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Faecal Analysis as an Indicator of the Dietary Quality Utilised by Free-Roaming Giraffe (*Giraffa camelopardalis*) in the Free State Province, South Africa

Andri Grobbelaar[1] | Gerbrecht Christina Josling[1] | Gernot Osthoff[2] | Francois Deacon[1]

[1]Department of Animal Sciences, Faculty of Natural and Agricultural Sciences, University of the Free State, Bloemfontein, Australia | [2]Department of Microbiology and Biochemistry, Faculty of Natural and Agricultural Sciences, University of the Free State, Bloemfontein, Australia

Correspondence: Francois Deacon (deaconf@ufs.ac.za)

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ABSTRACT

Accurate monitoring of wildlife diets and nutrient requirements is needed for effective biodiversity conservation. This also rings true for the world's tallest ruminant, the giraffe (*Giraffa camelopardalis*). The complexity of its anatomy is also reflected in its intricate ruminant, digestive properties. Being selective browsers, giraffes have evolved unique ways to effectively maximise the absorption of dietary nutrients and thereby maintain their critical energy balance. Using non-invasive faecal collections, the current study analysed 10 chemical parameters (dry matter, organic matter, ash, crude protein [CP_f], crude fat, gross energy, neutral-detergent fibre, acid-detergent fibre [ADF_{fOM}], acid-detergent lignin [ADL_{fOM}], and phosphorous) by chemical analyses, commonly used in domestic livestock health and nutrition monitoring. Fresh giraffe faecal samples were collected from six different locations, with different feeding practices, across different seasons from 2021 to 2023 in the Free State Province, South Africa. Results indicate that % CP_f, % ADF_{fOM}, and % ADL_{fOM} may successfully and significantly differentiate between different feeding practices and between seasons from faeces collected from giraffe populations in the Free State Province and could be used conjunctive with each other to determine diet quality and nutrient value.

1 | Introduction

The drastic decline in biodiversity during the last century calls for improved monitoring approaches in wildlife conservation (Bercovitch 2020; Pannoni et al. 2022). The need for more accurate but more economical ways to monitor animal population health has become crucial for species conservation on a large scale (Orellana et al. 2020). The use of faecal indices by means of chemical analysis can provide insight on the nutritional status of animals across different trophic levels (Čupić et al. 2021; Orellana et al. 2020; Verheyden et al. 2011). Combined with the assessment of habitat and environmental matrices, this approach can be used as an effective diagnostic tool for the assessment of animal welfare, diet, demography, behaviour and the management of protected areas globally (Webster et al. 2021a). Additional advantages of using faecal samples are that it offers a faster and less invasive method when compared to more traditional and stressful methods, such as oesophageal fistulisation, blood collection, and clinical examination during restraint (Leslie et al. 2008; Leslie and Starkey 1985). It also allows animals to be studied under natural conditions (Janecke and Smit 2011), with more regular opportunities for updates on animal and ecosystem interactions and health status (Orellana et al. 2020; Webster et al. 2021a, 2021b). Wildlife in southern Africa is increasingly being confined to fenced areas, such as smaller nature reserves and game farms. The monitoring of

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dietary quality and nutritional status are very important, since boundary fences limit their access to natural food sources. Confined spaces bring additional complications and over exposure to less favourable tree species and higher levels of less nutritive and digestible dietary components, such as tannins, fibres, and lignin. The translocation of extralimital giraffes (*Giraffa camelopardalis*) into protected areas and private land in the Free State Province has happened regardless of taking into account the natural habitat and tree species preferences of giraffes (Deacon and Tutchings 2018; Paulse 2018; Terblanche and Kok 1995). A practical measure to assess periods of potential stress of game species, before a decline in body condition occurs, would have numerous benefits for the effective management and translocations of game species, especially tree-dependent browsers and vulnerable species such as giraffes and kudus (*Tragelaphus strepsiceros*) (Clavadetscher et al. 2021; Dörgeloh et al. 1998; Mbatha and Ward 2006; Muller 2016; Stapelberg et al. 2008).

Similar to other ruminants, the digestive tract of the giraffe consists of the forestomaches (a rumen, reticulum, and omasum) in addition to the abomasum and intestines (Mitchell et al. 2015; Owen 1839; Sauer et al. 2017). The unique combination of digestive processes within giraffes, however, results in a very efficient use of the nutrients and a high, estimated digestibility of ~85% (Mitchell 2021). The daily rate of food consumption is similar to that of other ruminants—1.6% and 2.1% of the live weights of adult male and female giraffes, respectively (Pellew 1984a). In captivity, it has been estimated that adult bulls consume some 19 kg dry weight or 66 kg fresh weight browse daily, cows 16 kg dry weight, and 58 kg fresh weight (Jolly 2003). Different from grazers, the forestomaches of this browser species are smaller and the large intestines are longer. The smaller forestomaches are most likely an adaptation to the high-quality browse material selected by giraffes, resulting in a shorter needed rumination time (Mitchell 2021). Huge quantity of saliva is produced by the well-developed salivary glands, which assist in the fast movement of the cud through the rumen–reticulum (Mitchell 2021). It is likely that a mixture of plant cell contents and saliva, can bypass the rumen via an oesophageal groove, and be deposited directly into the stomach (Mitchell et al. 2015). The stomach walls of giraffes are covered in large tongue like papillae (Clauss et al. 2002; Sauer et al. 2016, 2017). The coverage is so vast and intricate that the surface area is one of the biggest known for ruminants, and greatly assists in effective absorption, relative to body size. It is estimated that 40% of the daily energy needed by giraffes (as browsers) is derived from volatile fatty acids (VFAs), produced by microbial fermentation in the rumen (Dagg 2014) and that the other 60% comes from the intestinal digestion of glucose (Mitchell 2021). The reverse is found in grazer-ruminants, where approximately 60% is produced by rumen microbial fermentation and only about 40% comes from intestinal digestion (Gordon 2003; Mitchell 2021). Further along, the large intestine facilitates substantial fermentation of undigested fibre (mainly hemicellulose). The main sites of fermentation are the rumen and large intestine, with only negligible 5.5% and 3.4% of total VFAs produced in the abomasum and small intestine, respectively (Clemens and Maloiy 1983).

The maximisation of dry matter (DM) intake is very important as it provides more nutrients to the rumen microbiome, which in turn provides more nutrients and building blocks for growth, reproduction and body condition (Mitchell 2021). Great variation in total % DM intake has, however, been calculated for giraffe housed in zoos (Gussek 2015), provided with different types of roughage and concentrate feeds. These ranges include 30%–48% (Hatt et al. 2005), 25%–51% (Clauss et al. 2001), 21%–30% (Clauss et al. 2002), or even as dramatically as from 8% to 40% (Kearney et al. 2003). One of the dietary problems associated with captive giraffe is the inadequate intake of dietary roughage, which leads to the development of ruminal acidosis (Clauss et al. 2002; Jolly 2003; Kearney and Ball 2001; Potter and Clauss 2005). Percentage of faecal DM (% DM_f) represents everything contained in a faecal sample except water; this includes protein fibre, fat and minerals, and so forth (Saha et al. 2023) and could therefore assist in providing an indication of DM intake. Provided a relatively good diet, consisting in high enough protein levels (±16%–18% crude protein [CP]), giraffes are very efficient digestors of the DM they eat (Hofmann 1973). By using both fermentation (via the rumen and hindgut), as well as straightforward digestion, the energy demands of their large body mass (Mitchell 2021) are met. As a result, very little of what giraffes eat is wasted and overall, the expected % DM_f is low.

Upon ingestion of the selected browse material, the foregut fermentation process of ruminants commences. Similar to other ruminants, giraffes depend on the symbiotic relationship with microorganisms in the rumen and the rest of the digestive system to digest and absorb energy locked in cellulose and hemicellulose (Dehority and Odenyo 2003; Ley, Hamady, et al. 2008; Roggenbuck et al. 2014; Van der Walt 2020; Youngblut et al. 2019; Zierer et al. 2018; Zoelzer et al. 2021). These microorganisms ferment fibres and produce, along with several other metabolites (Grobbelaar et al. 2024), the VFAs which are the major energy sources of the host (Saengkerdsub and Ricke 2013). The digestive workings of these microorganisms, the composition (quality and quantity) of the available browsing material and the overall physiology and health of the animals are represented in the "end product," that is, faeces. Through coevolution between the animal host and the microorganisms, faeces are the final reflector products of the original composition of the diet ingested by the animal and the different needed specialised functions provided by the microorganisms to nurture the animal (Codron and Codron 2009; Leslie et al. 2008; Ley, Hamady, et al. 2008; Ley, Lozupone, et al. 2008). Even a recent diet change, such as 1 day, was shown to have a noteworthy effect in the human gut microbiota (David et al. 2013). The mean retention times of particles in giraffes and okapi (*Okapia johnstoni*) have been reported to be approximately 40 h (Hummel et al. 2005; Mitchell et al. 2015) but the verdict is still out on the pace of the change in microbial communities of the reticulo-rumen of the giraffids (Roggenbuck et al. 2014).

Of all the herbivores, the giraffe remains a species whose nutritional management is considered to be a challenge (Hatt et al. 2005). Many captive giraffes die because of a chronic energy deficit (Potter and Clauss 2005) most likely due to the insufficient intake of the staple roughage component of the diet. Poor nutrition (usually energy and nitrogen [N]) and a low mineral intake may lead to poor lactation and may limit the ability of female ungulates to raise their offspring (Parker

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et al. 2009). For free-roaming giraffes, this limiting demographic parameter may reduce population growth in addition to predation and genetic causes (Lee 2015). Resulting that nutritional management and tree phenological changes are even more challenging for free-roaming giraffes than in captive controlled environments. Routine monitoring and information obtained from faecal analysis could be used to determine the time of initiating or discontinuing a supplemental feeding (SF) programme (Dörgeloh et al. 1998) and management of animal numbers (Janecke and Smit 2015). Faeces provide valuable pockets of information giving an insight to multiple wildlife health factors and the "holobiont" of the animal (Pannoni et al. 2022; Simon et al. 2019). The presence of unstratified rumen content and a homogenous rumen papillation pattern, resulting in similar rumen content throughout the digestive system, support the use of freshly excreted faeces as reliable representative indicator of giraffe gut health (Sauer et al. 2017).

The current study aims to provide insight into the feeding practices and seasonal changes in faecal quality composition, based on 10 different faecal parameters: % DM_f, organic matter (%OM_f), ash (% Ash_f), % CP_f, crude fat (% CF_f), gross energy (% GE_f), neutral-detergent fibre (% NDF_{fOM}), acid-detergent fibre (% ADF_{fOM}), acid-detergent lignin (% ADL_{fOM}), and phosphorus (% P_f). This would ultimately assist in assessing the nutritional quality of the diet accessible and consumed by giraffe populations occurring in areas outside of their historical distribution and under different management systems.

2 | Materials and Methods

2.1 | Study Animals and Area

More than 300 fresh faecal samples were collected from six giraffe populations from July 2021 to June 2023 in the Grassland Biome of the Free State Province, South Africa. Considered as an extralimital species, there is no reliable historical evidence of giraffes occurring naturally in central South Africa (Dagg 1962; Deacon and Parker 2016; Van Niekerk et al. 2019). All of the current study's populations were free-roaming and occurred within a 60-km radius from the city of Bloemfontein, located within the Free State Province (South Africa). Three different vegetation types of South Africa (Mucina and Rutherford 2006) were identified (Table 1) and correlated with the woody tree species previously described for the region (Janecke and Smit 2015; Mucina and Rutherford 2006).

Only fresh, moist faeces (after direct observation of defecation) were collected (Codron et al. 2005; Erasmus et al. 1978). Collections were done within 5–10 min after defecation, to limit environmental factors that may affect the chemical and biological constituents of faeces (Wrench et al. 1996). Samples were collected from the ground with a gloved hand and placed within plastic slider storage bags, kept under refrigeration (2°C–4°C) for a maximum of 3 days, whereafter it was vacuum sealed and stored at −20°C until analysis, which occurred within 18 months post collection. Plastic bags and immediate cooling or freezing methods were implemented to prohibit the development of mould/fungal growth, which would affect the chemical composition and concentrations (Wrench et al. 1996).

Only a limited subset of samples could be analysed for the determination of the faecal chemical fractions (DM, OM, Ash, CP, CF, ether extraction [EE], NDF, ADF, ADL, P). This decision was based on budgetary limitations and the extensively large costs associated with these types of analyses. Although a decisive attempt was made to select representative subsets from the different giraffe study populations, it was not achievable to be balanced with regard to seasons, feeding (i.e., management) practices, locations, age, and sexes. In an attempt to determine differences between seasons and dietary supplements, 47 faecal samples were selected for chemical analysis. As with most free-roaming wild ungulate studies, especially giraffe studies, our study design was unbalanced (Leslie and Starkey 1985) and sample size was small (Hatt et al. 2005). Chemical analysis results were pooled for Locations 1, 4, and 5 (A) and Locations 2, 3, and 6 (B), to differentiate between locations of which the management provide SF or locations where the giraffes are only provided with natural available vegetation (NAV), respectively. SF mainly composed of manufactured game pellets (e.g., Lubern Game Pellets, V14408) containing CP (minimum 100 g/kg), estimated energy (minimum 8 MJ/kg), moisture (maximum 120 g/kg), fat (minimum 30 g/kg), fibre (maximum 250 g/kg), calcium (maximum 10 g/kg), and phosphorous (minimum 4 g/kg). The provision of SF at Locations 1, 4, and 5, was done all year round and available when needed. Feed was supplied to giraffe in a special container that could not be reached by other herbivore species.

2.2 | Chemical Analysis of Faecal Samples

All faecal pellets were rinsed with distilled water, to remove superficial dust and pebbles, prior to analysis. As a result, no interpretations were made on the calculated % DM_f results as this did not represent the actual DM content or moisture concentration of the faecal samples.

After mixing the faecal pellets from each dung heap (Wrench et al. 1996), approximately 300 g of each defrosted faecal sample were weighed and dried to a constant dry weight at 60°C. The resultant dried faecal samples were ground in a CYCLOTEC 1093 sample mill (Foss, Denmark) to a 1-mm screen size and stored for subsequent testing (Codron et al. 2005; Milis et al. 2007; Wrench et al. 1996). Chemical analysis methods were employed to determine the concentrations of various components in the faecal samples, including DM (Latimer Jr. 2023a), OM and ash (Thiex et al. 2012), CP (Latimer Jr. 2023b), CF (EE) (Latimer Jr. 2023c), gross energy (provided in MJ/kg DM), NDF_{OM}, ADF_{OM} (Robertson and Van Soest 1981; Van Soest 1967), ADL_{OM} (Goering and Van Soest 1970), and P (Cavell 1955). To establish the OM and DM contents, the dried faecal samples underwent a secondary drying process by drying two 1.5–2 g subsamples at 105°C overnight and consecutively incinerating the same subsamples, after weighing at 250°C for 1 h followed by ashing at 550°C for 3 h. Data were converted to dry mass (DM) for statistical analyses and are described as percentage of faecal DM (Table S1 and Figure S1). Gross energy was calculated in MJ/kg per DM (Erasmus et al. 1978; Hatt et al. 2005;

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TABLE 1 | Locations 1–6 from which giraffe faecal samples ($n = 47$) were collected during different seasons from 2021 to 2023 in the Free State Province. The collected faecal samples were grouped based on the type of feeding practice followed on the property: Supplemental feeding (SF) or natural available vegetation (NAV). The assigned vegetation types and codes are based on previous research findings (Janecke and Smit 2015; Mucina and Rutherford 2006).

Location name, (size), feeding practice (sample size)	Locality coordinates; above sea level	Vegetation type (code) and landscape description
Location 1 (250 ha) SF ($n = 25$)	29°05′56″ S 26°14′07″ E; 1473 m	Bloemfontein Dry Grassland; Gh 5: A dolerite hill, located within the city of Bloemfontein; plant species composition consists of woody tree species, especially *Olea europaea subsp. africana* (Mill.) P.S. Green, Kew Bull. 34(1): 69 (1979) and *Searsia* F.A. Barkley, Fl. Texas [C.L. Lundell et al.] iii. 104 (1943) species, otherwise a deteriorated grassland with numerous forb and herbaceous species
Location 2 (500 ha) NAV ($n = 7$)	28°57′16″ S 26°23′29″ E; 1318 m	Western Free State Clay Grassland; Gh 9: A commercial game farm consisting of grassland plant species including woody tree species, such as *Vachellia karroo* (Hayne) Banfi & Galasso, Atti Soc. Ital. Sci. Nat. Mus. Civico Storia Nat. Milano 149(1): 149 (2008). Landscape typically includes hilly outcrops associated with the Bloemfontein area, with *Olea europaea* subsp. *africana*
Location 3 (7116 ha) NAV ($n = 5$)	28°35′50″ S 26°25′46″ E; 1417 m	Western Free State Clay Grassland; Gh 9: A large commercial game farm consisting of grassland plant species including numerous deciduous and semi-deciduous *Vachellia* Wight & Arn., Prodr. Fl. Ind. Orient. 1: 272 (1834) and *Ziziphus* Mill., Gard. Dict. Abr., ed. 4. [1547] (1754) tree species
Location 4 (100 ha) SF ($n = 3$)	29°03′00″ S 26°13′32″ E; 1383 m	Bloemfontein Dry Grassland; Gh 5: A private land, located just outside the Bloemfontein city outskirts consist of some hills and grasslands, with woody evergreen tree species such as *Olea europaea* subsp. *africana*, and *Searsia* species
Location 5 (700 ha) SF ($n = 4$)	29°24′47″ S 25°57′30″ E; 1399 m	Bloemfontein Dry Grassland; Gh 5: A privately-owned farm consisting of grassland and hilly outcrops with woody evergreen tree species
Location 6 (2500 ha) NAV ($n = 3$)	28°54′47″ S 25°50′11″ E; 1228 m	Vaal-Vet Sandy Grassland; Gh 10: A privately owned farm consisting of grassland and riverine plant species including woody tree species such as *Vachellia* and *Ziziphus*

Janecke and Smit 2015; McDonald et al. 2010; Milis et al. 2007; Zimmerman 1980). As a result, the NDF, ADF, and ADL values are provided on an OM basis (= NDF_{OM}, ADF_{OM} and ADL_{OM}), and silica and other minerals do not form part of the results.

Based on previous research, no differences were found in CP between faeces excreted during the day or night and therefore the time of sampling was not considered critical for this study (Erasmus et al. 1978; Janecke and Smit 2015; Zimmerman 1980). Only faeces collected from adult individuals were used for analyses and no differentiation was made between males and females (Wrench et al. 1996). Faecal samples were pooled per month and season: Winter, Dry (June–August), Spring, Dry (September–October), Summer, Wet (November–February) and Autumn, Wet (March–May) seasons.

2.3 | Calculations and Statistical Analysis

Principal component analysis (PCA) was used to visualise the variation in the data (weighted sum of the faecal parameter percentages) into a model plane, generating scores. PCA is an unsupervised method aiming to find the directions that best explain the variance in a dataset (X) without referring to class labels (Y) (Budaev 2010). The data are summarised into much fewer variables called scores which are weighted average of the original variables. Ten parameters (% DM_f, %OM_f), % Ash_f), % CP_f, % CF_f, (% GE_f, % NDF_{fOM}, % ADF_{fOM}, % ADL_{fOM}, and % P_f) were analysed from 47 faecal samples by means of correlation matrix (Figure 5). Median sample normalisation, log (base 10) data transformation and Pareto data scaling were used. PCA scores (seven detected groups) and factor rotation were computed and plotted in order to give a visual over-view of the samples and how they correlate to each other per variable (Figure 1 and Figure S2) PCA analysis was performed using the prcomp package in R (R Core Team 2024) (R-script provided in the Data S1). The calculation is based on singular value decomposition.

Descriptive statistics were used to describe the means, ranges and standard deviations for each of the 10 chemical parameters (Table 2) The data was analysed statistically using

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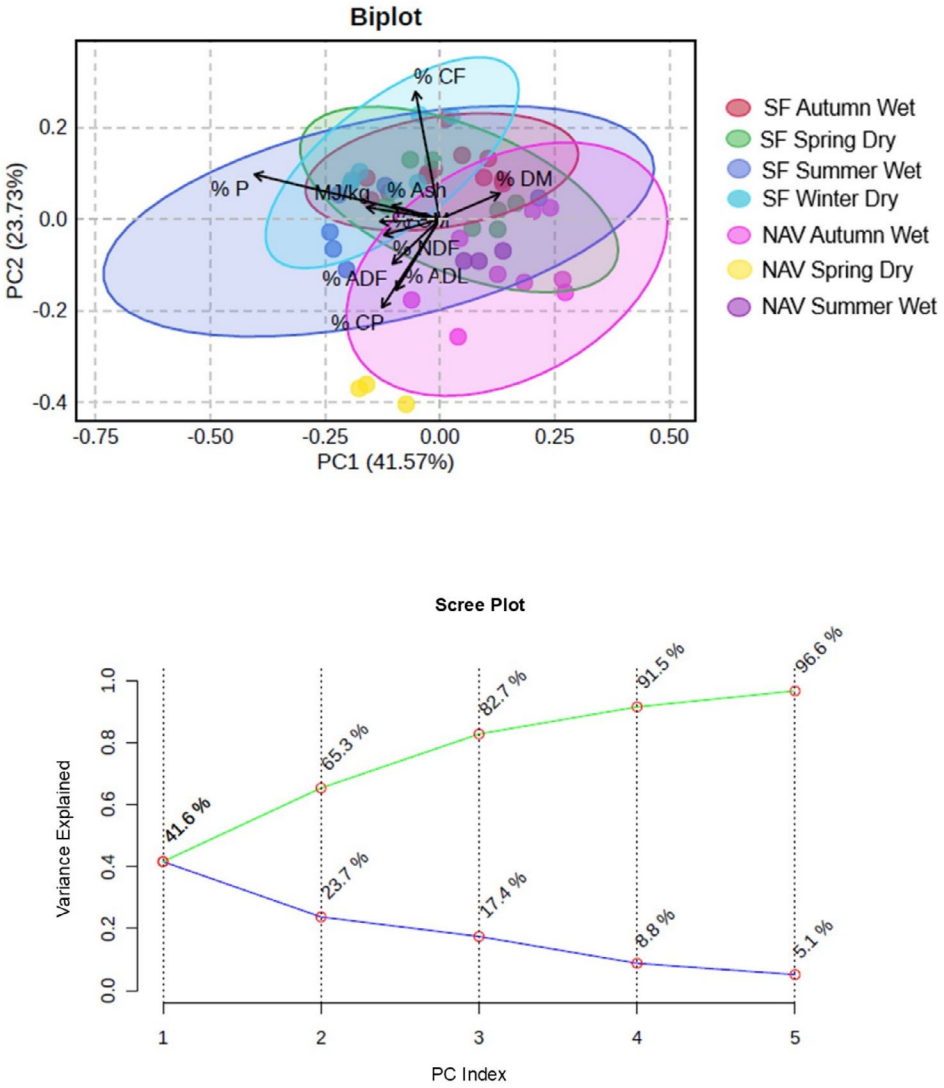


FIGURE 1 | A principal component analysis (biplot and scree plot) on giraffe faecal samples clustered on the type of feeding practice (supplemental feed [SF] and natural available vegetation [NAV]) provided to free-roaming populations at different locations in the Free State Province, over a 2-year period (2021–2023). Partial least square discriminant analysis of 10 faecal chemical parameter profiles of SF and NAV giraffes and seasons Winter, Dry; Spring, Dry; Summer, Wet and Autumn, Wet were used. Scree plot shows the variance explained by principal components. The green line on top shows the accumulated variance explained; the blue line underneath shows the variance explained by individual principal component.

MetaboAnalyst (Pang et al. 2024), an online statistical resource based on R (R Core Team 2024), making use of Fisher's least significant difference (LSD) method with an alpha value of 0.05 (confidence interval = 95%). Variables included two feeding practices (SF or NAV) and four seasons (Winter, Dry; Spring, Dry; Summer, Wet and Autumn, Wet). Box and Whisker charts are used to present the calculated means and ranges of the faecal parameters that are most indicative of dietary quality per feeding practice and season (Figures 2–4). Supporting Information is available on important features identified by one-way analysis of variance (ANOVA), post hoc analysis (Table S4), and pairwise permutational multivariate ANOVA (Table S5) performed on the 10 faecal chemical parameters analysed from faecal samples ($n = 47$).

A Pearson correlation matrix (with a significance level of 5%) was used to determine the relationships between the 10 different chemical parameters calculated from the 47 faecal samples (Figure 5), with the correlation matrix and corresponding p-values available in the Data S1.

3 | Results

Separate groupings, based on the calculated concentration percentages from the 10 giraffe faecal parameters could be illustrated using PCA (Figure 1 and Figure S2). Variables such as different feeding practices (SF or NAV) and seasons (Winter, Dry; Spring, Dry; Summer, Wet and Autumn, Wet) clearly showed different profile groupings.

The significant ($p < 0.05$) highest means for the chemical parameters calculated from giraffes provided with SF included: % OM_f (90.48%), % CF_f (4.66%), GE_f (20.64 MJ/kg), and % P_f (0.5%), while those only dependent on NAV had higher overall means for % DM_f (36.76%), % Ash_f (9.55%), % CP_f (13.84%),

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TABLE 2 | A summary of the descriptive statistics used to describe the means and standard deviations for the 10 faecal chemical parameters analysed from faecal samples ($n = 47$) from giraffes situated within the Free State Province. Fisher's least significant difference (LSD) method was used to calculate differences between the different feeding practices: Supplemental feeding (SF) and natural available vegetation (NAV) and between the four seasons (2021–2023).

	SF ($n = 32$)	NAV ($n = 15$)	Fisher's LSD between feeding practice groups		Winter, Dry ($n = 7$)	Spring, Dry ($n = 10$)	Summer, Wet ($n = 9$)	Autumn, Wet ($n = 21$)	Fisher's LSD between seasons (all groups, all locations)		Fisher's LSD between feeding practice groups and seasons	
Parameter	**Mean[a] (±SD)**	**Mean[a] (±SD)**	***f***	***p***	**Mean[a] (±SD)**	**Mean[a] (±SD)**	**Mean[a] (±SD)**	**Mean[a] (±SD)**	***f***	***p***	***f***	***p***
% DM_f	36.76↓ (±7.67)	38.88↑ (±6.84)	4.78	**<0.05**	34.07↓ (±8.87)	36.87 (±6.17)	36.76 (±8.99)	39.13↑ (±6.63)	—	>0.05	—	>0.05
% OM_f	90.48↑ (±1.92)	89.95↓ (±2.18)	6.79	**<0.05**	89.09↓ (±0.97)	92.07↑ (±1.97)	90.49 (±1.72)	89.75 (±1.83)	5.03	**<0.05**	4.26	**<0.05**
% Ash_f	9.55↓ (±1.92)	10.05↑ (±2.18)	7.51	**<0.05**	10.91↑ (±0.97)	7.93↓ (±1.97)	9.51 (±1.72)	10.25 (±1.83)	5.89	**<0.05**	4.26	**<0.05**
% CP_f	13.84↓ (±1.99)	18.50↑ (±2.67)	22.07	**<0.05**	13.48↓ (±0.90)	15.19 (±5.15)	16.50↑ (±1.29)	15.51 (±2.50)	—	>0.05	25.45	**<0.05**
% CF_f	4.66↑ (±1.06)	3.39↓ (±1.07)	16.43	**<0.05**	5.10↑ (±0.48)	3.17↓ (±1.05)	3.80 (±0.54)	4.69 (±1.22)	8.06	**<0.05**	9.90	**<0.05**
MJ/kg	20.64↑ (±0.97)	20.03↓ (±0.67)	6.62	**<0.05**	21.50↑ (±0.56)	20.09↓ (±0.96)	20.16 (±0.56)	20.39 (±0.89)	4.64	**<0.05**	7.26	**<0.05**
% NDF_{fOM}	67.95↓ (±3.93)	68.62↑ (±5.37)	10.76	**<0.05**	64.74↓ (±0.85)	72.75↑ (±3.91)	70.27 (±4.37)	66.22 (±2.88)	12.26	**<0.05**	12.17	**<0.05**
% ADF_{fOM}	55.26↓ (±2.75)	61.63↑ (±3.91)	12.97	**<0.05**	53.48↓ (±1.48)	57.40 (±6.05)	58.59↑ (±5.72)	57.96 (±2.18)	—	>0.05	22.53	**<0.05**
% ADL_{fOM}	37.90↓ (±3.28)	47.167↑ (±3.31)	39.04	**<0.05**	38.51↓ (±1.10)	40.35 (±8.26)	41.71↑ (±4.67)	41.52 (±4.71)	—	>0.05	20.43	**<0.05**
% P_f	0.50↑ (±0.20)	0.30↓ (±0.16)	8.15	**<0.05**	0.58↑ (±0.13)	0.42 (±0.17)	0.57 (±0.19)	0.34 (±0.19)	5.38	**<0.05**	5.77	**<0.05**

Abbreviations: % ADF_{fOM} = percentage faecal acid-detergent fibre based on an organic matter basis, % ADL_{fOM} = percentage faecal acid-detergent lignin based on an organic matter basis, % Ash_f = percentage faecal ash, % CF_f = percentage faecal crude fat, % CP_f = percentage faecal crude protein, % DM_f = percentage faecal dry matter, % NDF_{fOM} = percentage faecal-detergent fibre based on an organic matter basis, % P_f = percentage faecal phosphorous, ↑ = highest mean, ↓ = lowest mean, GE_f (MJ/kg) = faecal gross energy (mega joules per kilogram), LSD = least significant difference, NAV = natural available feeding, SF = supplemental feeding.

[a]Values rounded off to two decimals and provided in percentage.

Note: The bolded text ($p < 0.05$) indicates statistical significance.

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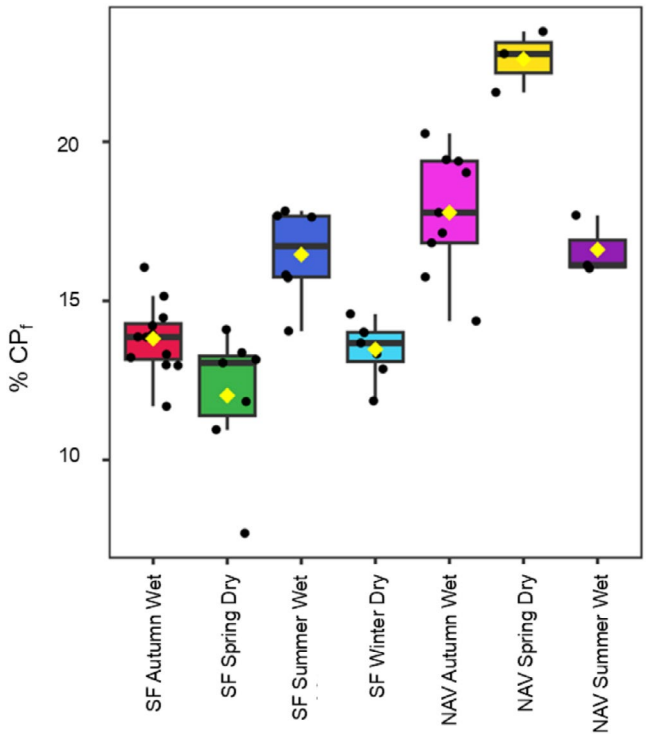


FIGURE 2 | Box and Whisker charts for the % Faecal Crude Protein (CP_f concentrations) grouped per feeding practice (supplemental feed [SF] and natural available vegetation [NAV]) and season (Autumn, Wet; Spring, Dry; Summer, Wet and Winter, Dry) calculated from free-roaming giraffe faecal samples ($n = 47$) collected from 2021 to 2023 in the Free State Province, South Africa.

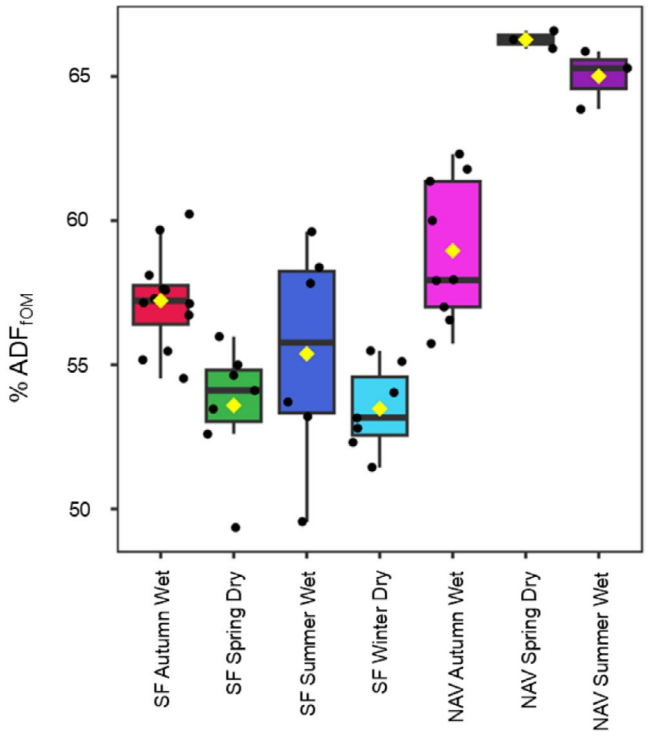


FIGURE 3 | Box and Whisker charts for the % faecal acid-detergent fibre (ADF_{fOM} concentrations) grouped per feeding practice (supplemental feed [SF] and natural available vegetation [NAV]) and season (Autumn, Wet; Spring, Dry; Summer, Wet and Winter, Dry) calculated from free-roaming giraffe faecal samples ($n = 47$) collected from 2021 to 2023 in the Free State Province, South Africa.

% NDF_{fOM} (67.95%), % ADF_{fOM} (55.26%), and % ADL_{fOM} (37.90%) (Table 2). The highest means for the chemical parameters calculated from giraffes in the Summer, Wet season included % CP_f (16.50%), % ADF_{fOM} (58.59%), and % ADL_{fOM} (41.71%), while lowest mean for these parameters were calculated for the Winter, Dry season (13.48%, 53.48%, and 38.51%, respectively) (Table 2).

Clear positive correlations (Distance measure Pearson r) between % CP_f, % ADL_f, and % ADF_f were noticed between the two different feeding practices and different seasons (Figure 5 and Tables S2 and S3).

4 | Discussion

In the current study, faecal analysis was done on different giraffe populations from various localities across different seasons but focus was also on the faecal composition of one specific individual in an attempt to minimise the subjective effects of various localities and different population physiological statuses. In both wild and captive browsers, a maximum of 2% of condensed tannin in a diet has been reported to maintain positive linear relationship between dietary N and N_f (faecal nitrogen) and can therefore be used to evaluate broad seasonal and spatial patterns of diet quality at the population level (Erasmus et al. 1978; Janecke and Smit 2015; Leslie et al. 2008; Robbins 1983; Verheyden et al. 2011), as were the objectives of this research. Given the robustness and accuracy across various seasons, % CP_f can be considered as an important indicator of nutrient intake and diet digestibility in ruminants (Awuma 2003; Cain et al. 2017; Mbatha and Ward 2006; McKinney et al. 2006; Mellado et al. 2005; Monteith et al. 2009; Orellana et al. 2020; Robinson et al. 2010; Stapelberg et al. 2008; Verheyden et al. 2011).

Additional factors, such as the intake of plant secondary compounds (PSCs), for example, tannins, should also be considered when evaluating excreted giraffe faces. PSCs create unpalatable detergents and with sufficient quantities are toxic and inhibit digestive enzymes and depress the digestion of browse (Caister et al. 2003; Furstenburg 1991; Furstenburg and Van Hoven 1994; Hassanpour et al. 2011; Mitchell 2021; Mkhize et al. 2015; Owen-Smith 1993; Robbins et al. 1987). Tannins, as well as lignin, decrease the protein and fibre digestibility of ruminants (Grant et al. 1995; McDonald et al. 2010; Moore and Jung 2001). It has been suggested that smaller ruminants, such as red deer (*Cervus elaphus*), that excrete both large amounts of N and large amounts of tannins in their faeces, develop a decline in their body condition (Carpio et al. 2015). It would therefore be logical to assume that in general, giraffes would prefer to avoid the ingestion of large tannin and lignin quantities. The effects of phenolic (e.g., tannin) and lignin concentrations on giraffe browsing habits are, however, not that straightforward (Mitchell 2021). It is known that certain problems exist when non-metabolic nitrogen (N_f) is used to determine the nutritional status of game species (Janecke and Smit 2015). Tannins and lignin, which are present in

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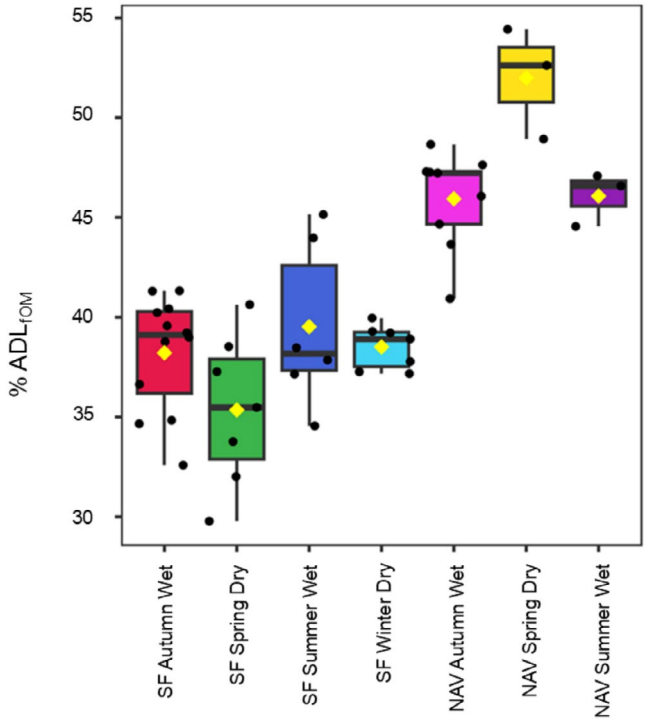


FIGURE 4 | Box and Whisker charts for the % faecal acid-detergent lignin (ADL_{fOM} concentrations) grouped per feeding practice (supplemental feed [SF] and natural available vegetation [NAV]) and season (Autumn, Wet; Spring, Dry; Summer, Wet and Winter, Dry) calculated from free-roaming giraffe faecal samples ($n = 47$) collected from 2021 to 2023 in the Free State Province, South Africa.

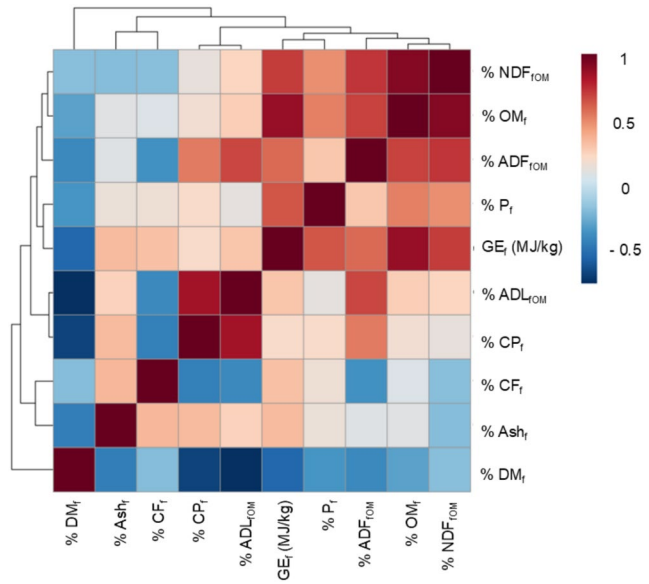


FIGURE 5 | A Pearson correlation matrix (with a significance level of 5%) to determine the relationships between the 10 different chemical parameters (percentage of dry matter [% DM_f], organic matter [%OM_f], ash [% Ash_f], crude protein [% CP_f], crude fat [% CF_f], gross energy [% GE_f], neutral-detergent fibre [% NDF_{fOM}], acid-detergent fibre [% ADF_{fOM}], acid-detergent lignin [% ADL_{fOM}] and phosphorus [% P_f]) calculated from free-roaming giraffe faecal samples ($n = 47$) collected from 2021 to 2023 in the Free State Province, South Africa.

most woody plants, may inhibit the ruminant's digestion of protein and fibre, which are then excreted as N_f (Botha and Stock 2005; Carpio et al. 2015; Hobbs 1987; Leslie et al. 2008; Leslie and Starkey 1987; Wrench et al. 1997). This inhibition may explain the increased percentage concentration of % CP_f, % NDF_{fOM}, % ADF_{fOM}, and % ADL_{fOM} from giraffe feeding from NAV (Figures 2–4 and Table 2), as discussed below.

Caution should be taken for using % N_f and % CP_f to indicate the quality of diet and animal condition, as it could be on overestimation of fodder digestibility and available diet N (Grant et al. 1995; Hobbs 1987; Holecheck et al. 1982; Howery and Pfister 1990; Irwin et al. 1993; Nunez-Hernandez et al. 1992; Robbins 1983; Robbins et al. 1987; Verheyden et al. 2011; Wofford et al. 1985; Wrench et al. 1997; Zimmerman 1980). % N_f is not a straightforward positive indicator of diet quality in terms of protein intake, but rather a complex interaction between diet quality (protein content) and any anti-nutritive factor (such as tannins) that is able to reduce N digestibility. Nevertheless, studies on various PSCs and foraging–digestive strategies of mammalian herbivores have highlighted physiological, behavioural and gut microbial adaptations that minimise the toxic and protein-precipitating nature of such compounds (Dearing et al. 2000, 2005; Iason 2005; Kohl et al. 2014; Menke et al. 2015; Milis et al. 2007). It is hypothesised that giraffes produce a voluminous amount of saliva that can neutralise the tannins they ingest (Mitchell 2021; Sauer et al. 2016). An argument has also been made that free-roaming herbivores will actively avoid plants with high levels of phenolic compounds (e.g., tannins) or with low-quality browse (Botha and Stock 2005; Grant et al. 2000). This would ultimately lead to less accurate % CP_f determination per seasonal variance (Janecke and Smit 2015). Other environmental conditions as well as the individual animal's own physiological status, genotype, health status and social conditions can also influence % CP_f and % N_f concentrations (Leslie et al. 2008; Wofford et al. 1985).

During this study, three chemical parameters (% CP_f, % ADF_{fOM}, and % ADL_{fOM}) showed the most potential in successful differentiating between variables such as feeding practice and season (Figures 2–4). For % CP_f, the Fisher's LSD between different feeding practices (SF and NAV) and seasons indicated a high f-value (25.45) and significance p-value (< 0.05) (Table 2). The same high f-values (22.53 and 20.43) and statistical significance (< 0.05) were also achieved for % ADF_f and % ADL_f, respectively, when compared between the two different feeding practices and different seasons (Table 2 and Figures 2–4).

A significant ($p < 0.05$) higher level in % CP_f was calculated for giraffe individuals occurring in NAV when compared to SF (Figure 2). This difference was evident across different feeding practices and seasons, as well (Table 2). A significant ($p < 0.05$) higher level in % ADL_f was calculated for giraffe individuals occurring in NAV when compared to SF (Figure 4). This difference was evident across different feeding practices and seasons, as well (Table 2). The higher availability of % CF_f and % GE_f (MJ/kg) could be as a result of the energy-rich SF provided to these animals throughout the year (Table 2). Increased percentage concentration of % CP_f, % NDF_{fOM}, % ADF_{fOM}, and % ADL_{fOM}

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from giraffe feeding from NAV in turn indicate the increased availability of lesser digestible plant structural material such as tannins, cellulose, and lignin present in natural vegetation (McDonald et al. 2010). Natural browse material is generally richer in CP and lignin contents than grazing material such as grass, which again is usually richer in fibres (Roggenbuck et al. 2014; Shipley et al. 1998). Browsing material usually may also contain other secondary plant metabolites such as tannins (Caister et al. 2003; Shipley et al. 1998). The minimum requirement for protein and energy to maintain normal body functions for free-roaming giraffe have been calculated to be above 12% of their body weight and above 8.3 MJ/kg of DM, respectively (Hall-Martin and Basson 1975; Pellew 1983a, 1983b, 1984a, 1984b).

The increased faecal concentrations of % CP_f (16.50%), % ADF_{fOM} (58.59%), and % ADL_{fOM} (41.71%) during the Summer, Wet season can be attributed to the seasonal availability of increased forage material during the growth season (McDonald et al. 2010) (Table 2 and Figures 2–4). CP_f is widely used as an index of dietary quality in the nutritional ecology of free-ranging and captive ruminants (Carpio et al. 2015; Grant et al. 2000; Janecke and Smit 2015; Leslie et al. 2008; Van der Waal et al. 2003; Verheyden et al. 2011). The availability of % CP and % N play an important function in the fermentation processes within the rumen (Dörgeloh et al. 1998; Grant et al. 1995). Microbiome activity is inhibited if N excretion exceeds N intake (Kinyamario and Macharia 1992). The critical level for where browsers (giraffe and kudu) are expected to lose body condition is estimated to be < 9% CP_f and < 16 g/kg N_f, respectively (du Bothma 2002; Grant et al. 2000; Van der Waal et al. 2003).

Results from the current study agree with those calculated from a previous study on giraffes also located within the Free State Province (Janecke and Smit 2015). The previous study was done over a 28-month study period and % CP values ranged from 18.75% to 21.88% CP during summer, decreasing in autumn 15% to 18.75% CP, and a continued decrease during winter 11.25% to 16.38% CP. In the short-term browsers, such as giraffes, should not be affected by seasonal changes as long as enough shrubs and trees are still available (Grant et al. 1995). Because specialist browsers such as giraffes can select the highest nutritional items available, for example, leaves, shoots, flowers, fruits, legumes, and twigs, a higher N_f concentration (i.e., % CP) is evident during the summer months (Erasmus et al. 1978; Grant et al. 1995; Janecke and Smit 2015; Kok and Opperman 1985; Owen-Smith 1994; Zimmerman 1980).

Similar to previous findings, the deciduous trees in the study areas had full leaf carriage in summer (Janecke and Smit 2015), resulting in a high quantity of browse and therefore protein being available. This increased protein availability could also be reflected in the higher N_f concentrations during the summer months. Given the robustness and accuracy across various seasons, % CP_f can be considered as an important indicator of nutrient intake and diet digestibility in ruminants (Awuma 2003; Cain et al. 2017; Mbatha and Ward 2006; McKinney et al. 2006; Mellado et al. 2005; Monteith et al. 2009; Orellana et al. 2020; Robinson et al. 2010; Stapelberg et al. 2008; Verheyden et al. 2011).

Performing the Fisher's LSD test between feeding practices along with seasonal differences, the highest f-values were calculated for % CP_f (25.45) ($p < 0.05$), % ADF_{fOM} (20.43) ($p < 0.05$), and % ADL_{fOM} (20.43) ($p < 0.05$) (Table 2). This supports the findings that these three faecal parameters add the most value in determining the nutritional status and seasonal stress in giraffes via faecal analysis. % CP_f (Figure 2) was the lowest during the Winter, Dry months and the highest in locations (NAV) where a variety of natural vegetation is available. The positive association between % CP_f and quality browse can also be seen with the increase in % CP_f during the wet season (Figure 2). The decrease in % CP_f during the drier months, indicates the lesser availability in dietary protein based on the seasonal availability of N in plant material (Čupić et al. 2021; Dörgeloh et al. 1998; Grant et al. 1995, 2000; Hall-Martin and Basson 1975).

Faecal CF is the measurement of fat content through EE and gives the approximate total fat content and includes some waxes, pigments, and other lipids to a minor degree in addition to true fats (Saha et al. 2023). The highest mean for % CF_f (5.10%) and GE_f (21.50 MJ/kg) during the Winter, Dry season can again be attributed to the availability of only evergreen tree species (Table 2). In the current study, these included, for example, *Olea europaea subsp. africana* (Mill.) P.S. Green, Kew Bull. 34(1): 69 (1979) and *Searsia* F.A. Barkley, Fl. Texas [C.L. Lundell et al.] iii. 104 (1943) spp. (Deacon et al. 2023; Janecke and Smit 2015; Kok and Opperman 1980; Theron 2005), known for waxy lipid compounds in its foliage as the plants mature during the winter months (Long et al. 2010). (Table 1). The availability of lesser nutritious evergreen plants is also supported by the lowest mean of % CP_f (13.48%) also calculated during the Winter, Dry season (Table 2 and Figure 2) (Janecke and Smit 2015). Faecal gross energy (% GE_f) is the heat, measured in mega joule (MJ) that is released when the faecal sample is completely oxidised in an adiabatic bomb calorimeter and refers to the total energy left in the faecal sample (McDonald et al. 2010; Saha et al. 2023) after the extraction for the fulfilment of the ruminant's metabolic processes. CF contains 2.25 times more energy on DM basis than carbohydrates (Saha et al. 2023), and therefore a higher CF_f content will result in a higher GE_f as evident from the current results (Table 2).

Faecal NDF (NDF_{fOM}) is the residue or insoluble fraction left after boiling a faecal sample in neutral detergent solution and mainly contains plant cell wall components, such as cellulose, hemicellulose, lignin, silica and tannins (Saha et al. 2023; Scholtz 2008). Though lignin is indigestible, hemicellulose and cellulose can be (in varying degrees) digested by the microbiome in the ruminant digestive tract (Saha et al. 2023). Faecal ADF_{OM} (ADF_{fOM}) is the residue remaining after boiling a forage sample in acid detergent solution and is a fibrous component representing the least digestible fibre portion of ingested forage and mainly includes lignin, cellulose, silica, and insoluble forms of N (Saha et al. 2023). Lignin is not a carbohydrate but rather a complex polyphenolic polymer that originates from three derivatives of phenylpropane and is contained in the fibrous portion of plant stems and leaves (McDonald et al. 2010; Saha et al. 2023). It is undigestible and hence has a negative impact on cellulose digestibility in ruminants (Gordon 2003). Similar to % CP_f, two other parameters % ADF_{fOM} (53.48%) (Figure 3) and % ADL_{fOM} (38.51%) (Figure 4) were also the lowest during the Winter, Dry months, as well as

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at locations with SF (55.26% and 37.90%), respectively (Table 2). Lower concentrations of % ADF_f and % ADL_f during Winter, Dry months could be the result of the lesser availability of high quality fibres (Čupić et al. 2021) or giraffes' ability to select more nutritious plants parts (Mitchell 2021). Lesser microbial protein synthesis in the rumen and associated decreases in faecal NDF and ADF and overall digestibility are also contributing factors (Jancewicz et al. 2017; Orellana et al. 2020). The use of good quality roughages as part of the feeding practice of SF could in turn be responsible for the lower faecal concentrations of ADF and ADL (Čupić et al. 2021; McDonald et al. 2010). The high positive correlations between the concentrations of CP_f, ADF_{fOM} and ADL_{fOM} are also clearly evident in the Pearson correlation matrix (with a significance level of 5%) (Figure 5). This supports the findings that these three faecal chemical parameters could be positive indicators of high-quality diets.

The significant ($p < 0.05$) highest mean for % P_f was calculated from giraffes provided with SF and from faeces collected during the Winter, Dry season (0.58%) (Table 2). The availability of P plays an important in the rumen, especially cellulolytic bacteria, which are dependent on this mineral for the breakdown of plant cell walls (Bryant et al. 1959; De Waal and Koekemoer 1997; Durand and Komisarczuk 1988; Harder et al. 2015). It has been suggested that P becomes a limiting nutrient for ruminants at <0.2% P_f (Grant et al. 1995). Previous findings have also indicated that % P_f is very low for giraffes (Grant et al. 1995). It is, however, uncertain if the low faecal P concentrations of giraffes, and browsers, in general, is a result of low P in browse (du Bothma 2002), or because browse P is utilised more efficiently. Speculation on the occurrence of osteophagia to gain a balanced ratio of Ca and P in the diet has occurred (Mitchell et al. 2005). Apart from GE_f (MJ/kg), lesser clear correlations with the other eight studied parameters were, however, found for % P_f (Figure 5), which could be a result of endogenous excretion of minerals into the gut (originating from the animal itself and not the diet) (McDonald et al. 2010) and hence is of limited use to determine nutritional status.

5 | Conclusions

From the 10 chemical parameters analysed during this study, it was calculated that % CP_f, % ADF_{fOM}, and % ADL_{fOM} are the most successful in differentiating between different feeding practices and seasons from faeces collected from giraffe populations in the Free State Province. The use of % CP_f to indicate nutritional status is a well-known application but should be considered conjunctive with % ADF_{fOM} and % ADL_{fOM} to determine if the increase in % CP_f is a result of increased faecal microbes or actual increase in diet quality. The provision of good quality SF as part of the feeding practice used at the study areas assists in maintaining the critical energy for giraffe populations occurring in areas outside of their historical distribution. This study contributes to the understanding of monitoring faecal chemical parameters and thereby preventing diet-related deaths in giraffes.

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Ethics Statement

Ethical approval was obtained prior to the commencement of the study. The study was approved by the Animal Research Ethics Committee (AREC) of the University of the Free State (UFS) and Nature Conservation (reference numbers: UFS-AED2022/0006). The process was initiated with the formulation of a formal project proposal, which was submitted for review and approval by the scientific review panel, the official animal welfare committee (AREC) of the UFS and the State Veterinarian for Section 20 of the Animal Diseases Act, 1984 (Act No. 35 of 1984).

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

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

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