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Nutrient Composition of Natural Diet Items and Faeces in Free-Ranging Southern Giraffes (*Giraffa camelopardalis giraffa*): A Pilot Study

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ABSTRACT

Food preference and selection of free-ranging giraffes have been well recorded, but limited data concerning the chemical composition of their diet and faeces are currently available. This pilot study added information on natural diet, nutritional quality and a description of faecal chemical composition of free-ranging giraffe in the Free State Province, South Africa. Measured crude protein levels in leaves were lower compared to previous reports. The leaf calcium (Ca) content was higher than the phosphorus (P) content in all samples, supporting concepts that giraffe may be P but not Ca limited. In the faecal samples of the present study, nitrogen and P concentrations were above the thresholds considered indicative of nutritional deficiency.

1 | Introduction

Two principal methods for assessing dietary ecology of megaherbivores are direct observations of feeding activity and faecal nutrient analysis (Parker and Bernard 2006; van Lieverloo et al. 2009). The latter is considered a practical, non-invasive method to measure nutritional status and has been widely applied to large herbivores, such as springbok, zebra, giraffe, and kudu (Abraham et al. 2023; Grant et al. 2000; Van der Waal et al. 2003; Wrench et al. 1997). Faecal nitrogen and phosphorus concentrations below the thresholds suggested by Van der Waal et al. (2003; 1.5% N of dry matter (DM) for mixed feeders and browsers) and Wrench et al. (1997; 0.2% P of DM) indicate a deficient diet. Several factors can influence the chemical composition of plants, such as mineral status of the soil, stage of growth, climate (sunlight, rainfall), and seasonality (Grant et al. 2000; Stapelberg et al. 2008; Tolsma et al. 1987; Underwood and Suttle 1999).

Giraffes (*Giraffa camelopardalis*) are classified as browsing, moderately selective ruminants (Hofmann 1989; Van Soest 1988) that primarily consume leaves and shoots from trees and/or shrubs (Pellew 1984a, 1984b). *Vachellia* and *Senegalia* species (previously known as *Acacia*) have been reported as the mainstay of the giraffe diet in previous studies (e.g., Ciofolo and LePendu 2002; Mahenya et al. 2016; Parker and Bernard 2005). However, giraffe diets can consist of 14 to over 90 plant species and vary greatly depending on range and season (Berry and Bercovitch 2016; Deacon et al. 2023; Gordon et al. 2016; Levi et al. 2022; Pellew 1984b). Giraffes have been observed chewing both other giraffe bones and those of other species, a behaviour known as osteophagia (Deacon et al. 2023; Hart and Hart 2023;

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Langman 1978; Wyatt 1971). A deficiency of phosphorus is the most likely cause of this behaviour (Bredin et al. 2008; Mitchell et al. 2005).

Limited data concerning the chemical composition of giraffe diets is available (Dagg 1960; Dougall et al. 1964; Field and Ross 1976; Hall-Martin and Basson 1975; Pellew 1984a; Sauer et al. 1982). The nutritional composition of some preferred plant species eaten by free-ranging giraffe from literature sources is summarised in Table S1. Kearney (2005) stated that more information on mineral concentrations in giraffe natural diets is required since the analyses of plants have focused on major nutrients that provide protein or energy. This pilot study aimed (1) to provide insights on the nutritional quality of browse eaten by free-ranging southern giraffes in two nature reserves in the Free State Province, South Africa, and (2) to describe their faecal chemical composition.

2 | Methods

2.1 | Ethics Statement

This study was approved by the Animal Research Ethics Committee at the University of the Free State (UFS-AED2023/0064) and National Department under the Section 20 permit (Ref. Number 12/11/1/4 (6087SdIR)).

2.2 | Study Sites

This study was conducted in Amanzi Private Game Reserve (APGR) and Sandveld Nature Reserve (SNR), both located in the Free State Province in South Africa. APGR is located in the Grassland Biome (Rutherford and Westfall 1994), with vegetation on the hills more representative of Winburg Grassy Shrubland (Mucina and Rutherford 2006). Butler (2017) reported that dominant vegetation includes woody trees like *Searsia ciliata, V. karroo*, and *Tarchonanthus camphoratus*. Different soil forms are characteristic of this reserve, such as gravel-rich Glenrosa and dry, clayey, duplex soils (Mucina and Rutherford 2006). The mean annual rainfall is 500 mm (Mucina and Rutherford 2006), with the highest rainfall from November to March, and temperatures varied from a maximum of 38.7°C in summer to a minimum of −9.2°C in winter (Butler 2017).

SNR is located on the Free State side of the Bloemhof Dam (Van der Merwe 2001), within the Kimberly Thorn Bushveld (Low and Rebelo 1996) or the eastern form of Kalahari Thornveld (Acocks 1988). This reserve features open savanna dominated by *Vachellia erioloba*, with scattered *Boscia albitrunca* and *V. karroo*, and grasses like *Themeda triandra* and *Cymbopogon plurinodis* found on predominantly sandy soils to loamy sand with a subsurface calcrete layer (Acocks 1988; Low and Rebelo 1996). The Vaal River and Vet River form the northwestern and southern boundaries of SNR, respectively (Avenant and Watson 2002). The mean annual rainfall ranges from 450 to 500 mm, with maximum monthly rainfall in January (Low and Rebelo 1996), and the mean temperature varies from 0°C in July to 33°C in January (Weather Bureau Department of Environment Affairs 1986). In this study, SNR was separated into two sections: Site A (southern side) and Site B (northern side) because giraffes do not have access to the southern side during some periods of the year.

2.3 | Sample Collection

During April to June 2024, samples from 17 browsing plants selected by free-ranging giraffes based on direct visual foraging observations were collected for laboratory analysis in both reserves: Study site 1 (APGR; 4 species) and Study site 2 (SNR; Site A: 5 species, Site B: 8 species). Mature leaves from multiple trees/shrubs per species were collected from the same plants and at the same height as giraffes had previously selected, and samples were pooled and stored in labelled paper bags until analysis. From January to July 2024, 25 fresh faecal samples were opportunistically collected from 11 individuals (5 females and 6 males) in APGR and from 14 individuals (5 females and 9 males) in SNR by rectal sampling during giraffe management procedures, avoiding the danger of contamination from soil. Faeces were stored in labelled plastic bags and kept in the freezer at −20°C until laboratory analysis. Browse and faecal samples were dried at 70°C and milled with a KN 295 Knifetec with a 1-mm screen size for subsequent chemical analysis.

Only a limited number of browse and faecal samples could be collected over a short period of time and analysed for chemical composition due to budgetary limitations. Furthermore, it was not achievable to evaluate changes in forage nutritional composition with regard to seasons, plant growth stages, soil types, and environmental conditions.

2.4 | Laboratory Analysis

All feed and faecal samples were analysed for dry matter (DM) chemical content (%) by the UFS Department of Animal Science Nutrition Laboratory. The nitrogen content was determined by Dumas Combustion Method (Hauck 1982; Kirsten 1983; N_f = faecal N) and multiplied by a factor of 6.25 to obtain crude protein (CP) in browse samples. Neutral detergent fibre (NDF) and acid detergent fibre (ADF) were determined using methods of Robertson and Van Soest (1981) and Goering and Van Soest (1970), respectively; both were corrected for residual ash. Calcium (Ca) was analysed by Atomic Absorption Flame Spectroscopy (AOAC 1990) and phosphorus (P) by Colorimetry (Cavell 1955). All analytical results are presented as % of DM.

The Mann–Whitney U test was used to compare faecal chemical components between sexes, using SPSS, and results were considered significant at $p \leq 0.05$.

3 | Results

Three *Vachellia* species (*V. erioloba*, *V. karoo*, and *V. tortilis*) were collected in this study, and *V. karroo*, *Searsia lancea*, and *Ziziphus mucronata* were common species in both reserves. Crude protein content of leaves ranged from 7.2% to 9.8% in APGR and from 7.9% to 12.9% in SNR. *S. lancea* (9.8%) and *V. erioloba* (mean: 11.6%) had the numerically highest values in

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TABLE 1 | Chemical composition (% of dry matter) in preferred plant species consumed by free-ranging giraffes in two nature reserves in the Free State Province of South Africa.

		Chemical composition (%)				
Location	**Plant species**	**CP**	**NDF**	**ADF**	**Ca**	**P**
APGR	*Searsia lancea*	9.8	40.3	28.2	1.9	0.2
	Tarchonanthus camphoratus	8.4	52.1	37.8	1.6	0.1
	Vachellia karroo	8.7	44.1	31.2	2.0	0.1
	Ziziphus mucronata	7.2	45.2	36.0	1.8	0.1
	Mean	8.5	45.5	33.3	1.8	0.1
SNR–Site A	*Grewia flava*	10.3	53.1	39.0	1.5	0.1
	Gymnosporia buxifolia	10.2	41.3	30.5	3.1	0.1
	Vachellia erioloba	12.3	49.3	39.1	1.6	0.1
	Vachellia karroo	10.1	38.8	30.1	2.4	0.1
	Ziziphus mucronata	10.0	39.7	30.8	2.6	0.1
	Mean	10.6	44.5	33.9	2.3	0.1
SNR–Site B	*Celtis africana*	11.6	19.0	17.1	4.1	0.1
	Ehretia rigida	11.2	38.4	28.6	1.6	0.1
	Grewia flava	12.9	42.3	30.3	1.7	0.1
	Gymnosporia buxifolia	7.9	43.0	31.3	2.1	0.1
	Searsia lancea	10.3	38.6	27.0	1.7	0.3
	Vachellia erioloba	10.9	49.3	38.4	1.7	0.1
	Vachellia tortilis	11.2	50.8	39.3	3.8	0.1
	Ziziphus mucronata	11.4	37.4	27.1	1.6	0.1
	Mean	10.9	39.8	29.9	2.3	0.1

Note: All values as % of dry matter.
Abbreviations: ADF, acid detergent fibre; APGR, Amanzi Private Game Reserve; Ca, calcium; CP, crude protein; NDF, neutral detergent fibre; P, phosphorus; SNR, Sandveld Nature Reserve.

APGR and SNR, respectively. *Tarchonanthus camphoratus* and *Z. mucronata* had the highest fibre content (both NDF and ADF) in APGR, while *V. erioloba* and *V. tortilis* were highest in SNR (Table 1). Ca content was numerically higher than P in all samples.

Faecal samples did not differ in mean N_f content between females and males in both reserves (Table 2). Higher faecal fibre contents were found in males compared with females in APGR (both NDF and ADF) and SNR (NDF). The concentration of Ca was higher than P in all faecal samples. In APGR, significant differences between sexes were only found in faecal NDF ($p = 0.028$) and Ca ($p = 0.028$) contents.

4 | Discussion

Giraffe browse acceptability is influenced by leaf chemical factors, including protein, minerals, fibre, secondary metabolites (e.g., condensed tannin), and water content (Cooper and Owen-Smith 1985; Sauer et al. 1982). Even though factors like seasonality and plant growth stage were not feasible to include in this study due to budget limitations, this study focused on evaluating the nutritional composition of mature leaves of browsing plants selected by giraffes in both reserves in one season. It is important to mention that giraffes fed on the same plant species in the same sections almost daily in both reserves.

In this study, the range of crude protein of leaves in both reserves was considerably lower compared to previous studies. Caister et al. (2003) reported crude protein in leaves from 10 plant species consumed by West African giraffe in Niger during the dry season varied between 8.2% and 28.6%. Similarly, Sauer et al. (1982) reported a range of 10.7% to 28.6% in 14 tree species eaten by South African giraffes. Owen-Smith (1982) stated that rumen microflora is positively influenced by a high-protein diet, increasing fermentation rates. Hence, plant species with high protein content may be more acceptable to giraffes (Parker 2004). In this study, *V. erioloba* and *S. lancea* had the numerically highest CP contents in SNR and APGR, respectively. The latter is usually avoided by giraffes unless desirable food is scarce (Deacon et al. 2023; Parker 2004; Sauer et al. 1982), whereas *Acacia* species are preferred due to their high water, low fibre, and high protein content (Cooper et al. 1988; Sauer

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TABLE 2 | Statistical analysis and faecal chemical composition (Mean ± Standard deviation% of DM) of free-ranging giraffes in two nature reserves in the Free State Province of South Africa, according to the location and sex.

		Chemical composition (%)				
Location	**Animal**	N_f	**NDF**	**ADF**	**Ca**	**P**
APGR	Female ($N=5$)	3.0 ± 0.4	58.7 ± 4.1	52.8 ± 1.9	4.9 ± 1.2	0.3 ± 0.1
	Male ($N=6$)	3.4 ± 0.5	65.3 ± 3.1	55.0 ± 4.0	3.0 ± 0.7	0.4 ± 0.8
	Female vs. Male	Mann–Whitney $U=10.0$	Mann–Whitney $U=3.0$	Mann–Whitney $U=9.0$	Mann–Whitney $U=3.0$	Mann–Whitney $U=7.5$
		p-value = 0.361	p-value = 0.028	p-value = 0.273	p-value = 0.028	p-value = 0.170
SNR	Female ($N=5$)	2.4 ± 0.1	60.2 ± 4.2	50.2 ± 1.9	4.3 ± 0.8	0.3 ± 0.0
	Male ($N=9$)	2.4 ± 0.2	63.3 ± 5.0	51.8 ± 2.3	3.7 ± 0.7	0.3 ± 0.1
	Female vs. Male	Mann–Whitney $U=11.0$	Mann–Whitney $U=13.0$	Mann–Whitney $U=12.0$	Mann–Whitney $U=10.0$	Mann–Whitney $U=18.0$
		p-value = 0.125	p-value = 0.205	p-value = 0.162	p-value = 0.096	p-value = 0.549
Both reserves	$N=25$	2.8 ± 0.5	62.3 ± 4.7	52.5 ± 3.0	3.9 ± 1.0	0.3 ± 0.1
	Female vs. Male	Mann–Whitney $U=65.0$	Mann–Whitney $U=31.0$	Mann–Whitney $U=55.0$	Mann–Whitney $U=25.0$	Mann–Whitney $U=61.0$
		p-value = 0.579	p-value = 0.015	p-value = 0.267	p-value = 0.006	p-value = 0.435

Note: All mean values as % of dry matter.
Abbreviations: ADF, acid detergent fibre; APGR, Amanzi Private Game Reserve; Ca, calcium; NDF, neutral detergent fibre; N_f, faecal nitrogen; P, phosphorus; SNR, Sandveld Nature Reserve.

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et al. 1982). Three species of *Vachellia* were preferred by giraffes in this study, whose %CP were lower compared to previous reports (Table S1).

The ADF content of *V. tortilis* (39.3%) in this study was higher compared to the study by Pellew (1984a), who reported the mean ADF content of this species consumed by the Masai giraffes in the Serengeti National Park varied from 23.5% ± 3.3% (new leaves) to 24.5% ± 0.7% (old leaves). In Khamab Kalahari Nature Reserve, *V. erioloba* and *Z. mucronata* were the most important species in giraffe diet (Deacon et al. 2023), despite the prussic acid content in pods and young leaves of *V. erioloba* that could pose a poisoning danger to animals (Smit 1999).

According to Dougall et al. (1964) and Pellew (1984a), browse preferred by giraffes contains approximately 1.4% Ca and 0.2% P (in %DM, although bioavailability is unknown). In this study, most browse species had %Ca similar to 1.4%. However, the highest Ca contents were reported on *Celtis africana* (4.1%), which value was slightly higher than what was reported for *Celtis australis* (3.65%) by Sharma and Gill (1969) and on *V. tortilis* (3.8%), which was previously reported with high Ca content by Dougall et al. (1964; 3.1%). Similarly, the %P of browse species in both reserves was similar to 0.2%. The mean Ca:P ratio of the browse samples was higher in SNR (19.2:1) than APGR (14.0:1), but those values were higher than the previous study by Pellew (1984a; 7.7:1). Dougall et al. (1964) found browse eaten by giraffes contained higher % Ca and lower %P (1.9 ± 2.3 vs. 0.2 ± 0.1), compared with diets of eland (1.0 ± 0.4 vs. 0.4 ± 0.2) and other ruminants (1.3 ± 1.0 vs. 0.3 ± 0.1). Nevertheless, Pellew (1984a) did not find a specific selection for browse with high Ca content by giraffes, but statistically, selection for browse with high P content was found in females during the wet season and throughout the year by males.

Janecke and Smit (2011) found seasonal variations in N_f concentrations of giraffes in one reserve in the Free State Province, with higher levels in summer (3.0%–3.5%) and lower levels in autumn (2.4%–3.0%) and winter (1.8%–2.3%). In this study, the N_f concentrations in female and male giraffes in SNR were similar to values reported by Janecke and Smit (2011) in autumn and winter as samples were collected from April to July. Similarly, the mean N_f concentrations in female and male giraffes in SNR were expected to be within the N_f range in autumn and summer since most samples were collected in May and January, respectively. Grant et al. (1995) recorded a N_f concentration of 2.0% ± 0.4% for giraffe in the savannah during the 1992–1993 drought in Kruger National Park (KNP), and a minimum value of 1.5% N_f was later indicated for giraffe feeding in the granitic areas (Grant et al. 2000), which is the threshold suggested by Van der Waal et al. (2003) for a deficient diet. The mean N_f concentrations of giraffe in this study were slightly higher than this threshold. Moreover, the mean N_f content from the whole group (2.8% ± 0.5%; $n = 25$) was similar to the study by Codron et al. (2007) for giraffes in KNP (2.6% ± 0.0%; $n = 118$). According to Robbins et al. (1987) and Van Soest (1994), the relationship between diet quality and %N_f should be interpreted cautiously in browsers due to the precipitating effects of protein of dietary tannins.

Ginnett and Demment (1997) suggested male giraffes can consume lower-quality forage and meet their metabolic and energy demands more quickly than females by increasing feeding rates. Brand (2007) added that males might maximise energy intake by feeding on taller tree species with higher leaf biomass. As expected, males in both reserves had higher faecal fibre contents compared to females. These values were within the range reported by Codron et al. (2007), with NDF ranging from 51.8% (dry season) to 70.8% (wet season) and ADF from 39.1% to 56.6%. Significant differences between sexes were only found in faecal NDF content in APGR.

Mitchell et al. (2005) reported calcium and phosphate concentrations in giraffe bones of 19.6 ± 1.0 g 100 g^{-1} bone (20%) and 9.5 ± 0.2 g 100 g^{-1} bone (9.5%), respectively (i.e., Ca:P ratio of 2:1). From birth to age 5, giraffe need about 20 g of Ca and 10 g of P daily for skeletal growth (Mitchell and Skinner 2003; Mitchell et al. 2005). Thereafter, their daily requirements decrease but increase in females by specific stresses like lactation (Mitchell et al. 2005). In this study, the P concentration in faeces was slightly higher than the threshold suggested by Wrench et al. (1997) for a deficient diet. According to Horst (1986) and Bravo et al. (2003), since saliva supplies up to 80% of endogenous faecal phosphorus, increased feeding time of males may cause more phosphorus to be excreted in faeces rather than urine. However, P content in giraffe faeces did not differ by sex in this study.

5 | Conclusion

Our pilot study adds data on the nutrient composition of free-ranging Southern giraffe diet in the Free State Province, South Africa. The data suggest that browse selected by giraffes in both reserves is not necessarily high in protein but can contain protein at concentrations sometimes observed in grasses consumed by grazing ruminants. Further research on seasonal changes in leaf chemical composition in terms of food selection would be encouraged to evaluate diet variations over seasons. Furthermore, preliminary data on faecal chemical composition of free-ranging Southern giraffes is provided. In this study, faecal indicators do not indicate nutritional deficiency in giraffes in both reserves at that time of the year. Faecal indicators can be valuable, non-invasive tools for monitoring habitat quality and ecological carrying capacity, not only for giraffes but for other sympatric herbivores that share similar dietary resources.

Author Contributions

R.P., G.O. and F.D. were involved in project conceptualisation and samples collection. R.P. analysed data and wrote the manuscript. G.O., M.C. and F.D. supervised and contributed to the manuscript writing. All authors reviewed and edited the manuscript prior to submission.

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Conflicts of Interest

The authors declare no conflicts of interest.

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Data Availability Statement

The data used to support the findings of this study are available from the corresponding author upon request.

References

Abraham, A. J., E. Duvall, E. le Roux, et al. 2023. "Anthropogenic Supply of Nutrients in a Wildlife Reserve May Compromise Conservation Success." *Biological Conservation* 284: 110149. https://doi.org/10.1016/j.biocon.2023.110149.

Acocks, J. P. H. 1988. "Veld Types of South Africa." Memoirs of the Botanical Survey of South Africa, 37, pp l–146.

AOAC. 1990. *Official Methods of Analysis*. 15th ed. Association of Official Analytical Chemists, Inc.

Avenant, N. L., and J. P. Watson. 2002. "Mammals Recorded in Sandveld Nature Reserve, Free State Province, South Africa." *Navorsinge Van Die Nasionale Museum, Bloemfontein* 18: 1–12.

Berry, P. S., and F. B. Bercovitch. 2016. "Seasonal and Geographical Influences on the Feeding Ecology of Giraffes in the Luangwa Valley, Zambia: 1973-2014." *African Journal of Ecology* 55: 80–90. https://doi.org/10.1111/aje.12324.

Brand, R. 2007. "Evolutionary Ecology of Giraffes (*Giraffa camelopardalis*) in Etosha National Park, Namibia." PhD thesis, Newcastle University, Newcastle Upon Tyne.

Bravo, D., D. Sauvant, C. Bogaert, and F. Meschy. 2003. "III. Quantitative Aspects of Phosphorus Excretion in Ruminants." *Reproduction Nutrition Development* 43, no. 3: 285–300.

Bredin, I. P., J. D. Skinner, and G. Mitchell. 2008. "Can Osteophagia Provide Giraffes With Phosphorus and Calcium?" *Onderstepoort Journal of Veterinary Research* 75, no. 1: 1–9. https://doi.org/10.4102/ojvr.v75i1.82.

Butler, V. P. 2017. "Feeding Ecology of the Greater Kudu (*Tragelaphus strepsiceros*) in the Central Free State." MSc thesis, University of the Free State, Bloemfontein.

Caister, L. E., W. M. Shields, and A. Gosser. 2003. "Female Tannin Avoidance: A Possible Explanation for Habitat and Dietary Segregation of Giraffes (*Giraffa camelopardalis peralta*) in Niger." *African Journal of Ecology* 41: 201–210. https://doi.org/10.1046/j.1365-2028.2003.00422.x.

Cavell, A. J. 1955. "The Colorimetric Determination of Phosphorus in Plant Materials." *Journal of Science and Food Agriculture* 6: 479–480.

Ciofolo, I., and Y. LePendu. 2002. "The Feeding Behaviour of Giraffe in Niger." *Mammalia* 66, no. 2: 183–194.

Codron, D., J. A. Lee-Thorp, M. Sponheimer, J. Codron, D. De Ruitter, and J. S. Brink. 2007. "Significance of Diet Type and Diet Quality for Ecological Diversity of African Ungulates." *Journal of Animal Ecology* 76: 526–537. https://doi.org/10.1111/j.1365-2656.2007.01222.x.

Cooper, S. M., and N. Owen-Smith. 1985. "Condensed Tannins Deter Feeding by Browsing Ruminants in a South African Savanna." *Oecologia* 67: 142–146. https://doi.org/10.1007/BF00378466.

Cooper, S. M., N. Owen-Smith, and J. P. Bryant. 1988. "Foliage Acceptability to Browsing Ruminants in Relation to Seasonal Changes in the Leaf Chemistry of Woody Plants in a South African Savanna." *Oecologia* 75: 336–342. https://doi.org/10.1007/BF00376934.

Dagg, A. I. 1960. "Food Preferences of the Giraffe." *Proceedings of the Zoological Society of London* 135: 640–642.

Deacon, F., G. N. Smit, and A. Grobbelaar. 2023. "Resources and Habitat Requirements for Giraffes' (*Giraffa camelopardalis*) Diet in the Northwestern Kalahari, South Africa." *Animals* 13, no. 13: 2188. https://doi.org/10.3390/ani13132188.

Dougall, H. W., V. M. Drysdale, and P. E. Glover. 1964. "The Chemical Composition of Kenya Browse and Pasture Herbage." *East African Wildlife Journal* 2: 86–121.

Field, C. R., and I. C. Ross. 1976. "The Savanna Ecology of Kidepo Valley National Forest." *East African Wildlife Journal* 14: 1–15.

Ginnett, T., and M. W. Demment. 1997. "Sex Differences in Giraffe Behavior at Two Spatial Scales." *Oecologia* 110: 291–300.

Goering, H. K., and P. J. Van Soest. 1970. "Forage Fiber Analysis (Apparatus, Reagents, Procedures and Some Applications)." Agricultural Research Service, United States Department of Agriculture. Agriculture Handbook 379. Government Printing Office, Washington, D.C.

Gordon, C. N., L. Eichenberger, P. Vorster, A. J. Leslie, and S. Jacobs. 2016. "Diet and Seasonal Dispersal of Extralimital Giraffe at Sanbona Wildlife Reserve, Little Karoo, South Africa." *Koedoe* 58, no. 1: 1–6. https://doi.org/10.4102/koedoe.v58i1.1346.

Grant, C. C., H. H. Meissner, and W. A. Schultheiss. 1995. "The Nutritive Value of Veld as Indicated by Faecal Phosphorous and Nitrogen and Its Relation to the Condition and Movement of Prominent Ruminants During the 1992-1993 Drought in the Kruger National Park." *Koedoe* 38, no. 1: 17–31. https://doi.org/10.4102/koedoe.v38i1.302.

Grant, C. C., M. J. S. Peel, N. Zambatis, and J. B. J. van Ryssen. 2000. "Nitrogen and Phosphorus Concentration in Faeces: An Indicator of Range Quality as a Practical Adjunct to Existing Range Evaluation Methods." *African Journal of Range & Forage Science* 17: 81–92. https://doi.org/10.2989/10220110009485743.

Hall-Martin, A. J., and W. D. Basson. 1975. "Seasonal Chemical Composition of the Diet of Transvaal Lowveld Giraffe." *Journal of the South African Wildlife Management Association* 5, no. 1: 19–21.

Hart, L. A., and B. L. Hart. 2023. "Flehmen, Osteophagia, and Other Behaviors of Giraffes (*Giraffa giraffa angolensis*): Vomeronasal Organ Adaptation." *Animals* 13, no. 3: 354. https://doi.org/10.3390/ani13030354.

Hauck, R. D. 1982. "Nitrogen-Isotope Ratio Analysis, Sec. 36-3.2.2, Conversion of Total Nitrogen to Ammonium-Nitrogen." In *Methods of Soil Analysis, Part 2, Chemical and Microbiological Properties*, edited by American Society of Agronomy, Crop Science Society of America, and Soil Science Society of America, 744. The American Society of Agronomy.

Hofmann, R. R. 1989. "Evolutionary Steps of Ecophysiological Adaptation and Diversification of Ruminants: A Comparative View of Their Digestive System." *Oecologia* 78: 443–457. https://doi.org/10.1007/BF00378733.

Horst, R. L. 1986. "Regulation of Calcium and Phosphorus Homeostasis in the Dairy Cow." *Journal of Dairy Science* 69, no. 2: 604–616.

Janecke, B. B., and G. N. Smit. 2011. "Phenology of Woody Plants in Riverine Thicket and Its Impact on Browse Availability to Game Species." *African Journal of Range & Forage Science* 28: 139–148. https://doi.org/10.2989/10220119.2011.642075.

Kearney, C. C. 2005. "Review of Free-Ranging Giraffe Diets." In *The Giraffe Nutrition Workshop Proceedings*, edited by D. A. Schmidt and R. Barbiers, 2–5. Lincoln Park Zoo.

Kirsten, W. 1983. *Organic Elemental Analysis: Ultramicro, Micro and Trace Methods*. Academic Prees/Hardcourt Brace Jovanovich.

Langman, V. A. 1978. "Giraffe Pica Behavior and Pathology as Indicators of Nutritional Stress." *Journal of Wildlife Management* 42, no. 1: 141–147. https://doi.org/10.2307/3800701.

Levi, M., D. E. Lee, M. L. Bond, and A. Treydte. 2022. "Forage Selection by Masai Giraffes (*Giraffa camelopardalis tippelskirchi*) at Multiple Spatial Scales." *Journal of Mammalogy* 103, no. 3: 737–744. https://doi.org/10.1093/jmammal/gyac007.

13652028, 2025, 6, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/aje.70095, Wiley Online Library on [26/06/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Low, A. B., and A. G. Rebelo. 1996. *Vegetation of South Africa, Lesotho and Swaziland: A Vegetation Map of South Africa, Lesotho and Swaziland*, 85. Department of Environmental Affairs and Tourism.

Mahenya, O., J. K. Ndjamba, K. M. Mathisen, and C. Skarpe. 2016. "Giraffe Browsing in Response to Plant Traits." *Acta Oecologica* 75: 54–62. https://doi.org/10.1016/j.actao.2016.07.001.

Mitchell, G., and J. D. Skinner. 2003. "On the Origin, Evolution and Phylogeny of Giraffe *Giraffa camelopardalis*." *Transactions of the Royal Society of South Africa* 58: 51–73. https://doi.org/10.1080/00359190309519935.

Mitchell, G., O. L. van Schalkwyk, and J. D. Skinner. 2005. "The Calcium and Phosphorus Content of Giraffe and Buffalo Skeletons." *Journal of Zoology (London)* 267: 55–61. https://doi.org/10.1017/S0952836905007247.

Mucina, L., and M. C. Rutherford. 2006. *The Vegetation of South Africa, Lesotho and Swaziland*. South African National Biodiversity Institute (SANBI).

Owen-Smith, N. 1982. "Factors Influencing the Consumption of Plant Products by Large Herbivores." In *The Ecology of Tropical Savannas*, edited by B. J. Huntley and B. H. Walker, 359–404. Springer.

Parker, D. M. 2004. "The Feeding Biology and Potential Impact of Introduced Giraffe (*Giraffa camelopardalis*) in the Eastern Cape Province, South Africa." MSc thesis, Rhodes University, South Africa.

Parker, D. M., and R. T. F. Bernard. 2005. "The Diet and Ecological Role of Giraffe (*Giraffa camelopardalis*) Introduced to the Eastern Cape Province, South Africa." *Journal of Zoology* 267: 203–210. https://doi.org/10.1017/S0952836905007399.

Parker, D. M., and R. T. F. Bernard. 2006. "A Comparison of Two Diet Analysis Techniques for a Browsing Megaherbivore." *Journal of Wildlife Management* 70, no. 5: 1477–1480.

Pellew, R. A. 1984a. "The Feeding Ecology of a Selective Browser, the Giraffe (*Giraffa camelopardalis tippelskirchi*)." *Journal of Zoology (London)* 202: 57–81.

Pellew, R. A. 1984b. "Food Consumption and Energy Budgets of the Giraffe." *Journal of Applied Ecology* 21, no. 1: 141–159.

Robbins, C. T., T. A. Hanley, A. E. Hagerman, et al. 1987. "Role of Tannins in Defending Plants Against Ruminants: Reduction in Protein Availability." *Ecology* 68: 98–107. https://doi.org/10.2307/1939852.

Robertson, J. B., and P. J. Van Soest. 1981. "The Detergent System of Analysis and Its Application to Human Foods." In *The Analysis of Dietary Fiber in Food*, edited by W. P. T. James and O. Theander, 123–158. Marcel Dekker Inc.

Rutherford, M. C., and R. H. Westfall. 1994. "Biomes of Southern Africa–An Objective Categorization." Memoirs of the Botanical Survey of South Africa No. 63, 1–94.

Sauer, J. J. C., J. D. Skinner, and A. W. H. Neitz. 1982. "Seasonal Utilization of Leaves by Giraffes, and the Relationship of the Seasonal Utilization to the Chemical Composition of the Leaves." *South African Journal of Zoology* 17: 210–219.

Sharma, D. D., and R. S. Gill. 1969. "Chemical Composition and Nutritive Value of the Leaves of Khirk Tree (*Celtis australis* Linn.)." *Journal of Research, Punjab Agricultural University* 6, no. 4: 942–947.

Smit, N. 1999. *Guide to the Acacias of South Africa*. Briza Publications.

Stapelberg, F. H., M. W. van Rooyen, and J. du P Bothma. 2008. "Seasonal Nutrient Fluctuation in Selected Plant Species in the Kalahari." *African Journal of Range & Forage Science* 25, no. 3: 111–119. https://doi.org/10.2989/AJRF.2008.25.3.3.600.

Tolsma, D. J., W. H. O. Ernst, R. A. Verweij, and R. Vooijs. 1987. "Seasonal Variation of Nutrient Concentrations in a Semi-Arid Savanna Ecosystem in Botswana." *Journal of Ecology* 75, no. 3: 755–770. https://doi.org/10.2307/2260204.

Underwood, E. J., and N. F. Suttle. 1999. *The Mineral Nutrition of Livestock*. CABI.

Van der Merwe, K. 2001. "An Investigation Into the Possible Causes of Decline in the *Acacia erioloba* Population of the Kathu Area." MSc thesis, University of the Free State, Bloemfontein.

Van der Waal, C., G. N. Smit, and C. C. Grant. 2003. "Faecal Nitrogen as an Indicator of the Nutritional Status of Kudu in a Semi-Arid Savanna." *South African Journal of Wildlife Research* 33, no. 1: 33–41.

van Lieverloo, R. J., B. F. Schuiling, W. de Boer, et al. 2009. "A Comparison of Faecal Analysis With Backtracking to Determine the Diet Composition and Species Preferences of the Black Rhinoceros (*Diceros bicornis minor*)." *European Journal of Wildlife Research* 55: 505–515.

Van Soest, P. J. 1988. "A Comparison of Grazing and Browsing Ruminants in the Use of Feed Resources." In *Increasing Small Ruminant Productivity in Semi-Arid Areas*, edited by E. F. Thomson and F. S. Thomson, 67–69. Kluwer Academic Publishers.

Van Soest, P. J. 1994. *Nutritional Ecology of the Ruminant*. 2nd ed. Cornell University Press.

Weather Bureau Department of Environment Affairs. 1986. *Climate of South Africa: Climate Statistics up to 1984*. Government Printer.

Wrench, J., H. Meissner, and C. Grant. 1997. "Assessing Diet Quality of African Ungulates From Faecal Analyses: The Effect of Forage Quality, Intake and Herbivore Species." *Koedoe* 40: 125–136.

Wyatt, J. R. 1971. "Osteophagia in Masai Giraffe." *African Journal of Ecology* 9: 157.

Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Table S1:** Mean values of chemical composition (% of dry matter) of preferred plant species eaten by free-ranging giraffe from literature sources.

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