Seasonal utilization of leaves by giraffes *Giraffa camelopardalis*, and the relationship of the seasonal utilization to the chemical composition of the leaves

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Food preferences of giraffe have been extensively investigated but few data concerning the chemical composition of the preferred species are available. The present study was aimed at ascertaining whether the differences in chemical composition of leaves of preferred food plants influence food selection. Furthermore, whether there are differences in the chemical composition of the specific plant species utilized at different localities and to provide information on the nutritive value of indigenous trees. Availability of the 54 preferred plant species studied was also considered. Moreover the seasonal utilization of the plants and its relation to their chemical composition was evaluated by a nonparametrical statistical method. The crude protein of the leaves of *Acacia* spp. is generally higher than in those of other species and they are therefore a better food source than e.g. *Combretum* spp. The leaves of preferred plants show the following seasonal trends: a decrease in moisture and protein content from January until August/September when they again increase; conversely, the two carbohydrate fractions, crude fibre and nitrogen-free extract, increase during the corresponding period until August/September, whereafter they decrease again. Variations in the ether extract and ash fractions show few or no trends. Leaf moisture content was always greater during the night than during the day. This may be important for supplementing water gain in times of drought.
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Voedselvoorkeur en voedselseleksie van kameelperde is al ondersoek; min data is egter beskikbaar oor die chemiese samestelling van die voorkeurvoedselplante. 'n Doel van die huidige studie was om vas te stel of die chemiese samestelling van voorkeurvoedselplante enige invloed het op die kameelperde se seleksie daarvan. Nog 'n doelwit was om vas te stel of spesifieke voedselplante se chemiese samestelling verskil in die verskillende lokaliteite, en om inligting in te win oor die voedingswaarde van inheemse bome. Die beskikbaarheid van die 54 voorkeurplantsoorte is ook in aanmerking geneem. Verder is die seisoenale benutting van die plantsoorte deur kameelperde en die verwantskap met die chemiese samestelling geëvalueer deur gebruik te maak van nie-parametriese statistiese metodes. Die proteïeninhoud van die blare van *Acacia*-spesies is oor die algemeen hoër as dié van ander spesies en is dus 'n beter bron van voedsel as bv. *Combretum* spp. Die blare van voorkeurplante toon die volgende seisoenale tendense; 'n daling in vog en proteïeninhoud vanaf Januarie tot Augustus/September, wanneer dit weer toeneem, terwyl altwee koolhidraatfraksies nl. ruvesel en stikstofvrye ekstrak toeneem gedurende hierdie periode tot Augustus/September, wanneer dit afneem. Variasie in eterekstrak en asfraksies toon min of geen tendense. Blaarvoginhoud was altyd hoër in die nag as gedurende die dag, wat belangrik mag wees as 'n bykomstige bron van water onder droogtetoestande.
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Research on food preference and selection by giraffes (Foster & Dagg 1972; Leuthold & Leuthold 1972; Hall-Martin 1975; Kok & Opperman 1980) has not yet indicated why giraffes prefer the leaves of particular plants. The aim of the present study was to determine seasonal changes in the chemical composition of the leaves in terms of utilization while taking availability of the different plant species into account.

Fox (1938) and Dagg (1959) analysed the leaves and twigs of certain *Acacia* species but they were unable to determine the order of preference in terms of chemical composition. Their conclusions are based on a single leaf collection and only three fractions were analysed viz., crude protein, ether extract and ash. Furthermore, food preferences of giraffes were only qualitatively ascertained.

Hall-Martin & Basson (1975) analysed the stomach contents of giraffes shot each month over a period of one year. Because the leaves of specific plant species could not be differentiated from those of similar species, and because micro-organisms in the rumen, saliva and digestive secretions influence the chemical composition, their study is not suitable for the determination of actual seasonal changes in dietary chemical composition.

Nevertheless their results indicate that the crude protein and moisture content of the leaves seem to be the most important fractions influencing selection of food plants. Yet how the giraffes determine what to select remains an open question. On the one hand olfactory cues probably play an important role in the selection of food by herbivores (Matthews & Knight 1963) but other sensory cues such as vision and taste may be important. Preferences can furthermore be modified by learning and by difficulties in obtaining a specific food item. In addition, preference may be influenced by frequency of occurrence as well as nutritional requirements. The results reported in this paper could most probably be applied advantageously in the determination of the most suitable foods for giraffes in zoological gardens.

Materials and Methods

Sampling

Samples of the 54 preferred food plants selected by giraffes in the Timbavati (TPNR), Jack Scott (JSNR) and Koos Meintjies (KMNR) Nature Reserves, as determined by Hall-Martin (1975), Van Aarde & Skinner (1975) and Sauer, Theron & Skinner (1977), were collected at eight six-weekly intervals throughout 1976. Each sample consisted of two to four sub-samples of equal volume of material collected from the same trees throughout the year at approximately the same time of day, thereby reducing the effect of time of collection and intraspecific variation on the chemical composition of samples. The methods of collection furthermore simulated the feeding behaviour of the giraffes. When new growing shoots were available the soft and juicy food parts were first selected by the giraffes. When not available they concentrated on the mature leaves. The samples of new-growing shoots included leaflets, twigs and thorns while samples of the matured food items were comprised only of leaves. Shed leaves were not sampled. Each sample weighed approximately 100 g and these were stored at 4° C, and sealed in glass containers until analysed.

Chemical analysis

Duplicate quantitative chemical analyses of each sample for moisture content, crude protein, ether extract, crude fibre, ash and nitrogen-free extract were performed in accordance with the standards of the Association of Official Agricultural Chemists (Horwitz 1965). The analyses were carried out as described by van der Merwe (1970). All values for the fractions determined on a dried mass basis were converted to a wet mass basis.

Statistical methods

Percentage utilization of a specific plant species was correlated with all the different wet and dry chemical fraction values of the same plant species throughout the year to determine if seasonal changes in any of the fractions correlated with the variation in utilization of that plant selected by giraffes. Seasonal changes in every fraction were also correlated with seasonal changes in every other fraction of the same plant species to ascertain whether there are general relationships in the seasonal changes of the different fractions of these indigenous trees.

The Kendall Partial Rank Coefficient (τ) was used since it is a nonparametrical method of calculation and is better applied to the specific data as a result of the limited amount of data and because of the lack of proof of normality (Hajèk 1969). One advantage of τ over r_s (Spearman Rank Correlation Coefficient) is that the effects of variation by a third variable upon the relation between the two variables correlated, are eliminated (Siegel 1956). Where related samples were analysed the Wilcoxon matched pairs signed-ranks test was used, and where independent samples were analysed the Mann Whitney U-test was used to determine the significance of differences (Siegel 1956).

The percentage error between the two duplicate analyses of each fraction of each sample was ascertained by making use of the following formula:

$$\% \text{ error} = \frac{\text{difference between 2 duplicates}}{\bar{x} \text{ of the two duplicates}} \times \frac{100}{1}$$

If the percentage error between the duplicate samples of the crude protein was higher than 5,0% the analysis was repeated in duplicate. The critical values for the other fractions were 10,0% because of the less accurate analytical methods and due to the fact that the smaller a specific fraction is, the larger the influence of a relatively small experimental error on the percentage error.

Results and Discussion

Only those plants whose seasonal changes in chemical composition showed some relationship ($P<0{,}01$) with the variation in utilization by giraffes (Table 1) are discussed. In 62,5% of the plant species studied, there was no significant relationship between utilization and changes in the chemical composition of the leaves (Table 2). Data on the chemical composition of these species are available in Sauer (1977).

Assumptions and Shortcomings

In the TPNR the percentage utilization of different plant species was determined from analyses of monthly collections of stomach contents of giraffes from July 1971 to June 1972 (Hall-Martin 1975). Since the leaves in the present study were collected for chemical analysis during 1976 the assumption was made that the utlization of plant species by giraffes is more or less the same from one year to the next. Furthermore, the assumption was made that the quantitative amounts of foodstuffs in leaves of every plant species remain more or less constant from one year to the next.

In JSNR food preferences and percentage utilization were ascertained by recording observations and time spent feeding, but only from February to August 1974 (Van Aarde & Skinner 1975) thus limiting the amount of data on utilization that could be correlated with the change in chemical composition of the leaves and reducing the value of results obtained. The same applies to the data on utilization of preferred food plants of giraffes in KMNR which were recorded from February to August 1975 (Sauer *et al.* 1977).

Important food plants studied

Acacia caffra (Thund.) Willd.

Acacia caffra is the most important and preferred food plant of giraffes in JSNR and is the plant species utilized most during both the wet and dry seasons (Van Aarde & Skinner 1975). *A. caffra* is abundant in this Reserve (Mason 1973). It is of lesser importance as a food plant in KMNR (Sauer *et al.* 1977). Nevertheless it is a preferred food plant since only a few trees were found in this reserve and all were heavily browsed.

The percentage utilization of *A. caffra* by giraffes is significantly correlated with seasonal changes in protein content ($\tau = 0{,}67$) and with fat content (ether extract fraction) ($\tau = 0{,}67$) (Table 1). Percentage utilization furthermore correlates negatively with crude fibre content in the oven-dried sample ($\tau = -0{,}67$). Unfortunately data on utilization were limited to five months of the year during the wet and three months during the dry season (van Aarde & Skinner 1975).

The protein content in the dry matter was highest in new growth sampled in JSNR during October 1975 (18,6%). It then gradually decreased until September 1976. Because of the influence of the fluctuating moisture content which has been taken into account, this tendency for change in

Table 1 The relationship (τ) between percentage utilization of the leaves of preferred food plants by giraffes and the different important food analysis fractions

		Food analysis fractions						
Plant species	Locality	Moisture	Nitrogen-free extract	Crude Protein Wet	Crude Protein Dry	Crude fibre	Ether extract	Ash
Acacia caffra	JSNR			0,67		−0,67	0,67	
Acacia karoo	JSNR		−0,68	0,96		−0,98		−0,98
Acacia karoo	KMNR	0,66	−0,68	0,98		−0,98		−0,96
Acacia senegal	TPNR			0,91				0,66
Combretum apiculatum	KMNR	−0,67		0,67		0,67		
Combretum apiculatum	TPNR				0,59			
Combretum hereroense	KMNR					0,65		
Combretum hereroense	TPNR			0,59				
Combretum imberbe	KMNR				0,59	0,65	1,00	
Combretum zeyheri	TPNR				0,73	−0,62		−0,73
Colophospermum mopane	TPNR			0,35			−0,89	
Dichrostachys cinerea	TPNR				0,90			
Diospyros mespiliformis	TPNR		0,80			0,56		0,61
Peltophorum africanum	KMNR		0,95	0,91			0,97	
Rhus lancea	KMNR			−0,33		0,92		
Sclerocarya caffra	TPNR				0,68			
Terminalia prunioides	TPNR		0,38	0,60				
Ziziphus mucronata	TPNR				0,82	−0,69		
		2	5	10	6	10	4	5

Table 2 Preferred plant species studied that do not show significant relationships between changes in chemical composition and the variation in utilization of the leaves by giraffes (Sauer 1977)

Nature reserves		
Timbavati	Jack Scott	Koos Meintjies
Acacia caffra	*Acacia ataxacantha*	*Acacia erubescens*
A. exuvialis	*Berchemia zeyheri*	*A. nilotica*
A. gerrardii	*Burkea africana*	*A. robusta*
A. nigrescens	*Cassine aethiopica*	*A. tortillis*
Bolusanthus speciosus	*Combretum erythophyllum*	*Burkea africana* *Euclea crispa*
Combretum imberbe	*C. molle*	*Pappea capensis*
Lannea stuhlmanii	*Cussonia paniculata*	*Spirostachys africana*
Spirostachys africana	*Dombeya rotundifolia* *Fagara capensis*	
Albizia harveyi	*Maytenus heterophylla*	
	Olea africana	
	Protea caffra	
	Phus leptodictya	

the protein content of the leaves of *Acacia caffra* is masked in the wet samples.

In comparing the different chemical fractions of *Acacia caffra* leaves sampled on JSNR there is a significant correlation between the crude fibre and nitrogen free extract (τ = 0,71). The crude fibre is also significantly correlated with the ether extract fraction (τ = 0,57).

When the corresponding chemical fractions of *A. caffra* leaf samples from two different localities were compared, there were no significant correlations with the exception of the ether extract fraction (τ = 0,93), although in most cases the corresponding fractions did show similar tendencies and correlated positively but not significantly. It is also important to mention that there were no leaves left that could have been sampled during the dry season in KMNR (Sauer *et al.* 1977). In JSNR the leaves were always available and sampled throughout the year.

Acacia karoo Hayne

A. karoo is also a preferred food plant of giraffes. It is a dominant plant species in JSNR (Wells 1964). However, only a few trees could be found in KMNR all of which were heavily browsed (Sauer *et al.* 1977).

In both these nature reserves percentage utilization is significantly correlated with protein content in the dried matter: JSNR (τ = 0,96) and KMNR (τ = 0,98) (Table 1). Percentage utilization is furthermore significantly correlated with the nitrogen-free extract (τ = −0,68) and with the crude fibre (τ = −0,98). The same tendencies are seen in KMNR: nitrogen-free extract (τ = −0,68), crude fibre (τ = −0,98) and ash (τ = −0,96) (Table 1).

It can therefore be concluded that giraffes prefer juicy leaves of *A. karoo*. Incidentally, perhaps because of their higher protein content and/or because of their lower crude fibre content, the values of nitrogen-free extract (NFE) and ash in the young leaves were comparable with those of the older leaves.

When the chemical fractions of the leaves sampled on the two different localities are compared, all fractions are significantly correlated except the protein fractions. The specific values of the different fractions sometimes differ greatly.

In comparing the different fractions from leaves sampled in JSNR, the moisture content is significantly correlated with the crude fibre (τ = 0,80) and NFE (τ = 1,0). In KMNR the significant correlation between the protein content and the ether extract fraction (τ = 0,78) and ash fraction (τ = 0,98) is possibly fortuitous.

Acacia senegal (L.) Willd.

A. senegal is possibly the most preferred food plant of giraffes in TPNR and is utilized throughout the year (Hall-Martin 1974). The specific three trees from which leaves were sampled were over-utilized and had been pruned into umbrella-like shapes by browsing. However, only a few *A. senegal* could be found in TPNR, and these were prevented from growing higher than 9 m due to browsing by giraffes.

Percentage utilization of the leaves is significantly correlated with their protein content (τ = 0,91) and with their ash content (τ = 0,66; Table 1). The average protein content of *A. senegal* ($\bar{x}$ = 28,6%) exceeds that of all other plant species studied. This may be owing to the fact that no leaves could be sampled from May to October 1976, when the protein content of the leaves of most plants studied was generally low. There is an increase in the protein content from December to April 1976.

Combretum apiculatum Sond.

C. apiculatum is an important food plant of giraffes in TPNR. This tree is utilized throughout the year with the exception of a few weeks during September and October when the trees shed their leaves (Hall-Martin 1975). In KMNR this species was utilized by giraffes during the dry season (Sauer *et al.* 1977). In both localities *C. apiculatum* trees are numerous and a dominant plant species in at least one plant community (Hall-Martin 1975; Sauer *et al.* (1977).

Percentage utilization of the leaves by giraffes is significantly correlated with changes in protein content (τ = 0,67) and with changes in crude fibre content (τ = 0,67) in the Koos Meintjies Nature Reserve. It is furthermore significantly correlated with changes in moisture content (τ = −0,67; Tables 1 & 3). However, the last two significant correlations may be fortuitous since, in all plants studied, the moisture content is inversely related to the crude fibre content.

The chemical composition of *C. apiculatum* has previously been determined by several researchers (Bonsma 1942; Groenewald, Joubert & Tölken 1967; Joubert & Eloff 1971; Roth & Osterberg 1971). The percentage values of the different fractions differ in all cases. The protein content and crude fibre content of the leaves sampled in different areas differ significantly when compared. However, the tendency for seasonal changes shows the same trend in the majority of cases. There is a decrease in crude protein content from January to September and an increase in crude fibre content from January to August (Bonsma 1942).

The samara fruits of *C. apiculatum* were sampled and analysed during January 1976 to compare the chemical composition of the fruit with the leaves of the same trees.

Table 3 Relationship (τ) between the moisture content and other important fractions of the preferred food plant species of giraffes as ascertained by the Weende food analysis of Henneberg and Slohmann in Van der Merwe (1970). Kendall partial rank correlation coefficents for the variables significantly ($P<0{,}01$) related to each other

	Kendall partial rank correction coefficients				
Plant species	Nitrogen-free extract	Crude protein	Crude fibre	Ether extract	Ash fraction
Acacia caffra		0,67			
A. exuvialis	−0,98	0,60	−0,87		
A. gerrardii	−0,47	0,73	0,73		
A. nigrescens	−0,87		−0,84		
Bolusanthus speciousus	−0,86		−0,86		
Combretum apiculatum	−0,81	0,61	−0,81		−0,52
C. hereroense					−0,71
C. imberbe		−0,50			
Dichrostachys cinerea	−0,81		−0,43		−0,90
Diospyros mespiliformis		0,50		−0,78	
Lannea stuhlmanii	−0,20		−0,60	−0,73	
Sclerocarya caffra			−0,60	−0,47	−0,87

The mean moisture content of leaves ($\bar{x}$ = 52,9%) was less than that of fruit (71,0%). The mean crude protein content ($\bar{x}$ = 11,0%) was also less than that of fruit (12,2%). On the other hand the crude fibre content of fruit (28,7%) was consistently higher than that of leaves ($\bar{x}$ = 22,1%). The ash content of leaves ($\bar{x}$ = 0,9%) was consistently higher than that of the samara fruit (0,3%) and the ether extract fraction of fruit (2,3%) was lower than the average ether extract fraction of leaves ($\bar{x}$ = 2,5%).

When the corresponding chemical analysis fractions of *C. apiculatum* leaves sampled in two different localities are compared the average moisture content (52,9%) in TPNR is significantly greater than the moisture content in KMNR (43,3%). In the other fractions there are no significant differences.

In comparing the different fractions from leaves sampled in TPNR the moisture content is significantly correlated with the crude protein content (τ = 0,61). The moisture content furthermore is significantly correlated with the following fractions: crude fibre (τ = −0,81) NFE (τ = −0,81) and the ash fraction (τ = −0,52) (Table 3).

Combretum hereroense Schinz

Although *C. hereroense* is one of the less important food plants of giraffes in TPNR, and is only utilized from February to September (Hall-Martin 1974), it is the second most important food plant during the dry season in KMNR (Sauer *et al.* 1977). *C. hereroense* is one of the dominant plant species in KMNR and it is not widely distributed in TPNR (Hall-Martin 1975; Sauer *et al.* 1977). Thus it seems that availability of food plants may be an important factor that influences selection and preference by giraffes.

Percentage utilization of the leaves is significantly correlated with changes in protein content ($\tau = 0{,}59$) in TPNR (Table 1). In KMNR percentage utilization is significantly correlated with changes in crude fibre content ($\tau = 0{,}65$) (Table 1). This correlation may be fortuitous since the crude fibre content in most plants studied increased from January to August. The moisture content of this plant species changes relatively little throughout the year in both study areas.

The samara fruit of *C. hereroense* was sampled during July 1976 and the flowers during October 1976 in TPNR. Both these parts were previously seen to be utilized by giraffes. The chemical composition of these parts differs largely from the leaves of the same species. The moisture content of the fruit (54,9%) is lower than the moisture content in the leaves (56,8%) and both are lower than the flowers (62,0%). The protein, crude fibre and ether extract fractions of the fruit are higher than the corresponding fractions in the leaves, while the mean ash content ($\overline{x} = 1{,}12\%$) of leaves is higher than that of flowers (0,17%) and samara fruit (0,31%).

The mean crude protein content of leaves in TPNR ($\overline{x} = 4{,}67\%$) and KMNR ($\overline{x} = 4{,}64\%$) is relatively low in comparison with the other food plants studied. This may be responsible for the low utilization of *C. hereroense*. Giraffes most probably consume the leaves of this plant species due to the lack of leaves on preferred food plants during the dry season.

In comparing the different fractions from leaves sampled in TPNR there is a significant correlation between the moisture and ash fractions ($\tau = -0{,}71$). Furthermore there is an inexplicable significant correlation, perhaps fortuitous, between the ether extract fraction and the nitrogen-free extract (NFE) ($\tau = 0{,}90$). In KMNR there is an unaccountable significant correlation between the ether extract and crude fibre fraction ($\tau = 0{,}81$).

Combretum imberbe Wawra

C. imberbe is one of the less important food plants in the diet of giraffes and is only utilized during the dry season when feeding stress forces giraffes to feed on *C. imberbe* (Sauer *et al.* 1977).

Percentage utilization of the leaves is significantly correlated with changes in the ether extract fraction throughout the year ($\tau = 1{,}00$) in KMNR. It is unlikely that giraffes utilize *C. imberbe* to provide for their energy requirements. Since the mean ether extract content ($\overline{x} = 1{,}39\%$) of *C. imberbe* is relatively low when compared with the leaves of the other plant species sampled in the KMNR (Tables 1 & 2). It is therefore possible that the correlation is fortuitous or giraffes may be attracted by the aromatic flavour.

Tendencies for change in corresponding fractions from *C. imberbe* leaves sampled from two different study areas in most cases correlated significantly. However, the mean moisture content of the leaves ($\overline{x} = 65{,}2\%$) in TPNR is much higher than in those sampled in KMNR ($\overline{x} = 49{,}5\%$). The other chemical fractions in the leaves from KMNR are all higher than those in the leaves sampled in TPNR. In comparing the different fractions from leaves sampled, the change in crude fibre is significantly correlated with changes in crude protein ($\tau = 0{,}79$) and ether extract ($\tau = 0{,}64$).

Combretum zeyheri Sond.

C. zeyheri is also one of the less important food plants of giraffes and is utilized from September to February (Hall-Martin 1974). The fact that this plant species is utilized during the period when food is abundant might indicate that *C. zeyheri* is a preferred food plant. However the reason for this feeding behaviour is because *C. zeyheri* is one of the dominant plant species in TPNR but, utilization is nevertheless limited in relation to availability and it is lightly browsed in comparison to the preferred plant species. Futhermore, *C. zeyheri* is deciduous and thus was not utilized from March to August.

Percentage utilization of the leaves is significantly correlated with changes in the protein content in the dry mass fraction ($\tau = 0{,}73$) and negatively correlated with the change in the crude fibre content ($\tau = -0{,}62$) and the change in ash content ($\tau = -0{,}73$) (Table 1). From this it can be concluded that *C. zeyheri* is utilized because of the relatively high protein content from November to January, and that it is fortuitous that utilization is negatively correlated with the low crude fibre and ash content.

In comparing the different fractions of leaves sampled throughout the year there is a negative correlation between the protein and ash fractions in the dried mass value ($\tau = -0{,}71$). During the period of active growth the protein content of the leaves is relatively high and crude fibre and ash content relatively low. This tendency is, as can be expected, a general phenomenon that could be recognized in most of the plant species studied.

Colophospermum mopane Kirk ex Benth.

C. mopane is one of the important food plants of giraffes during the cold dry season in TPNR. This plant species is primarily utilized between July and October (Hall-Martin 1974). Furthermore, it is one of the dominant plant species in the north of TPNR.

Percentage utilization is significantly correlated with the change in protein content throughout the year ($\tau = 0{,}35$) (Table 1). In addition it is significantly correlated with changes in ether extract content ($\tau = -0{,}89$) (Table 1). This may be owing to the fact that giraffes avoid this food plant to some degree because of the terpentine and other aromatic compounds that are unmistakably perceptible in damaged leaves and in the ether extract fractions of the leaves (Bonsma 1976).

The protein content of the leaves sampled during this study is, with the exception of the October sample, higher than those sampled and analysed by Bonsma (1942). The same phenomenon is seen in the crude fibre fraction. When the fractions are compared the changing trends are of the same order (Bonsma 1942).

The protein content of *C. mopane* leaves and twigs sampled in the Matopos, Zimbabwe was higher during January (15,4%), February (20,0%) and October (17,0%). However, throughout the cold dry season from May to August the protein content of the leaves in the Matopos (Roth & Osterberg 1971) was lower than that in the present study and that given by Bonsma (1942). There is a greater fluctuation in the crude fibre content but it is always more than that found in the other two studies. This may be owing to the fine twigs that were sampled with the leaves. The ash and ether extract fractions are higher than those of the present study. Changing tendencies in all the different fractions show the same pattern of change in all three of the abovementioned studies as well as those of Groenewald *et al.* (1967).

Dichrostachys cinerea Wight & Arn.

D. cinerea is an important food plant of giraffes in TPNR and less important in the KMNR (Hall-Martin 1974; Sauer *et al.* 1977). Utilization of this plant species is in direct relation to availability and it could thus be seen as a preferred food plant.

Percentage utilization is significantly correlated with the change in protein content of the leaves (τ = 0,90) and the change in moisture content (τ = 0,81) (Tables 1 & 2). This correlation may be fortuitous for it is a general phenomenon that a high protein content is characteristic of the new active growth during the wet season when moisture content of the new growth is also higher. It seems that giraffes utilize this plant species because of the relatively high protein content ($\bar{x}$ = 15,9%) in TPNR. In KMNR the amount of data on utilization is insufficient to draw any conclusions.

In comparing the different fractions of leaves sampled in TPNR there is a decrease in moisture content that is significantly negatively correlated with an increase in the following fractions: ash content (τ = −0,90), crude fibre content (τ = −0,43) and NFE content (τ = −0,81). These fractions also correlate significantly with each other.

When the changing trends for corresponding fractions of *D. cinerea* leaves sampled from the two different study areas are compared, fractions show more or less the same kind of change. The exceptions can only be explained in terms of the relatively large influence of the moisture factor.

Diospyros mespiliformis Hochst ex A.DC.

D. mespiliformis is one of the less important food plants of giraffes and is only utilized from August to October (Hall-Martin 1975). This plant species is associated with termite mounds and also forms an important part of riverine growth.

Percentage utilization is significantly correlated with the two carbohydrate fractions in the leaves: NFE (τ = 0,80) and the crude fibre (τ = 0,56) (Table 1). Utilization is also significantly correlated, perhaps fortuitously, with the ash content in the leaves (τ = 0,61). *D. mespiliformis* is not a preferred food plant and is only utilized during the time of the year when the preferred food plants are not available. Thus these correlations could not be of much value.

In comparing the different fractions in the leaves of *D. mespiliformis* there is a significant correlation between moisture content and ether extract (τ = −0,78). Furthermore there is a significant correlation between the change in moisture content and the protein content in the dry material of the leaves (τ = 0,5).

Peltophorum africanum Sond.

P. africanum is an important food plant of giraffes in KMNR. It is utilized during the wet warm season when food is abundant (Sauer, *et al.* 1977).

Percentage utilization of this species is significantly correlated with the following three chemical fractions: crude protein (τ = 0,91), ether extract (τ = 0,97) and NFE (τ = 0,95) (Table 1). The relatively low mean values: crude protein ($\bar{x}$ = 41,1%), ether extract (1,6%) and NFE (30,2%) and the low moisture content during April 1976 indicate a limited value for these correlations since they are possibly fortuitous and that there is no specific reason for the relatively high percentage utilization of *P. africanum* by giraffes from March to May 1976. This plant species is utilized to a very small degree in TPNR which is a much better and more suitable habitat for giraffes, and where this plant species is much more plentiful (Hall-Martin 1975).

In comparing the chemical fractions the change in protein content is significantly correlated with the change in crude fibre content (τ = −0,60) and the ash content (τ = −1,00) in the dried mass fractions.

Rhus lancea L.f.

Although *R. lancea* is not an important food plant of giraffes it was utilized to some degree throughout the year. It is one of the dominant plant species in KMNR (Sauer *et al.* 1977). *R. lancea* is a semi-deciduous plant species and was available throughout the year. It can not be regarded as a preferred food plant.

Percentage utilization is significantly correlated with the change in crude fibre content (τ = 0,92) and is negatively correlated with the change in protein content (τ = −0,33) (Table 1). This is possibly fortuitous due to the fact that the majority of plants studied, show an increase in crude fibre content from the beginning of the wet season to the end of the dry season. Furthermore, the giraffes increasingly fed on *R. lancea* as the preferred food became less available (Sauer *et al.* 1977).

In comparing the different chemical fractions of *R. lancea* there is a positive correlation between the ether extract fraction and the two carbohydrate fractions: crude fibre (τ = 0,86) and NFE (τ = 0,86).

Sclerocarya caffra Sond.

S. caffra is one of the less important food plants of giraffes and is only utilized from November to March. *S. caffra* is a sub-dominant species in TPNR and thus characteristic of this environment.

Although there are only four values on utilization of the leaves of this plant species by giraffes (Hall-Martin 1975) they indicate a positive correlation with the change in the dried mass crude protein content from November to March (τ = 0,68) (Table 1).

In comparing the chemical fractions of *S. caffra* leaves there are negative correlations between the moisture fraction and the following fractions; ether extract fraction (τ = −0,47), crude fibre (τ = −0,60), ash (τ = −0,87) and NFE (τ = −0,73). This seems to be a general phenomenon in most of the plants studied. There is a decrease in the moisture content from the end of the warm wet season (November to March) to the end of the cold dry season (April to July) (Hall-Martin 1975). During this time there is an increase in the crude fibre, NFE, ether extract and ash contents (Table 3).

When the chemical composition of the maroela fruit determined on a dried mass basis (Groenwald *et al.* 1967) is compared with the leaves the crude protein of the fruit (4,0%) is much lower than the mean protein content in the leaves ($\bar{x}$ = 12,9%). The crude fibre content in the leaves ($\bar{x}$ = 51,1%) is also much higher than the fruit (16,9%). The ether extract fraction in the fruit (7,3%) is higher than in the leaves (x = 2,3%). Groenewald *et al.* (1967) did not ascertain the moisture content of the fruit as it was collected in nature and this factor has a great influence on the percentage values of all fractions determined on a dried mass basis.

Terminalia prunioides Laws.

T. prunioides is an important preferred food plant species of giraffes and is extensively utilized from November to June (Hall-Martin 1974). In TPNR this plant species is abundant and many trees and shrubs could be found in all plant communities.

The percentage utilization of *T. prunioides* by giraffes is significantly correlated with changes in the protein content of the leaves throughout the period of utilization (τ = 0,60) (Table 1). With the exception of the moisture fraction, percentage utilization correlates negatively with all the other chemical fractions although only to a minor degree. It seems as if this plant species is specifically being utilized owing to the relatively high protein content of the leaves in comparison with the other plant species studied in TPNR ($\bar{x}$ = 16,06% through the year).

The protein content in the dried mass increases from December to April and then decreases until the leaves are shed. This tendency could also be seen in the leaves of *T. prunioides* from Otjovasandu, South West Africa, that were analysed by Joubert & Eloff (1971). The crude fibre content of the leaves from TPNR decreases from January to April and then increases until the leaves are shed in November. The mean crude protein content from TPNR is much higher and the crude fibre and ash content lower than those sampled in Otjovasandu (Joubert & Eloff 1971).

Ziziphus mucronata Willd.

Z. mucronata is one of the important preferred food plants of giraffe and it is extensively utilized during the wet warm season when food in general is abundant. *Z. mucronata* was utilized in all three study areas and in all cases the utilization was in direct relation to the availability of the leaves of this deciduous plant species (Hall-Martin 1975; Sauer *et al.* 1977; Van Aarde & Skinner 1975).

In TPNR percentage utilization is significantly correlated with the change in protein content in the leaves (τ = 0,82). Furthermore the percentage utilization is negatively correlated with the change in crude fibre content (τ = −0,69). This may be fortuitous, for the majority of plant species studied show an increase in crude fibre content from January to September. In the remaining two study areas (JSNR and KMNR) the amount of data on utilization are limited and no meaningful conclusion could thus be drawn from them.

In TPNR the mean crude protein content is higher ($\bar{x}$ = 19,9%) than in the other two study areas, JSNR ($\bar{x}$ = 19,4%) and KMNR ($\bar{x}$ = 14,9%). These values are relatively high in comparison to the other 51 plant species of which leaves were sampled and analysed. It is also higher than the protein content of *Z. mucronata* leaves which have been sampled from the South West Cape (13,0%) (Groenewald *et al.* 1967).

The moisture content of the leaves of *Z. mucronata* is relatively high and the crude fibre and nitrogen-free extract relatively low in comparison with the other 51 plant species studied although they do not differ significantly. Thus it may be possible that the giraffe select this plant species because of the juicy soft leaves that are also correlated with a high protein content.

In comparing the chemical fractions from the different study areas there are positive correlations in most cases. With the exception of the ash fraction it seems that the changing trends of the different fractions are more or less the same for the three areas but that the specific values of fractions from different localities that were sampled during the same time of the year sometimes differ drastically.

In comparing the chemical fractions of *Z. mucronata* leaves sampled in one locality, there is, in all three cases, a decrease in crude protein content and moisture content from October to June. In the corresponding time there is an increase in the crude fibre content and in the nitrogen-free extract. The ether extract fraction gradually increases until February and then decreases until this plant species sheds its leaves.

Conclusions

Explanation of food preference

The percentage utilization of the leaves of the different plant species browsed by giraffes is mostly significantly correlated with the crude protein content in both the dry and wet samples. Compared to the other fractions however, this does not mean that the giraffes select the food plant species for their protein content. The giraffes seem to prefer the new growing shoots when available. These food parts may be more succulent and have a relatively high protein content, and then one must bear in mind that chemical composition is only one of the selection criteria that may influence food selection by herbivores. Furthermore, of the 35,5% of the species that showed a significant correlation between utilization and chemical composition a total of only eight out of 54 species sampled, showed a significant correlation with the crude protein.

In TPNR which is a better habitat and where monthly data on utilization are available for a full year, percentage utilization correlates positively with changes in crude protein content in 13 out of 18 plant species studied (Table 4) and with moisture content in nine out of 18 cases studied. This is an indication that succulence of leaves may well be an important factor influencing selection of food plants by giraffes (Tables 4 & 5).

Comparison between *Acacia* and *Combretum* species

When the mean values of all fractions of the *Acacia* and *Combretum* species are compared it is apparent that the *Acacia* species have a higher crude protein content, with the exception of *Combretum imberbe* (Table 5). The *Combretum* species in general have a higher crude fibre, NFE, ether extract and ash content and a lower moisture content than the *Acacia* species (Table 5).

When the utilization, protein content and succulence of the most preferred *Acacia* species are compared to the

Table 4 Total number of significant positive correlations (τ) between percentage utilization of the tree leaves by giraffes and the different nutrient analytical fractions of 51 feeding plants studied. Non-significant positive correlations, negative and no correlations are also given (Sauer 1977)

	Timbavati Private Nature Reserve			Jack Scott Nature Reserve			Koos Meintjies Nature Reserve		
	A	B	C	A	B	C	A	B	C
Crude protein	8	5	5	1	6	5	2	10	5
Crude fibre	3	7	8	0	5	7	2	9	6
Ether extract	0	10	8	1	5	6	1	8	8
Ash	4	7	8	0	5	7	1	7	9
NFE	3	6	9	0	6	6	2	9	6
Moisture	3	6	9	2	6	8	3	5	9

A = Significant positive correlation ($P<0{,}01$); B = Non-significant positive correlations; C = Negative or no correlations

Combretum species there are no significant differences between the species for any of these variables over a full year (Figure 1). However, both these plant groups are preferred species although the *Acacia* species are more sought after. Unfortunately no data are available on the chemical composition of plant species available, but not utilized, by giraffes, to compare with these two groups of plants.

From January to August the utilization of preferred *Acacia* species by giraffes shows a positive correlation with both the protein content (r = 0,87) and the succulence (r = 0,32) of the leaves (Figure 1). But as the utilization of the *Acacia* species increases from February to August the utilization of the *Combretum* species decreases (Figure 1).

The reason why utilization of both plant groups decreases drastically during the latter half of the dry season is because these trees are all deciduous and thus shed their leaves (Figure 1). The *Acacia* species loose their leaves gradually replacing the lost leaves simultaneously. Furthermore, different species do not shed their leaves during the same time just as they do not flower and produce fruit simultaneously. This is important for the survival of browsing animals since it reduces feeding stress. The decline in utilization from August to November (Figure 1) does not provide an indication of availability, thus the low percentage utilization is simply because very few leaves, flowers and fruit were available to feed on (Figure 1).

Utilization of the *Combretum* species increases gradually from May to September while the succulence of the leaves declines markedly. Concomitantly utilization of the *Acacia* species decreases (Figure 1). The leaf protein content of the *Combretum* species remains more or less constant during this period but the protein content decreases in the leaves of the *Acacia* species. Taking availability into account, the utilization of these preferred food plants by giraffes correlates positively with the protein content of the leaves throughout the year, while during the wet warm season the succulence of the leaves may be important (Table 5, Figure 1) although there is no significant correlation between utilization and succulence in specific *Acacia* species.

Table 5 Comparison of mean values of four dry-matter fractions, moisture and NFE (wet sample fractions) of all *Acacia* and *Combretum* species studied. (All values are given as percentages)

Plant species	H_2O	Protein	Fat	Crude fibre	Ash	NFE
Acacia species						
Timbavati Nature Reserve						
Acacia exuvalis	62,04	15,33	2,40	16,20	0,43	24,70
A. gerrardii	54,79	14,98	0,71	21,12	0,61	26,55
A. nigrescens	63,05	13,03	4,21	20,04	0,49	22,25
A. senegal	60,99	28,58	3,76	16,23	0,39	19,77
Jack Scott Nature Reserve						
A. ataxacantha	53,51	17,37	4,05	17,06	0,46	26,45
A. caffra	57,07	16,37	4,94	19,23	0,57	25,50
A. karoo	60,46	17,31	2,94	15,94	0,42	25,17
Koos Meintjies Nature Reserve						
A. caffra	62,85	17,59	3,74	14,61	0,18	23,68
A. erubescens	59,20	19,37	4,08	18,53	0,45	23,57
A. karoo	52,19	11,58	2,50	14,50	0,44	34,64
A. nilotica	52,04	12,90	5,06	13,67	1,06	32,21
A. robusta	55,59	14,25	2,95	24,83	0,36	26,05
A. tortilis	46,10	16,49	3,61	19,83	0,82	32,66
Combretum species						
Timbavati Nature Reserve						
Combretum apiculatum	52,92	11,05	2,59	22,10	0,96	29,59
C. hereroense	56,85	10,73	3,28	21,67	1,12	27,06
C. imberbe	65,21	12,53	3,72	27,56	0,92	18,93
C. zeyheri	55,46	14,28	3,53	21,02	0,52	26,74
Jack Scott Nature Reserve						
C. erythrophyllum	59,07	13,31	5,84	20,56	1,37	23,97
C. molle	51,34	10,84	5,40	23,02	1,01	28,92
Koos Meintjies Nature Reserve						
C. apiculatum	43,39	11,31	2,98	22,47	0,59	35,84
C. hereroense	49,94	11,45	3,17	20,82	0,80	33,04
C. imberbe	49,54	12,29	2,87	21,14	0,81	33,25

When the mean protein content of *Acacia* species is compared with that of the other 31 plant species studied, it is apparent that the protein content is higher in *Acacia* spp. with the following exceptions; *Terminalia prunioides, Fargara capensis, Ziziphus mucronata* and *Dichrostachys cinerea*. *D. cinerea* is also a member of the Leguminosae that could possibly make use of the *Rhizobium* bacteria in the root nodes to bind free nitrogen from the atmosphere and thus make it available for protein synthesis in the plant.

General tendencies

In most plants studied the moisture decreases from

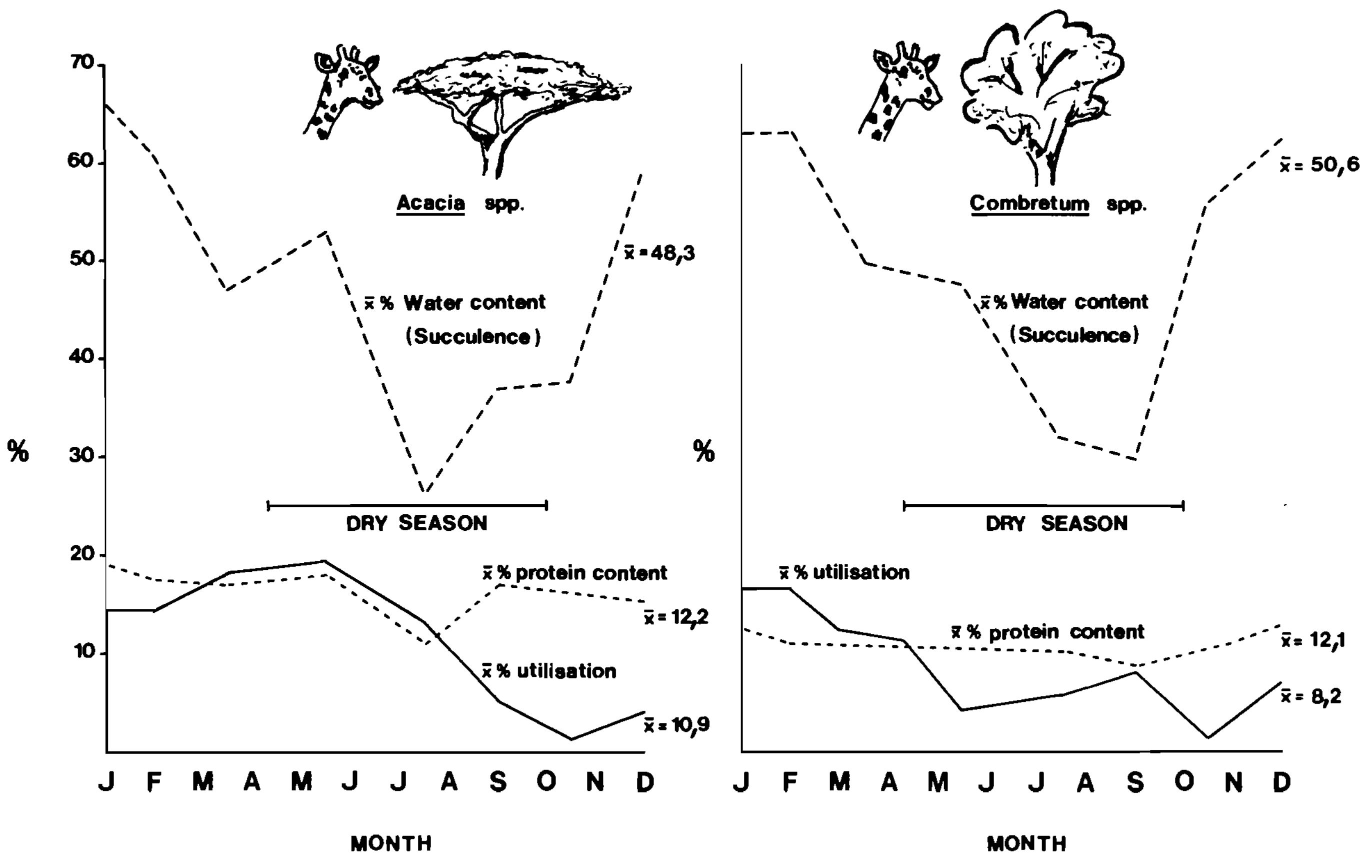

Figure 1 A composite diagram of the average percentage utilization of the five preferred *Acacia* species (*senegal, caffra, erubescens, karoo* and *tortilis* in order of preference) browsed by giraffes in relation to the mean protein content and succulence of leaves compared to the five preferred *Combretum* species (*erythrophyllum, apiculatum, imberbe, zeyheri* and *molle*) on the same basis. Preferred food plant species were selected by taking availability (based on botanical surveys) and food selection data into account.

December until approximately August/September and then increases again. With the decrease in moisture content there is usually an increase in the crude fibre and nitrogen-free extract content of the leaves. Further general phenomena are the significant negative correlations between the NFE values and the relatively large moisture fractions and significant positive correlations between the moisture fractions and the crude protein content. The same tendencies for change in the crude fibre and crude protein have been mentioned elsewhere (Bonsma 1942; Joubert & Eloff 1971).

The ash fractions of the different plant species vary to a large degree in the eight samples of one fraction of a specific plant species and in most cases no tendencies for change could be recognized. In the cases that do show changes there is an increase in the ash content from January until approximately August/September (*Acacia karoo, Dichrostachys cinerea* and *Peltophorum africanum*). This tendency has also been found in *Acacia nigrescens* and *Combretum molle* (Sauer 1977). More reliable results could possibly have been obtained by washing the leaves with water so as to eliminate dust pollution but this procedure would have resulted in an unreliable moisture content.

There are no general trends in ether extract fractions, not even in the same genus, for example the different *Acacia* species show no resemblance. Thus the ether extract fractions show only a relationship within a specific plant species and may be influenced by many ecological factors within the specific environment.

Where the chemical composition of a specific plant species from different localities is compared, the trends in corresponding fractions are more or less the same. The values of fractions sampled during the same month do sometimes differ drastically. It could be concluded that it is wrong to generalize, for the chemical composition of a specific plant species varies from one area or environment to the next.

It was also found that there is a significant difference ($P < 5,0$) in the moisture content of tree leaves of the same plant species when sampled during the night compared to the day (Table 6). Thus it is true that if a browser feeds during the night it will take in more moisture with the food it eats. This may be critical for herbivores during drought periods in general and for desert herbivores in particular if applicable to such areas.

Influence of the moisture fractions

In a study of this nature where utilization of a plant species is compared with the quantitative amount of foodstuffs in the leaves, it is important to take the moisture content into account with the fractions that have been determined on a dried mass basis to ascertain the wet fractions of the leaves as they are found and selected by the herbivores in nature. In several cases it was found that when the percentage moisture was relatively high, fractions present in low concentrations were influenced to such a degree that the opposite trends in e.g. the protein content in the dry and wet fraction of the same plant species were found. This was the case in *Burkea africana, Combretum molle, Cussonia paniculata, Protea caffra* and *Acacia erubescens* (Sauer 1977).

Table 6 Difference between the day and night moisture content of *Bolusanthus speciosus* and *Acacia nigrescens* leaves in Timbavati Private Nature Reserve during 1976

	Moisture content %		
Month	Time of sampling 12h00 to 14h00	Time of sampling 24h00 to 02h00	Difference
Bolusanthus speciosus			
January	72,1	79,8	7,7
February	60,2	72,5	12,3
March	31,8	45,6	13,8
September	73,6	78,4	4,8
November	65,0	78,9	13,9
December	63,9	75,7	11,8
$\bar{x}$	61,1	71,8	10,7
Acacia nigrescens			
January	63,8	71,4	7,6
February	65,0	76,8	11,8
March	58,8	76,0	8,2
June	56,8	62,4	5,6
August	66,1	70,9	4,8
September	64,9	75,3	10,4
November	62,0	71,5	9,5
December	61,3	67,1	5,8
$\bar{x}$	62,3	71,4	9,1

Suggested future experimentation

The food samples should be analysed further by fermentation with giraffe rumen liquid to ascertain which plant species is the better source of food by determining which sample ferments fastest and easiest. Hydrogen gas production could be used as criterion. One could also establish which plant species produces the best ultimate spectrum of volatile fatty acids (fermentation end products). From this one could ascertain the energy output in ATP, since the energy source is of importance in the intermediate metabolism in the giraffe.

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