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Leopard Tortoises (*Geochelone pardalis*) in Valley Bushveld, Eastern Cape, South Africa: Specialist or Generalist Herbivores?

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Abstract. – The natural diet of leopard tortoises (*Geochelone pardalis*) was determined in Valley Bushveld in the Addo district of the Eastern Cape, South Africa, via visual observations of feeding and fecal analysis. We found that plants of 28 species were consumed by leopard tortoises. Six species comprise 75% of the diet with the geophyte *Albuca* sp. accounting for nearly a third of the diet. A preference index and two electivity indices were used to determine principal and preferred food items in relation to their occurrence in the habitat. The α_i value of Chesson (1978) was found to be the best in terms of interpretation. The grass *Cynodon dactylon* and the geophyte *Albuca* sp. were found to be the principal food species, while the exotic cactus *Opuntia ficus-indica* and the forb *Abutilon sonneratianum* were preferred. Non-plant items found in fecal samples included bones, insects, and sand. Leopard tortoises may be considered as intermediate between generalist and specialist herbivores, feeding on many plant species as they occur in the environment, but showing some preferences.

Key Words. – Reptilia; Testudines; Testudinidae; *Geochelone pardalis*; tortoise; diet; preference index; preferred food; principal food; South Africa

Information on the diet of southern African tortoises is largely vague or anecdotal. Leopard tortoises (*Geochelone pardalis*) are considered to have a wider dietary range than other African tortoises (Greig and Burdett, 1976), feeding on grasses, forbs, succulents, and fruits (Pienaar et al., 1983; Boycott and Bourquin, 1988; Branch, 1988; Baard, 1994). There are few studies of the diet of leopard tortoises available and these are often only lists of species eaten (e.g., Branch and Braack, 1987; Milton, 1992). These lists are limited in value unless food consumption is considered in relation to its availability (Rall and Fairall, 1993). In the present study, the diet of leopard tortoises in Valley Bushveld, South Africa, is described and related to food plant availability in order to test the hypothesis that leopard tortoises are generalist, or unselective, herbivores. Dietary preference indices devised by Davies et al. (1986), as well as the α_i value and the electivity index ε_i of Chesson (1978, 1983) were calculated and their applicabilities discussed.

MATERIALS AND METHODS

Study Area. — The study site was located on Tembani and Mimosa farms (33°17'S; 25°32'E), 10 km northwest of the original core area of Addo Elephant National Park (AENP), in the Eastern Cape, South Africa. The rainfall averages 396 mm per annum, although during the year of the study (January 1995 to January 1996) a total of 527 mm was measured. The farms are recent (1994) acquisitions to the AENP (L. Moolman, *pers. comm.*) consisting largely of Valley Bushveld degraded by the pastoral and cultivation practices of the previous owners. Addo bush was recognized by Acocks (1975) as a subdivision of Valley Bushveld, being characterized by a practically impenetrable scrub consisting mainly of *Portulacaria afra*, *Schotis afra*, and *Euclea undulata*, while the thorny shrubs *Azima tetracantha* and *Capparis sepiaria*, and the lianas *Sarcostemma viminale* and *Rhoicissus digitata* are also common (Penzhorn and Olivier, 1974; Olivier, 1986). The invasive species *Salsola kali* and *Cynodon dactylon* form large stands in previously cultivated areas. The exotic cacti *Opuntia ficus-indica* and *O. aurantiaca* are also present in the study area.

Diet Composition. — South African tortoises feed at a low level in the vegetation on species easily accessible to them (Els, 1989; Rall and Fairall, 1993). Plant specimens were collected at the study site in an attempt to obtain a representative collection of the vegetation available for tortoise consumption. Plant species collected included those species observed to be eaten and species growing at a height corresponding to the maximum reach of adult leopard tortoises, i.e., < 50 cm above ground. The green plant material was used to prepare a reference collection of epidermi. Plants were identified to the lowest possible taxonomic group by reference to material housed in the Ria Olivier Herbarium, University of Port Elizabeth. Nomenclature follows Gibbs-Russell et al. (1981). Monthly presence of green foliage on dietary plant species was determined for the period January 1995 until December 1996. Ten individuals of each dietary plant species were examined monthly to determine seasonal availability of green foliage to the animals. The phenology of flowers and fruit was also noted.

Leopard tortoise diet was determined from direct feeding observations as well as analysis of fecal material for the period from December 1994 until January 1996. An observed feeding record was noted as one, or more, bites of a single food source. This record was then recorded as one observation on that particular food source. Plants observed eaten by animals were collected for later identification and to form part of a reference plant collection for fecal analysis. Fecal samples were collected from individual animals by picking the tortoise up, whereupon it usually defecated. Fecal samples were also collected from unknown animals as they were encountered in the field during the course of fieldwork. Fecal samples were oven dried at 70°C for 24 hrs and then stored individually until examination.

Tortoise fecal samples contain plant parts little changed from their pre-ingestion state (Els, 1989; Milton and Dean, 1995), which facilitated easy identification of most plant food items. Microscopic fecal analysis (see below) was undertaken as a supplement as some plant species may undergo more complete digestion than others.

Methods used for the fecal analysis followed Gaylard (1994). Each fecal sample was physically broken up and a portion was digested in 4 ml concentrated nitric acid over low heat for ca. 2 min. Samples were then made up to 100 ml with distilled water and boiled and stirred for 5 min. The resulting mixture was centrifuged for 15 minutes at 2000 RPM and the supernatant discarded. This process removed most of the leaf mesophyll while keeping the epidermis intact. The remaining cuticle fragments were stored in 5 ml FAA (25% distilled water, 60% absolute alcohol, 10% formalin, and 5% glacial acetic acid) until analysis. A sub-sample of prepared fecal sample was placed on a microscope slide and viewed at 400X magnification. Epidermal fragments were identified by comparison to reference material (see below). Different plant species encountered in the fecal samples were taken as separate feeding records in order to keep the analysis of data simple, i.e., one fecal sample could yield 4 feeding records if it contained the remains of 4 different plant species.

The compilation of the reference material followed Gaylard (1994). Leaf material, from known plant species collected in the study area, was cut into 15 mm lengths and boiled in 10% nitric acid in a vacuum flask. Depending on the texture of the leaf, the epidermis begins to peel away after 5–10 min. The contents of the flask were then washed under running tap water. The cuticle layer was then removed and lightly stained with haematoxylin dye and permanently mounted on a microscope slide. Both adaxial and abaxial surfaces of the leaf were prepared for the reference collection.

The frequencies of food plant species observed to be eaten and those recovered in fecal samples were compared using a Kolmogorov-Smirnov test at the 0.05 confidence limit (Zar, 1996) to test if fecal analysis is a reliable indicator of tortoise diet.

Preference Indices. — Measuring dietary selection of an animal requires a comparison of the relative abundance of food species available with the relative abundance of food species consumed (Norbury and Sanson, 1992). Relative availability of plants was expressed as estimated plant cover, determined using the canopy line-intercept method (Barbour et al., 1987). Plants encountered at 10 mm intervals, at ground level, along 30 m line transects were identified during March 1995. Nineteen transects were located randomly across the study area. By using a small interval, rarer plants in the environment should be detected. Species present in the diet but not intercepted during the transects were assigned a value less than the minimum value measured for any species at the site.

Animals are said to be selective in their diet if they feed on dietary species in quantities that are disproportionate to their availability (Johnson, 1980). Dietary selection, or preference, is defined as an animal's choice of food from an array of different food species (Norbury and Sanson, 1992). The concept of preferred food is therefore distinct from that of the principal food species. Principal food species are those which the animal eats in the greatest quantities, while preferred foods are those which are proportionally more frequent in the diet than in the environment.

To determine preferred and principal foods of leopard tortoises a preference index (PI) (% consumption / % availability) (Davies et al., 1986), an α_i value and an electivity index ε_i (see below) (Chesson, 1978, 1983) were calculated for each dietary species in relation to the availability of each species. A preference index greater than one indicates selection for that species, whereas a value less than one indicates that the species is being utilized less than the availability would suggest (Davies et al., 1986).

The α_i value can be interpreted as the proportion of the diet which would consist of food type *i* if all food types were present in equal densities in the environment (Chesson, 1978, 1983). This relative measure indicates the preference of a consumer for a food type relative to the other food types present, unlike the preference index of Davies et al. (1986) which does not take into account the other food types present. Assuming reduction of food density is insignificant compared to the total amount of food available, then α_i is estimated by the maximum likelihood (ML) estimator:

$$\alpha_{i_i} = \frac{r_i/n_i}{\sum_{j=1}^{m} r_j/n_j}, \quad i = 1, \ldots, m$$

where r_i and n_i are the proportions, or the percentages of food type *i* in the diet and environment, respectively (Chesson, 1978).

For a range of food species it may be better to display preference as an electivity index ε_i which ranges from -1 to +1 with 0 representing no preference (Chesson, 1983). This can be done with α_i, $i = 1,..., m$, by calculating the preference for food type *i* relative to the average preference for all other food types, then multiplying the result by 2 and subtracting 1. In terms of the α_i this electivity value, ε_i, is given by:

$$\varepsilon_i = \frac{m\alpha_i - 1}{(m-2)\alpha_i + 1}, i = 1, ..., m$$

Unlike Ivlev's (1961) index of electivity, ε_i can take any value between -1 and 1, irrespective of food densities in the environment. It also has a natural interpretation in terms of the preference of food type *i* relative to the average preference for the alternative food types, rather than being merely an arbitrary quantity ranging between -1 and 1 (Chesson, 1983).

Plant foods were classed as preferred or principal species based upon the values derived from the above equations. Species with preference index values of 10 or greater are considered to be preferred. Food species with an α_i value of 0.05 or greater are considered preferred and species with a positive electivity index value are considered preferred. Principal foods were defined as those with an average frequency of greater than 5% in the diet.

The Proportional Similarity Index (PSI) of Feinsinger et al. (1981) was used to estimate if leopard tortoises are dietary specialists or generalists:

$$PS = 1 - 0.5 \sum_i |p_i - q_i|$$

where p_i is the proportion of resource species in state *i* out of all species used by the population, and q_i is the proportion of *i* species in the resource base available. Here values range from 1.0 for the broadest possible niche to [minimum q_i] for the narrowest possible niche (Feinsinger et al., 1981).

RESULTS

We made a total of 147 visual observations from 68 individuals, representing 22 plant species being eaten by leopard tortoises (Table 1). A further 6 taxa, not observed eaten, were occasionally identified in 52 fecal samples (Table 1). Visual observations and fecal records were combined to give a total list of dietary species for leopard tortoises. Geophytes constituted 46.9%, succulents 19.6%, grasses 18.6%, and other plants 14.9% of the diet (Table 2). Animal remains (vertebrate and invertebrate) were found in 9 out of 52 fecal samples (Table 3). Most dietary plant species had accessible green foliage throughout the year (Table 4).

No significant difference was observed in frequencies of plant food species between fecal samples and visual observations (Kolomogorov-Smirnov, $[d_{max}]_{0.05, 24, 139} = 23$, $0.02 < p < 0.05$). Therefore, fecal analysis gives a representative indication of the diet of leopard tortoises in Valley Bushveld.

Preference indices (PI), α_i values, and electivity indices (ε_i) are shown for each dietary species in Table 2. A Proportional Similarity Index (PSI) was calculated for leopard tortoises at the study site as 0.497.

Table 1. Plants consumed by leopard tortoises and species observed in the fecal samples. (Frequency represents the percentage of occurrence out of 147 visual observations, and 52 fecal samples, representing 161 individual feeding records).

	Visual Observation		Fecal Samples	
Taxon	Occur.	Freq.	Occur.	Freq.
Poaceae				
Cynodon dactylon	9	6.12	22	13.66
Digitaria eriantha	2	1.36	2	1.24
Eragrostis racemosa	1	0.68	3	1.86
Panicum deustum	0	0	3	1.86
Tragus berteronianus	6	4.08	5	3.11
Liliaceae-Hyacinthaceae				
Albuca sp.	51	34.69	35	21.74
Urginea altissima	17	11.56	10	6.21
Liliaceae-Asphodelaceae				
Bulbine latifolia	1	0.68	1	0.62
Bulbine spp.	11	7.48	2	1.24
Aloe ciliaris	1	0.68	0	0
Amaryllidaceae				
Brunsvigia gregaria	0	0	1	0.62
Aizoaceae				
Galenia spp.	6	4.08	6	3.73
Crassulaceae				
Crassula expansa	12	8.16	12	7.45
Crassula spp.	1	0.68	1	0.62
Cotyledon sp.	1	0.68	0	0
Fabaceae				
Acacia karroo	0	0	2	1.24
Indigofera sp.	0	0	2	1.24
Trifolium sp.	2	1.36	0	0
Schotis afra	0	0	1	0.62
Malvaceae				
Abutilon sonneratianum	1	0.68	2	1.24
Sterculiaceae				
Hermannia althaeoides	2	1.36	1	0.62
Cactaceae				
Opuntia ficus-indica	13	8.84	14	8.70
Opuntia aurantiaca	1	0.68	0	0
Commelinaceae				
Commelina spp.	5	3.40	6	3.73
Oxalidaceae				
Oxalis spp.	1	0.68	4	2.48
Asteraceae				
Sonchus/Venedium spp.	1	0.68	2	1.24
Mesembryanthemaceae				
Drosanthemum hispidum	2	1.36	0	0
Sapindaceae				
Pappea capensis	0	0	1	0.62
Unidentified	0	0	17	10.56
Stick/twigs	0	0	6	3.73

DISCUSSION

The total of 28 plant species observed in the diet of leopard tortoises in this study (Table 1) is considerably less than the 75 plant species recorded as eaten by leopard tortoises in the Karoo (Milton, 1992), or the 51 species recorded in the Kalahari (Rall and Fairall, 1993). The Karoo and the Kalahari are both areas of lower plant species diversity and richness than Valley Bushveld (Low and Rebello, 1996). Milton's (1992) and Rall and Fairall's (1993) studies were conducted over a longer time period than the present study, hence it is likely that given a sufficient sampling effort, Valley Bushveld leop-

Table 2. Plants consumed by leopard tortoises at the study sight with availability of plants (% of total plant cover) and indices of preference. (Consumption is a combination of visual and fecal records). Cons. = Consumption; Avail. = Availability; Pref. = Preference; Elect. = Electivity.

Taxon	Cons. %	Avail. %	Pref. Index	α_i	Elect. Index
Poaceae					
Cynodon dactylon	10.88	14.71	0.74	0.0006	-0.97
Digitaria eriantha	1.40	2.62	0.53	0.0004	-0.98
Eragrostis racemosa	1.40	0.48	2.92	0.0022	-0.89
Panicum deustum	1.05	0.27	3.89	0.0029	-0.86
Tragus berteronianus	3.86	0.85	4.54	0.0034	-0.84
Liliaceae-Hyacinthaceae					
Albuca sp.	30.18	5.27	5.73	0.0044	-0.79
Urginea altissima	9.47	0.96	9.86	0.0075	-0.67
Liliaceae-Asphodelaceae					
Bulbine latifolia	0.70	0.17	4.12	0.0031	-0.85
Bulbine sp.	4.56	0.40	11.40	0.0086	-0.63
Aloe ciliaris	0.35	<0.01	35.00	0.0264	-0.17
Amaryllidaceae					
Brunsvigia gregaria	0.35	0.93	0.38	0.0003	-0.98
Aizoaceae					
Galenia sp.	4.21	18.07	0.23	0.0002	-0.99
Crassulaceae					
Crassula expansa	8.42	3.54	2.38	0.0018	-0.91
Crassula sp.	0.70	0.02	35.00	0.0264	-0.17
Cotyledon sp.	0.35	<0.01	35.00	0.0264	-0.17
Fabaceae					
Acacia karroo	0.70	2.03	0.34	0.0003	-0.98
Indigofera sp.	0.70	0.07	10.00	0.0076	-0.67
Trifolium sp.	0.70	1.25	0.56	0.0004	-0.98
Schotis afra	0.35	<0.01	35.00	0.0264	-0.17
Malvaceae					
Abutilon sonneratianum	1.05	<0.01	105.00	0.0795	0.38
Sterculiaceae					
Hermannia althaeoides	1.05	2.07	0.51	0.0004	-0.98
Cactaceae					
Opuntia ficus-indica	9.47	<0.01	947.00	0.7167	0.97
Opuntia aurantiaca	0.35	0.03	11.67	0.0088	-0.62
Commelinaceae					
Commelina spp.	3.86	0.19	20.32	0.0154	-0.42
Oxalidaceae					
Oxalis sp.	1.40	0.61	2.30	0.0017	-0.92
Asteraceae					
Sonchus/Venedium spp.	1.05	0.58	1.81	0.0014	-0.93
Mesembryanthemaceae					
Drosanthemum hispidum	0.70	13.89	0.05	<0.0001	-1.00
Sapindaceae					
Pappea capensis	0.35	<0.01	35.00	0.0264	-0.17

ard tortoises may be observed to eat a wider variety of plants.

Six species (Table 1) made up 75% of the diet of leopard tortoises at the study site. Karoo leopard tortoise diet was dominated by numerous grasses and succulents (Milton, 1992) as was the diet of Kalahari leopard tortoises (Rall and Fairall, 1993). The limited dietary selection by leopard tortoises in Valley Bushveld may reflect higher nutrient contents of plants, particularly principal foods, and/or a greater concentration of principal and preferred foods (see Aucamp et al., 1978). Two plant species constituted 61% of desert tortoise (*Gopherus agassizii*) diet (Burge, 1977), five plant species constituted 80% of the diet of gopher tortoises (*G. polyphemus*) (Macdonald and Mushinsky, 1988), and four contributed to the bulk of the diet of Madagascan ploughshare tortoises (*Geochelone yniphora*) (Juvik et al., 1980). In all these cases, the dominant food plants were also the most abundant in the environment. This was not the situation with the leopard tortoise's diet in our study, with the dominant species in the diet occurring at relatively low densities in the environment.

Table 3. Non-plant items found in the feces of leopard tortoises, n = 52. (Frequency is percentage occurrence.)

Item	Occurrence	Frequency
Chordata		
Tortoise bones	1	1.92
Other bones	1	1.92
Fur	1	1.92
Insecta		
Tenebrionidae	2	3.85
Carabidae	2	3.85
Mollusca		
Achataena shell	2	3.85
Sand	4	7.69
Stone	1	1.92

Tortoises may be: a) non-selective feeders, taking food in proportion to environmental availability and showing little selection among common food types; or b) selective feeders, preferring particular foods, but when these are not available, taking less preferred species in proportion to their abundance (Gibson and Hamilton, 1983). Feinsinger's Proportional Similarity Index (Feinsinger et al., 1981) indicated that the foraging habits of leopard tortoises in Valley Bushveld lie midway between a specialist and a generalist (PSI = 0.497). Macdonald and Mushinsky (1988) obtained a PSI value of 0.566 for gopher tortoises (*G. polyphemus*). In the latter study, animals consumed food plant species in relation to the plant's abundance in the environment, unlike leopard tortoises in our study. Leopard tortoises in Valley Bushveld feed selectively on certain plant species, i.e., the relative abundance of certain plants in their diets does not reflect the relative availability of those species in the environment. Similar findings were made for South American yellow- and red-footed tortoises (*Geochelone denticulata and G. carbonaria*) (Bjorndal, 1989; Moskovits and Bjorndal, 1990).

Many workers have stressed the importance of succulents in the diet of leopard tortoises (e.g., Branch, 1988; Broadley, 1989; Baard, 1994), particularly as a source of water in a semi-arid habitat. A quarter of all species eaten by Karoo leopard tortoises were succulents (Milton, 1992; Milton and Dean, 1995). Although the diet of Kalahari leopard tortoises was dominated by grasses, these animals showed a marked preference for succulents. Valley Bushveld contains a large succulent flora (Cowling, 1983; Lubke et al., 1986; Hoffman and Cowling, 1991; Moolman and Cowling, 1994) and yet leopard tortoises ate relatively few (Table 1). Although few succulents were eaten, the exotic succulent *Opuntia ficus-indica* was a preferred item in Valley Bushveld (preference index = 947, $\alpha_i = 0.72$, $\varepsilon_i = 0.97$, Table 1). This fact is interesting in itself. These animals are selecting an exotic species, a species they did not evolve with, preferentially over indigenous food sources, possibly as a valuable water and food source. This has many implications particularly in relation to the spread of this exotic weed; a relationship that requires further investigation.

Table 4. Monthly availability of green forage and fruit on food plants of leopard tortoises in Valley Bushveld.

Species	J	F	M	A	M	J	J	A	S	O	N	D
Poaceae												
Panicum deustum	x	x	x	x	x	x			x	x		
Cynodon dactylon	x	x	x	x	x	x			x	x		
Digitaria eriantha	x	x	x	x	x			x	x			
Tragus berteronianus	x	x	x	x	x			x	x			
Eragrostis racemosa	x	x	x	x	x	x			x	x		
Liliaceae-Hyacinthaceae												
Albuca sp.	x	x	x	x	x	x	x	x	x	x	x	x
Urginea altissima		x	x	x	x	x						
Liliaceae-Asphodelaceae												
Bulbine abyssinica	x	x	x	x	x			x	x			
Bulbine latifolia	x	x	x	x	x	x			x	x		
Aloe ciliaris	x	x	x	x	x	x	x	x	x	x	x	x
Amaryllidaceae												
Brunsvigia gregaria		x	x	x	x	x						
Aizoaceae												
Galenia sp.	x	x	x	x	x	x		x	x	x		
Crassulaceae												
Crassula expansa	x	x	x	x	x	x	x	x	x	x	x	x
Crassula sp.	x	x	x	x	x	x	x	x	x	x	x	x
Cotyledon sp.	x	x	x	x	x	x	x	x	x	x	x	x
Fabaceae												
Acacia karroo	x	x	x	x	x			x	x			
Indigofera sp.	x	x	x	x	x			x	x			
Trifolium sp.	x	x	x	x	x	x			x	x		
Schotis afra	x	x	x	x	x	x	x	x	x	x	x	x
Malvaceae												
Abutilon sonneratianum	x	x	x	x	x	x	x	x	x	x	x	x
Sterculiaceae												
Hermannia althaeoides	x	x	x	x	x	x	x		x	x		
Cactaceae												
Opuntia ficus-indica	x	x	x	x	x	x	x	x	x	x	x	x
O. ficus-indica fruit		x	x	x	x							
Opuntia aurantiaca	x	x	x	x	x	x	x	x	x	x	x	x
Commelinaceae												
Commelina spp.	x	x	x	x	x	x			x	x		
Oxalidaceae												
Oxalis sp.		x	x	x	x	x						
Asteraceae												
Sonchus/Venedium spp.		x	x	x	x	x	x					
Mesembryanthemaceae												
Drosanthemum hispidum	x	x	x	x	x	x	x	x	x	x	x	x
Sapindaceae												
Pappea capensis	x	x	x	x	x	x	x	x	x	x	x	x

Geophytes, of which Valley Bushveld is also a center of endemism (Moolman and Cowling, 1994), dominate the diet with five species comprising nearly 45% of items eaten (Table 1). The diet of both Karoo and Kalahari leopard tortoises contained few geophytes (Milton, 1992; Rall and Fairall, 1993; Milton and Dean, 1995) although this may reflect the relatively low abundance of these plants in these habitats. Geophytes are relatively common in Valley Bushveld and are a principal food item in the diet of leopard tortoises. These plants may play a role akin to that suggested for succulents in the diet of Karoo and Kalahari leopard tortoises, i.e., a source of water, as the leaves are relatively succulent.

Kalahari leopard tortoises utilize plant foods according to seasonal abundance (Rall and Fairall, 1993). Similar findings have been obtained for numerous tortoise species (e.g., Coombs, 1979; Turner et al., 1984; Moskovits and Bjorndal, 1990). No seasonal differences were noted in the diets of Karoo leopard tortoises (Milton, 1992) and the principal (*Albuca* sp.) and preferred (*Opuntia ficus-indica*, *Abutilon sonneratianum*) food plants of leopard tortoises in Valley Bushveld were available throughout the year (Table 4). It is not apparent that leopard tortoises feed on plants in relation to their seasonal availability, although *Cynodon dactylon* (a principal food) had green foliage only during the spring and summer (Table 4). Leopard tortoises went into torpor during the colder winter months (June to August) and no feeding was observed to occur. Thus the winter shortage of some food species may not be important to these animals.

Many wildlife species ingest soil, either deliberately or accidentally, while feeding (Sokol, 1971; Beyer et al., 1994). Leopard tortoises were not observed to intentionally ingest sand. The relatively high frequency of sand in the fecal samples (Table 3) may be a result of incidental ingestion, although numerous species of tortoise have been observed to practice geophagia intentionally (e.g., Boycott and Bourquin, 1988). Sand may serve as an abrasive agent enhancing digestion (Rick and Bowman, 1961; Sokol, 1971, Macdonald and Mushinsky, 1988; Moskovits and Bjorndal, 1990), as well as an important source of nutrients, especially sodium and phosphorus (Kramer, 1973; Beyer et al., 1994). In captivity, leopard tortoises have been observed to consume small stones which may be retained in the gut (MCM, *pers. obs.*).

The diet of herbivores is generally low in nutrients (Bjorndal and Bolten, 1993). Animal matter may be an additional source of nutrients for tortoises and has been found in the feces of numerous species (e.g., Van Zyl, 1966; Cloudsley-Thompson, 1970; Macdonald and Mushinsky, 1988; Els, 1989; Milton, 1992; Hambler, 1994). Miscellaneous animal matter was found in 9 of the 52 fecal samples examined in the present study (Table 3). The consumption of materials such as animal matter and sand may also have an associative effect, i.e., enhancing the assimilation of certain nutrients (Bjorndal, 1991).

Conclusions reached from usage-availability studies depend on the investigator's notion of what components are available to the animal (Johnson, 1980). For determining preferred food species in an animal's diet it is proposed that the use of the α_i value of Chesson (1978) offers the most realistic figures. The preference index of Davies et al. (1986) gives values indicating preference (i.e., greater than 10) to species which were observed to be incidentally ingested, e.g., *Schotis afra*, or which were eaten on a once-off basis, thus giving a false impression of food preferences. The electivity value (ε_i) of Chesson (1983) is not very easy to interpret and therefore is not favored. Thus, for representing preference for a food species, the α_i value of Chesson (1978) should be used due to its ability to relate preference to all other food items in the diet and its ease of interpretation.

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