkable finding that the ingested diet had a PEP index (15) that was greater than that of any of the individual species assayed (Table 5). The high intake of *Camissonia claviformis* leaves (42% of all bites and PEP near 20) was largely responsible for the high PEP of the overall diet; only leaves of *Malacothrix glabrata* had a higher PEP index.

Although juvenile tortoises appeared to favor high PEP plants and plant parts, this index does not explain all foraging choices. For example, *Chaenactis fremontii* was relatively frequently encountered (Fig. 1) and had leaves high in PEP (Table 6) but did not receive many bites (Table 4). Conversely, *Cryptantha angustifolia* leaves and inflorescences had negative PEP indices but relatively many were eaten. It is possible that some high PEP plants may be avoided due to morphologic (e.g., thorns, calcareous hairs, woody parts) or toxic properties, and that low PEP plants might prove beneficial if they contain specific nutrients that are limiting (Oftedal, 2002). Alternatively, the high PEP intakes achieved by feeding on some high PEP plants may permit the ingestion of other plants of lower quality without compromising the overall diet.

The selectivity shown by juvenile tortoises in this study was only possible because of the array of species available to them. In a drier year many species with high water needs would not germinate. For example, *Camissonia claviformis* is known to have a very high photosynthetic rate that implies a very high rate of transpirational water loss (Mooney et al., 1976). As this species requires abundant soil moisture to sustain such high photosynthetic activity, germination during drier years might prove lethal. A high rate of photosynthesis also entails a high concentration of the photosynthetic enzyme ribulose bisphosphate carboxylase-oxygenase (rubisco), which is a primary reason for the relatively high protein content of its leaves (Mooney et al., 1976; Table 6). Although tortoises had not previously been reported to eat this species, its observed importance in this study is consistent with the hypothesis that tortoises in the Mojave Desert may have a disproportionate dependence on annuals with high photosynthetic rates that only germinate in wet years (Oftedal, 2002). If the desert tortoise originated in wetter and less extreme desert steppes and grasslands, as has been proposed (Van Devender, 2002; Morafka and Berry, 2002), its reliance on annuals that lack extreme xeric adaptations (other than avoidance of drought conditions) may have a long evolutionary history.

How Representative is FISS? — The wider implication of this study is that tortoises must have access to an array of plants, including high PEP species, if they are to be able to select a diet of high nutritional quality. Yet it is possible that the choices made by tortoises in this study were constrained by their enclosure. The conclusions of this study can only be considered of general application to the extent that the vegetation in the enclosure was representative of tortoise habitat.

The enclosure was constructed in January–February 1995 on an undisturbed site (Morafka et al., 1997), but some soil disturbance during construction was unavoidable. The surface was raked after construction to remove footprints, and subsequent human activity in the enclosure was kept to a minimum to prevent development of compacted trails. At initial inspection in April 1998 we saw little evidence of prior human activity, although the relatively high biomass of split grass in the intershrub space could have been associated with earlier soil disturbance. The number of annual species inside the enclosure was comparable to that in the area immediately outside (other than in a wash which had additional species), suggesting that the fencing did not diminish seed dispersal into the pen, or that an adequate seed bank remained from prior years. During the trial we attempted to minimize impact by walking on discrete trails, although these trails did develop some compaction. After the trial the estimated biomass inside the enclosure was similar to that outside the enclosure (Table 2). We believe that the plant community within the enclosure was similar in composition and biomass to that outside. However, both areas had no doubt been substantially altered by the successful and prodigious invasion by split grass (*Schismus* spp.), two species of similar exotic annual grasses that are native to Eurasia and North Africa (Conert and Türpe, 1974) but are now widespread in the Mojave Desert.

The confinement of juvenile tortoises to the enclosure may have reduced foraging choices as they were unable to utilize washes and wash edges for foraging, an important foraging site for adult tortoises in the western Mojave Desert (Jennings, 1993). For example, desert dandelion (*Malacothrix glabrata*), a species with high PEP leaves, was observed to remain green and moist in the neighboring wash when it was senescing in the enclosure, and might have provided a foraging opportunity. Being subject to predation by ravens, juveniles may be less prone to utilize exposed areas like washes, but this warrants further study.

One possible source of error was the relatively high density of tortoises in the enclosure. For the enclosure, tortoise density was 58/hectare, less than in an earlier FISS enclosure (152–344/hectare in FISS 1; Morafka et al., 1997) but considerably more than has been reported from the Mojave desert (0.4–0.8; Berry, 1990, cited by Morafka et al., 1997). While it is possible that the estimates for the wild are low, given the difficulty in identifying small burrows and the small proportion of time juveniles spend on the surface (Morafka et al., 1997), the population density in FISS 2 was likely greater than occurs in nature. This high density may have reduced availability of preferred foods. We found that more than 90% of brown-eyed primrose (*Camissonia claviformis)* plants had sustained moderate to heavy feeding effects by the end of the trial. However, plant damage was also caused by larvae of the white-lined sphinx moth (*Hyles lineata*) that were feeding on the leaves of this species, and we did not distinguish damage by caterpillars from damage by tortoises. In either case, the net effect was a reduction in availability of primrose leaves, especially towards the end of the trial. The relatively low use rate (14%) of encountered *C. claviformis* plants may have been related to this reduced leaf availability as our impression was that tortoises most often bypassed plants without available leaves. Thus primrose leaves might have been an even greater part of the diet at lower tortoise densities.

The present study confirms the tremendous value of naturally vegetated enclosures for research on the biology of juvenile tortoises, as proposed by Morafka et al. (1997). The efficacy of these enclosures is particularly apparent in studies which can take advantage of the high sampling frequency associated with high juvenile tortoise density. It is unlikely that the quantity of data collected in this study could have been obtained in a wild population over such a short time period, and yet a short time period is essential to minimize the confounding effects of changing plant phenologies. This is especially problematic in a desert environment in which annuals race through phenological development in order to set seed before soils desiccate (Rundel and Gibson, 1996; Smith et al., 1997).

Implications for Tortoise Conservation. — Tortoises may be unique among desert herbivores in that they must rely so extensively on urates to eliminate excess potassium. Herbivorous iguanine lizards also excrete potassium urates, but this is as a supplement to salt gland secretions (Minnich, 1970; Nagy, 1972, 1975). The need to produce urates places a tremendous burden on the nitrogen economy of tortoises (Oftedal, 2002). For example, juvenile desert tortoises in captive conditions have difficulty retaining nitrogen for growth even when fed a diet containing 20% protein if the potassium level of the diet is very high (Oftedal et al., 1994).

Table 7. Effect of cattle grazing on diets of adult tortoises, after Avery (1988).

					Ivanpah Valley in 1993			
	Plants Analyzed for PEP[2]				Early (Apr-May)		Late (May-June)	
Species[1]	PEP g/kg	Site[3]	Stage[4]	Part[5]	Grazed % of bites	Protected % of bites	Grazed % of bites	Protected % of bites
Chaenactis fremontii	18.42	FISS	imfr	lv		22		
Malacothrix glabrata	23.21	FISS	imfr	lv	48	60		45
Stylocline micropoides	0.49	DTNA	imfr	entire	3			
Cryptantha angustifolia	-6.58	FISS	imfr	lv	8			33
Cryptantha circumscissa	-0.99	DTNA	imfr	entire	14	1		
Cryptantha micrantha	-0.05	PV	imfr	entire	2			
Cryptantha pterocarya	-2.05	FISS	mfr	entire	7			
Pectocarya spp.	-1.47	PV	imfr	entire	9			
Erodium cicutarium	12.76	FISS	imfr	lv			1	
Camissonia boothii	17.05	FISS	imfr	lv	2	8		
Camissonia spp.	19.95	FISS	imfr	lv	2	8	1	
Schismus barbatus	1.85	FISS	mfr	fr			93	22
Linanthus aureus	9.10	EV	fl	entire			2	
Loeseliastrum matthewsii	5.06	FISS	fl	infl	2			
Ingested diet		Calculated PEP (g/kg)			11.4	21.1	2.3	8.7

[1]See Table 1 for common names; *Camissonia* spp. = evening primrose spp., *L. aureus* = desert gold. [2]All samples collected in late April and early May 1998 except *L. aureus* which was collected in March 1995. [3]Sites of collection abbreviated as follows: FISS = Ft Irwin (this study); DTNA = Desert Tortoise Research Natural Area, Kern Co., CA ; PV = Piute Valley, Clark Co., NV; EV = Eldorado Valley, Clark Co., NV. [4]Stage as follows: fl = flowering, imfr = immature fruit; mfr = mature fruit. [5]Plant part as follows: lv = leaves, infl = inflorescence (with peduncle, bracts, etc.), fr = fruit.

The PEP index was devised as a means of weighting the relative contributions of water and nitrogen to solving the potassium excretion problem (Oftedal, 2002). However, the PEP index is only approximate, as it does not take into account such variables as differences in protein digestibility, fecal losses of water and potassium, water obtained from metabolic processes, or factors influencing evaporative water loss. Water flux varies greatly among seasons and years in juvenile tortoises, as shown in an earlier study at FISS (Nagy et al., 1997).

The survival of any animal species depends on its ability to locate, ingest, and utilize sufficient quantities of essential nutrients. If nutrient intakes are inadequate, animals may have compromised immune function, be susceptible to disease, suffer a compromised reproductive effort (Henen, 1997), fail to grow, and ultimately die. An evaluation of the diets of juvenile tortoises at Ft. Irwin indicated that they were able to self-select a diet of high quality (as judged by the PEP index). They did this by directing foraging activity at the highest quality parts of high-quality plants, species which were available because of the high winter rainfall that preceded this study. Substantial nitrogen retention, and hence rapid growth, is probably only possible in years of high germination of annuals, although diets in other years may be important to prevent the backward slide in body protein reserves and health that can occur during drought (Henen, 1994, 1997). The ability of juvenile tortoises to select high quality parts may have been enhanced due to their small bite size, but there is no reason to believe larger tortoises would not also benefit from similar selectivity in feeding.

The potential for tortoises to take advantage of high rainfall years depends on access to high PEP plant species. In this context the finding that cattle grazing may induce marked differences in the species of annuals upon which adult tortoises feed assumes additional importance. Avery (1998) studied tortoise diets within and outside a cattle exclosure in the eastern Mojave Desert, in Ivanpah Valley, San Bernardino Co., California. In 1993 tortoises in grazed habitat ate less desert dandelion (*M. glabrata*), Fremont pincushion (*Chaenactis fremontii*), and evening-primroses (*Camissonia* spp.), but more *Cryptantha* spp. (in early spring) and more split grass (in late spring). Avery (1998) noted that cattle depleted some annuals, such as *M. glabrata*. Using PEP data from the present study as well from other sites (Oftedal, 2002, and unpubl. data) it is possible to calculate the effect of such diet shifts on tortoise diets (Table 7). This calculation is approximate as the parts eaten and the phenological stages concerned were not reported. If available, we used data on the parts eaten by Ft. Irwin juveniles; otherwise analytical results for entire plants were used. In early spring, the estimated PEP index of the Ivanpah diet (weighted by percentage of bites per species) declined from about 21 in the protected area to 11 in the grazed area; in late spring the PEP index declined from about 9 in the protected area to 2 in the grazed area. These calculations indicate a potential for substantial impact of cattle grazing on the nutritional quality of tortoise diets.

Tortoises may be particularly vulnerable to anthropogenic factors that alter the amount and diversity of high PEP plants in the Mojave Desert. This could include damage from off-road vehicle use, competition from invading exotic plants, the impact of air pollution near urban or industrial areas, and global warming as it affects patterns of rainfall in the desert. For example, if brown-eyed primrose (*C. claviformis*) had not germinated and grown in 1998, and if tortoises had eaten the same proportions of other plants, the PEP index for the diet would have dropped from 15 to 11. For these reasons management of biological reserves and other protected habitats for tortoises should maintain not only the total amount of food available, but also the nutritional quality of that food.

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