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Nutritional Quality of Native and Introduced Food Plants of Wild Desert Tortoises

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ABSTRACT.—Digestibilities of dry matter, energy, water, and nitrogen were determined for four foods of desert tortoises (*Gopherus agassizii*) that were kept individually in outdoor pens where food intake and feces output could be measured quantitatively. Two native plants, the forb *Malacothrix glabrata* and the grass *Achnatherum (Oryzopsis) hymenoides*, and two exotic plants, the forb *Erodium cicutarium* and the grass *Schismus barbatus*, were collected in the field during the seasons that wild tortoises consumed them (spring for the forbs, summer for the then-dead and dry grasses), and were then offered to the penned tortoises. The digestibilities of the nutrients in the two forbs were similar, ranging from 63–70% for dry matter, 69–73% for energy, 72–79% for nitrogen, and 70–75% for water. Which forb was the more nutritious depends on what determines feeding rate (appetite) in tortoises. If tortoises eat to obtain a given volume of food ("full stomach") daily, then the exotic forb provides significantly more digestible energy and nitrogen, but if tortoises eat to obtain a given amount of digestible energy ("meet energy needs") daily, then the native forb provides significantly more nitrogen and water. The dry matter and energy digestibilities of the two grasses were much lower than the forbs, but were similar to each other, ranging from 46–50%. However, both grasses provided little or no nitrogen, and the tortoises lost more water than they gained while processing grasses. The type of food plant (forb or grass) and its phenological stage, rather than its geographic origin (native or exotic), best predicted its nutritional value.

Food is a primary resource needed by reptiles, and food quality can be critically important to survival, especially for herbivorous reptiles, because plant foods vary in quality much more than do foods of animal origin. Reptiles have probably coevolved with many of their prey species, and herbivores have probably adapted more or less to the chemical and structural antiherbivore properties their food plants have evolved (Van Soest, 1982; Crawley, 1983). What happens to herbivorous reptiles such as desert tortoises when exotic plants invade their habitat?

The Mojave Desert has become increasingly colonized by two introduced annual plants: the forb *Erodium cicutarium* (filaree, family Geraniaceae) and the grass *Schismus barbatus* (split grass, family Graminae). When winter rainfall is adequate, these two species may carpet the desert floor so densely that after they dry up in summer, wildfires may occur where they never had before these plants invaded (Brooks and Berry, 1996). Is this change in flora beneficial or detrimental to the desert tortoises (*Gopherus agassizii*) in the Mojave Desert? This turtle is the California State Reptile, and it has been listed as a Threatened Species by the U.S. Fish and Wildlife Service, due to a precipitous decline in population densities in the late 1980s.

There are reasons to suspect that the invasion of exotic plants, among other changes in their environment, may be influencing the nutritional status of these tortoises. We hypothesized that filaree and split grass, both of which are eaten in large amounts by wild desert tortoises (Marlow, 1979; Nagy and Medica, 1986; Barboza, 1995a; Esque et al., 1996; Henen, 1996), were of lower nutritional quality than two native food plants. We conducted standard input-output feeding trials (see recent reviews by Robbins, 1993; Stevens and Hume, 1995) on these four plant species to measure the digestibilities of the major nutrients (energy, nitrogen, and water) in order to compare the nutritional qualities of these plants.

MATERIALS AND METHODS

Animals.—We obtained 14 desert tortoises (*Gopherus agassizii*) of various ages and sizes (400–4500 g body mass) from Clark County, Nevada, where they had been captured prior to construction of a flood control project. A fifteenth tortoise, from the Mojave Desert in San Bernardino County, California, was added to the study for the second set of feeding trials, because two original tortoises did not survive the intervening years. Tortoises in the study were free of upper respiratory tract disease (URTD) symptoms. They were housed separately in outdoor pens (2.4 m × 1.2 m × 0.6 m high) made of plywood, with open tops except for one corner that was covered to provide shade for thermoregulatory purposes. The shaded corner contained a Styrofoam and concrete building block nesting box. The plywood floors were covered with a 5–10 mm layer of washed sand. Four

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metal picture hooks were glued to the shell of each tortoise around the cloaca (two on the plastron, two on the carapace) so that plastic bags could be attached to collect feces uncontaminated by sand. A minimum-maximum thermometer was hung 50 cm above the floor in the shade of one pen to monitor daily air temperatures. The tortoises were allowed three weeks to become accustomed to the cages and experimental diets before measurements began.

Diets.—Feeding trials were done using four species of plants that free-living desert tortoises eat (Marlow, 1979; Nagy and Medica, 1986; Esque et al., 1996): desert dandelion (*Malacothrix glabrata*), which is a native annual wildflower (or forb); red-stemmed filaree (or heron's bill; *Erodium cicutarium*), an introduced forb; Indian rice grass (*Achnatherum* (formerly *Oryzopsis*) *hymenoides*), a native perennial grass; and split grass (*Schismus barbatus*), an introduced annual grass. We collected these plants in the field (western Mojave near the towns of Lancaster, Little Rock, and Mojave) at the time of year that tortoises eat them: spring for the forbs, and summer for the grasses (which are usually dead and dry when eaten). Clean, above-ground parts of the plants that we judged tortoises could and would eat were cut off and sealed in plastic bags upon collection. The green forbs and the *Schismus* grass, which was mostly brown but not completely dry were quickly frozen, and portions were thawed as needed for feeding trials. We froze freshly-collected diet items because (1) forbs mature and senesce quickly in the Mojave Desert, so their availability in a lush condition is restricted to a relatively short period; (2) freezing preserves freshness and quality of macronutrients, although it may alter slightly the availability of some vitamins (Macrae et al., 1993); and (3) although freezing may change digestibility of leaves by disrupting cell walls, the effect is apparently small or negligible—1–2% increase in digestible energy content in leafy human foods like collards and spinach (Adams, 1975). The very dry *Achnatherum* grass was not frozen. Plants were cut into 2–4 cm lengths before feeding.

Feeding Experiments.—During the first year (1991), feeding trials on *Erodium cicutarium* were done in spring and early summer, then trials on *Schismus barbatus* were run in summer and early autumn. In the second year of measurements (1994), *Malacothrix glabrata* was studied in spring, switching to *Achnatherum hymenoides* in summer. Between feeding trials, tortoises were maintained in their outdoor pens either on natural field diets or on chopped fresh vegetables (green beans, summer squash, leaf lettuce, broccoli, carrots), and they were also fed locally-available wild forbs (e.g., *Sonchus oleraceus*). We offered each experimental diet to tortoises for 15–20 d before measurements began. This is approximately the time required for green foods to transit the gut of tortoises (Nagy and Medica, 1986; Meienberger et al., 1993). Food movement through tortoises was traced using indigestible plastic tape, which is a good marker for particulate matter (Warner, 1981; Van Soest, 1982) and works well in desert tortoises, which pass food along the gut as in a tubular flow system (Meienberger et al., 1993). Tortoises were force-fed eight 3 × 25-mm strips of colored plastic "surveyor's" tape to mark the beginning of a pulse of food through the gut, and we began measuring food consumption at that time. As soon as the tape markers were voided, the date was noted to determine gut transit time (TT, after Warner, 1981), and we collected all feces defecated between that marker and the next marker. Each ten days, for 3–4 more times, we marked the beginning of a new trial on the same diet by feeding more plastic tape (using different colors each time). Thus, we obtained 3–4 measurements per animal per diet for transit time, food consumption, feces production, and nutrient digestibilities.

Each day, weighed amounts of fresh foods were offered, and the remaining food from the previous day, if any, was collected into pre-weighed plastic containers for drying and weighing. Most tortoises ate all offered food each day; thus little selective feeding occurred. Samples of fresh diets were taken periodically for measurement of water and nutrient contents. Feces from collection bags were cleaned of urates (if any) and stored in pre-weighed plastic containers for subsequent drying and weighing. We calculated total dry matter consumed between the times of marker ingestion and marker excretion from measurements of fresh food offered times dry matter content of food, minus dry matter in uneaten food. Apparent digestibility of dry matter (%) was calculated as dry matter ingested minus dry matter defecated between markers, divided by dry matter ingested.

Drinking water was not provided during feeding trials, but before each new diet was begun, tortoises were placed in pans containing fresh water for an hour to allow them to hydrate themselves. All animals were weighed at two day intervals. Because their body masses can drop quickly as a result of urination events, we used maximum body mass of each tortoise in subsequent data analyses.

Sample Analyses.—Fresh samples of diets and uncontaminated (by urine or sand) subsamples of feces were dried to constant mass (in duplicate) at 60 C to determine water contents by mass loss. These samples were then ground to pass a 1 mm^2 screen and kept in a desiccator

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pending analyses. Energy contents were measured (in duplicate) using a Phillipson microbomb calorimeter, and nitrogen contents were determined (in duplicate or triplicate) either at UCLA by the micro-Kjeldahl technique involving the indophenol-blue method on a Technicon continuous-flow analyzer, or at UC Davis' Division of Agricultural and Natural Resources Analytical Laboratory in a nitrogen gas analyzer (Leco model FP428) using an induction furnace and thermal conductivity (Sweeney, 1989).

Statistics.—The allometric relationship between food intake and body mass was evaluated by least squares regression analysis of $\log_{10}$-transformed variables. An F-test was used to determine significance of the regressions. Differences in apparent digestibilities were evaluated first by one-way analysis of variance on all diets combined, then by pair-wise comparisons using paired t-tests or Mann-Whitney U-tests as appropriate for data sets having either homoskedastic or heteroskedastic distributions. The probability level of 0.05 was used as threshold for statistical significance of differences between means or medians. Values reported are means and standard deviations (SD).

RESULTS

Many of the results from the feeding trials on the two introduced plant species (*Erodium cicutarium* and *Schismus barbatus*) are reported in Meienberger et al. (1993). Ambient temperatures (shade) during the *Erodium* and *Schismus* feeding trials were relatively stable, and daily maximum values averaged 34 C, while minima averaged 16 C (Meienberger et al., 1993). During the *Malacothrix* trial (May and June), daily maxima averaged 28 C and minima averaged 15 C, and average temperatures during the *Achnatherum* trial were 37 C (maximum) and 19 C (minimum). Temperatures in the insulated nest boxes were less variable, ranging from 33 to 17 C. Tortoises were usually active in mid morning and late afternoon, and rested in the shade or in their nest boxes at other times.

Some tortoises either did not eat or ate only sporadically, and produced little or no feces, so they were excluded from subsequent analyses of nutrient digestibility. Those tortoises that ate consistently gained body mass while eating the native forb (12 animals), and lost mass while eating the native dry grass (eight tortoises). Daily dry matter (DM) intake rates averaged 3.5 (±1.47) g DM/d for the *Malacothrix* diet, and were significantly lower for the *Achnatherum* diet, averaging 1.5 (±1.19) g DM/d. When the tortoises were eating the introduced plants, they also consumed the forb faster than the grass, on a DM basis. However, average daily rates of exotic plant consumption, on a whole-animal basis, were lower than for the corresponding native species, mainly because the tortoises were three years younger and thus were smaller when they were eating the exotic diets. Body masses averaged 1265 g (range: 249–3110 g) during the introduced plant feeding trials in 1991, and during the native plant trials in 1994, tortoise masses were 47% greater, averaging 1863 g (range: 330–4440 g).

Within a trial, the larger tortoises ate more food between the ingestion of a marker and its defecation (=total food intake, g $\mathrm{DMI_{total}}$) than did the smaller ones. The allometric relationship for the *Malacothrix* trial is described by the equation: $\mathrm{g\ DMI_{total}} = 1.43\ (\mathrm{g\ BM})^{0.46}$, where g BM is body mass in grams ($r^2 = 0.63$, $N = 12$, $F = 17.2$, $P = 0.002$), and the allometric equation for the *Achnatherum* trial is: $\mathrm{g\ DMI_{total}} = 0.044\ (\mathrm{g\ BM})^{0.83}$, with $r^2 = 0.64$, $N = 8$, $F = 10.5$, and $P = 0.018$. The allometric regressions for the exotic and native forb diets are similar (Fig. 1), as are the regressions for the two grass diets, indicating that, on average, tortoises consumed 2–3 times as much DM when eating forbs as when eating grasses.

The nutrient composition of the two forbs were similar to each other, as were the two grasses. The forbs contained more water and nitrogen than did the grasses, but the total chemical potential energy contents were similar among all diets (although *Malacothrix* contained about 9% less energy/g DM than the others, suggesting that *Malacothrix* had a greater ash content; Table 1). The proportions of these nutrients that were apparently digestible were greatest in the forbs, ranging from 63 to 79% (Table 1). The digestibility of dry matter, energy and nitrogen was significantly higher in the native forb than in the exotic forb, but water in the exotic forb was more assimilable than in the native annual wildflower. Less than half of the dry matter and energy in the grasses was digestible, and the grasses contributed essentially no net nitrogen; apparent digestibilities for these nutrients did not differ significantly between grass species. Tortoises lost more water in feces than they gained from the diet when eating the dry grasses, thus apparent water digestibilities for grasses were negative, with the drier *Schismus* costing tortoises the most body water to process (Table 1).

The nutrient gain from a food can be calculated as the product of its nutrient content and nutrient digestibility. We calculated nutrient gains on the basis of both fresh mass and dry mass of the foods. Surprisingly, the exotic forb *Erodium* provided a greater amount of energy, per g of fresh or dry mass, than did the native forb *Malacothrix* (Table 2). This was due to the higher water content and lower energy content

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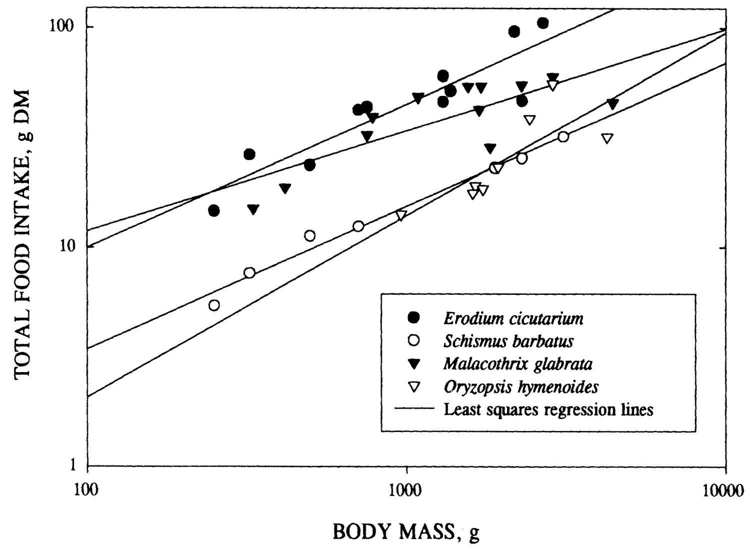

FIG. 1. Allometric relationship (double logarithmic plot) between total food consumed between the times of marker ingestion and egestion (Total Food Intake in g dry matter) and body mass of captive desert tortoises (*Gopherus agassizii*) voluntarily consuming various food plants. Each data point represents the mean of 2–4 trials for one tortoise on a single diet. The approximately three times greater intake of forb dry matter, after accounting for the greater digestibility of forbs, indicates that tortoise digestive tracts contained about two times more dry matter when they were eating forbs (closed symbols) as when eating grasses (open symbols).

of *Malacothrix. Erodium* provided 22% more nitrogen on a fresh matter basis, but 15% less nitrogen on a dry matter basis than *Malacothrix.* Both forbs provided the same amounts of digestible water on a fresh mass basis, but the native forb yielded more water on a dry matter basis. There were no significant differences in the digestible energy, nitrogen or water contents of the two grasses, except for the higher digestible energy yield (fresh matter basis) of *Schismus* compared to *Achnatherum* (Table 2).

When tortoises were eating the exotic diets, apparent digestibility of energy was positively correlated with transit time: when food stayed in the gut longer, more of its energy was digested and absorbed (Meienberger et al., 1993). For the native plant diets in this study, however, no significant correlations between energy digestibility and gut passage time were detectable ($P > 0.34$).

DISCUSSION

The nutritional value of a food can be evaluated at a variety of levels, ranging from its gross chemical composition, up to its actual contribution to the lifetime nutrition of the individual consumer, the latter incorporating ecological factors such as the daily, seasonal, and annual availability and palatability of the food item, as well as the varying nutritional needs of the animal. In this study, we focused on two parameters that are important nutritional indicators (percent nutrient digestibility and digestible nutrient amount per g DM), and on one parameter that is more ecologically relevant (digestible nutrient per g fresh matter). Water contents of plants are highly variable and can change rapidly in the field, so evaluating nutritional value of foods on a fresh mass basis includes a second variable (water content) which complicates comparisons. However, animals in the field are ingesting fresh food matter, not just its dry mass. Thus, both ways of expressing food nutritional value are important.

The native grass and the exotic grass differed little in the apparent digestibilities of their nutrients, or in the amounts of nutrients available per unit of fresh or dry mass (Tables 1 and 2). However, the two forbs did differ, with the dry matter, energy and nitrogen in the native forb *Malacothrix glabrata* being more readily digestible than in the exotic forb *Erodium cicutarium* (Table 1). However, on a fresh mass basis, the exotic forb was the more nutritious overall, providing 50% more digestible energy and 22% more digestible nitrogen per g fresh matter than did the native forb. On a dry matter basis, the exotic forb provided a bit more digestible energy, but the native forb yielded more digestible nitrogen (18%) and water (49%) than the exotic *Erodium.*

The primary reason underlying the nutritional differences between these forbs is the higher water content of *Malacothrix* (Table 1). If wild

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TABLE 1. Composition and apparent digestibilities (AD) of four important native and introduced food plants of desert tortoises. Data for *Erodium* and *Schismus* are from Meienberger et al. (1993). Values are means (SD). Means for apparent digestibilities having common superscripts within rows are not significantly different.

Nutrient	Food plant: *Erodium cicutarium* (exotic forb)	*Malacothrix glabrata* (native forb)	*Schismus barbatus* (exotic grass)	*Achnatherum hymenoides* (native grass)
Diet composition				
Dry matter (DM), g/g fresh	0.246	0.171	0.934	0.763
	(0.071)	(0.001)	(0.069)	(0.055)
Water, g/g fresh	0.754	0.829	0.066	0.237
	(0.071)	(0.001)	(0.069)	(0.055)
Energy, kJ/g DM	17.2	15.6	17.1	16.8
	(0.7)	(0.7)	(0.6)	(0.2)
Nitrogen, mg/g DM	25.0	26.9	8.0	8.7
	(2.0)	(1.3)	(2.0)	(0.3)
Apparent digestibility, %				
Dry matter	63.3	70.1	49.7^{a}	46.9^{a}
	(5.0)	(2.5)	(8.4)	(5.1)
Water	74.8	70.4	−1416	−386
	(8.3)	(5.8)	(532)	(152)
Energy	68.8	72.6	48.3^{a}	46.3^{a}
	(4.5)	(2.6)	(8.0)	(6.1)
Nitrogen	72.4	79.1	−6.9^{a}	7.2^{a}
	(5.0)	(1.4)	(18.3)	(10.1)

tortoises eat until they fill their stomachs, then a stomach full of fresh *Erodium* will provide more digestible energy and crude protein, and about the same amount of digestible water (Table 2) as does *Malacothrix*. However, if the appetites of tortoises are determined primarily by energy balance, as in other vertebrate groups (Robbins, 1993; Murphy, 1996), and tortoises consume just enough food to satisfy their energy needs (consumption thus being correlated with dry matter intake), then the native forb is the more nutritious. *Malacothrix* provides 12% more digestible N per kJ digestible energy and 42% more digestible water per kJ digestible en-

TABLE 2. Nutritional value of two native and two exotic food plants of desert tortoises. Values are means (SD) of apparently digestible (assimilable) nutrient contents, on the basis of both fresh mass and dry mass of the food. Data for *Erodium* and *Schismus* are from Meienberger et al. (1993). Means for apparent digestibilities having common superscripts within rows are not significantly different.

Nutrient	Food plant: *Erodium cicutarium* (exotic forb)	*Malacothrix glabrata* (native forb)	*Schismus barbatus* (exotic grass)	*Achnatherum hymenoides* (native grass)
Energy (digestible)				
Fresh food basis, kJ/g fresh	2.68	1.94	7.71	5.94
	(0.09)	(0.07)	(0.27)	(0.78)
Dry matter basis, kJ/g DM	10.9	11.4	8.26^{a}	7.78^{a}
	(0.4)	(0.4)	(0.29)	(1.02)
Nitrogen (digestible)				
Fresh food basis, mg/g fresh	4.45^{a}	3.64^{a}	−0.56^{b}	0.23^{b}
	(0.31)	(0.07)	(0.30)	(1.10)
Dry matter basis, mg/g DM	18.1	21.3	−0.55^{a}	0.30^{a}
	(1.3)	(0.4)	(0.32)	(1.44)
Water (digestible)				
Fresh food basis, g/g fresh	0.56^{a}	0.58^{a}	−0.93^{b}	−0.91^{b}
	(0.12)	(0.49)	(0.19)	(0.36)
Dry matter basis, g/g DM	2.29	3.41	−1.00^{a}	−1.20^{a}
	(0.48)	(0.28)	(0.21)	(0.47)

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ergy than does *Erodium* (calculated from Table 2). Thus, conclusive evaluation of the nutritive value of tortoise foods must incorporate information about what regulates tortoises' feeding rates.

Current knowledge about appetite in chelonians is very meager (Skoczylas, 1978; Guard, 1978). Appetite may be influenced by factors other than energy. As the summer drought progresses and food plants dry up, juvenile desert tortoises (Nagy and Medica, 1986) and chuckwalla lizards (also Mojave Desert herbivores; Nagy, 1972) cease eating. Similarly, during spring seasons of extreme drought years when no new winter annuals are available, adult tortoises may reduce food intake by 85% or more (Peterson, 1996a, b; Henen, 1997) compared to intake rates during wetter years when new winter annuals are available. However, females that rehydrated by drinking water from summer rains consumed dry annuals (ca. 95% was dry *Schismus barbatus*) at a rate over four times higher (ca. 7 g DM/d by 1.6-kg females; Henen, 1994, 1997) than those eating either grass diet in this study. Thus, their appetites may be strongly influenced by osmotic stress experienced during droughts (summer or extended).

Tortoises select and eat dry grasses in summer (Nagy and Medica, 1986; Esque et al., 1996; Henen, 1996) Our results indicate that these grasses provide little or no crude protein, and these foods actually cause tortoises to lose more water than the grasses provide (about 0.9 g of body water lost per g grass ingested, Table 2). Why do tortoises eat dry grasses? Even though the energy digestibility in grasses is relatively low (about 49%), they provide about three times more apparently digestible energy per g fresh matter than do the forbs (Table 2). Thus, a full stomach of dry grass would yield three times more energy that does a full stomach of succulent forbs. During the year, free-living females showed substantial storage of lipid only after (1) rehydrating via drinking summer rain water, and (2) subsequently consuming dry grasses (Henen, 1997). These stored lipids enabled females to survive winter, fueling energy metabolism without catabolizing significant amounts of body protein, and probably facilitated development of follicles before hibernation occurred.

However, for reasons that are not clear, the tortoises in this study voluntarily consumed the grass diets at very low rates compared to the forbs they ate, so they obtained much less energy while eating grasses. The dehydrating property of these grass diets may have inhibited tortoises from consuming large amounts of them. Free-living tortoises with full urinary bladders after drinking rain water can consume much larger amounts of dry grasses in summer (Nagy and Medica, 1986; Henen, 1997) than measured in this study. We offered drinking water to tortoises before the grass feeding trials began, and most drank, but they still experienced increasing osmotic stress while eating the grasses. Blood samples taken before (following hydration by drinking) and after the *Achnatherum* trial indicated that plasma osmotic pressures increased by 80 mosM, and plasma potassium concentrations tripled, going from 7 to 22 mM in the first seven weeks of the trial (S. T. Chao and B. T. Henen, unpubl. data). Osmotic or ionic effects of foods may influence appetite in desert tortoises.

Free-living tortoises do consume some dead, dry leaves of forbs along with the grasses they eat in summer (Nagy and Medica, 1986). This may improve nutrient digestibilities due to the beneficial interactions that have been demonstrated in freshwater turtles eating mixed diets (Bjorndal, 1991). However, this seems unlikely, because the nutrient digestibilities in desert tortoises eating a mixed spring diet (Nagy and Medica, 1986) were all lower than those reported herein for single-species diets. A disadvantage of consuming dry forbs is that the osmotic and ionic loads associated with eating dry leaves of forbs in summer may be large. Potassium ion (K^+) in particular may pose a substantial problem due to its apparent toxicity to herbivorous desert reptiles (Shoemaker et al., 1972; Minnich, 1979; Nagy and Medica, 1986; Oftedal et al., 1996). Potassium concentrations in forbs are high (500–1200 μmol/g DM) in summer, but K^+ in grasses is much lower, ranging only from 40 to 420 μmol/g DM (Nagy, 1973; Nagy et al., 1976). Thus, dry grasses may be the least toxic foods available to tortoises in summer. Phenological differences in the nutrient composition of desert plants and their components (e.g., flowers versus leaves), of which little is known, may help explain why tortoises consume dry grasses in summer.

The low or even negative nutrient yield of dry grasses may be due to their senescent stage. Earlier in its life cycle, when it is green, *Schismus barbatus* yields much more energy and nitrogen to desert tortoises (Barboza, 1995b), and is nutritionally comparable to green forbs and green leaves of an herbaceous desert perennial plant, *Sphaeralcea ambigua* (Table 3). The digestive capabilities of desert tortoises eating green leaves (apparent digestibility of energy = 54–75%, Table 3) are similar to those of other herbivorous chelonians eating green plant matter, including gopher tortoises, *Gopherus polyphemus* (ADE = 61%, Bjorndal, 1987), freshwater turtles, *Pseudemys nelsoni* (ADE = 75%, Bjorndal and Bolten, 1990), and marine turtles, *Chelonia mydas* (ADE = 50–69%, Bjorndal, 1985). Other herbivorous

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TABLE 3. Summary of nutrient digestibilities for desert tortoises eating various diets. Values are percent apparent digestibilities [=100(food intake − feces output)/(food intake)].

Diet, reference\nutrient	Dry matter	Energy	Nitrogen	Water
Grasses				
Schismus barbatus, dry (this study)	49.7	48.3	−6.9	−1416
Schismus barbatus, green (Barboza, 1995b)	63.0	59.1	53.6	
Achnatherum hymenoides, mostly dry (this study)	46.9	46.3	7.2	−386
Forbs				
Erodium cicutarium, green (this study)	63.3	68.8	72.4	74.8
Malacothrix glabrata, green (this study)	70.1	72.6	79.1	70.4
Mixed spring diet (90% forbs, 10% grass) (Nagy and Medica, 1986)	61.6	54.3	20.5	63.2
Herbaceous perennial				
Sphaeralcea ambigua, green (Barboza, 1995b)	69.2	75.4	80.7	

reptiles also have similar ADEs when eating green foods: chuckwalla lizards, *Sauromalus obesus*, and desert iguanas, *Dipsosaurus dorsalis* at 56–57% (Nagy and Shoemaker, 1975), and green iguanas, *Iguana iguana* at 59–66% (Marken Lichtenbelt, 1992), as well as in herbivorous mammals eating green desert vegetation (jackrabbits, *Lepus californicus*, at 52–73%; Shoemaker et al., 1976). All of these animals probably have some capacity to ferment cell walls (Bjorndal et al., 1990; Stevens and Hume, 1995), but their foreguts are not specialized fermentation chambers as found in ruminant mammals. Nevertheless, their energy digestibilities are nearly as high as in ruminants, most likely because of the highly digestible nature of green, growing leaves (Parra, 1978). Thus, by selecting easily-digestible diets, desert tortoises are able to obtain relatively large amounts of nutrients from their plant diets in spring.

The desert tortoises' summer diet of mainly dry grass can provide much energy, if enough is consumed, even though it actually removes more water and nitrogen from a tortoise than it provides (Henen, 1997). The low availability or absence of new annuals in summer of some years removes new annuals as a dietary alternative to dry grasses at these times. Tortoises are adapted to tolerate unusually wide swings in body composition (Nagy and Medica, 1986; Peterson, 1996a, b; Henen, 1997). This capacity, in conjunction with stored water in their urinary bladders and possibly stored protein, may permit desert tortoises to exploit foods that are not nutritionally complete, but which can yield some benefit nevertheless.

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