Sighting frequency and food habits of the leopard tortoise, *Geochelone pardalis*, in northern Tanzania

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Abstract

Sighting frequency and food habits of the leopard tortoise (*Geochelone pardalis*) were studied in northern Tanzania from October 1993 to June 1996. Sighting frequency varied significantly between protected (0.22 mhr^{-1}) and unprotected sites (0.59 mhr^{-1}), and between Arusha (0.27 mhr^{-1}) and Serengeti sites (0.56 mhr^{-1}).

The tortoise diet comprised mostly plants (97.8%) and rarely inorganic matter (2.2%). A total of 47 plant species from 21 families was eaten. Forbs made up 74.5% of the plant items and monocots the remainder. Succulents contributed 51.0% of the plant items eaten while grasses and legumes accounted for 16.8% and 13.5%, respectively. Some plant items were eaten more frequently than their occurrence in the habitats.

Key words: diet, leopard tortoise, sighting frequency, Tanzania

Résumé

On a étudié la fréquence des observations et les habitudes alimentaires de la tortue léopard (*Geochelone pardalis)* dans le nord de la Tanzanie d'octobre 1993 à juin 1996. La fréquence des observations variait significativement entre les sites protégés (0,22 m/h) et les sites non protégés (0,59 m/h), et entre les sites d'Arusha (0,27 m/h) et ceux du Serengeti (0,56 m/h).

Le régime alimentaire des tortues comprenait surtout des plantes (97,8%) et, rarement, des matières inorganiques (2,2%). On a rapporté un total de 47 espèces végétales appartenant à 21 familles. Les monocotylédones représentent 74,5% des éléments végétaux et les monocotylédones, le reste. Les plantes succulentes comptent pour 51,0% des plantes broutées tandis que les plantes grasses et les légumineuses représentent respectivement 16,8% et 13,5%. Certaines plantes étaient broutées plus souvent qu'elles n'étaient présentes dans les habitats.

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Introduction

Although the leopard tortoise (*Geochelone pardalis*) is thought to be common in Tanzania, it is feared that it may no longer inhabit parts of its former range due to over-collection for the export trade (Moll, Klemens & Njalale, 1993). Even if the current status were known, the lack of baseline data makes it difficult to draw conclusions about population trends (Swingland & Klemens, 1989). Furthermore, there is a lack of information on food habits, which is important for conserving the species and its habitats. Data from South Africa have shown that leopard tortoises feed on a wide variety of items compared to other African tortoises, their diet including grass, forbs, succulents, fruits and fungi (Broadley, 1989). However, the data cannot be extrapolated here because seasonal availability and preference (Milton, 1992; Rall & Fairall, 1993) affect the tortoise diet.

The purpose of this study was to investigate the sighting frequency and food habits of leopard tortoises, to provide baseline information for monitoring the species in Tanzania.

Materials and methods

Study area

Data were collected from Tarangire and Lake Manyara National Parks in Arusha Region, Serengeti National Park, Serengeti District, and neighbouring villages in northern Tanzania (Fig. 1). The climate in these areas is

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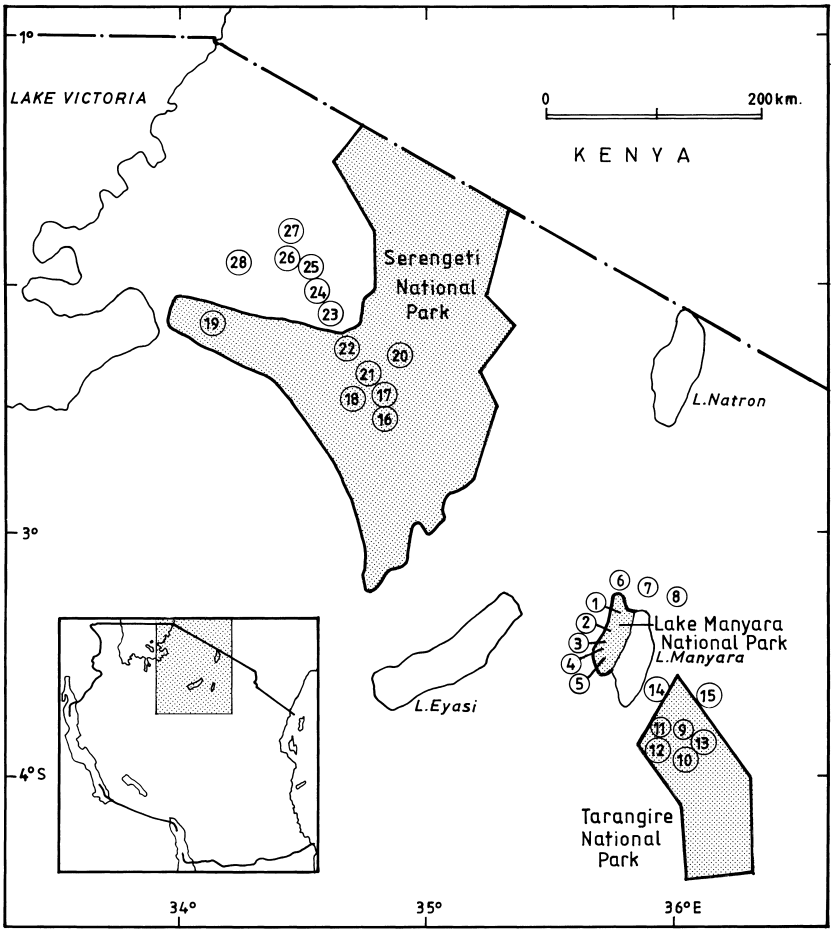


Fig 1 Location of study area and tortoise sites described in Table 1

typically semi-arid, with the 'short rains' falling in November–December and the 'long rains' in March–May. Field studies were carried out during the rains, when leopard tortoises are active.

Location of tortoise sites

Locations of tortoise sites were identified through interviews with park rangers and local people acquainted with the habitats preferred by the tortoises, as well as by direct observation. Twenty-eight sites were located in the study area, ten of which were classified as unprotected from human disturbance. The criteria used included location in a less-patrolled section of a protected area, proximity to known collecting centres, and indications of exploitation obtained from interviews with local people (Klemens & Moll, 1995).

Tortoise observations

Suitable habitats (e.g. grass, bush undergrowth, termitaria, under rocks and logs, burrows and road edges) were searched for leopard tortoises. Three field assistants were usually used for these searches, but the number of assistants was increased for larger sites to ensure adequate coverage.

Counts of tortoises were conducted in the morning, between 08.00 and 12.00 hours, when leopard tortoises are most active. Other records were obtained from sightings of tortoises while driving at 30–40 kph or walking through the study area. The bias resulting from this method (Norton-Griffiths, 1978) was minimized by the presence of a good road system and tracks traversing most of the sites. Road counts have been used in Kazakhstan for *Agrionemys horsfieldii* (Kubykin, 1988) and in

Madagascar for surveying *Geochelone radiata*, for which they were shown to give reliable population estimates (Goodman, Pidgeon & O'Connor, 1994).

The number of live and dead tortoises found and the number of man-hours (mhr) spent searching (hours of search × number of searchers) were recorded for each site. Assessment of abundance was based on sighting frequency calculated as the average number of tortoises observed per man-hour of search at different sites (Lambert, 1981). This technique provided a useful (albeit gross) estimate of relative abundance for comparison between sites.

The data were analysed to compare protected and unprotected populations for sites of comparable habitat type and quality.

Food habits

Observations on the food habits of leopard tortoises were made in the Serengeti National Park and adjacent villages by recording the items being eaten. Due to the lack of time available it was not possible to quantify all the parameters necessary for a detailed study of food preference (Owen-Smith & Cooper, 1987a). Preference was analysed using the χ^2 test, by comparing the occurrence of the plant species in the diet relative to their frequency in the habitats in which tortoises were seen feeding. At each sighting the plant species present within a 1 m radius were recorded. The relative frequency of a species was calculated as a proportion of the total number of frequencies of all species recorded (Mueller-Dombois & Ellenberg, 1974).

The data were analysed to show the frequency of the various food items in the diet and their preference by leopard tortoises.

Results

Sighting frequency

Sighting frequency ranged from 0 to 0.86 and 0 to 1.40 tortoises mhr^{-1} at protected and unprotected sites, respectively (Table 1). The frequency was compared between protected and unprotected sites on the hypothesis that tortoises were more abundant at the protected sites. However, sighting frequency was significantly lower at protected ($0.22 \pm 0.12\ mhr^{-1}$) than unprotected sites ($0.59 \pm 0.09\ mhr^{-1}$) (Mann–Whitney *U*-test, $d = 4.029$, $n_1 = 19$, $n_2 = 55$, $P = 0.000$). The highest frequency of sightings was recorded in Robanda village, with an average of $0.74 \pm 0.1\ mhr^{-1}$ (range 0.46–1.18, $n = 32$ counts). The nearby Mareshi and Nyabuta sites yielded 0.68 and $0.42\ mhr^{-1}$, respectively; Ikoma Gate and Banagi sites in Serengeti National Park 0.19 and $0.25\ mhr^{-1}$, respectively. The Endabash site in Lake Manyara National Park yielded $0.67\ mhr^{-1}$, all of which were dead. However, three live animals were seen from a vehicle in the area on two occasions. Sighting frequency was considerably lower at the Tarangire sites, ranging from 0 at several sites to $0.19\ mhr^{-1}$ at the Burungi A site. No significant difference in sighting frequency was detected between protected and unprotected sites ($0.40\ mhr^{-1}$) when the Robanda village sample was excluded (Mann–Whitney *U*-test, $d = 1.82$, $n_1 = 19$, $n_2 = 23$, $P =$ NS). Comparison between the Serengeti ($0.56 \pm 0.10\ mhr^{-1}$) and Arusha ($0.27 \pm 0.15\ mhr^{-1}$) sites showed a significant difference (Mann–Whitney *U*-test, $d = 3.017$, $n_1 = 16$, $n_2 = 58$, $P = 0.003$), with leopard tortoises being more abundant at the Serengeti sites.

Food habits

A total of 124 feeding observations were made in which 139 items were eaten. Plants comprised 97.8% of the food items eaten and inorganic matter (bone fragments and ashes) the remainder (2.2%). In total, 47 plant species from 21 families were eaten. Forbs comprised 74.5% of the plant items ($n = 136$) and monocots (Commelinaceae, Cyperaceae and Poaceae) the remainder (Table 2). Succulents (Cactaceae, Commelinaceae, Euphorbiaceae, Portulacaceae, Vitaceae and Zygophyllaceae) contributed 51.0% of the plant items eaten while grasses (including sedges) and legumes (Fabaceae) accounted for 16.8% and 13.5%, respectively. There was a significant difference in the occurrence of the plant items eaten relative to their frequency of occurrence in the vegetation communities ($\chi^2 = 250.71$, df = 22, $P \ll 0.001$) (Table 2).

Cissus rotundifolia, a succulent forb, was eaten most frequently (23.5%) followed by *Indigofera schimperi* (8.8%), *Justicia anselliana* (4.4%) and *Tribulus terrestris* (4.4%). Grass species eaten most frequently included *Dactyloctenium aegyptium* (3.1%) and *Tragus berteronianus* (2.2%). *Chloris pycnothrix* (2.2%) and *Themeda triandra* (2.2%) featured less in the diet despite their high frequency of occurrence in the vegetation. Crop species eaten were *Cucurbita maxima* (3.7%) and *Phaseolus vulgaris* (0.7%).

Table 1 The average number of leopard tortoises seen per man-hour at the study sites in northern Tanzania. Location numbers are shown in parentheses (see Fig. 1 for corresponding location numbers). The total number of tortoises found over the study period at each site is shown

Location	Total number of tortoises		*n*	mhrs	Slighting frequency (tortoises mhr^{-1})
	Live	Dead			
Lake Manyara National Park					
Main Gate (1)	0	3	11.84	0.07	
Msasa (2)	0	1	None	–	–
Ndala (3)	5	4	2	10.47	0.31
Bagayo (4)	2	0	1	4.00	0.25
Endabash (5)	3	13	3	22.80	0.67
Monduli District					
Mlimani village (6)	4	0	1	3.33	0.60
Migombani village (7)	6	1	None	–	–
Esilalei (8)	1	0	None	–	–
Tarangire National Park					
Kambi ya Nyani (9)	2	2	1	2.00	0*
Kuro (10)	0	2	1	1.86	0
Burungi A (11)	0	1	1	5.30	0.19
Burungi B (12)	0	0	1	2.80	0
Matete (13)	0	1	None	–	–
Hanang District					
Njemu (14)	0	2	1	2.00	0*
Mswakini (15)	0	1	1	2.47	0.40
Serengeti National Park					
Seronera (16)	7	2	None	–	–
Nyaruswiga (17)	15	1	1	9.00	0.33
Serena (18)	7	0	None	–	–
Kirawira (19)	1	0	2	6.96	0*
Togoro (20)	4	0	None	–	–
Banagi (21)	21	0	2	12.93	0.19
Ikoma Gate (22)	8	1	1	8.00	0.25
Serengeti District					
Robanda village (23)	192	13	32	305.86	0.74
Mareshi (24)	12	5	2	15.34	0.68
Nyabuta (25)	33	5	11	64.08	0.42
Fort Ikoma (26)	35	2	7	41.60	0.30
Kijiji Park (27)	16	0	None	–	–
Sibola (28)	15	1	None	–	–

mhrs = man-hours of search; *n* = number of counts; * = number of tortoises sighted during census.

Discussion

Sighting frequency

Although sighting frequency was significantly lower at the protected sites, no significant difference was detected when the Robanda village sightings were excluded. This suggests that the difference was because of the consistently high number of tortoises recorded in the village. The high number of tortoises at Robanda village is probably due to the ecotonal habitat (Auffenberg & Franz, 1982; Branch, 1984) created by cultivation and pastoralism. Both activities have converted the natural thicket vegetation into short grass habitat interspersed with patches of thickets and *shambas*. Milton (1992) has also shown that changes in Karoo vegetation caused by livestock grazing result in a decrease in perennial grass and shrub cover, with a consequent

Table 2 Occurrence of plant species in the leopard tortoise's diet

Food species	Relative frequency (%)	% occurrence ($n = 136$)
MONOCOTS		
COMMELINACEAE		
Commelina africana L.	1.3	3.7
C. benghalensis L.	1.1	0.7
C. foskalaei Vahl	1.4	2.9
C. latifolia A. Rich.	*	0.7
C. petersii Hassk	*	0.7
CYPERACEAE		
Cyperus rotundus L.	1.7	1.5
POACEAE		
Chloris pycnothrix Trin.	8.2	2.2
Dactyloctenium aegyptium (L.) Beauv.	0.4	2.9
Digitaria milanjiana (Rendle) Stapf	2.2	0.7
Eragrostis congesta Oliv.	1.1	1.5
Heteropogon contortus (L.) Roem. & Schult.	4.4	0.7
Panicum atrosanguineum A. Rich	0.4	0.7
P. massaiense Mez.	2.8	1.5
P. maximum Jacq.	2.2	0.7
Themeda triandra Forsk.	12.2	2.2
Tragus berteronianus Schult	2.0	2.2
Urochloa brachyura (Hack.) Stapf	1.1	1.5
U. pullulans Stapf	0.2	0.7
DICOTS (FORBS)		
ACANTHACEAE		
Justicia anselliana (Nees) Anders	3.5	4.4
Blepharis stuhlmanii Lindau	0.2	0.7
Crossandra subcaulis C.B.Cl	0.2	0.7
Dyschoriste radicans Nees	0.4	0.7
AMARANTHACEAE		
Alternanthera pungens H.B.K.	0.6	0.7
Achyranthes aspera L.	1.7	0.7
CACTACEAE		
Opuntia vulgaris Mill.	1.1	0.7
CONVOLVULACEAE		
Ipomoea mombassana Vatke	0.2	0.7
CRASSULACEAE		
Kalanchoe lanceolata (Forsk.) Pers.	0.3	2.2
CUCURBITACEAE		
Cucumis hirsutus Sond	0.4	1.5
Cucurbita maxima Lam.	*	3.7
EUPHORBIACEAE		
Euphorbia prostrata Ait.	0.2	0.7
E. hirta L.	0.4	2.2
Phyllanthus nummulariifolius Poir	0.4	1.5
FABACEAE		
Indigofera schimperi Jaub. & Spach	1.1	8.8
Phaseolus vulgaris L.	*	0.7
Tephrosia pumila (Lam.) Pers.	1.7	2.9
MALVACEAE		
Sida ovata Forsk.	0.2	0.7

(*Continued*)

Table 2 continued

Food species	Relative frequency (%)	% occurrence ($n = 136$)
MOLLUGINACEAE		
Glinus latoides L.	0.9	1.5
NYCTAGINACEAE		
Boerhavia diffusa L.	0.2	0.7
POLYGALACEAE		
Polygala erioptera D.C	0.4	1.5
PORTULACACEAE		
Portulaca grandiflora Hook.	1.1	0.7
P. quadrifida L.	1.4	1.5
RUBIACEAE		
Pentenisia ouranogyne S. Moore	0.2	0.7
TILIACEAE		
Corchorus trilocularis L.	*	0.7
VITACEAE		
Cissus quadrangularis L.	*	0.7
Cissus rotundifolia (Forsk.) Vahl	6.2	23.5
Cyphostemma serpens (A. Rich.) Descoings	0.2	0.7
ZYGOPHYLLACEAE		
Tribulus terrestris L.	2.2	4.4

χ^2 test: $\chi^2 = 250.71$, df $= 22$, $P \ll 0.001$.
n = total number of feeding records.
* = relative frequency not recorded.

increase in the succulent and ephemeral component of the vegetation, boosting the population of leopard tortoises using the area. In *Chersina angulata*, Branch (1984) found more animals in partially cleared thickets than in the surrounding climax vegetation. Highfield & Bayley (1995) and Bayley & Highfield (1996) also encountered higher density *Testudo graeca graeca* populations in cultivated areas than in the natural forest areas. The abundance of tortoises in the cultivated areas was ascribed to the new habitat created by *Opuntia ficus* that was introduced as fencing material. Like the hedging species used in Robanda (*O. vulgaris*, *Agava sisalana*), the thorny *O. ficus* provides good protection from predators and humans, as well as a food source and good shade.

The low sighting frequency at the protected sites was perhaps due to prolonged drought at the Arusha sites leading to higher tortoise mortality and low recruitment. No live animals were recorded at several Tarangire sites, and at one Manyara site (Endabash) most of the tortoises found were dead. The tortoises probably died of hyperthermia, as most carapaces were intact. Drought was also cited by local communities in Mto wa Mbu as the most important factor leading to the decline of tortoise numbers in their area (Kabigumila, 1998b).

The Arusha Region is one of the major collecting centres for tortoises destined for the export trade (Klemens & Moll, 1995). A local contact at the Njemu site on 19 May 1994 reported that leopard tortoises used to be abundant in the area, but that numbers had declined because of over-collection. The collector's camp located in the neighbourhood had been closed two months before this survey took place. A visit to Mwada (along the main road to Dodoma) the following day revealed that sixteen leopard tortoises had been collected that week for a dealer from Arusha. In November 1993, the Antipoaching Unit confiscated fifteen adult leopard tortoises from poachers in Arusha Town. The tortoises were presumably collected for farming purposes because they were all adults, and most operators were issued licences during that period. Moreover, the animals were far beyond the size preferred for export (100–155 mm carapace length, Kabigumila, 1998a). No evidence of tortoise collection was detected in Serengeti although the sites lie along the main road to Mwanza and Musoma (Kabigumila, 1998a). This may partly account for the higher sighting frequency

at the unprotected sites. Other workers (Lambert, 1982; Klemens & Moll, 1995) have reported reductions in tortoise abundance following commercial collection. Klemens & Moll (1995) reported the sighting frequency of *Malacochersus tornieri* in northern Tanzania as ranging from 0.23 to 0.33 mhr^{-1} in collected habitats and 0.5–8.5 mhr^{-1} in uncollected habitats. Lambert (1984) reported comparable figures for *T.g. graeca* in collected areas of northwest Africa as 0.3 mhr^{-1}, compared to 3.3 mhr^{-1} for *T.g. ibera* in largely uncollected populations in western Turkey. The latter compared with 4–10 mhr^{-1} for *T.g. graeca* recorded in the Algiers region prior to pressure from collection for trade (Lambert, 1984).

Sighting frequency was significantly different between the Serengeti and Arusha sites. This was also supported by local opinion; half the respondents in Robanda village ($n = 154$) claimed they saw more than two leopard tortoises per day, compared to less than one-fifth of the respondents in Mto wa Mbu ($n = 154$) (Kabigumila, 1998b). The difference might partly be due to higher rainfall in the Serengeti, in addition to collection for the export trade at some of the Arusha sites. Lambert (1982) reported similar differences between *T.g. ibera* in western Turkey and *T.g. graeca* in northwestern Africa. The difference in tortoise abundance was partly explained by the more favourable climate in Turkey, in addition to habitat loss through agriculture and population reduction through collection in northwestern Africa (Lambert, 1982).

Opportunities for comparison of the present data with other leopard tortoise populations, and with other closely related species (e.g. *Geochelone sulcata*, *G. platynota*, *G. elegans*) are limited due to the paucity of such studies. However, comparison with other xeric-dwelling, albeit smaller species (e.g. *T. hermanni*, *T.g. graeca*, *T.g. ibera*, *M. tornieri*) shows higher sighting frequencies than in the present study. In most populations, variations existed between disturbed and undisturbed populations, suggesting a negative impact of humans on tortoise density.

Conservation status

Because there are no baseline data from Tanzania, it is difficult to say whether there is a trend in the abundance of leopard tortoises, or if the species is more abundant than elsewhere. However, local opinion (Kabigumila, 1998a) and the present data suggest that the leopard tortoise is still common in the Serengeti, but rare at the Arusha sites.

Food habits

Observations recorded in this study on the food habits of leopard tortoises are consistent with those by previous workers (Loveridge & Williams, 1957; Milton, 1992; Rall & Fairall, 1993). Diet is largely vegetarian, comprising a wide variety of plant items. However in the present study, leopard tortoises ate mostly succulent forbs, in contrast to tortoises in South Africa whose principal food item was grass, comprising 69.7–71.0% of the diet (Milton, 1992; Rall & Fairall, 1993). The grass item was taken in proportion to its availability (Milton, 1992; Rall & Fairall, 1993).

Climate is known to influence the relative availability of grass and other food items. The mesic grasslands of the eastern parts of South Africa are characterized by a stable and less seasonally defined climate with uniform rains (Greig & Burdett, 1976). Such a climate may give rise to abundant green grass and thus a preponderance of grass in the diet. In northern Tanzania, the less predictable and less reliable rainfall may result in low grass production (Coe, Bourn & Swingland, 1979). However, observations in western Serengeti suggest that green grass is more abundant than other food items. Thus, the food habits of leopard tortoises may be explained by factors other than grass abundance. The herb layer in western Serengeti is dominated by tall grass (Herlocker, 1976), which may not be accessible to leopard tortoises because they feed at a low level (Rall & Fairall, 1993). Therefore, leopard tortoises have to rely on short grass, succulents and low-growing forbs for their food supply. These items can be obtained by foraging in short grass and road verge habitats where the said food items are relatively more abundant (Kabigumila, 1998b). Although leopard tortoises are sympatric with *Kinixys spekii*, the two species may not be in competition for food as the latter are omnivorous, feeding on herbs, invertebrates and fungi (Hailey & Coulson, 1995). Furthermore, *K. spekii* occurs mostly in moist, dense riverine vegetation or around thicket patches (Hailey & Coulson, 1995). Thus, leopard tortoises in the Serengeti may have evolved the succulent diet to avoid competition with ungulate herbivores for short grass. Succulents may be avoided by ungulates because they contain toxic secondary compounds (Milton, 1992).

Sinclair (1975) has shown that during the wet season, over 90% of the green biomass on the short grass plains of Serengeti is consumed by ungulates. This suggests that large herbivores may limit the amount of food and cover available to smaller herbivores (Janzen, 1975; Kreulen, 1979). However, Lambert, Campbell & Kabigumila (1998) contend that food may not be a limiting factor to tortoises in the Serengeti. Hailey & Coulson (1995), who suggested that green vegetation available as food, even during years of poor rainfall, was well beyond the leopard tortoise feeding requirements, also support this. It has been suggested that considering their size, leopard tortoises might consume large amounts of herbage, thereby competing with livestock for grazing (Boycott & Bourquin, 1988). However, Rall & Fairall (1993) have argued that as leopard tortoises feed at a low level in the vegetation and exist at low densities, they are not expected to have a great influence on biomass. This may also be true in the Serengeti where the relatively inactive ectothermic leopard tortoises browse more frequently than they graze, and exist at low numbers in the habitats (this study). Other workers in the Serengeti National Park have shown that small herbivores such as grasshoppers (Sinclair, 1975) and African grass rats *Arvicanthis niloticus* (Senzota, 1983) may consume more biomass than any other herbivorous taxon.

The leopard tortoise diet included many species of plants from different families, but most were only eaten very occasionally in proportion to their availability. Nevertheless, the animals appeared to select certain species, e.g. *C. rotundifolia* (Vitaceae), *I. schimperi* (Fabaceae), *J. anselliana* (Acanthaceae), *T. terrestris* (Zygophyllaceae) and *Commelina africana* (Commelinacea), despite their low frequency in the vegetation. Owen-Smith & Cooper (1987b) have shown that the selection of plant species is influenced by the animal's nutrient requirements, palatability, digestibility and succulence, while physical structure and chemical defences of plants act as deterrents. Because succulents have a high water content (Stanley-Price, 1977), the significant use of these items in the present study indicates that leopard tortoises may have the ability to survive in the absence of free water. Although leopard tortoises elsewhere were seen to drink on several occasions (Kabigumila, 1998b), this was never observed in the Serengeti tortoises. The use of succulents and forbs in arid areas or during drought periods has also been confirmed in South African leopard tortoises (Milton, 1992; Rall & Fairall, 1993). They suggested that the negative relationship between the frequency of grass and succulents in the diet shows that leopard tortoises are capable of switching diets according to the relative availability of the two food items. Succulents have also been documented in the diet of other arid-dwelling tortoises (*Psammobates oculifer*: Rall & Fairall, 1993; *Gopherus agassizii*: Turner *et al.*, 1984; *Geochelone elephantopus*, Fritts, 1983).

Table 3 Plant species eaten by leopard tortoises that are suspected to contain toxic substances

Plant species	Active secondary compound
Alternanthera sp.	Cyanin
Cissus spp.	Oxalic acid
Commelina spp.	Cyanin
Cucumis hirsutus	Cucurbitacin
Euphorbia spp.	Cyanin
Kalanchoe sp.	Cotyledontoxin
Opuntia vulgaris	Oxalic acid
Portulaca quadrifida	Potassium oxalate
Tribulus terrestris	Sapogenin; hepatoxin

Sources: Watt & Breyer-Brandwijk (1962); Pratt & Gwynne (1977).

Among the plants eaten by leopard tortoises were species with spines (e.g. *O. vulgaris* and *T. terrestris*) and those suspected to contain toxic secondary compounds, e.g. sapogenin, oxalic acid, cyanin, cucurbitacin and cotyledontoxin (Table 3). In East Africa, *T. terrestris* is said to be poisonous to sheep and causes stomach bloat in cattle and goats (Pratt & Gwynne, 1977). In South Africa, *T. terrestris* causes swelling of the head with fatal results in livestock (Watt & Breyer-Brandwijk, 1962; Pratt & Gwynne, 1977), but it is a critical food item to both *G. pardalis* and *P. oculifer* (Rall & Fairall, 1993). Milton (1992) also recorded plants with spines and those containing cardiac glycosides, oxalic acid and alkaloids in the leopard tortoise diet, although livestock and antelopes generally avoid such plants. In *T. hermanni*, Meek (1985) recorded the presence of toxic alkaloids in five (41.6%, $n = 12$) of the food plants eaten.

Because very little is known about the nutrient requirements and digestion of leopard tortoises in Tanzania and elsewhere (Rall & Fairall, 1993), it is difficult to speculate about the data presented here. However, it could be suggested that the plant items were selected because of their high water content and digestibility. Furthermore, leguminous species like *I. schimperi* may be selected for their easily digestible protein content (Rall & Fairall, 1993). Previous workers with leopard tortoises (Milton,

1992; Rall & Fairall, 1993) and with *Aldabrachelys elephantina* (Hnatiuk, 1978) have also reported selection of food items. On Galapagos, *G. elephantopus* inhabiting xeric islands have evolved saddle-backs that enable the animals to extend their heads higher to reach the upper stems of succulent *Opuntia* (Fritts, 1983). The animals are known to depend on *Opuntia* for water during prolonged drought (Fritts, 1983).

It is possible that tortoises and other arid-dwelling reptiles that lack sufficient mobility to search for free water are adapted to cope with physical and chemical substances of plants by various means including: (a) excretion of some of the substances (oxalates) in crystalline form as uric acid crystals rather than urea (Milton, 1992), which requires some water for its elimination (Pritchard, 1967); (b) ingesting supplementary minerals to nullify the toxic effects of secondary compounds in food plants (Esque & Peters, 1994), and (c) consuming small amounts of the various items to avoid lethal doses.

The succulent diet of leopard tortoises in the Serengeti may have implications for the ranging patterns of tortoises there. Because succulents and forbs are patchily distributed within the habitats compared to grass, and all things being equal, leopard tortoises in the Serengeti are likely to have larger home ranges than those of animals from South Africa that feed mostly on grass (Milton, 1992; Rall & Fairall, 1993). In addition, such food patches may serve as focal points for tortoise activities (e.g. courtship and copulation) (Jennings, 1993). Destruction of these patches (by fire, overgrazing, off-road driving or vegetation clearance) may not only reduce the preferred foods, but may also disrupt other social activities (Jennings, 1993).

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