

Diet Selection by the Desert Tortoise in Relation to the Flowering Phenology of Ephemeral Plants

W. BRYAN JENNINGS^{1,2}

¹Section of Integrative Biology, University of Texas at Austin, Austin, Texas 78712 USA;

²Present Address: Department of Zoology, Box 351800, University of Washington, Seattle, Washington 98195 USA
[E-mail: wbjenn@u.washington.edu; Fax: 206-543-3041]

ABSTRACT. – During spring 1992 in the western Mojave Desert, California, I measured desert tortoise (*Gopherus agassizii*) diet and monitored the flowering phenology of all study site plants. Rainfall between January and March 1992 was well above average and nearly all plant species from the area flowered. Although tortoises ate at least 44 plant species, only 10 species comprised 81.4% of their diet. These preferred plants flowered at different times, which led to much temporal variability in tortoise diet. Tortoises preferred succulent to dry plants, and selected plants during certain phenological states, suggesting that plant palatability varied with phenological state. Tortoises selectively ate plant parts (e.g., leaves or flowers) suggesting that plant parts differed in palatability and/or nutrition. Although the nutritional importance of these preferred plants has yet to be demonstrated, the loss or diminished abundance of native plants through replacement by exotic species may adversely affect tortoise nutrition and conservation.

KEY WORDS. – Reptilia; Testudines; Testudinidae; *Gopherus agassizii*; tortoise; ephemeral plants; flowering phenology; foraging ecology; herbivore; nutritional ecology; rainfall; western Mojave Desert; California; USA

Desert tortoise (*Gopherus agassizii*) populations in the western Mojave Desert have suffered severe declines over the past few decades (U.S. Fish and Wildlife Service [USFWS], 1994; Berry, 1997). Although tortoise mortality in affected populations has been attributed to myriad factors (USFWS, 1994), the upper respiratory tract disease syndrome is believed to have been a major force driving this decline (Berry, 1997). Because disease susceptibility in desert tortoises may be linked with diet (Jacobson et al., 1991), population recovery will benefit from a better understanding of tortoise nutritional requirements.

In the western Mojave Desert, desert tortoises forage on annual and herbaceous perennial plants (Berry, 1978; Jennings, 1993; Jennings and Fontenot, 1993; Spangenberg, 1994). Because ephemeral plant biomass during spring depends upon the previous autumn and winter rains (Beatley, 1969), little biomass is produced following dry winters while in spectacular contrast the desert is lushly carpeted by wildflowers after wet winters. The longevity of adult tortoises, which is on the order of decades (Woodbury and Hardy, 1948; Germano, 1992), shows that these animals are able to withstand the year to year vagaries in food and water availability. The wet years seem to contribute the most to individual growth (Medica et al., 1975).

Phenology of ephemeral plants adds complexity to within-season forage availability. For example, the flowering of ephemeral plants in the western Mojave Desert appears not to be simultaneous, but rather a chronological sequence spanning the entire spring (Jennings, 2001). This phenological sequence in flowering ephemerals has also been observed at other desert localities (Beatley, 1974; Burk, 1982; Vidiella et al., 1999). Thus food plant availabil-

ity may be temporally variable within years and possibly predictable from a tortoise's perspective. Another potential consequence of flowering phenology is that the palatability and nutritiousness of plants could vary among the phenological states of plants (Nagy and Medica, 1986; Nagy et al., 1998). Studies of tortoise foraging ecology should therefore span the entire tortoise activity season so that changes in tortoise diet as well as changes in the phenological states of their food plants can be monitored.

Jennings (1993) demonstrated that adult desert tortoises in the western Mojave Desert during spring 1992 did not eat plant species in relation to their availability, and they exhibited marked seasonal variation in diet. The purpose of this paper is to develop the latter result by describing the seasonal variation in tortoise diet in light of the phenology of their preferred food plants, which hopefully will lead to a better understanding of their nutrient requirements.

METHODS

This study was conducted between 1 March and 21 June 1992 at the Desert Tortoise Research Natural Area (DTNA), a 100 km² nature preserve located in the western Mojave Desert, Kern County, California. I gathered data on tortoise diet and flowering phenology from the northwest corner of the DTNA, an area with elevations ranging from 800–915 m. The vegetation community was comprised of creosote bush scrub (Vasek and Barbour, 1988), which overlies various landforms including flat sandy areas, sandy washes, and low-rocky hills (Jennings, 1993). Annual precipitation occurs primarily during the winter months (1937–99 data from

the nearest climate station, Randsburg; National Climate Data Center [NCDC], 2000).

Tortoise diet was estimated from direct observations of 16 free-ranging adult tortoises (8 males and 8 females), 14 of which were equipped with radiotransmitters for concurrent studies involving the physiological ecology and health of wild desert tortoises (e.g., Peterson, 1996; Henen et al., 1998; Christopher et al., 1999; Wallis et al., 1999). I also observed two additional tortoises encountered opportunistically during spring 1992. Dietary observations were recorded as follows. Each morning, a study animal was located using radiotelemetry before that individual emerged from its cover site (i.e., burrow or shrub) to commence foraging. Individuals usually had two daily foraging bouts (i.e., morning and afternoon), but occasionally foraged once, or not at all, on any given day. Daily foraging data were usually obtained from a single animal with a recording of all food items taken by that animal on that day. Once the tortoise emerged, I then followed the individual at distances of 4 to 8 m to observe all foraging behaviors yet to minimize animal disturbances. When a tortoise was observed feeding, the plant species, plant parts consumed (i.e., stems, leaves, flowers, and seeds), number of bites taken, whether the plant was in a succulent or dried state, and the date and time were recorded on a micro-cassette recorder. Plants were considered "succulent" if they were green and "dry" if they were brown. Nomenclature for plant species follows Hickman (1993).

Data on flowering phenology for annual and perennial species were obtained through daily observations of plants on the study site. Flowering phenology of each species was partitioned into five stages: *emergence* (ephemerals only): plant shoots emerged above the surface; *first flowering*: minority of individuals in flower; *peak flowering*: most individuals in flower; *past-peak flowering*: majority of individuals still succulent but few still in flower; and *dried*: majority of individuals completely dry or, in the case of shrubs, completely in seed with no flowers remaining (see Jennings, 2001).

I evaluated the influence of plant phenology on tortoise diet in two analyses. First, I compared the number of bites, per week, taken by tortoises on their top ten forage species to the species-specific "phenology profiles." These phenology profiles indicate when in the spring 1992 the various phenological stages of each food plant were available to tortoises. The goal of this analysis was to ascertain the degree by which tortoises were focusing their attention on particular phenological states of their preferred food plants. On a finer scale, I determined whether or not tortoises targeted certain parts of plants for consumption. In this analysis, I partitioned the above-ground plant form into four categories (parts): stems, leaves, flowers, and seeds, so that the frequency of use of these plant parts by tortoises could be tabulated. I quantified overall consumption of each plant part during spring 1992 by counting the number of plants in which at least a single bite on a given plant part was taken by a tortoise.

RESULTS

The western Mojave Desert received above average precipitation in early 1992, as the Randsburg weather station recorded 134.5 mm during February and 78.3 mm in March, far exceeding the monthly averages of 32.5 mm and 24.4 mm for these two months (NCDC, 2000). This heavy rainfall resulted in the germination and flowering of at least 71 species of annuals and herbaceous perennials and 7 species of shrubs on the study site. Study animals emerged from their burrows between 24 March and 2 April, then began foraging. Following emergence from hibernation, tortoises continued almost-daily foraging bouts until June 21 by which time all study animals had become inactive inside their respective burrows. The 16 study animals were observed to take 35,388 bites from 2423 individual plants.

Although tortoises sampled at least 44 species of plants, only 10 preferred species (7 annuals and 3 herbaceous perennials) comprised the bulk (81.4%) of their diets (Table 1). This summary, however, obscures within-

Table 1. Top 10 preferred species of plants* in desert tortoise diet during spring 1992 at the DTNA.

Species	Common Name	Family	Life Form	No. Bites	% Bites
<i>Lotus humistratus</i>	Hairy Lotus	Fabaceae	Annual	10512	29.7
<i>Mirabilis bigelovii</i>	Four O' Clock	Nyctaginaceae	Herbaceous Perennial	3820	10.8
<i>Chamaesyce albomarginata</i>	Rattlesnake Weed	Euphorbiaceae	Herbaceous Perennial	3801	10.7
<i>Astragalus layneae</i>	Layne Locoweed	Fabaceae	Herbaceous Perennial	2902	8.2
<i>Prenanthes exigua</i>	Egbertia	Asteraceae	Annual	1977	5.6
<i>Astragalus didymocarpus</i>	Two-seeded Milkvetch	Fabaceae	Annual	1623	4.6
<i>Camissonia boothii</i>	Booth's Evening Primrose	Onagraceae	Annual	1367	3.9
<i>Erodium cicutarium</i>	Stork's Bill	Geraniaceae	Annual	1150	3.3
<i>Chorizanthe brevicornu</i>	Brittle Spineflower	Polygonaceae	Annual	919	2.6
<i>Phacelia tanacetifolia</i>	Lacy Phacelia	Hydrophyllaceae	Annual	710	2.0
Totals				28781	81.4

*Other foods eaten by tortoises by decreasing number of bites included: dead leopard lizard (*Gambelia wislizenii*), 695 bites (2%); *Amsinckia tessellata*, 590 bites (2%); *Cryptantha circumscissa*, 561 bites (2%); *Plantago ovata*, 430 bites (1%); *Mentzelia* spp., 428 bites (1%); *Eriastrum eremicum*, 404 bites (1%); *Gilia minor*, 342 bites (1%); *Stylocline micropoides*, 334 bites (1%); unknown plant material, 322 bites (1%); and *Camissonia palmeri*, 266 bites (1%).

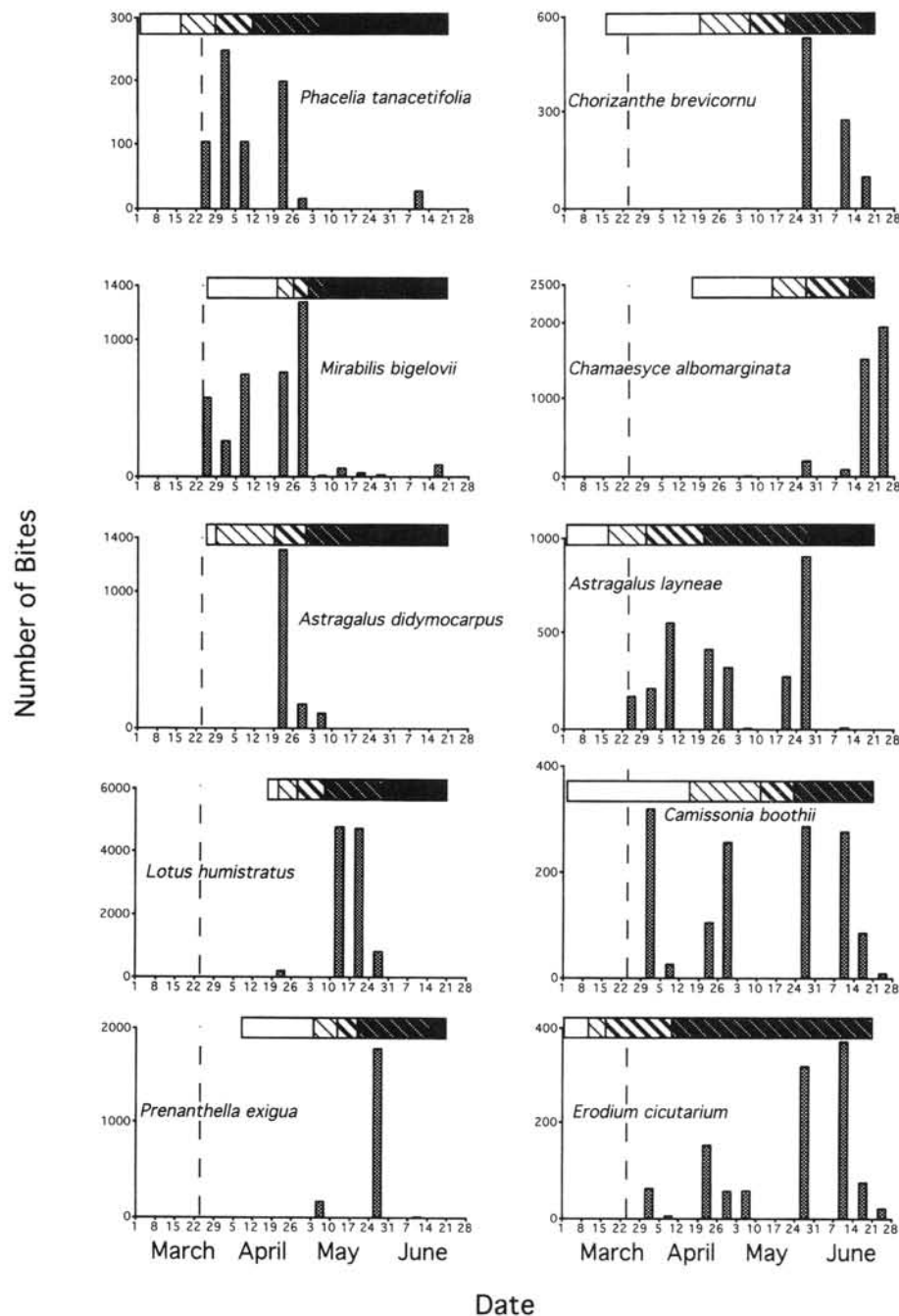


Figure 1. Temporal variation in tortoise diet and flowering phenology of the top 10 preferred forage plants. Vertical bars on each graph represent the numbers of bites per week on a particular plant species. Horizontal bars at the top of each graph show the flowering phenology stages of the same plant (from left to right: plain white bar = emergence; white bar with thin diagonal dark lines = first flowering; white bar with thick diagonal lines = peak flowering; dark bar with white diagonal lines = past-peak flowering; and black bar = dried (see text for definitions of these phenological stages; after Jennings, 2001).

season variation in tortoise diet. Tortoises primarily fed upon individuals of *Phacelia tanacetifolia* and *Mirabilis bigelovii* during early spring before switching to *Astragalus didymocarpus*, *Lotus humistratus*, and *Prenanthes exiguus* in middle spring then later eating *Chorizanthe brevicornu* and *Chamaesyce albomarginata* near the end of spring (Fig. 1). Several other plants, *Camissonia boothii*, *Astragalus layneae*, and *Erodium cicutarium*, were eaten by tortoises throughout spring (Fig. 1).

Tortoises focused their foraging efforts on specific phenological stages of their preferred food plants. For instance, tortoises fed from individuals of *P. tanacetifolia*, *M. bigelovii*, *A. layneae*, *C. boothii*, and *E. cicutarium* at the earliest possible opportunity when these plants were in the emergence or first flowering stages (Fig. 1). Other plant species such as *A. didymocarpus*, *L. humistratus*, *P. exiguus*, *C. brevicornu*, and *C. albomarginata* were not consumed until these plants progressed into peak flowering and even past-peak flowering stages (Fig. 1). Regardless of when

Table 2. Frequency of consumption of plant parts by desert tortoises at the DTNA during spring 1992. Values represent the numbers of plants eaten. Common names for each species are given in Table 1.

Species	Total	Stems	Leaves	Flowers	Seeds
<i>Lotus humistratus</i>	1008	1008	1008	168	999
<i>Mirabilis bigelovii</i>	40	38	40	16	1
<i>Chamaesyce albomarginata</i>	101	101	101	101	1
<i>Astragalus layneae</i>	72	56	69	23	0
<i>Prenanthes exigua</i>	134	134	0	133	114
<i>Astragalus didymocarpus</i>	126	123	123	126	0
<i>Camissonia boothii</i>	161	110	148	34	21
<i>Erodium cicutarium</i>	206	103	104	30	152
<i>Chorizanthe brevicornu</i>	56	56	55	41	0
<i>Phacelia tanacetifolia</i>	35	28	27	29	1

tortoises initiated their consumption of preferred food plants they abruptly ceased to feed on any plants that had advanced to a dried state (Fig. 1). In fact, dried plants only comprised 4.2% of all tortoise diet and tortoises did not begin eating dried plant material until the last few weeks of spring, a time when most plants on the study plot were dry.

The frequency of consumption of different plant parts may provide insights into the timing of tortoise preference of these plants during spring. Tortoises generally consumed the stems, leaves, and flowers of their preferred plants, though some peculiarities in plant part selection were also observed (Table 2). For example, the flowers of *M. bigelovii*, *A. layneae*, *C. boothii*, and *E. cicutarium* seemed to be consumed far less often than stems and leaves on these plants (Table 2). The flowers of *M. bigelovii* and *A. layneae* may have been too difficult to reach by tortoises because the flowers on these herbaceous perennials tended to grow well above ground. This explanation cannot apply to *C. boothii*, as tortoises invariably bit off the flowers of these plants and allowed them to drop to the ground uneaten. Seeds were generally not eaten, exceptions including *L. humistratus*, *P. exigua*, and *E. cicutarium* (Table 2).

DISCUSSION

The western Mojave Desert received higher than average rainfall during winter 1992 (Jennings, 2001). From the perspective of a tortoise, spring 1992 must have been an outstanding year regarding food and water availability because nearly all species of plants known to occur on the study site flowered and became available as potential forage. Emergence and flowering of some ephemeral plants was well underway by the time tortoises emerged from hibernation and were available for forage until the end of June when tortoise aboveground activity ceased (Jennings, 1993). I did not monitor tortoise activity over the summer months, so it is unknown to what extent further foraging occurred. However, because only a trace amount of rain fell in the area during summer 1992 (NCDC, 2000), and since summer tortoise activity is believed to be dependent upon summer rainfall (Nagy and Medica, 1986), as occurs in the eastern Mojave Desert (Turner, 1982), it seems unlikely that much foraging could have taken place at the DTNA during this time. Marlow (1979), who studied tortoise behavior and

physiology at the DTNA between 1969–1978, also noticed that peak foraging activity occurred during spring; this was followed by a dramatic slowdown in activity in early summer, which in turn led to a long period of little activity lasting until the following spring.

Despite the tremendous availability of potential food plants throughout spring tortoises concentrated their foraging efforts upon a small fraction of the ephemeral flora. Only 10 species of plants accounted for more than 80% of tortoise diet. The flowering phenologies of these preferred plants were quite variable, with some plants coming into full bloom in early spring, others in mid-spring, and still others in late spring (Jennings, 2001). Tortoises kept pace with this turnover of preferred foods resulting in dramatic seasonal variation in their diet. Data indicate that the flowering of plants during spring occurs as an orderly sequence with each species flowering at a specific time (Jennings, 2001). If the flowering phenologies of ephemeral plants occurred in such a recurrent manner, then tortoises may effectively predict when to locate preferred foods, thereby economizing their daily foraging efforts and behavior in general.

Although tortoises usually ate preferred plants in entirety, they tended to target these plants during particular phenological stages, thereby suggesting that the different phenological states may have varied in palatability (and possibly nutritional value) to tortoises. For example, tortoises ate some plants in their emergence stage, namely *M. bigelovii* and *C. boothii*, thereby primarily consuming the vegetative portions of these plants, not the flowers and seeds. The apparent rejection of certain plant parts by tortoises may be explained by either inaccessibility to high-growing flowers on relatively large forage plants (i.e., *M. bigelovii* and *A. layneae*) or possibly on palatability grounds (i.e., *C. boothii*). Why, for instance, do tortoises bite off and then reject the flowers of *C. boothii* without eating them?

Consuming succulent plants usually enable tortoises to maintain water and nitrogen budgets, whereas eating dry plants may cause water and nitrogen deficits (see Nagy et al., 1998). Thus, it is not surprising that tortoises generally prefer, when available, succulent as opposed to dry forage plants (Nagy and Medica, 1986; Jennings and Fontenot, 1993; Spangenberg, 1994). In the present study, comparisons between the phenologies of the preferred plants with

the dates when tortoises consumed them showed that tortoises precisely stopped eating individuals of a particular plant species once the plants became dry. Interestingly, Nagy and Medica (1986) discovered that tortoises in the eastern Mojave Desert actually became osmotically stressed by a spring diet of succulent plants. Notwithstanding, succulent forage plants must somehow be more beneficial than detrimental to tortoises, perhaps in the long-term, despite apparent short-term osmotic imbalances caused by their consumption. Indeed, physiological studies of desert tortoises suggest that individuals can tolerate temporary imbalances in nutrients to withstand the harsh desert environment and maintain nutrient balances to grow and reproduce in the long-term (Nagy and Medica, 1986; Peterson, 1996; Henen, 1997).

The results of this study underscore the importance of observing foraging tortoises throughout their activity season, otherwise perceptions of tortoise dietary habits may be incomplete owing to the variable flowering phenologies of forage plants. Of equal importance may be the documentation of flowering phenologies for primary forage plants as differences in nutritional states of plants may change with age. Tortoises in this study exhibited food preferences at the level of plant species, phenological state of a plant, and plant parts. This selective foraging behavior implies that the palatability, and possibly nutritive value, of plants varies among plants and their parts (Nagy et al., 1998).

Although at least 71 species of ephemeral plants were available for forage, over 80% of tortoise diet was based on only 10 plant species. Tortoise dietary requirements may therefore be quite specialized, at least for populations in the western Mojave Desert. An implication of such apparent selectivity is that habitat degradation leading to the loss or diminished abundance of preferred plants could have deleterious consequences for tortoise health. For example, proliferation of exotic annual plant species such as *Schismus* spp. and *Bromus* spp. in the Mojave Desert (Brooks, 1992; Jennings, 1993; Esque, 1994) may be negatively impacting native ephemeral species either through competition (Brooks, 2000) or aiding fire propagation in an environment where fire was historically absent (Jennings, 1997; Brooks, 1999, 2002). Indeed, the 10 preferred plant species identified in this research occur in extremely low densities and are therefore vulnerable to extirpation (Jennings, 1993). Further evidence that these plants may be extremely important to the welfare of tortoises comes from observations of the truly astounding abilities of tortoises to successfully locate these rare plants (Jennings, 1993). Discovering these subtle but potentially critical details of tortoise foraging ecology is only the first step in comprehending tortoise ecological and nutritional requirements. Nutritional assays (including water content) of desert plants can then address tortoise foraging ecology in finer detail, which may ultimately explain why tortoises are so selective in their diet.

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