DIET OF FREE-RANGING DESERT TORTOISES *(Gopherus agassizii)* IN THE NORTHEASTERN SONORAN DESERT, ARIZONA

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FINAL REPORT

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ABSTRACT

Using plant fragment and microhistological analyses of scat, we studied the diet of free-ranging desert tortoises at seven sites in saguaro-foothill paloverde desertscrub in the northeastern Sonoran Desert in Arizona: Bonanza Wash, Eagletail Mountains, Four Peaks, Granite Hills, Little Shipp Wash, Mineral Mountain, and Sand Tank Mountains. Twenty-five fecal pellets (scat) collected from a study site constituted a "sample." Each pellet was numbered, described, disaggregated, and sorted for identifiable plant fragments.

Quantitative estimates of the relative biomass of plant species in the seasonal or annual scat samples were obtained using microhistological methods on the residues from the 25-pellet samples in the fragment analyses. Lists of plants were prepared for each of four plots in the spring diet study in March and April, 1996, to augment plant lists compiled during summer-fall tortoise population surveys. Additional plant species were found in each study area: Eagletail Mountains (5 new species), Four Peaks (22 plus 10 nearby), Granite Hills (25), and Little Shipp Wash (20).

Using fragment analysis, we identified 133 taxa in the tortoise diet. Plant foods included trees and shrubs (12.0% of the 133 taxa), subshrubs/woody vines (11.3%), grasses (12.9%, 8.3% annuals), succulents (6.0%), herbaceous perennials (12.0%), and dicot annuals (45.9%, 36.8% spring). Annuals (including grasses and dicots) accounted for 54.1% of the diet taxa. Only 5 taxa (3.8%) were introduced species: *Bromus rubens* (red brome), *Schismus barbatus* (Mediterranean grass), *Brassica tournefortii* (a mustard), *Centaurea melitensis* (Malta star thistle), and *Erodium cicutarium* (filaree).

A total of 52 taxa (39.1%) occurred in 5 (20%) or more of the 25-pellet samples, including trees and shrubs (8), subshrubs/woody vines (5), spring annual grasses (3), succulents (2), herbaceous perennials (6), and dicot annuals (28). Only 5 of 31 annual grasses and dicots are summer species. Eighteen species that occur in 50% or more of the samples stand out as important in the diet, including a tree, shrubs, a woody vine, spring annual grasses, and dicot annuals. *Cercidium microphyllum* (foothill paloverde), *Cryptantha barbigera* (nievitas), *E. cicutarium*, and *Pectocarya recurvata* (combbur) were in 75% or more of the samples while *Bromus rubens* was in every sample. Plants eaten out of season were mostly spring taxa (94.3%: 39 annual dicots, 5 annual grasses, 4 subshrubs, 1 shrub, 1 tree). The only summer taxa found in spring scat were *Boerhavia intermedia* (spiderling), *Carnegiea gigantea* (saguaro), and *Euphorbia setiloba* (spurge).

Microhistological analysis revealed a total of 41 taxa eaten. The most important food items (based on relative biomass in the scat) were grasses or the *Janusia gracilis*-mallow cohort (JAMA). Mallows are *Abutilon*, *Herissantia*, *Hibiscus*, *Sida*, and *Sphaeralcea*. Grasses and JAMA together make up the bulk of the tortoise diets at all of the sites. Desert tortoises in Arizona Upland Sonoran Desert habitats are relatively specialized herbivores that eat primarily grasses or *Janusia*/mallows. These two groups of plants (16 taxa) accounted for at least 90% of the biomass in most of the samples.

INTRODUCTION

The desert tortoise (*Gopherus agassizii*) is an herbivore found from the Mohave (Mojave) Desert in Arizona, California, and Utah south through the Sonoran Desert in Arizona, California, and Sonora into subtropical Sinaloan thornscrub and tropical deciduous forest in central and southern Sonora and northern Sinaloa, Mexico (Treviño et al., 1992; Fritts and Jennings, 1994; Germano et al., 1994). There has been a great deal of interest in the ecology and conservation of the desert tortoise, especially since the Mojave population (all tortoises north and west of the Colorado River) was listed by the U.S. Fish and Wildlife Service (USFWS) as Threatened in 1990 (USFWS, 1990).

In recent years, desert tortoise diets have been the focus of "bite count" studies in the western Mohave Desert at the Desert Tortoise Natural Area, California (Jennings, 1992), and in the eastern Mohave Desert in the Ivanpah Valley, California (Avery and Neibergs, in press), and the Beaver Dam Slope area of southwestern Utah and northwestern Arizona (Esque, 1994).

The earliest dietary account for the desert tortoise in the Sonoran Desert was by Ortenburger and Ortenberger (1927) who only found grasses in the stomachs of tortoises they examined in Pima County, Arizona. With the exception of microhistological analyses of scat from the New Water Mountains, La Paz County (Hansen et al., 1976), and the Picacho Mountains, Pinal County (Vaughan, 1984), most observations of desert tortoise feeding in the Sonoran Desert in Arizona were incidental to other field work. These observations are summarized in Johnson et al. (1990) and Arizona Interagency Desert Tortoise Team (1996). In 1991, Arizona Game and Fish Department biologists began a study of the ecology and diet in tortoise populations in the Harcuvar Mountains and Little Shipp Wash, Yavapai County, Arizona, using bite counts (Dickinson et al., 1995; Snider, 1993). Tortoises were observed to eat 12 species of plants in the Harcuvars and 22 in Little Shipp Wash.

We studied the diet of free-ranging desert tortoises at seven sites in saguaro (*Carnegiea gigantea*)-foothill paloverde (*Cercidium microphyllum*) desertscrub in the northeastern Sonoran Desert in Arizona using plant fragment and microhistological analyses of scat. In a companion study, we examined the nutritional and mineral content of important plant foods.

STUDY SITES AND METHODS

Study Sites. Desert tortoise scat were collected from seven localities in central and western Arizona (Fig. 1). Detailed descriptions of the sites are given in the following reports: Bonanza Wash (Woodman et al., 1992); Eagletail Mountains, Granite Hills, and Little Shipp Wash (Hart et al., 1992; Shields et al., 1990; Woodman et al., 1993, 1994a,b); Four Peaks (Murray, 1993; Murray and Schwalbe, 1993; Murray and Schwalbe, 1997), Mineral Mountain (Woodman et al., 1993), and Sand Tank Mountains (Dames and Moore, 1994). Vegetation at all seven sites contain elements of saguaro/foothill paloverde desertscrub, but there is much variation within and among sites, with some localities also represented by plant species characteristic of both Sonoran and

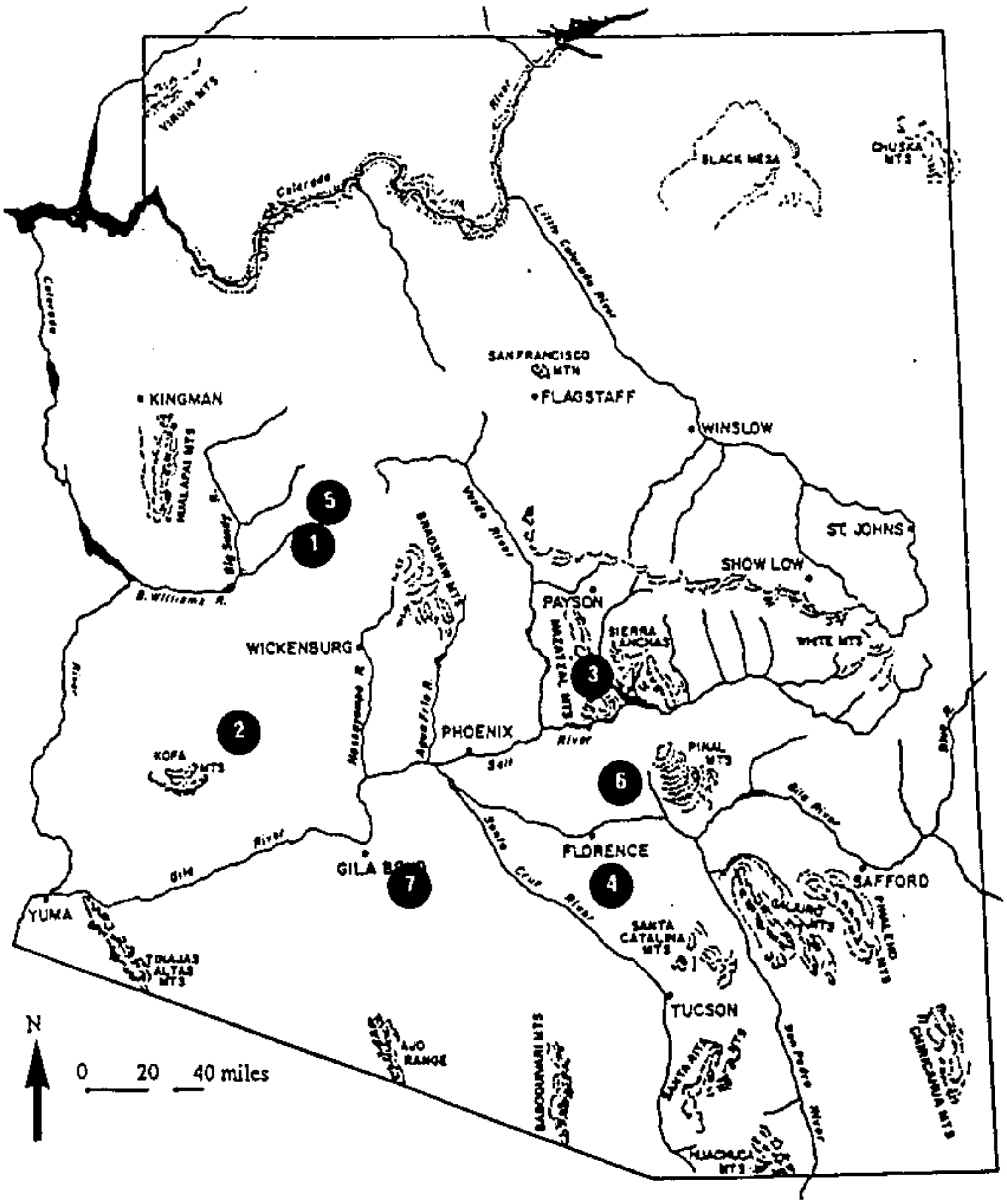

Figure 1. Map showing study sites. 1=Bonanza Wash, 2=Eagletail Mountains, 3=Four Peaks, 4=Granite Hills, 5=Little Shipp Wash, 6=Mineral Mountain, 7=Sand Tank Mountains.

Mohave desertscrub, desert grassland, and, in some cases, interior chaparral (Brown, 1982; Burgess, 1995; Lowe, 1964). Geology at most of the study sites is granitic in origin, with the notable exception of the Eagle Tail Mountains, which, in the area of the plot, are composed primarily of rhyolite and volcanic ash (tuff) (Woodman et al., 1994a).

Fecal Pellet Samples. When possible, 25 individual tortoise fecal pellets (scat) were collected from each of the study sites. We define a "sample" for a study site as 25 individual scat from that site in a season or year. We attempted to collect scat from varied localities at a particular study site to minimize the likelihood of collecting several scat from the same tortoise in a given 25-pellet sample. A 25-pellet sample from throughout a study area reflects diets of many tortoises. To investigate seasonal variation in diet, we analyzed scat collected in the summer-fall (August-October) and in the spring (March-April).

A total of 25 fecal samples (each sample usually containing 25 fecal pellets) from the seven study sites were analysed for dietary content (Table 1). Samples from the 1992 summer-fall tortoise plot surveys were provided by Peter Woodman and Steve Boland (Bonanza Wash), Scott Hart (Little Shipp Wash, Mineral Mountains), David Silverman (Granite Hills), Elizabeth B. Wirt (Sand Tank Mountains). Roy Averill-Murray provided samples from Four Peaks for September 1992 and August-October 1995. The remainder of the samples were collected by Ana L. Reina G. and Thomas R. Van Devender in 1995-1996.

With the exception of Bonanza Wash #1 (n = 22) and Eagletail Mountains # 4 and 5 (den samples, n = 20 and 11, respectively), 25 pellets were collected from each site (Table 1). The Eagletail den samples are from one or a few tortoises foraging in a smaller area. Little Shipp Wash #5 was the gut content of a single tortoise found dead in the field. Whenever possible, samples were of fresh pellets, typically dark in color with little obvious weathering. When insufficient fresh pellets were found, fresh and weathered pellets were mixed (6 samples), and those samples were considered to relect annual diets (Table 1).

Scat were so common at Four Peaks in April of 1996 that the pellets were separated into fresh, old (obviously weathered), and very old (bleached) samples. In years with wet winters, few pellets survive into the next year. Pellets were most obviously being devoured by termites but may well be eaten by coyotes (*Canis latrans*) or other mammals. The color and condition of pellets in packrat (*Neotoma albigula*) houses or dens or tortoise dens are unreliable indicators of age.

During the study period, scat samples were collected in summer-fall (1992, 1995-1996) and spring (1996). Fresh pellets were especially difficult to find in March and April when the spring annuals were peaking. Only two of 14 fresh pellet samples were obtained in the spring, limiting interseasonal comparisons. Fresh scat were more numerous in August-September.

Spring Flora Surveys. Lists of plants were prepared for each of the plots as part of previous tortoise population studies. Since the tortoise plots have all been surveyed in summer-fall, the spring annual floras were poorly represented. The presence, size, abundance, and diversity of

Table 1. Desert tortoise fecal pellet and gut samples from Sonoran Desert study areas in Arizona. Fresh = fresh condition with dark color, mixed = mixture of fresh and older, weathered pellets, old = light-colored weathered pellets, very old = bleached weathered pellets, gut = stomach content of dead tortoise, den = pellets of indeterminate age from a single den.

1. Bonanza Wash #1 (n = 22): P. Woodman and S. Boland, September-October 1992; fresh.
2. Mineral Mountains #1 (n = 25): S. Hart, September-October 1992; mostly fresh.
3. Sand Tank Mountains #1 (n = 25): E. B. Wirt, August-October 1992; mixed.
4. Eagletail Mountains #2 (n = 25): T. R. Van Devender, September 21, 1995; fresh.
5. Eagletail Mountains #3 (n =25): A. L. Reina G. and T. R. Van Devender, March 21-23, 1996; mixed.
6. Eagletail Mountains #4 (n = 20): A. L. Reina G. and T. R. Van Devender, March 21-23, 1996; den.
7. Eagletail Mountains #5 (n = 11): A. L. Reina G. and T. R. Van Devender, March 21-23, 1996; den.
8. Four Peaks #1 (n = 25): R. Murray, September 1992 (mostly fresh).
9. Four Peaks #2 (n = 25): R. Murray, August 2-October 3, 1995 (daily); fresh - one pellet each day.
10. Four Peaks #3 (n = 25): R. Murray, August 2-18, 1995; fresh.
11. Four Peaks #4 (n = 25): R. Murray, August 19-September 1, 1995; fresh.
12. Four Peaks #5 (n = 25): R. Murray, September 2-October 3, 1995; fresh .
13. Four Peaks #6 (n = 25): A. L. Reina G. and T. R. Van Devender, April 11, 1996; fresh.
14. Four Peaks #7 (n = 25): A. L. Reina G. and T. R. Van Devender, April 11, 1996; old.
15. Four Peaks #8 (n = 25): A. L. Reina G. and T. R. Van Devender, April 11, 1996; very old.
16. Granite Hills #1 (n = 25): D. Silverman, September 7-October 21, 1992; fresh.
17. Granite Hills #2 (n = 25): T. R. Van Devender and J. F. Wiens, September 18, 1995; fresh.
18. Granite Hills #3 (n = 25): T. R. Van Devender and J. F. Wiens, September 18, 1995; mixed.
19. Granite Hills #4 (n = 25): A. L. Reina G. and T. R. Van Devender, March 23, 1996; fresh.
20. Granite Hills #5 (n = 25): A. L. Reina G. and T. R. Van Devender, March 23, 1996; mixed.
21. Little Shipp Wash #1 (n = 25): S. Hart, September 1992; fresh.
22. Little Shipp Wash #2 (n = 25): T. R. Van Devender, September 20, 1995; mixed.
23. Little Shipp Wash #3 (n = 25): T. R. Van Devender, September 20, 1995; fresh.
24. Little Shipp Wash #4 (n = 25): A. L. Reina G. and T. R. Van Devender, April 5, 1996; mixed.
25. Little Shipp Wash #5 (n = 1): T. R. Van Devender, September 19, 1995; gut.

spring annuals are highly correlated with the amount and distribution of winter-spring rainfall. Ana Lilia Reina G. and Thomas R. Van Devender surveyed the four plots in the diet study in March and April of 1996. As needed, specimens were collected and identified in the University of Arizona Herbarium; voucher specimens were deposited into this collection.

Fragment Analyses. Fragment and microhistological analyses of tortoise fecal pellets yield very different results. Fragment analysis has great power to document the diversity of plants consumed by tortoises, especially annuals. It does not provide an accurate reflection of the less-diagnostic material (grass blades, digested leaves, etc.) that forms the bulk of the pellet matrices. The majority of the diet biomass apparently is non-reproductive materials, not the seeds and fruits typically identified in fragment analysis. In a few instances, tortoises were observed eating plant species that did not show up in the fragment analysis for that study site. In those cases, those plant species are indicated as dietary observations at the appropriate site.

Fecal pellets can be analyzed from a particular season or averaged for a year or more. Luckenbach (1982) pointed out that scat fade from shiny black to bleached white as they weather. In many cases, individual pellets are readily recognized as spring or summer scat due to the presence of seasonal annuals, herbaceous perennials, or cactus seeds. Woodbury and Hardy (1948) pointed out that tortoises can go long periods without defecating and plant materials remain in the large intestine over the winter. Pellets that are protected in burrows, rock shelters, or packrat (*Neotoma albigula*) houses may not fade and appear fresh for longer periods. Seasonal samples were selected as fresh scat from open sites. Other scat can be combined into bulk annual samples.

Each pellet in a sample was numbered, described, disaggregated, and sorted for identifiable plant specimens. Preliminary analyses were done by Jessie C. Piper. Specimens were counted although they represented only a small fraction of the mass of the pellet, and the results are mostly presented in percentages of presence or absence.

Microhistological Analyses. Microhistological analyses provide good estimates of the total biomass of plant foods eaten. Many of the diverse food plants documented in diets in fragment analyses are missed in microhistological analyses either because their vegetative parts are less diagnostic at the cellular level (the fragments identified were removed from the samples) or not common enough to be discerned when the entire sample was reduced to microscopic scale. The mass of identified fragments removed from the samples was insignificant compared to total mass of the scat, so this removal did not affect the relative estimates of biomass of plant foods eaten.

Microhistological analysis of plant epidermis in dung of herbivores is a standard range management technique (Free et al., 1970; Hansen et al., 1973; Ward, 1970). In this method, fecal samples are ground to uniform fragment size in a Waring blender and mounted on slides for microscopic analysis. Fragments are identified using epidermal characters including cell, stomate, and trichome (hairs) structure and patterns. Reasonable amounts of epidermis are recognizable after passing through the most efficient herbivore digestive systems (e.g., cattle, desert tortoise) including the epidermis of highly digestible annuals and herbaceous perennials.

Identifiable fragments are counted in each microscope field allowing percent density, frequency, and relative density to be calculated. The latter measure is highly correlated with the dry weight of plants consumed (Sparks and Malachek, 1968). Although 35-40% of the fragments in a field cannot be identified, technicians are trained to accurately quantify hand compounded mixtures. Microhistological analysis identifies and quantifies the less-distinctive but dominant leaf and stem tissues not easily identified in fragment analysis. The plants identified in fragment analyses helped the technician refine the microhistological analyses.

Microhistological analysis was first applied to an herbivorous reptile in Hansen's (1974) study of the diet of chuckwalla in the Grand Wash Cliffs in the western Grand Canyon, Mohave County, Arizona. Hansen et al. (1976) reported microhistological analyses of tortoise scat from the Beaver Dam Slope in Utah, and the Grand Wash Cliffs and New Water Mountains in Arizona. A more extensive study analyzed tortoise scat from the Picacho Mountains of Arizona (Vaughan, 1985). Esque et al. (1990) maintained that bite counts were superior to microhistological analyses of fecal pellets due to differential digestion of flower parts and succulent vegetation. However, their comparison of plants "bitten" to the occurrence of plants in scat was flawed because the percent relative density which is highly correlated with the dry weight of plant matter ingested in most species was not used (Sparks and Malechek, 1968). A plant could occur in high frequency in fecal pellets and not have a high relative density/biomass.

Using the residues from the 25-pellet samples in the fragment analyses, quantitative estimates of the plant species in the seasonal samples were then determined by Theresa M. Foppe in the Composition Analysis Laboratory, at Colorado State University, using the microhistological analytical methods of Sparks and Malechek (1968) and Ward (1970). The weight of plant foods consumed can be reliably estimated through counts of the numbers of plant fragments (ground to uniformly small sizes) identified per area (mean relative density).

RESULTS

Spring Flora Survey. Additional species were found in each study area: Eagletail Mountains (5), Four Peaks (22 plus 10 nearby on the Four Peaks road), Granite Hills (25), and Little Shipp Wash (20; Table 2). Revised plant lists for the sites are presented in Appendices 1-4. Many species recorded in previous years were only seen dead or not seen in 1996 (e.g., Eagletail Mountains -- 16 taxa and Little Shipp Wash -- 12 taxa), reflecting the relatively poor spring rainfall. Additional ephemerals are to expected on the plots in wetter years.

Fragment Analyses. The most common identifiable fragments were seeds, fruits (including composite achenes, grass florets, and borage nutlets), leaves, and spines/thorns. The number of taxa in 200 individual pellets in the Four Peaks samples ranged from 1 to 13 (average 5.2 taxa/pellet; data from pellet analysis forms). The frequencies (number of pellets with taxon/total pellets in sample) of plants identified in the 25 fecal pellet samples are presented in Appendices 5-9. The number of taxa per sample for 24 samples ranged from 15 to 43 (average 29.2). Little

Table 2. Spring survey of the local floras of Arizona desert tortoise plots. ET = Eagletail Mountains, Mariciopa County, FP = Four Peaks Maricopa County, GH = Granite Hills, Pinal County, LS = Little Shipp Wash, Yavapai County. N = new addition to flora, D = dead plants from previous year, P = spring annuals recorded in previous year but not seen in 1996.

TAXA	ET	FP	GH	LS
SHRUBS				
Abutilon abutiloides				N
Anisacanthus thurberi		N		
Baccharis sarothroides		N*		
Bebbia juncea		N		
Condalia warnockii		N		
Krameria erecta			N	
PERENNIAL GRASSES AND SEDGES				
Aristida purpurea var. purpurea			N	
Cynodon dactylon	E	N*		
Eleocharis rostellata				N**
Hilaria belangeri		N		
Juncus bufonius				N**
Scirpus americanus				N**
SPRING ANNUAL GRASSES				
Bromus carinatus		N		
Bromus hordaceus	E	N*		
Hordeum murinum subsp. glaucum	E	N*		N
Poa bigelovii			N	
Puccinellia parishii				N**
Schismus barbatus	E	N	N	
Vulpia microstachys var. ciliata		N		N
Vulpia microstachys var. pauciflora		N		N
ASEASONAL ANNUAL GRASS				
Eragrostis cilianensis	E			P
SUCCULENTS				
Nolina microcarpa		N		

Table 2 (cont'd).

		ET	FP	GH	LS
		HERBACEOUS PERENNIALS			
Acourtia nana					N
Allionia incarnata				N	
Anemone tuberosa			N	N	
Asclepias nyctaginifolia			N*		
Castilleja angustifolia var. dubia			N		
Cheilanthes parryi		N			
Delphinum sp.					N
Machaeranthera asteroides			N*		
		SPRING ANNUALS			
Amsinckia intermedia				N	
Amsinckia tessellata		P			
Astragalus nuttallianus					N
Bowlesia incana				N	P
Brassica tournefortii	E	P			
Camissonia californica			D		
Centaurea melitensis	E				P
Chaenactis carphoclinia		D			
Chaenactis stevioides				N	
Chorizanthe brevicornu		P			
Chorizanthe rigida		P			
Cryptantha barbigera		N	N	N	N
Cryptantha maritima		P			
Cryptantha pterocarya		N		N	
Daucus pusillus				N	
Descurainia pinnata			N, D		P
Draba cuneifolia					P
Eriogonum deflexum		P			P
Eriogonum thomasii		P			
Eriogonum trichopes		P			P
Eriophyllum lanulosum				N	
Erodium texanum				N	
Eucrypta chrysanthemifolia		P		N	N
Filago californica			N		
Galium proliferum			N*		
Gilia flavocincta			N*	N	
Harpagonella palmeri					P
Hybanthus attenuatus					N
Lasthenia chrysotoma			N	N	
Lepidium lasiocarpum			N*		P
Lepidium virginicum var. medium			N		P
Lotus humistratus		P	N	N	N

Table 2 (cont'd).

		ET	FP	GH	LS
			SPRING ANNUALS (CONT'D)		
Lupinus concinnus			N		N
Lupinus sparsiflorus		P			
Malva parviflora	E		N*		
Microseris linearifolia				N	
Nemacladus glanduliferus			P		
Parietaria hespera				N	N
Pectocarya platycarpa			N	N	
Pectocarya recurvata			N	N	N
Perityle emoryi		N			
Phacelia crenulata		P			
Plagiobothrys arizonicus			N	N	
Pterostegia drymarioides				N	
Salvia columbariae		P	D		
Senecio flaccidus var. monoensis					P
Silene antirrhina		P	D		P
Sisymbrium irio	E	P			
Sonchus oleraceus	E	N			
Spergulina marina					N**
Stylocline micropoides				N	
Thysanocarpus curvipes			N		N

Shipp Wash #5 (gut sample) only yielded 7 taxa. Table 3 summarizes the plant taxa identified in fecal pellets or observed eaten by tortoises on the plots. Due to determination of fragments to different taxonomic levels, the total of 133 taxa is somewhat larger than the actual number of species: i.e., *Lepidium* sp. was either *L. lasiocarpum* or *L. virginicum* (peppergrasses), *Plantago* sp. was either *P. fastigiata* or *P. patagonica* (Indian wheats), etc. The plant foods included trees and shrubs (12.0% of the 133 taxa eaten), subshrubs/woody vines (11.3%), grasses (12.9%, 8.3% annuals), succulents (6.0%), herbaceous perennials (12.0%), and dicot annuals (45.9%, 36.8% spring). Annuals (including grasses and dicots) account for 54.1% of the diet taxa. Only 5 taxa (3.8%) are introduced species: *Bromus rubens* (red brome), *Schismus barbatus* (Mediterranean grass), *Brassica tournefortii* (a mustard), *Centaurea melitensis* (Malta star thistle), and *Erodium cicutarium* (filaree).

A total of 52 taxa (39.1%) occurred in 5 (20%) or more of the 25 pellet samples (Table 3) including trees and shrubs (8), subshrubs\woody vines (5), spring annual grasses (3), succulents (2), herbaceous perennials (6), and dicot annuals (28). Only 5 of 31 annual grasses and dicots are summer species. Eighteen species that occur in 50% or more of the samples stand out as important in the diet, including a tree (*Cercidium microphyllum*), shrubs (*Calliandra eriophylla, Encelia farinosa, Hyptis albida*), subshrubs (*Ditaxis lanceolata, Sphaeralcea ambigua*), a woody vine (*Janusia gracilis*), spring annual grasses (*Bromus rubens, Vulpia microstachys, V. octoflora*), and dicot annuals (*Chorizanthe brevicornu, Cryptantha barbigera, Erodium cicutarium, Lotus salsuginosus, Pectocarya recurvata, Plantago* sp., *Silene antirrhina*). *Cercidium microphyllum* (foothills paloverde), *Cryptantha barbigera* (nievitas), *E. cicutarium*, and *P. recurvata* (combbur) were in 75% or more of the samples while *Bromus rubens* was in every sample.

The occurrence in half or more of the 25 samples may not be significant because some species were only represented by occasional specimens in a few pellets. For example, most of the records of *Encelia farinosa* (brittlebush) were 1-3 achenes although a tortoise eating a single flower head would consume many achenes. In contrast, the maximum numbers of specimens per pellet per sample were high for other taxa: *Bromus rubens* (14-500), *Cryptantha barbigera* (1-109), *Pectocarya recurvata* (8-87), *Plantago* sp. (10-218), *Silene antirrhina* (2-218), *Vulpia microstachys* (17-282), and *V. octoflora* (3-335). For other species such as *Ditaxis lanceolata, Janusia gracilis* (desert vine), and *Sphaeralcea ambigua* (globe mallow), the numbers of specimens identified do not reflect their importance very well because less diagnostic trichomes (epidermal hairs) were so numerous that they often formed the matrix of the pellet.

Aseasonal Foods. A surprising result of the fragment analyses were the abundance in fresh scat (either fresh samples or fresh pellets in mixed samples) of remains of plant species from another season. Table 4 presents 224 records (presence in a fecal sample or feeding observation) of 53 taxa of food plants eaten out of season. A total of 20 observations (not all in Table 4) of tortoises eating dead spring annuals including grasses (*Bromus rubens* [6], *Schismus barbatus* [2], *Vulpia microstachys, V. octoflora*) and dicots (*Amsinckia* sp., *Brassica tournefortii, Cryptantha nevadensis, Lepidium lasiocarpum, Lotus* sp., *Lupinus sparsiflorus, Phacelia* sp., and *Plantago fastigiata* [3]) were made in September-October 1992 at Bonanza Wash and the Eagletail

Table 3. Plant taxa identified in tortoise fecal pellets samples from Sonoran Desert study plots in Arizona. BW = Bonanza Wash, Yavapai County, ET = Eagletail Mountains, Maricopa County, FP = Four Peaks plot, Maricopa County, GH = Granite Hills, Pinal County, LS = Little Shipp Wash, Yavapai County, MM = Mineral Mountains, Pinal County, ST = Sand Tank Mountains, Maricopa County, TOT = percentage of 25 samples with taxon. Values = numbers of samples, OB = observation only. Taxa in 20% or more of the samples in bold.

No. samples:	BW (1)	ET (4)	FP (8)	GH (5)	LS (5)	MM (1)	ST (1)	TOT (25)
TAXA								
			TREES AND SHRUBS					
Acacia greggii			7		3	1		.44
Calliandra eriophylla		1	8		5	1		.60
Cercidium microphyllum	1	2	6	5	4	1	1	.80
Encelia farinosa		3	5	4	2	1	1	.64
Eriogonum fasciculatum			3	4	1	1		.36
Fouquieria splendens		1	2				1	.16
Hyptis albida		3	3	4	4	1	1	.64
Krameria erecta					OB			
Krameria grayi				1				.04
Larrea divaricata		2		2	1			.20
Lycium berlandieri				OB				
Olneya tesota		2		1			1	.16
Prosopis glandulosa					4			.16
Prosopis velutina			3					.12
Quercus turbinella					1			.04
Simmondsia chinensis			6			1		.28
N = 16	1	7	9	8	10	7	4	
			SUBSHRUBS AND WOODY VINES					
Ambrosia deltoidea				3		1	1	.20
Ambrosia dumosa		OB		2		1		.12
Ambrosia eriocentra					1			.04
Ayenia microphylla					1			.04
Carlowrightia arizonica					1			.04
Ditaxis lanceolata		3	5	5	1	1	1	.64
Dyssodia porophylloides	1							.04

Table 3 (cont'd).

No. samples:	BW (1)	ET (4)	FP (8)	GH (5)	LS (5)	MM (1)	ST (1)	TOT (25)
Herissantia crispa			3			1		.16
Janusia gracilis	1		7	3	2	1		.56
Lotus rigidus			1		1			.08
Mirabilis bigelovii			4		1			.20
Porophyllum gracile			1					.04
Psilostrophe cooperi					1			.04
Sphaeralcea ambigua			4	4	4	1		.52
Sphaeralcea sp.	1						1	.08
N = 15	3	1	7	5	9	6	3	
PERENNIAL GRASSES								
Aristida purpurea				1	1		1	.12
Bouteloua sp.					OB			
Erioneuron pulchellum			1	1	1		1	.16
Hilaria belangeri					2			.08
Pleuraphis rigida					1			.04
Tridens muticus						1		.04
N = 6	0	0	1	1	5	1	1	
SPRING ANNUAL GRASSES								
****Bromus rubens***	1	4	8	5	5	1	1	1.0
Poa bigelovii				1				.04
**Schismus barbatus*				OB	OB			
Vulpia microstachys	1		8		5			.56
Vulpia octoflora	1	4	6	5		1	1	.72
N = 5	3	2	3	4	3	2	2	
SUMMER ANNUAL GRASSES								
Bouteloua aristidoides					OB			
Bouteloua barbata					OB		1	.04
Brachiaria arizonica					OB			
Panicum hirticaule	1			?1				.08
N = 4	1	0	0	1	3	0	1	

Table 3 (cont'd).

No. samples:	BW (1)	ET (4)	FP (8)	GH (5)	LS (5)	MM (1)	ST (1)	TOT (25)
ASEASONAL ANNUAL GRASSES								
Aristida adscensionis		OB		OB				
Muhlenbergia microsperma								
N = 2	—/0	—/1	1/1	—/1	—/0	—/0	1/1	.08
SUCCULENTS								
Carnegiea gigantea			2					.08
Ferocactus cylindraceus			1	1		1		.12
Ferocactus sp.		1						.04
Dasylirion wheeleri			1					.04
Mammillaria grahamii					1			.04
Opuntia acanthocarpa			1			1		.08
Opuntia phaeacantha			1	1	5			.28
Opuntia sp.								
N = 8	—/0	1/2	4/6	4/3	—/2	1/3	1/1	.44
HERBACEOUS PERENNIALS								
Allionia incarnata	1	1			OB		1	.12
Boerhavia coccinea				1			1	.08
Ayenia filiformis		1	4		5			.40
Castilleja sp.					1			.04
Cheilanthes parryi				1				.04
Cirsium neomexicanum	1		2		3	1		.24
Ditaxis sp.	1							.04
Eriogonum sp.				1	2			.12
Euphorbia arizonica			1				?1	.08
Euphorbia eriantha		1						.04
Euphorbia melanadenia			2		2		1	.20
Euphorbia polycarpa/micromera			5	5		1	1	.48
Euphorbia sp.	1	1	1	3	3			.36
Evolvulus alsinoides					1			.04
Portulaca suffrutescens				1				.04

Table 3 (cont'd).

No. samples:	BW (1)	ET (4)	FP (8)	GH (5)	LS (5)	MM (1)	ST (1)	TOT (25)
SPRING ANNUALS (CONT'D)								
Lupinus concinnus		2	2	1	2			.28
Lupinus sparsiflorus				1				.04
Lupinus sp.				1				.04
Microseris linearifolia					1			.04
Parietaria hespera		1	2	2	1			.24
Pectocarya platycarpa				1				.04
Pectocarya recurvata	1	4	8	5	5	1	1	1.0
Perityle emoryi		1			1			.08
Phacelia crenulata		4			1			.20
Phacelia distans			4	3				.28
Plagiobothrys arizonicus			1		3			.16
Plantago fastigiata		4				1		.20
Plantago patagonica						1		.04
Plantago sp.			8	5	4		1	.72
Rafinesquia neomexicana			1					.04
Silene antirrhina	1	3	6	3	4	1	1	.76
Sphaeralcea ?coulteri		3						.12
Thysanocarpus curvipes			2	1	4	1		.32
N = 46	5	23	26	23	23	14	12	
SUMMER ANNUALS								
Boerhavia coulteri				1				.04
Boerhavia intermedia	1	2	6		2		1	.48
Boerhavia wrightii	1	1	2					.16
Boerhavia sp.				1				.04
Euphorbia abramsiana		2		3			1	.24
Euphorbia hyssopifolia			4					.16
Euphorbia setiloba	1	3	4	1				.36
Ipomoea sp.			1		4	1		.24
Mollugo cerviana			3					.12
Pectis papposa		1						.04
?Pectis					1			.04

Table 3 (cont'd).

No. samples:	BW (1)	ET (4)	FP (8)	GH (5)	LS (5)	MM (1)	ST (1)	TOT (25)
HERBACEOUS PERENNIALS (CONT'D)								
Selaginella arizonica N = 16	—/4	—/4	3/7	4/7	—/7	1/3	—/5	.32
SPRING ANNUALS								
Amsinckia tessellata		3	1	1				.20
Astragalus nuttallianus		3	5	3	3		1	.60
Astragalus sp.							1	.04
Bowlesia incana			1					.04
**Brassica tournefortii*		OB						
Calycoseris wrightii		2					1	.12
Camissonia sp.			1					.04
**Centaurea melitensis*			1					.04
Chorizanthe brevicornu		4	4	2	2		1	.52
Cryptantha barbigera	1	3	6	4	3	1	1	.76
Cryptantha maritima		3						.12
Cryptantha nevadensis				OB				
Cryptantha sp.		2	1		OB			.12
Daucus pusillus		3	3	1	3	1		.44
****Erodium cicutarium***	1	2	7	4	4	1		.76
Eucrypta chrysanthemifolia		2	6	3	2	1	1	.60
Filago sp.			1					.04
Filago/Stylocline				5	3			.32
Gilia/Linanthus			1					.04
Harpagonella palmeri		1			2	1		.16
Lepidium lasiocarpum		4		2				.24
Lepidium cf. virginicum			7					.28
Lepidium sp.					3	1	1	.20
Linanthus bigelovii							1	.04
Lotus humistratus		1		1	2	1		.20
Lotus salsuginosus		1	6	5	1	1		.56
Lotus strigosus			1			1	1	.12
Lotus sp.	1		2	4	2			.32

Table 3 (cont'd).

No. samples:	BW (1)	ET (4)	FP (8)	GH (5)	LS (5)	MM (1)	ST (1)	TOT (25)
SUMMER ANNUALS (CONT'D)								
Portulaca oleracea				1				.04
Portulaca halimoides					1			.04
N = 13	3	5	6	5	4	1	2	
ASEASONAL ANNUALS								
Amaranthus sp.		1	1	3	4	1		.40
Chenopodium sp.					1		1	.08
N = 2	0	1	1	1	2	1	1	
Total = 133	20	47	66	60	69	38	34	

Table 4. Plant taxa identified in fresh tortoise fecal pellets from Arizona sites that were eaten in another season. BW = Bonanza Wash, Yavapai County, ET = Eagletail Mountains, Maricopa County, FP = Four Peaks plot, Maricopa County, GH = Granite Hills, Pinal County, LS = Little Shipp Wash, Yavapai County, M = Mineral Mountains, Pinal County, ST = Sand Tank Mountains, Maricopa County. Values = numbers of samples, OB = observation only. Taxa in 10 or more samples in bold.

TAXA / **No. samples**	ET (4)	FP (8)	GH (5)	LS (5)	**MM** (1)	ST (1)	TOT (25)
TREES AND SHRUBS							
Cercidium microphyllum			1				1
Encelia farinosa	1	4	2		1	1	9
N = 2	1	4	3	0	1	1	10
SUBSHRUBS AND WOODY VINES							
Ambrosia deltoidea			1		1	1	3
Ambrosia dumosa					1		1
Ambrosia eriocentra				1			1
Lotus rigidus				1			1
N = 4	0	0	1	2	2	1	6
SPRING ANNUAL GRASSES							
Bromus rubens	**1**	**5**	**3**	**4**	**1**		**14**
Poa bigelovii			1				1
**Schismus barbatus*			OB				1
Vulpia microstachys		4		2			6
Vulpia octoflora	1	4	3		1	1	10
N = 5	2	13	8	6	2	1	32
SUCCULENTS							
Carnegiea gigantea		2					2
N = 1	0	2	0	0	0	0	2

Table 4 (cont'd).

No. samples:	ET (4)	FP (8)	GH (5)	LS (5)	MM (1)	ST (1)	TOT (25)
			SPRING ANNUALS				
Amsinckia tessellata	1		1				2
Astragalus nuttallianus		2	1	1		1	5
Astragalus sp.						1	1
**Brassica tournefortii*	OB						1
Calycoseris wrightii						1	1
Chorizanthe brevicornu	1	1	2	1		1	6
Cryptantha barbigera	**1**	**5**	**2**	**2**	**1**	**1**	**12**
Cryptantha maritima	1						1
Cryptantha nevadensis			OB				1
Cryptantha sp.		1					1
Daucus pusillus	1	1	1	1	1		5
Erodium cicutarium		**4**	**3**	**2**	**1**		**10**
Eucrypta chrysanthemifolia	1	4	1	1	1	1	9
Filago sp.		1					1
Filago\Stylocline			3	3			6
Harpagonella palmeri				1	1		2
Lepidium lasiocarpum	1		2				3
Lepidium cf. virginicum		4					4
Lepidium sp.				2	1	1	4
Linanthus bigelovii						1	1
Lotus humistratus	1		1	1	1		4
Lotus salsuginosus	**1**	**4**	**3**	**1**	**1**		**10**
Lotus strigosus		1			1		2
Lotus sp.		3	3	1			7
Lupinus concinnus	1		1				2
Lupinus sparsiflorus			1				1
Lupinus sp.			1				1

Table 4 (cont'd).

No. samples	ET (4)	FP (8)	GH (5)	LS (5)	MM (1)	ST (1)	TOT (25)
SPRING ANNUALS (CONT'D)							
Microseris linearifolia				1			1
Parietaria hespera		1	2	1			4
Pectocarya recurvata	2	5	3	3	1	1	15
Perityle emoryi	1			1			2
Phacelia crenulata	1			1			2
Phacelia distans		3	3				6
Plagiobothrys arizonicus		1		1			2
Plantago fastigiata	1				1		2
Plantago patagonica					1		1
Plantago sp.		4	3	3		1	11
Silene antirrhina	1	4	1	2	1	1	10
Thysanocarpus curvipes		1		1	1		3
N = 39	16	19	21	21	14	11	172
SUMMER ANNUALS							
Boerhavia intermedia		1					1
Euphorbia setiloba		1					1
N = 2	0	2	0	0	0	0	2
Total = 53	19	40	23	29	19	14	224

Mountains by Peter Woodman, at the Granite Hills by David Silverman, and at the Mineral Mountains by Scott Hart. Additional bite count observations made by Vanessa Dickinson and John Snider in June-October for 1991-1993 at Little Shipp Wash included *Schismus barbatus*, *B. tournefortii*, and *C. nevadensis*, species that were not identified in the fragment analyses (Dickinson et al., 1995).

The plants eaten out of season were mostly spring taxa (94.3%: 39 annual dicots, 5 annual grasses, 4 subshrubs, 1 shrub, 1 tree). The only summer taxa found in spring scat were *Boerhavia intermedia* (spiderling), *Carnegiea gigantea* (saguaro), and *Euphorbia setiloba* (spurge). Fully 98.2% of the aseasonal feeding records were spring taxa! The most common taxa eaten out of season in descending order (Table 4) were: *Pectocarya recurvata* (15), *Bromus rubens* (14), *Cryptantha barbigera* (12), *Silene antirrhina* (12, desert catchfly), *Plantago* sp. (11), *Erodium cicutarium* (10), *Lotus salsuginosus* (10, deer vetch), and *Vulpia octoflora* (10, six-weeks fescue). Combinations of the *Lotus* taxa (18), *Vulpia octoflora\V. microstachys* (17) and the *Plantago* taxa (15) augment their importance. These 14 taxa account for 50.4% of the out-of-season feeding records.

The abundance of dead spring annuals eaten in the summer and fall is even more impressive. For example, *Bromus rubens* was present 82-100% of the 25 pellets in four samples of fresh pellets collected from Four Peaks by Roy Murray in September and October of 1995 (Appendix 7). The number of florets per pellet was 1-164; 3-14 pellets per sample had 20 or more.

Microhistological Analyses. Microhistological analyses of the residues from the 25-pellet samples in the fragment analyses (Tables 1 and 3, Appendices 5-9) are presented in Tables 5-9. These mean relative densities are general indicators of the biomass of plants eaten in the diet. A total of 41 taxa were recorded including seven miscellaneous categories. The 31 taxa identified to genus include trees and shrubs (33.3%), a succulent (2.4%), grasses (33.3%), and annuals (22.2%). Taxa only identified in the microhistological analyses including *Agropyron* (wheatgrass, likely misidentification, not in area), *Abutilon* (Indian mallow), *Atriplex* (saltbush), *Cercocarpus* (mountain mahogany), *Ephedra* (Mormon tea), *Eriophyllum* (an annual composite), *Hibiscus* (rose mallow), *Marina* (a small legume), *Salsola* (Russian thistle), *Sida*, and *Sporobolus* (dropseed) raise the total number of dietary taxa to 143. Thirteen taxa accounted for 10% or more of the diet in at least one sample. They included shrubs (*Abutilon, Hyptis*), subshrubs (*Herissantia, Hibiscus, Sphaeralcea*), a woody vine (*Janusia*), herbaceous perennials (*Eriogonum, Evolvulus, Sida*), grasses (*Aristida, Bouteloua, Sporobolus*), and a single annual (*Plantago*). The only evidence of eating introduced species was low levels of *Bromus* (0.3-5.5%), *Erodium* (0.3-0.8%), and *Salsola* (1.3%).

The most important food items were in general grasses or the *Janusia*-mallow cohort (JAMA). Mallows are *Abutilon, Herissantia, Hibiscus, Sida*, and *Sphaeralcea*. In the Eagletail Mountains, the most xeric study site, tortoises were eating mostly *Janusia* (27.8-68.2%) as well as *Abutilon* (1.1-29.3%), *Eriogonum* (0-11.3%), and *Hibiscus* (0-11.5%). Grasses were less important (13.2-24.2%; Table 6). For the Bonanza Wash, Mineral Mountains, and Sand Tank

Table 5. Mean percent relative density (x) and standard deviation (SD) of discerned microhistological fragments from tortoise fecal samples from the Bonanza Wash (BW), Mineral Mountains (MM), and Sand Tank Mountains (ST), Arizona. Based on 5 slides of 20 fields per sample. F = fresh pellets, M = mixture of fresh and old pellets. Percentages of 10% or more in bold.

TAXA	BW (M) (9\10-92)		MM (F) (9\10-96)		ST (M) (8\10-92)	
	x	sd	x	sd	x	sd
TREES, SHRUBS AND WOODY VINES						
Abutilon			**15.7**	**3.1**	5.3	2.3
Cercidium	0.5	1.2				
Hyptis			0.5	0.7	0.8	1.1
Janusia			6.2	2.8	8.3	3.0
Sphaeralcea	**17.7**	**7.3**	**15.9**	**3.9**		
N = 5	**18.2**		**38.3**		**14.4**	
GRASSES						
Aristida	**46.0**	**7.1**	**57.6**	**6.9**	**58.3**	**4.2**
Bouteloua			0.3	0.8	**24.4**	**4.7**
Bromus			0.8	1.2		
Erioneuron	6.3	2.9				
Hilaria/Pleuraphis	0.5	1.0	0.3	0.7	0.4	0.8
Muhlenbergia			1.9	2.7	1.1	1.7
Poa	1.0	2.1				
Sporobolus	**26.8**	**5.9**				
N = 8	**76.6**		**60.8**		**84.2**	
HERBACEOUS PERENNIAL						
Evolvulus			0.3	0.7		
N = 1	0		0.3		0	
ANNUALS						
hydrophyll	1.4	1.9				
Oenothera					0.4	0.8
Plantago			0.3	0.6	0.4	0.9
N = 3	1.4		0.3		0.8	
MISCELLANEOUS						
seed					0.6	1.4
N = 1	0		0		0.6	
TOTAL = 18	**8**		**11**		**10**	

Table 6. Mean percent relative density (x) and standard deviation (SD) of discerned microhistological fragments from tortoise fecal samples from the Eagletail Mountains, Maricopa County, Arizona. Based on 5 slides of 20 fields per sample. D = pellets of inteterminate age from den. F = fresh pellets, M = mixed fresh and old pellets. Percentages of 10% or more in bold.

TAXA	#2 (F) (9-95) x	sd	#3 (M) (3-96) x	sd	#4 (D) (9-95) x	sd	#5 (D) (9-95) x	sd
TREES, SHRUBS AND WOODY VINES								
Abutilon	**29.3**	**3.3**	**13.1**	**2.8**	1.1	1.5	5.0	2.1
Acacia	4.4	2.0	0.5	1.1				
Atriplex	0.7	1.6						
Ephedra					0.7	1.5		
Hibiscus			**11.5**	**4.8**			0.5	1.2
Hyptis					1.2	1.7	1.6	2.4
Janusia	**27.8**	**4.9**	**28.1**	**3.6**	**46.5**	**6.1**	**68.2**	**5.4**
Olneya			0.5	1.1				
Quercus	0.6	1.2						
N=9	**62.8**		**54.5**		**49.5**		**75.3**	
SUCCULENT								
cactus	1.1	1.5						
N = 1	1.1		0		0		0	
GRASSES								
Aristida	**10.4**	**3.4**	**10.0**	**4.3**	8.7	3.5	;	
Bouteloua	3.5	2.4	**11.2**	**2.8**			1.7	1.6
Bromus	3.3	2.6	2.0	2.8	4.0	1.3	2.2	1.3
Erioneuron					0.5	1.1		
Hilaria/Pleuraphis			1.0	2.3			3.5	3.3
N = 5	**17.2**		**24.2**		**13.2**		**19.5**	
HERBACEOUS PERENNIALS/ANNUALS								
Eriogonum			**11.3**	**3.7**				
Marina	4.1	4.3						
N = 1	4.1		**11.3**		0		0	

Table 6 (cont'd):

TAXA	#2 (F) x	#2 (F) sd	#3 (M) x	#3 (M) sd	#4 (D) x	#4 (D) sd	#5 (D) x	#5 (D) sd
ANNUALS								
Astragalus	2.9	2.1			2.9	2.0	4.6	1.9
Erodium					0.5	1.1		
Oenothera			1.5	2.3			0.3	0.8
Plantago	**10.1**	**6.6**	7.7	3.2	**27.2**	**6.5**		
N = 4	**13.0**		9.2		**30.6**		4.9	
MISCELLANEOUS								
seed	1.8	2.6	1.1	1.5	2.4	3.8		
N = 1	1.8		1.1		2.4		0	
TOTAL = 22	13		14		11		10	

Table 7. Mean percent relative density (x) and standard deviation (SD) of discerned microhistological fragments in tortoise fecal pellets from Four Peaks, Maricopa, County, Arizona. Based on 5 slides of 20 fields per sample. F = fresh pellets, M = mixed fresh and old pellets, W = old, weathered pellets, B = very old, bleached pellets. * = questionable, not in area. Percentages of 10% or more in bold.

TAXA	#1 (F) (10-92) x	sd	#2 (F) (9\10-95) x	sd	#3 (M) (9\10-95) x	sd	#4 (F) (9\10-95) x	sd	#5 (F) (9\10-95) x	sd	#6 (F) (4-96) x	sd	#7 (W) (4-96) x	sd	#8 (B) (4-96) x	sd
TREES, SHRUBS AND WOODY VINES																
Abutilon	**24.5**	**2.4**	**34.0**	**3.7**	**33.2**	**9.0**	**54.9**	**6.9**	6.9	3.6			**26.9**	**5.5**	7.5	1.9
Cercidium					2.5	3.8	0.6	1.4					1.4	3.1		
Cercocarpus					0.9	1.9							1.4	2.0		
Eriogonum					**11.8**	**5.7**	1.2	1.6								
Hyptis			2.3	3.4	**11.9**	**4.5**	2.5	2.8					0.6	1.3		
Janusia	3.2	1.4	6.4	2.3			**13.3**	**5.5**	4.1	2.3			4.7	1.7		
Larrea					0.8	1.8										
Olneya			0.8	1.7												
Sphaeralcea	2.5	1.1	9.0	5.4	5.0	4.8	6.2	2.6	1.2	1.1	0.5	1.1			6.5	2.5
N = 9	**30.2**		**52.5**		**66.1**		**78.7**		**12.2**		0.5		**35.0**		**14.0**	
SUCCULENTS																
cactus			0.8	1.9												
N = 1	0		0.8		0		0		0		0		0		0	
GRASSES																
**Agropyron*							0.7	1.5								
Aristida	**63.5**	**7.3**	**25.2**	**3.8**	4.3	4.3	**13.7**	**4.8**	**83.0**	**6.9**	**82.8**	**5.6**	**54.3**	**8.8**	**85.1**	**3.2**
Bouteloua											0.3	0.7	0.7	1.5		
Bromus	0.3	0.8	5.5	2.0	4.8	3.2	0.6	1.3			0.4	0.8			0.7	0.9
Erioneuron	1.1	1.6	0.8	1.9	1.7	2.3			0.4	0.9						
Muhlenbergia	0.4	0.9														
Sporobolus	4.2	3.4	3.4	5.7	1.6	2.2	0.6	1.3								

Table 7 (cont'd).

TAXA	#1 (F) x	sd	#2 (F) x	sd	#3 (M) x	sd	#4 (F) x	sd	#5 (F) x	sd	#6 (F) x	sd	#7 (W) x	sd	#8 (B) x	sd
GRASSES (cont'd):																
Tridens									0.5	1.0						
N = 8	69.5		34.9		12.4		15.6		83.9		83.5		55.0		85.8	
HERBACEOUS PERENNIALS																
Evolvulus			6.4	2.5	0.7	1.5	0.6	1.3					4.1	2.9		
Marina					4.7	3.9	0.7	1.5								
Sida											15.3	3.8				
N = 3	0		6.4		5.4		1.3		0		15.3		4.1		0	
ANNUALS																
Astragalus					0.8	1.8			0.4	0.8						
Erodium											0.8	1.2				
Eriophyllum					0.7	1.5	0.6	1.3								
Lupinus					5.7	2.2			1.7	1.9			1.3	1.8		
Oenothera	0.3	0.8														
Plantago			4.7	4.4	4.2	3.0	1.8	1.6	1.4	2.1			2.1	1.9		
Salsola													1.3	1.8		
N = 7	0.3		4.7		11.4		2.4		3.5		0.8		4.7		0	
MISCELLANEOUS																
bean							1.8	1.6								
composite									0.5	1.0						
pollen													0.6	1.3		
seed					2.5	2.3									0.3	0.7
unknown forb					1.5	2.1										
unknown forb I			0.8	1.7									0.7	1.6		
unknown forb II					0.9	1.92	0.6	1.3								
N = 7	0		0.8		4.9		0.6		0.5		0		1.3		0.3	
TOTAL = 35	9		13		20		16		10		6		13		5	

Table 8. Mean percent relative density (x) and standard deviation (SD) of discerned microhistological fragments from tortoise fecal samples from the Granite Hills, Pinal County, Arizona. Based on 5 slides of 20 fields per sample. F = fresh pellets, M = mixed fresh and old pellets. Percentages of 10% or more in bold.

TAXA	#1 (F) (9\10-92) x	sd	#2 (F) (9-95) x	sd	#3 (M) (9-95) x	sd	#4 (F) (5-96) x	sd	#5 (M) (3-96) x	sd
TREES, SHRUBS, AND WOODY VINES										
Abutilon	8.7	3.1							5.0	2.8
Cercidium	0.5	0.7								
Hyptis	1.8	1.5	0.3	0.6			0.3	0.7		
Janusia	**61.5**	**9.2**	**64.3**	**6.4**	**80.9**	**6.6**			**70.7**	**6.9**
Olneya	0.8	1.0	0.3	0.6	0.6	0.8			1.0	1.4
Sphaeralcea	6.0	2.4	**15.9**	**4.9**	9.6	4.4			4.9	2.7
N = 6	**79.3**		**80.8**		**91.1**		0.3		**81.6**	
SUCCULENTS										
cactus			0.3	0.7						
N = 1	0		0.3		0		0		0	
GRASSES										
Aristida	**12.5**	**2.1**	**17.6**	**3.1**	4.8	3.3	**94.2**	**3.8**	**14.8**	**6.0**
Bouteloua	1.9	2.6	0.6	0.8	0.5	1.0				
Bromus	0.4	0.9					2.5	2.9		
Erioneuron	6.5	4.3	0.3	0.6						
seeds, glumes									2.2	2.2
N = 5	**21.3**		**18.5**		5.3		**96.7**		**17.0**	
HERBACEOUS PERENNIAL										
Marina									0.4	0.9
N = 1	0		0		0		0		0.4	
ANNUALS										
Astragalus			0.4	1.0						
Erodium	0.3	0.7								
hydrophyll										
Lupinus					1.6	1.8			0.5	1.1
Plantago			0.3	0.6	0.9	2.0	2.7	2.3		
N = 5	0.3		0.7		2.5		2.7		0.5	
MISCELLANEOUS										
seed					0.5	1.0				
N = 1	0		0		0.5		0		0	
TOTAL = 19	11		10		8		4		8	

Table 9. Mean percent relative density (x) and standard deviation (SD) of discerned microhistological fragments from tortoise fecal samples from Little Shipp Wash, Yavapai County, Arizona. Based on 5 slides of 20 fields per sample. F = fresh pellets, G = gut content of dead tortoise, M = mixed fresh and old pellets. * = questionable, not in area. Percentages of 10% or more in bold.

TAXA	#1 (M) (9-92)		#2 (F) (9-95)		#3 (F) (9-95)		#4 (M) (4-96)		#5 (G) (9-95)	
	x	sd	x	sd	x	sd	x	sd	x	sd
TREES, SHRUBS, AND WOODY VINES										
Abutilon	**26.1**	2.6	**36.6**	5.8	**23.8**	3.9	**38.7**	3.6		
Cercocarpus							1.6	2.3		
Herissantia									**64.6**	8.3
Hyptis					0.6	1.4	0.7	1.6		
Janusia	3.6	2.7			0.5	1.1	0.6	1.3	2.2	1.6
Larrea			0.5	1.1						
Sphaeralcea	3.9	3.5	7.7	3.9	1.2	2.8	0.9	2.0		
N = 7	33.6		44.8		26.1		41.7		66.8	
SUCCULENTS										
cactus			3.1	0.4	2.9	2.2			1.3	2.0
N = 1	0		3.1		2.9		0		1.3	
GRASSES\SEDGES										
**Agropyron*	1.2	2.6								
Aristida	**21.7**	3.7	0.0	7.5	**23.1**	7.7	**21.9**	5.9	4.3	3.3
Bouteloua									**17.7**	5.5
Bromus			0.7	1.5	1.5	1.4				
Cyperus/Carex	0.5	1.2			0.6	1.4	0.9	2.0		
Erioneuron	1.4	2.0								
Hilaria/Pleuraphis									3.9	2.9
Juncus									0.5	1.1
Sporobolus	**21.7**	5.1	4.6	4.1	4.4	2.1	**10.0**	7.6		
Tridens							5.2	3.2		
N = 10	46.5		45.3		29.6		38.0		26.4	
HERBACEOUS PERENNIALS										
Evolvulus	**18.7**	3.5	3.1	0.4	**40.3**	6.2	**14.0**	6.0		
Sida									5.0	2.3
N = 2	18.7		3.1		40.3		14.0		5.0	
ANNUALS										
Astragalus	0.5	1.2			0.5	1.1	5.6	3.8		
Lupinus	0.6	1.3								
Oenothera									0.5	1.1
Salvia			0.7	1.5						
N = 4	1.1		0.7		0.5		5.6		0.5	
MISCELLANEOUS										
arthropod parts			1.4	1.9						
composite			1.7	1.3	0.6	1.4				
N = 2	0		3.1		0.6		0		0	
TOTAL = 26	11		11		12		11		9	

Mountains samples, grasses were the dominant (60.8-84.2%, especially *Aristida* [46.0-58.3%]) food plants, with JAMA secondary (13.6-37.8%; Table 5). In the Granite Hills, the samples were dominated by *Janusia* (61.5-80.9%), with lesser amounts of grasses (5.3-21.3%; Table 8). An April sample lacking *Janusia* had 94.2% *Aristida*. At Four Peaks and Little Shipp Wash, the two most mesic sites, dominance fluctuated between JAMA and grasses (Tables 7 and 9). The importances of the herbaceous perennials *Evolvulus* and *Sida* are notable in these samples. Grasses and JAMA together make up the bulk of the tortoise diets at all of the sites: Bonanza Wash (94.3%), Mineral Mountains (98.6%), Sand Tank Mountains (97.8%), Eagletail Mountains (59.8-93.2%), Four Peaks (50.6-99.9%), Granite Hills (95.8-97.6%), and Little Shipp Wash (55.1-93.2%).

DISCUSSION

Comparison of Methods. The 133 taxa recorded in the tortoise diet (Table 3) illustrate the power of fragment analyses to document the great diversity of plants consumed by tortoises, especially annuals. It does not provide an accurate reflection of the less-diagnostic material (grass blades, digested leaves, etc.) that forms the bulk of the pellet matrices. The majority of the diet biomass apparently is non-reproductive materials, not the seeds and fruits typically identified in fragment analysis. Fragment analyses were able to document the surprising frequencies of spring annual grasses and dicots eaten dried in summer and fall (Table 4).

Microhistological analyses provided good estimates of the total biomass of plant foods eaten. These dietary staples were relatively few in number -- only 13 species were present at levels of 10% or more in one of the 25 samples. Most of the samples (and diets) were dominated by grasses or *Janusia*/mallows. Most of the diverse food plants documented in the diets in fragment analyses are missed in microhistological analyses either because their vegetative parts are less diagnostic at the cellular level (the fragments identified were removed from the samples) or not common enough to be discerned when the entire sample was reduced to microscopic scale. The annuals in general, especially *Chorizanthe brevicornu*, *Cryptantha barbigera*, *Lotus* spp., *Pectocarya recurvata*, and *Silene antirrhina*, etc.), were missing. Microhistological analyses recorded more *Aristida*, *Bouteloua*, *Hilaria\Pleuraphis*, and *Sporobolus* than fragment analyses but less *Bromus* and no *Vulpia*.

Diet Summary. Desert tortoises in Arizona Upland Sonoran Desert habitats are relatively specialized herbivores that primarily eat grasses or *Janusia*/mallows. These two groups of plants (16 taxa) accounted for at least 90% of the biomass in most of the samples. In the xeric Eagletail Mountains sample, grasses are uncommon and *Janusia*/mallows dominated tortoise diets. In the higher areas where grasses are more common, either group can be dominant.
In this context, it is prudent to note that these staple plants are those preferred by grazing livestock.

The additional 102 taxa of plants documented in fragment analyses demonstrates that desert tortoise diets have more general aspects as well. The 61 dicot annuals (75.4% spring) identified in the pellets, some in very large numbers, indicate that tortoises readily consume plants that rarely account for significant amounts of their diets. The pronounced consumption of annual plants likely reflects strong selective pressures for some kind of dietary supplements -- extra protein, trace minerals, vitamins, etc. deficient in the grass-*Janusia*/mallow staples. Analyses of the nutrient and mineral contents of the dietary plants will help understand the value of these secondary foods. In the final report on a companion study to this one, we will address the relationship of diet to nutrition (Van Devender and Schwalbe, in prep.).

Another enigma is that it is unlikely that some of the plant foods (*Ambrosia* spp., *Carnegiea gigantea*, *Encelia farinosa*, etc.) were eaten deliberately, raising the possibility that tortoises eat miscellaneous plant debris accumulated in protected pockets. Moreover, the consumption of large numbers of spring ephemerals eaten dried in summer and fall illustrates the importance of eating dried plants. Nagy and Medica (1986) found that the ability to drink rain water in the occasional warm-season storms helped to relieve physiological stress by flushing excess potassium and salts from the bladder and allowing tortoises to utilize dry grasses and forbs to accumulate energy. Well-hydrated tortoises achieve positive energy balances and are able to store lipids as potential energy reserves. Peterson (1993) concluded from his studies in the western and eastern Mohave Desert in California that the desert tortoise was not physiologically adapted to live in the desert but was a "tenuous relic of a less rigorous climate". During drought, tortoises lost body mass, body water contents declined, and solute concentrations of blood plasma increased to very high levels. Only when tortoises drank water were body mass, water content, and fluid concentrations restored allowing them to forage on dry plants and probably make an energy profit and store fats.

Our results suggest that even in the biseasonal Sonoran Desert, where tortoises achieve positive water balance more often than those in the Mohave Desert, and most of the foraging behavior is from late July to October, the consumption of dried plants is important. For several weeks after the beginning of the summer monsoon, the only plants available to well-hydrated tortoises are from previous seasons. In drier years, sporadic rainfall is enough to hydrate tortoises but not for substantial growth of plants. Except in the driest years, tortoises are not likely to be critically stressed by drought because they rehydrate in spring and/or summer and grasses-*Janusia*/mallows and dead annuals are generally available. Critical physiological stress is much more likely in the Mohave Desert with only winter rainfall and greater difficulty in eating dried plants due to longer periods of dehydration. Arizona Upland Sonoran Desert habitats on boulder ridges from 760 to 1070 m elevation in central and southern Arizona are prime desert tortoise habitat due to adequate biseasonal rainfall (shorter periods of dehydration), relatively high winter minimum temperature (partly due to cold air drainage), and a diverse flora rich in grasses, *Janusia*/mallows, and annuals. Tortoise ecology in these habitats is clearly derived from the behavior of their southern cousins in Sonora and Sinaloa that dwell in tropical thornscrub and deciduous forest habitats.

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