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Diet Composition of Forest Inhabiting Cape Buffalo (*Syncerus caffer caffer*) in Western Ethiopia

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ABSTRACT

This study investigated the diet composition of Cape buffalo in Jorgo-Wato Protected Forest. Diet composition was determined through feeding quadrat survey method. Grass as a mode of diet contributed 82.6%, whereas browse contributed 17.4% to the annual diet of Cape buffalo. Graminoids (Poaceae and Cyperaceae) formed the bulk of food available and eaten by Cape buffalo in both seasons (dry and wet season). However, the contributions of graminoids were higher in the dry season than the wet season, whereas the contribution of browse was high in the wet than the dry seasons. *Panicum hochstetteri* and *Setaria poiretiana* have the highest availability, acceptability and dietary contribution in the diet of Cape buffalo in Jorgo-Wato Protected Forest. Faecal nitrogen and phosphorus content analysis indicated mean nitrogen of 18.4±0.53 g kg^{-1} in the wet and 17.7±0.71 g kg^{-1} in the dry seasons. It also revealed mean faecal phosphorus content of 4.3±0.39 g kg^{-1} in the wet and 3.9±0.36 g kg^{-1} in the dry seasons. The mean faecal nitrogen and phosphorus content of Jorgo-Wato buffalo were above the minimum threshold level in both seasons. Though Cape buffalo inhabit pure forested habitat, they found replacement in the forest to find adequate shade tolerant grass species that produce sprouts and green foliage throughout the year. Faecal nitrogen and phosphorus analysis also revealed that forest inhabited Cape buffalo obtain more quality diet than those dwelling in open savanna habitats especially in the dry season where forages dieback over the course of the dry season. Despite the pure forested habitats of Jorgo-Wato Protected Forest, Cape buffalo has confirmed that they remain grazers even in forested habitats of limited grass diversity.

Key Words: African Buffalo; Diet Composition; Diet Quality; Ethiopia; Forest Inhabited

INTRODUCTION

Knowledge of animal diet is central to the study of animal ecology and management (Petrides 1975, Johnson 1980) because it is vital to understand the relationship between species and their environment (Bar et al. 1984). Large herbivores consume a variety of food items in order to fulfill their nutritional requirements (Bailey et al. 1996). They forage in different habitats where food availability and quality vary seasonally (Walker 1993). The availability and quality of diet is insufficient for various groups of ungulates leading to the death of herbivores in savanna ecosystems (Sinclair 1977). Diet composition of savanna buffalo in savanna and savanna wooded habitats has been relatively well understood (Leuthold 1972, Sinclair 1977, Prins 1996, Venter and Watson 2008, Tshabalala et al. 2009). However, studies about diet composition of Cape buffalo (*Syncerus caffer caffer* Sparrman, 1779) in forested habitats are limited. African buffalo (= Cape buffalo) consume a wide range of grass species (Tshabalala et al. 2009), but prefer species with green leaves, low fibre and high nutrient contents (Sinclair 1974, Macandza et al. 2004). They are known as hyper-grazers (Skinner and Smithers 1991, Prins 1996) as grass makes about 75-100% of their diet (Codron et al. 2007). Their digestive system also confirms that they are typically bulk feeders (Hofmann 1989). African buffalo, however, forced to use more browse during the drought season (Novellie et al. 1991) like the buffalo of Addo Elephant National Park (De Graaf et al. 1973). However, as stated by Landman et al. (2018), the high browse reported in the diet of Addo buffalo was not a valid measure as foraged species were identified from the rumen of starved buffalo that took large browse and died during drought season likely due to poor adaptation to browse diet (Hofmann 1989, Novellie et al. 1991).

Forage utilization of African buffalo varies based on season, habitat types, quality and quantity of the diet. However, they are able to regulate their dietary components in accordance with the spatial and temporal changes of resources (Sinclair 1977, Prins 1996, Macandza et al. 2004). Their feeding and ranging behaviour are also associated with the availability of water. Hence, seasonal variations in the availability of food and water have shown to alter the ranging and feeding habits of African buffalo (Funston et al. 1994). Forage species were recorded as available at the feeding station if the plant were alive, irrespective of the level of desiccation or utilization (Owen-Smith 1982). Availability can be seen in terms of season and habitats to indicate how often accepted species were available in each habitat and season as an indicator of feeding opportunity (Owen-Smith and Cooper 1987). Forage species were either accepted or rejected at the feeding station (Johnson 1980) and can be classed as staple or preferred. Staple species are those occur in greatest quantity in the diet, whereas preferred species are those ones more frequent in the diet than in the environment due to its palatability. A staple forage species can be preferred forage, but a preferred forage species can be staple forage species only when available in large quantities in the environment (Petrides 1975).

African buffalo feed selectively in the wet season, but unselective in the dry season due to forage reduction (Sinclair 1977, Skinner and Chimimba 2005). Consequently, they feed on low quality food (Mloszewski 1983, Landman and Kerley 2001) and browse on woody shrubs (Stark 1986). African buffalo add browse to their diet when grass is limited, but spend less time browsing in areas of abundant grass and in the wet season (Cromhout 2006). However, browse accounted for 54% of the buffalo's diet in *Combretum* woodland of the Zambezi Valley, Zimbabwe due to limitation in the availability of grass (Jarman 1971). As described by Mloszewski (1983), African buffalo have been observed browsing to some degree in areas of low grass availability. For instance, buffalo have been reported browsing in Uganda (Field 1968), Tanzania (Sinclair 1977), Botswana (Gagnon and Chew 2000) and South Africa (Landman and Kerley 2001).

The nutritional quality of game animals can be examined through the analyses of faecal nitrogen and phosphorus contents (Grant et al. 1995, Wrench et al. 1996, Wrench et al. 1997, Grant et al. 2000). Nitrogen is mostly associated with the amount of protein and play critical roles in an animal's life (Mattson 1980) compared to other food types (Parker et al. 2009). Several studies confirmed that crude protein in faeces is positively correlated with crude protein in the diet (Wrench et al. 1997, Kamler and Homolka 2005, Nicholson et al. 2006). The amount of faecal phosphorus content has also been used to predict the dietary phosphorus contents of herbivores (Holechek et al. 1985). Faecal phosphorus and nitrogen concentrations below 2.0 g kg^{-1} and 13.0 g kg^{-1}, respectively, are indicators of low quality food. Low phosphorus gradually reduces reproduction (Grant et al. 2000) and nitrogen deficiency decreases growth of herbivores (Grasman and Hellgren 1993; Grant et al. 2000). Though the feeding ecology of African buffalo had been well studied, the dietary composition of the species varies across its ranges (Sinclair 1977, Prins 1996, Perrin and Brereton-Stiles 1999, Landman and Kerley 2001, Macandza et al. 2004). Moreover, the results of most of these studies have local significance as the study sites vary in vegetation composition, habitat types, climate and landscape level. Hence, studying the dietary compositions of Cape buffalo in Jorgo-Wato Protected Forest is highly crucial as Cape buffalo has not been known to dwell in pure forested habitats.

THE STUDY AREA

The Jorgo-Wato Protected Forest (JWPF) is one of the top National Forest Priority Areas located in the western parts of Ethiopia between West Wollega and Buno Bedele Administrative Zones. JWPF is about 509 km far from Addis Ababa along Addis Ababa-Gimbi main road, and 68 km south of Gimbi, the capital of West Wollega Administrative Zone. The forest is situated between 8° 40' 20" to 8° 48' 06" N latitude and 35° 48' 01" to 35° 56' 40" E longitude (Figure 1). JWPF has a total area of 8,503.49 ha, including both natural and plantation forests. The study area receives a unimodal annual rainfall. The mean annual rainfall of the area was about 1805 mm from 1992 to 2014. The highest mean monthly rainfall was about 324 mm in July and the lowest of 9 mm in

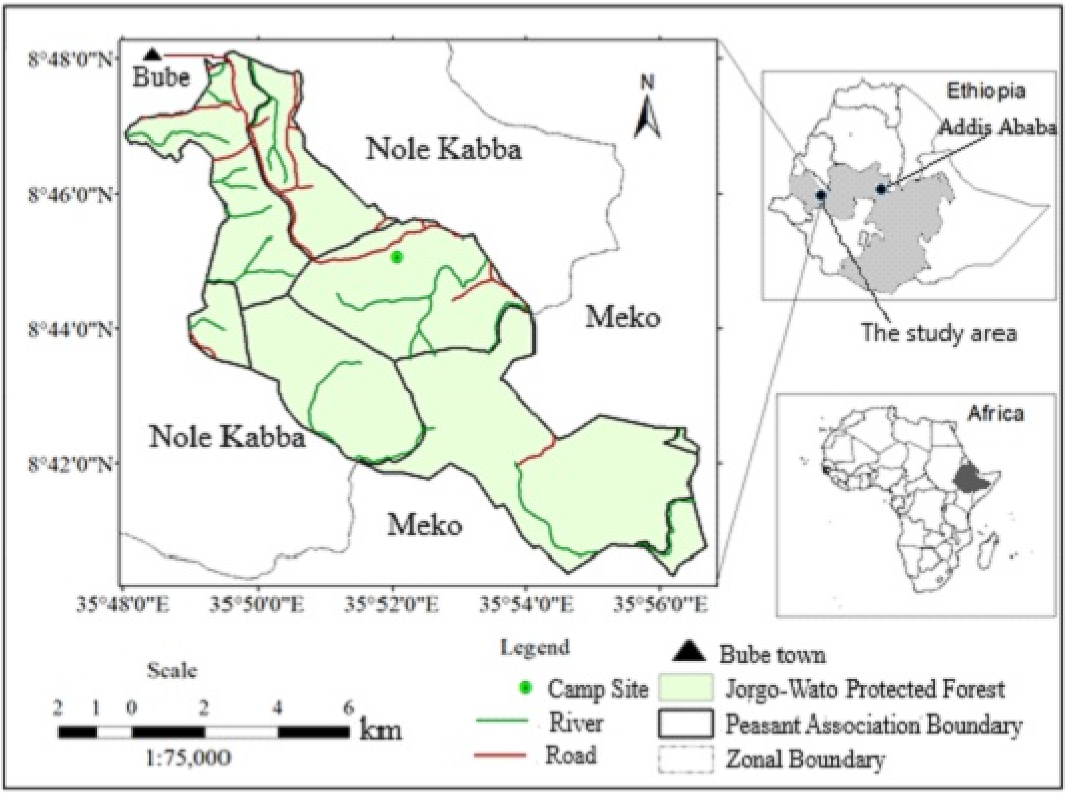

Figure 1. Location map of Jorgo-Wato Protected Forest.

December. The mean monthly maximum temperature was 28 ºC in February and March, but the mean minimum was 12 ºC in July and August.

METHODS

Feeding quadrat method was chosen to determine the diet composition of African buffalo as suggested by various authors (Grobler 1983, Macandza et al. 2004, Venter and Watson 2008, Magome et al. 2008). The feeding quadrat method was supplemented by faecal analysis (Landman and Kerley 2001, Macandza et al. 2004, Paola et al. 2005) to examine forage species, which could be consumed out of areas covered by feeding quadrat survey. A feeding quadrat survey was carried out by backtracking buffalo of fresh tracks. Feeding signs were located and identified through opportunistic observations (Blake 2002b), by searching fresh footmarks and feeding signs in areas where buffalo frequented (Perrin and Brereton-Stiles 1999) and by moving along the dry weather road that pass through the forest. Fresh tracks and feeding signs were followed once attributed to the buffalo. Plant species grazed by buffalo were less likely to cause confusion with feedings of other herbivores due to their distinctive footmarks and feeding patterns. Observed signs, which were too old, ambiguous and not attributed to buffalo were ignored. The backtracking of buffalo track was conducted every morning during data collection, which sometimes ended up with observations of resting buffalo in thicket riverine and bottomland vegetation or dense forest. However, they were not safely approached because they usually fled to avoid danger.

When fresh buffalo tracks were located, grasses and herbs were quantified using 1 × 1 m quadrats laid at feeding station (Bullock 2006) along the foraging path of African buffalo (Magome et al. 2008, Venter and Watson 2008). This was done for five effective days four times per year over a period of two years encompassing the wet and dry seasons. The quadrats were laid randomly at 10 m intervals at feeding stations of buffalo. Each day, 11 to 16 quadrats were sampled for all potential species available and utilized by buffalo (Arsenault and Owen-Smith 2008, Venter and Watson 2008). Samples of grazed species were collected and pressed for identification and preparation of reference slides (Macandza et al. 2004). Shrubs were surveyed using 10 m^2quadrat (Greenwood and Robinson 2006) laid around each 1 m^2 quadrats used for grasses and herbs. In this study, browse species refers to herbs, shrubs and woody plants, whereas the family Poaceae and Cyperaceae were classed as graminoids (Steuer et al. 2010). Collected forage species were also identified into different families and forage categories.

Dung piles were collected from different habitats and air-dried before faecal analysis (MacLeod et al. 1996). Faecal samples of the same season of a year were amalgamated to form composite samples (Homolka 1987, Katona and Altbacker 2002). Thirty-two (Wet=16; Dry=16) composite faecal samples were used to determine faecal nitrogen and phosphorus contents (Magome et al. 2008, Ndawula et al. 2011). The percentage of nitrogen was determined by means of Kjeldahl analysis method (Van Soest 1994). Phosphorus was determined by wet digestion and read by a spectrophotometer (Wrench et al. 1996). Both phosphorus and nitrogen contents were presented and quantified as dry matter. Faecal Crude Protein (FCP%) was calculated as 6.25 (Standard value) × N% (nitrogen) (Van Soest 1994) and Dietary Crude Protein (DCP) as DCP% = 1.677 (Standard value) FCP% - 6.93 (Standard value) (Sinclair 1977, Prins 1996). Seasonal differences in diet and patterns of diet change were tested using a Chi-square test of association (Zar 1996). Chi-square goodness of fit was used to test all single categorical data. One-way analysis of variance (ANOVA) was used to test differences in the percentage contributions of different forage categories to the diet of buffalo. Forage species that contributed $\geq$ 2.5% in the diet of buffalo were considered as staple species assuming that each of the 39 identified forage species had an equal chance (≈2. 56%) to contribute to the diet of the study animal as described by Tshabalala et al. (2009). The proportion of plants used as diet was calculated as the ratio of a species used in the diet to all species used, while forage availability was computed as the ratio of the total number of feeding sites where a species was noted to the total number of feeding sites surveyed (Tomlinson 1980, Magome et al. 2008, Hensman et al. 2012). Acceptability was computed as the ratio of the number of quadrats in which a species was consumed to the total number of quadrats in which the species was recorded as available (Owen-Smith and Cooper 1987, Venter and Watson 2008). Acceptability of forage species was categorized as low ($\leq$0.49) and high ($\geq$0.50) as reported by Macandza et al. (2004). The mean faecal nitrogen and phosphorus contents between seasons were tested by t-test (Zar 1996). The level of significance accepted was 0.05. Statistical analyses were performed using a combination of statistical tools such as Statistical Package for Social Sciences (IBM SPSS 24), PAST Version 3.15 software and Epi-InfoTM-7.

RESULTS

Thirty-nine plant species were identified as annual dietary composition of Cape buffalo populations in JWPF. Out of this, 32 were recorded in the wet and 28 in the dry seasons. Among these, 21 species were common to both seasons. Forage species were classed into four growth forms. Accordingly, graminoids accounted for the largest identified forage species (16), followed by herbs (14) and shrubs (7) and climbers (2). The difference in the number of forage species utilized by buffalo in wet and dry seasons was not significant (χ^2 = 0.87, df=1, P >0.05), but significant among the forage categories (χ^2= 11.11, df = 3, P = 0.05). In addition, five cultivated crops belonging to the family Poaceae such as *Zea mays, Sorghum bicolor, Triticum aestivum, Hordeum vulgare* and *Eragrostis tef* were consumed by Cape buffalo around JWPF.

The proportions of forage species used by buffalo in wet and dry seasons are presented in Table1. In the wet season, *Panicum hochstetteri*, *Setaria poiretiana, Achyranthes aspera, Bidens ghedoensis, Bidens pilosa, Cyperus distans* and *Galinsoga quadriradiata* were identified as the main forage species. They accounted for 83.2% of the wet season diet composition of buffalo. The top three staple species: such as *P. hochstetteri* (27.5%), *S. poiretiana* (17.5%) and *C. distans* (20.0%)formed 65% of the wet season diet. Among the staple forage species, *P. hochstetteri* and *S. poiretiana* were used in proportion to their availability, whereas other species were considered both as staple and preferred species in the wet season. Plant species that were staple in the wet season, but totally absent in the dry season were *B. ghedoensis, B. pilosa* and *G. quadriradiata*.

In the dry season, Cape buffalo foraged on seven staple grass species, such as *P. hochstetteri, S. poiretiana, Digitaria abyssinica, Cynodon dactylon, Eragrostis* spp., *Cyperus fischerianus* and one staple shrub species (*Dracaena afromontana*), which together formed 85.9% of the diet. *Panicum hochstetteri* (40.3%) and *S. poiretiana* (26.1%) alone accounted for 66.4% of dry season diet of buffalo. *Cyperus fischerianus*, *Eragrostis* spp., *D. abyssinica*, *C. dactylon* and *D. afromontana* were staple species in the dry season, but these were reduced in the wet season.

Eight forage species such as *P. hochstetteri, S. poiretiana, D. abyssinica, C. dactylon*, *A. aspera, C. distans, G. quadriradiata* and *D. afromontana* were annual staple forage species, which accounted for 81.4 % of the annual diet composition of Cape buffalo. *Panicum. hochstetteri* (33.9%), *S. poiretiana* (21.8%) and *C. distans* (11.1%) were the top three staple forage species that constituted about 66.8% of the annual diet composition of Cape buffalo. All annual staple plant species were found in both seasons except *G. quadriradiata,* which was found only in the wet season. In this study, only forage species that contributed ≥1% in the diet of the Cape buffalo populations either in the wet or dry seasons were subjected to seasonal dietary contribution analyses as shown in Table 1.

Graminoids formed 82.6% ± 2.4 of the annual diet composition of Cape buffalo, followed by herbs (13.5% ± 0.3) and shrubs (3.7% ± 0.5). Graminoids were used more in the dry season (90.2% ± 2.9) than the wet season (75.2% ± 2.2), whereas herbs were used more in the wet season (24.4%±1.2) than the dry season (2.6%±0.2). Shrubs were consumed more in the dry season (6.8%) than in the wet season (0.6%) (Figure 2). The seasonal contribution of forage categories to the diet of Cape buffalo differed significantly ($F_{34} = 32.70$, $P < 0.05$).

Grass contributed 82.6% of the annual diet of Cape buffalo, whereas browse contributed 17.4%. In both seasons, grass formed the greatest proportion of buffalo diet. Browse was higher in the wet season (25%±0.4) than the dry season (9.8%±0.2) (χ2 =6.64, df= 1, P<0.05), whereas the contribution of grass in the diet of Cape buffalo was higher in the dry season (90.2%±2.9) than the wet season (75.2%±2.2), but the difference was not significant (χ2 = 1.37, df=1, P >0.05).

Table 1. Forage species (mean ± SD) which contributed ≥1% in the diet of Cape buffalo either in the wet or dry season in JWPF.

Family	Forage species	Annual	Wet	Dry	χ2, df=1
	Graminoids =11				
Poaceae	*Panicum hochstetteri* Steud.	33.9±9.1	27.5 ±1.1	40.3±1.3	77.07***
Poaceae	*Setaria poiretiana* (Schult.) Kunth	21.8±6.1	17.5±2.5	26.1±1.7	50.27***
Poaceae	*Digitaria abyssinica* Hochst. ex A.Rich.	3.6±2.5	1.8±0.1	5.3±0.6	74.14***
Poaceae	*Andropogon abyssinicus* R.Br. ex Fresen.	1.3±0.8	1.9±0.7	0.7±0.5	0.14
Poaceae	*Cynodon dactylon* (L.) Pers.	2.6±1.5	1.5±0.7	3.6±0.8	19.93***
Poaceae	*Eragrostis* spp. Wolf	1.4±1.6	0.2±0.4	2.5±0.0	1.60
Poaceae	*Pennisetum thunbergii* Kunth	1.1±0.6	0.7±0.3	1.5±0.3	0.77
Poaceae	*Hyparrhenia hirta* (L.) Stapf.	1.0± 0.4	0.7±0.3	1.3±0.2	6.19*
Poaceae	*Hyparrhenia cymbaria* (L.) Stapf.	0.8±0.3	0.6±0.2	1.1±0.3	1.31
Cyperaceae	*Cyperus distans* L.f.	11.1±12.6	20.0±0.5	2.2±4.7	25.04***
Cyperaceae	*Cyperus fischerianus* Schimp. ex A.Rich.	1.9±1.8	0.6±1.2	3.2±0.4	6.42*
	Herbs =8				
Amaranthaceae	*Achyranthes aspera* L.	2.5±2.8	4.5±0.1	0.5±1.2	0.18
Asteraceae	*Bidens ghedoensis* M.esfin	1.8±2.5	3.6±1.0	-	-
Asteraceae	*Bidens pilosa* L.	1.9± 2.7	3.8±0.7	-	-
Asteraceae	*Guizotia scabra* (Vis.) Chiov.	0.5±0.8	1.2±0.2	-	
Asteraceae	*Galinsoga quadriradiata* Ruiz. & Pav.	3.2±4.5	6.3±1.2	-	-
Acanthaceae	*Hypoestes forskaolii* (Vahl.) R.Br.	1.4± 0.4	1.1±0.4	1.6±0.7	10.21***
Lamiaceae	*Satureja paradoxa* (Vatke) Engl.	0.5±0.7	1.1±0.3	-	-
Polygonaceae	*Persicaria nepalensis* (Meisn.) Miyabe	0.6±0.9	1.3±1.0	-	-
	Shrubs =1				
Dracaenaceae	*Dracaena afromontana* Mildbr.	2.7± 3.1	0.5± 0.2	4.9±0.7	9.4**
	Total	95.6	96.4	94.8	

*P <0.05; **P<0.01; ***P<0.001

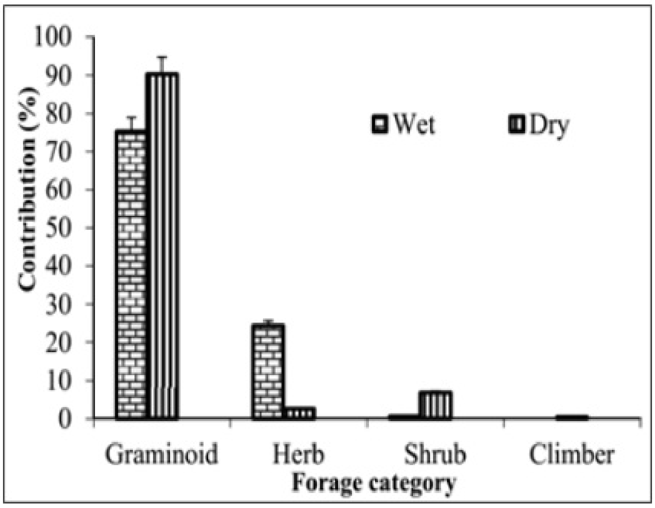

Figure 2. Seasonal dietary contributions (%) of different forage categories to the diet of Cape buffaloes in JWPF (Mean ±SE).

Seasonal availability of 20 forage species that contributed ≥1% in the diet of Cape buffalo either in the wet or dry seasons are shown in Figure 3. Fourteen forage species were available to the buffalo populations, in both the wet and dry seasons, whereas six species were available only in the wet season. *Panicum hochstetteri* (29.9%), *S. poiretiana* (21.1%), *H. forskaolii* (6.3%), *A. aspera* (5.4%) and *C. distans* (3.5%) were available to Cape buffalo in both seasons and together accounted for 66.2% of available forages. *Panicum hochstetteri* and *S. poiretiana* were the top two forage species consistently available for Cape buffalo in greatest proportion in wet and dry seasons. These species alone formed 51% of the total available forages of the buffalo populations in JWPF. *Panicum hochstetteri* was available more in the dry season (32.7%) than the wet season (27.2%) ($\chi2$ =11.51, df =1, P < 0.05). Similarly, *S. poiretiana* was available to Cape buffalo more in the dry season (24.7%) than the wet season (17.4%), but the difference was not significant ($\chi2$=0.48, df =1, P > 0.05). The availability of *H. forskaolii* and *A. aspera* was similar in the wet and dry seasons, and the difference was not significant ($\chi2$=2.14, df=1, P>0.05; $\chi2$=1.08, df =1, P>0.05) for the two species, respectively. *Cyperus distans* was available more in the wet season (9.4%) than in the dry season (1.4%) and the difference was significant ($\chi2$=6.37, df =1, P <0.05).

In the wet season, most forage species were available for Cape buffalo in open, plantation and riparian forest habitats, but less in dense forest. *Panicum hochstetteri* and *H. forskaolii* were the two forage species that had better availability (>2%) in the dense forest. *Panicum hochstetteri* had >3% availability in all habitats and seasons, whereas *S. poiretiana* had >4.5% availability in all habitats, but less in the dense forest in the wet (0.7%) and dry (1.5%) seasons. In the wet season, *C. distans* was available in most habitats, but it was low in the dry season. The availability of grass was high in the plantation habitat, open forest and riparian forest, but low in dense forest in both seasons. *Panicum hochstetteri, S. poiretiana, C. distans* and *H. forskaolii* were easily available for Cape buffalo in the wet season, whereas *P. hochstetteri, S. poiretiana* and *H. forskaolii* in the dry season in the study habitats. The overall forage species availability recorded among the four habitats was significantly different in the wet season ($\chi2$ =744.58, df = 69, P<0.05) and in the dry season ($\chi2$ =902.30, df=54, P <0.05).

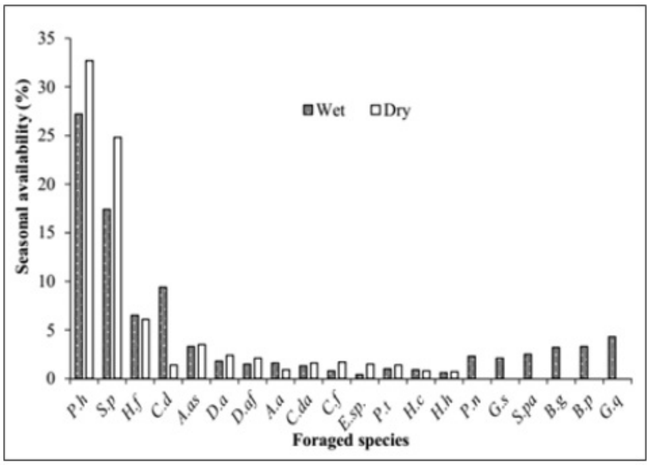

Figure 3. Seasonal changes in the availability (%) of forage species recorded in more than 5 quadrats and contributed ≥1% in the diet of Cape buffaloes either in the wet or dry seasons in JWPF (*P.h= P.hochstetteri,S.p=S.poiretiana, H.f=H. forskaolii, C.d=C.distans,A.as=A.aspera,D.a=D.abyssinica,D.af=D.afromontana,A.a=A.abyssinicus, C.da=C.dactylon, C.f=C.fischerianus, E.*sp.*=Eragrostis*spp.*, P.t=P. thunbergii, H.c=H. cymbaria, H.h=H. hirta, P.n=P. nepalensis, G.s=G. scabra, S.pa=S. paradoxa, B.g= B. ghedoensis, B.p=B. pilosa,G.q=G. quadriradiata*).

Graminoids were the most commonly available forage categories to the Cape buffalo constituting 65.2% ±6.3 in the wet and 72.7% ±8.5 in the dry seasons in JWPF (Figure 4). Herbs make about 33.0%±3.5 in the wet season and 14.4%±2.7 in the dry seasons, whereas shrubs contributed 1.8%±0.7 in the wet season and 9.6%±2.4 in the dry season. Climbers were the least available forage categories to Cape buffalo constituting about 3.5%±1.6 only in the dry season. Forage categories available to the Cape buffalo in the wet and dry seasons differed significantly ($F_{3,4} = 31.94$, $P < 0.05$).

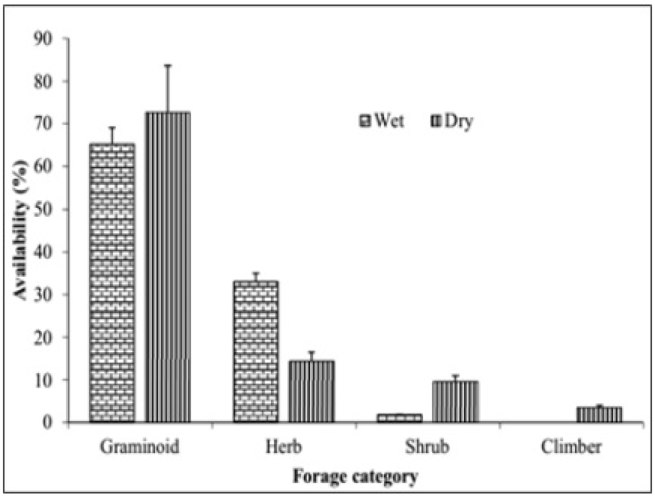

Figure 4. Forage categories (%) available to the Cape buffaloes in the wet and dry seasons in JWPF.

Acceptability index was calculated for 20 foraged species that contributed ≥1% in the diet of the Cape buffalo either in wet or dry seasons. In the wet season, 12 (60%) of them showed high acceptability, whereas 8 (40%) showed low acceptability by the buffalo populations. In the dry season, however, acceptability was calculated only for 14 forage species out of which 12 (86%) showed high acceptability, and 2 (14%) species showed low acceptability (Figure 5). *Panicum hochstetteri, S. poiretiana* and *D. abyssinica* were the top three species that showed high and consistent acceptability in both seasons. *Cyperus distans* and *A. abyssinicus* also showed high acceptability in the wet and dry seasons ($\chi 2 = 1.89$, df=1, $P < 0.05$ and $\chi 2 = 1.3$.df=1, $P > 0.05$), respectively. *Achyranthes aspera* showed low acceptability in the dry season (0.12), but high acceptability in the wet season (0.86), and the difference was significant ($\chi 2 = 27.94$, df=1, $P < 0.05$). *Cynodon dactylon, D. afromontana, Eragrostis* spp. and *C. fischerianus* that showed low acceptability in the wet season showed high acceptability in the dry season ($\chi^2 = 16.50$, df=1, $P < 0.05$, $\chi 2 = 6.50$, df=1, $P < 0.05$, $\chi 2 = 50.84$, df=1, $P < 0.05$ and $\chi^2 = 9.44$, df=1, $P < 0.05$), respectively. *Hypoestes forskaolii* had low acceptability both in the wet (2%) and dry (25%) seasons.

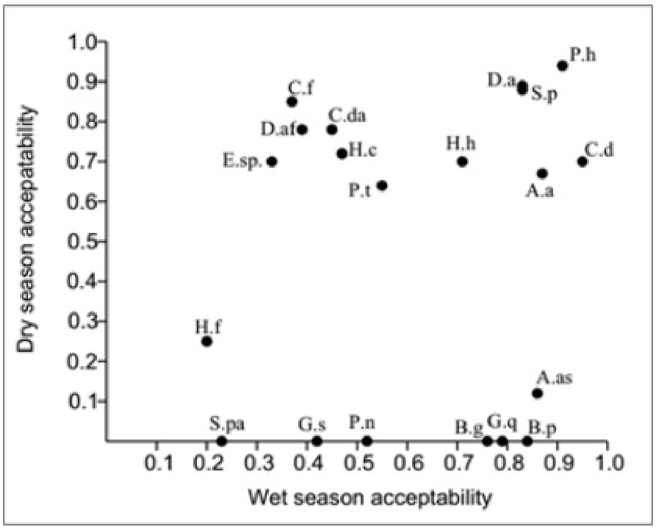

Figure 5. Seasonal acceptability of forage species that contributed ≥1% in the diet of Cape buffaloes either in the wet or dry seasons in JWPF (*P.h= P. hochstetteri, S.p= S. poiretiana, H.f= H. forskaolii, C.d= C. distans, A.as= A. aspera, D.a = D. abyssinica, D.af= D. afromontana, A.a= A. abyssinicus, C.da= C. dactylon, C.f= C. fischerianus, E.*sp.*= Eragrostis* sp., *P.t= P. thunbergii, H.c= H. cymbaria, H.h= H. hirta, P.n= P. nepalensis, G.s= G. scabra, S.pa= S. paradoxa, B.g= B. ghedoensis, B.p = B. pilosa, G.q= G. quadriradiata*).

Faecal analysis of buffalo revealed that the nitrogen content of the dung ranged from 17.3 to 21.0 g kg^{-1} in the wet and 14.6 to 19.6 g kg^{-1} in the dry seasons. The mean nitrogen content of buffalo dung was 18.4±0.53 g kg^{-1} in the wet and 17.7±0.71 g kg^{-1} in the dry seasons. This difference was not significant (t=1.48, df=15, $P > 0.05$). Likewise, faecal phosphorus content ranged from 2.5 to 5.6 g kg^{-1} in the wet season and 2.4 to 5.3 g kg^{-1} in the dry season. The mean faecal phosphorus content was 4.3±0.39 g kg^{-1} in the wet and 3.9±0.36 g kg^{-1} in the dry season. The difference in the mean phosphorus contents between the wet and dry seasons was also not significant (t=0.91, df=15, $P > 0.05$). Faecal crude protein and DCP contents of buffalo were 11.7%±0.84 and 12.7%±0.5 in the wet season, respectively. Similarly, FCP and DCP contents were 10.6%±0.44 and 10.8%±0.76 in the dry season, respectively.

DISCUSSION

Feeding quadrat survey showed that 39 forage species were utilized by Cape buffalo in JWPF. These forage species were classed into graminoids, herbs, shrubs and climbers. Among these, grasses formed the bulk of the buffalo diet (82.6%) in JWPF. Similar studies conducted in the succulent thicket habitat of Addo Elephant National Park and Great Fish River Reserve, South Africa showed that the diet of buffalo largely consisted of grass species (Landman and Kerley 2001, Tshabalala et al. 2009). Earlier studies conducted in savanna and savanna woodland habitats have also reported large quantities of grass in the diets of African buffalo (Sinclair 1974, Mloszewski 1983, Beekman and Prins 1989, Prins 1996, Macandza et al. 2004). Moreover, the diet composition of Jorgo-Wato buffalo was similar to the diet composition of forest buffalo reported from Lope National Park, Gabon, in which grasses (Poaceae) and sedges (Cyperaceae) predominated their diet (Van derHoek et al. 2012). African buffalo are known to be hyper-grazers (Prins, 996) because 75–100% of their diet have been represented by grasses (Codron et al. 2007). As described by Landman and Kerley (2001), grass contributed 71.9 % of buffalo diet in the succulent thicket habitat of the Addo Elephant National Park, South Africa. Similarly, this study reconfirmed that buffalo are true grazers as they still dictate their savanna mode of feeding even if they inhabit pure forested habitats of JWPF. Furthermore, the greatest proportions of grass in the diet of Jorgo-Wato buffalo disproved the assumption that they have shifted their diet into browse like buffalo of Addo Elephant National Park (De Graaf et al. 1973). A study carried out in the Eastern Cape thicket of Addo Elephant National Park showed that African buffalo are grazers, not browsers even in grass-limited habitats (Landman et al. 2018).

The proportion of browse used by Jorgo-Wato buffalo (17.4%) was within the estimated ranges of browse use (5 to 26%) as determined by Stark (1986). However, browse may appear to be less significant for Jorgo-Wato buffalo as reported by Prins and Beekman (1989) because of the availability of few, but adequate fresh and shade tolerant grass species throughout the year. This view is supported by Mloszewski (1983), who stated that buffalo browse only when the availability and quality of grass is reduced. Likewise, buffalo did not browse in the Hluhluwe-Umfolozi Game Reserve, South Africa, due to high nutritional quality of forages (Perrin and Brereton-Stiles 1999). Buffalo are limited from browsing because their digestive system and rumen microbes are not well adapted to browse diet (Hofmann 1989, Novellie et al. 1991). In this study, the higher proportion of browse in the wet season than the dry season could be ascribed to the higher availability of the herbaceous layer in the wet season, agreeing with Lesoli (2008), who reported that high rainfall in the wet season increases the proliferation of high herbaceous biomass. Moreover, the mixed growth patterns of annual herbs with grasses in the wet season could make Cape buffalo to accidentally consume more herbs than the dry season as revealed by Venter (2006). But in the dry season, Cape buffalo browse some shrub species in the riverine and dense forests. Previous studies have shown that African buffalo continuously include browse into their regular diet regardless of shortage of forages (Mloszewski 1983, Macandza et al. 2004). However, the diet of Cape buffalo was dominated by grass than browse similar to most studies conducted else in African countries (Table 2).

Table 2. Grass and browse contents (%) in the diet of African buffaloes collated from different study areas

Reference	Study site	Grass %	Browse %	Country
This study	JWPF	82.6	17.4	Ethiopia
Leuthold, 1972	Tsavao National Park	98.5	1.5	Kenya
Sinclair, 1974	Serengeti-Mara Region	99	1	Tanzania-Kenya
Beekman and Prins, 1989	Lake Manyara National Park	95	5	Tanzania
Tshabalala *et al.*, 2009)	Great Fish River Reserve	69.5	30.5	South Africa
Landman and Kerley, 2001	Addo Elephant National Park	71.9	28.1	South Africa
Jarman, 1971	Zambezi valley	46	54	Zimbabwe
Cromhout, 2006	Eastern Kalahari region	82	18	South Africa
Macandza *et al.*, 2004	Kruger National Park	Not described numerically, but they were principally grazers		South Africa
Muposhi *et al.*, 2014	Umfurudzi Park	Not described numerically, but they spent 20% of their time browsing		Zimbabwe

Most forage species recorded in the diet of Jorgo-Wato buffalo have not previously been reported as dietary composition of African buffalo across the range of the species (Sinclair 1977, Prins 1996, Landman and Kerley 2001, Macandza et al. 2004, Tshabalala et al. 2009). Previous studies described that forage species utilized by African buffalo vary between seasons and habitat types (Sinclair 1977, Prins 1996). Similarly, the variation in the forage species composition of Jorgo-Wato buffalo could be ascribed to variation in species composition of the area and an indication of Cape buffalo's dietary adaptation to a newly colonized pure forested range or habitat. Most diet profiles of savanna buffalo have been commonly reported from savanna and savanna dominated woodlands (BeekmanandPrins1989, Funston et al. 1994, Macandza et al. 2004, Cromhout 2006), but limited from pure forested habitats. Staple dietary composition of Jorgo-Wato buffalo, which has been directly reported as dietary composition of African buffalo elsewhere was *C. dactylon* (Landman and Kerley, 2001, Tshabalala et al. 2009). However, the other staple forage species were *P. hochstetteri*, *S. poiretiana, C. distans*, *D. abyssinica, D. afromontana* and *G. quadriradiata* are absent from previous reported diet profile of African buffalo, but other species from the same genus are widely recognized (Leuthold 1972, Macandza et al. 2004, Venter and Watson 2008, Bekhuis et al. 2008, Tshabalala et al. 2009). Moreover, *A. aspera* is a staple forage that has not been reported as diet of African buffalo elsewhere.

Cynodon dactylon was described as staple forage of African buffalo in the Addo Elephant National Park (Landman and Kerley 2001), in Lake Manyara National Park (Prins 1996) and in Great Fish River Reserve (Tshabalala et al. 2009). In contrast, the annual dietary contribution of *C. dactylon* was reported to be low in Doornkloof Nature Reserve, South Africa (Venter 2006). In JWPF, *C. dactylon* occurs in small glades and adjacent steep slope as stated by Paley and Kerley (1998), and used more in the dry season. In this study, the proportion of *C. dactylon* in the diet of buffalo was higher in the dry season than in the wet season. The low dietary contribution of *C. dactylon* in the wet season could be attributed to its stoloniferous growth habit, which was evolved in some grass species as an escape strategy from large herbivores (Wolfson and Tainton 1999, Skarpe and Hester 2008).

Panicum hochstetteri and *S. poiretiana* were the two staple perennial grasses that form the backbone of the Cape buffalo diet in both seasons. *Panicum hochstetteri* had higher acceptability and availability than *S. poiretiana* in both seasons. Both species were known to exist in open, riverine and plantation forests due to their shade loving habit. Though *P. hochstetteri* has not been reported in the previous diet profile of African buffalo, the significance of *Panicum* species for African buffalo has been well documented (Funston et al. 1994, Prins 1996, Perrin and Brereton-Stiles 1999). African buffalo have been reported to depend on *Panicum* species throughout the entire year in Hluhluwe-Umfolozi Game Reserve, South Africa (Perrin and Brereton-Stiles 1999). As reported by Macandza et al. (2004), *P. maximum* and *P. coloratum* have contributed the largest amount of buffalo diet in Kruger National Park. Similarly, *P. deustum* has contributed a significant amount to the diet of African buffalo in the wet and dry seasons in the Great Fish River Reserve in South Africa (Tshabalala et al. 2009). Contrary to this result, *Setaria* species has been reported to be consistently avoided by buffalo in Hluhluwe-Umfolozi Game Reserve (Perrin and Brereton-Stiles 1999) and Kruger National Park, South Africa (Macandza et al. 2004). However, *S. neglecta* was the principal diet of African buffalo in Great Fish River Reserve in the dry season, but neglected in the wet season (Tshabalala et al. 2009). In this study, *S. poiretiana* had high acceptance in both seasons, which could be due to its availability or a new dietary adaptation of Cape buffalo to forested habitats, where the diversity of grass species is scarce. *Setaria poiretiana* was grazed more when it was younger than old, probably due to its fresh and green foliage that attracts Cape buffalo for grazing.

Cyperus distans was the staple forage species that constitutes the bulk of buffalo diet in the wet season. This could be attributed to its high availability and acceptability in the forest during this season. In JWPF, *C. distans* were available in open forest, plantation forest and in riparian forest in the wet season. However, *Cyperus* species are mostly limited to the riverine and riparian banks of upwelling groundwater as reported by Prins (1996). As described by Sinclair (1977), African buffalo spent much of their time in the riverine and riparian banks which could contribute for the higher proportion of *Cyperus* species to be consumed in the dry than the wet season. Similarly, *Cyperus* species have been used as buffer food in the dry season and formed the bulk of the buffalo diet in the Masai ecosystem (Prins 1996). In contrast, the proportion of *C. distans* was reduced in the diet of Jorgo-Wato buffalo in the dry season, which could be attributed to its low availability. *Cyperus* species have been also reported as dietary composition of African buffalo in Doornkloof Nature

Reserve, South Africa (Venter and Watson 2008) and Nouabale-Ndoki National Park, Republic of Congo (Blake 2002a), but their contribution was minimal.

The importance of *Digitaria* species in the diet of African buffalos have been widely reported in several studies elsewhere (Leuthold 1972, Macandza et al. 2004, Cromhout 2006, Tshabalala et al. 2009, Muposhi et al. 2014). Some *Digitaria* species such as *D. macroblephara* and *D. eriantha* have been reported as staple diets of African buffalo in Tsavo National Park (Leuthold 1972) and Great Fish River Reserve (Tshabalala et al. 2009), respectively. *Digitaria abyssinica* was also a staple diet of buffalo, which contributed more in the dry season than the wet season. This was in agreement with Macandza et al. (2004), who found that African buffalo in the Kruger National Park favour *D. eriantha* in the late dry season.

Staple forage species such as *A. aspera, G. quadriradiata* and *D. afromontana* have not been reported as diet of African buffalo, but other species from the same family were reported for *G. quadriradiata* and *D. afromontana* in the diet of forest buffalo in Campo-Ma'an National Park, Cameroon (Bekhuis *et al.* 2008). The contribution of *A. aspera* to the diet of buffalo was highest in the wet, but decreased in the dry season. This could be due to the reduction of foliage, and their flowers produce long adhesive spiny structure that might disfavour buffalo when aged. *Galinsoga quadriradiata* is an annual herb, which sprouts quickly and grows fast following rains in the early wet season and made about 6.3% of buffalo diet, but totally deteriorated over the course of the dry season. Increased consumption of this species was in the wet season or when young due to its high palatability, which gradually declines as it gets longer and older with time. *Dracaena afromontana* is shrub that mostly grows as the undergrowth of dense forests around montane forested areas. Its dietary contribution to Cape buffalo was high in the dry season, but less in the wet season. Seasonal variation in the diet contribution of *D. afromontana* could be associated with a habitat shift of Cape buffalo due to human disturbances.

Cape buffalo favoured only few forage species. Among the 39 forage species identified as diet of Cape buffalo, *P. hochstetteri, S. poiretiana* and *C. distans* alone made about 66.8% of the annual diet composition, whereas the remaining 33.2% are formed by 36 forage species. Though African buffalo consume diverse plant species (Leuthold 1972, Sinclair 1974, Prins 1996), only few forage species had dominated the diet of Jorgo-Wato buffalo agreeing with previous views that only few species available to African buffalo make the bulk of their diet (Leuthold 1972, Prins and Beekman 1989). In JWPF, Cape buffalo did not show overall seasonal dietary shift, but, largely and consistently depended on *P. hochstetteri* and *S. poiretiana,* particularly in the dry season. *Panicum hochstetteri* and *S. poiretiana* had high availability and acceptability in both seasons.

African buffalo are known to forage on a wide variety of herbs, shrubs and browse species (Sinclair 1977, Landman and Kerley 2001, Cromhout 2006). Similarly, *Bidens ghedoensis*, *Bidens pilosa* and *Galinsoga quadriradiata* were herbs consumed in the wet season, but these species were less in the dry season. The distribution and habitat availability of these herbs were low, but restricted to small forest glades and edges. *Bidens ghedoensis* and *B. pilosa* were staple forage species in the wet season as determined by feeding quadrat survey. *Achyranthes aspera* and *D. afromontana* were a staple forage in the wet and dry seasons, respectively. *Achyranthes aspera* had similar availability in both seasons, but its habitat availability was higher in open and riparian forests in the wet and dry seasons, respectively. *Achyranthes aspera* had high acceptability in the wet season (0.86), but low in the dry season (0.12). *Dracaena afromontana* had similar seasonal availability, but its habitat availability was higher in dense forest than other habitat types. The dietary contribution of *D. afromontana* increased in the dry season, which could be ascribed to the temporal habitat shift of Cape buffalo for more suitable habitats (Sinclair 1977, Prins and Beekman 1989, Funston et al. 1994, Macandza et al. 2004) and avoidance of humans.

Feeding quadrat survey method was used to identify forages to easily the species level. This could be ascribed to the bunch growth habit of most forages, and buffalo's preference for tall forages made them to have more remnants after grazed by African buffalo. As revealed by Sanders et al. (1980), direct observation of foraged species provides a more accurate picture of the diet composition of range animals. African buffalo mostly feed on tall grasses (Beekman and Prins 1989) and did not graze the whole forage species to the ground without leaving evidence behind. The minimum threshold level of faecal nitrogen for the normal health status of African buffalo was 13.0 g kg^{-1} below which their body condition deteriorates rapidly (Leslie and Starkey 1985, Irwin et al. 1993, Grasman and Hellgren 1993, Grant et al. 2000). The faecal nitrogen content of Jorgo-Wato buffalo was 18.4 g kg^{-1} and 17.7 g kg^{-1} in the wet and dry seasons, respectively, which was above the minimum threshold level in both seasons. In

Doornkloof Nature Reserve, South Africa, Venter and Watson (2008) found that the mean faecal nitrogen concentration was 15.3 g kg^{-1} in the wet and 12.9 g kg^{-1} in the dry seasons. This was above the minimum threshold level of faecal nitrogen content required (13 g kg^{-1}) in the wet season, but almost equivalent to the minimum threshold level of in the dry season (Leslie and Starkey 1985, Irwin et al.1993, Grasman and Hellgren 1993, Grant et al. 2000). Previous studies have reported a mean faecal nitrogen content of 10.7 g kg^{-1} in Tswalu Kalahari Reserve, South Africa (Cromhout 2006) and 11.5 g kg^{-1} in Kruger National Park (Grant et al. 1995). The differences in the concentration of faecal nitrogen across different buffalo ranges could be attributed to the variation of nitrogen across landscapes, foraged species and soil types (Grant et al. 1995). Bottom lands have a high accumulation of nutrients and moisture (Morison et al. 1984), which facilitates rapid growth and continuous sprouting of plants that attract African buffalo in the dry season. In JWPF, bottom land and riparian gorges are expected to have high nitrogen and phosphorus as described by Weel et al. (2015). Faecal nitrogen content below 13.0 g kg^{-1} in wildebeest, zebra, cattle and impala was followed by a rapid body decline (Grant et al. 1995, Wrench et al. 1997, Grant et al. 2000) and increased nutritional stress (Grant et al. 2000). According to the physical condition evaluation criteria of ungulates (Riney 1960) and African buffalo in particular (Cromhout 2006), the body condition of Jorgo-Wato buffalo was good (hook bones barely visible) and areas between hook and pin bone was flat. This was in agreement with the finding of Grant et al. (1996), who reported a strong correlation between body condition and nitrogen content. Faecal crude protein and dietary crude protein are positively correlated in herbivores. Several studies have confirmed that FCP and DCP were positively correlated in herbivores (Leslie and Starkey 1985, Wrench et al. 1997, Nicholson et al. 2006). The minimum DCP required for the normal health status of buffalo is 7% (Sinclair 1977). In this study, the mean DCP of buffalo was estimated to be 12.7% in the wet and 10.8% in the dry seasons, which were greater than the aforementioned minimum DCP values set by Sinclair (1977).

As reported by Grant et al. (2000), the minimum faecal phosphorus content required for herbivores was 2 g kg^{-1}. Previous study conducted in Doornkloof Nature Reserve, South Africa revealed mean faecal phosphorus content of 2.9 g kg^{-1} in the wet and 2.0 g kg^{-1} in the dry seasons, which was above the minimum threshold level for the wet season, but the same as to the threshold level for the dry season (Grant et al. 2000). In this study, a mean faecal phosphorus content of 4.3 g kg^{-1} in the wet and 3.9 g kg^{-1} in the dry seasons were recorded, which were above the minimum threshold level (2 g kg^{-1}) as indicated by Grant et al. (2000). In the Kruger National Park, a mean faecal phosphorus content of 4.5 g kg^{-1} and 2.1 g kg^{-1} was recorded for African buffalo in the wet and dry seasons, respectively (Grant et al. 2000). A faecal phosphorus content of less than 2.0 g kg^{-1} indicates phosphorus deficiency (Wrench et al. 1997), which reduces reproduction if it consistently remains below the threshold level (Grant et al. 1995, Wrench et al. 1997, Grant et al. 2000). The faecal phosphorus content of Jorgo-Wato buffalo was different from previous reports, which could be attributed to the variation of phosphorous between landscapes, grass, browse, seasons and soil types (Grant et al. 1995).

African buffalo face shortages of food and poor digestibility in the dry season (Grant et al. 1995). Palatability (Scholes and Walker 1993), digestibility (Bartiaux-Thill and Oger 1986) and DCP of forage species (Irwin et al. 1993) were proven to be positively correlated with nitrogen contents, but inversely correlated with fibre content (Buys 1990). In the dry season, the level of fibre content increase, but DCP declines (Owen-Smith 1982). The high and consistent faecal nitrogen and phosphorus contents of buffalo in both seasons indicated that Jorgo-Wato buffalo had no basic dietary deficiency. As revealed by Kingdon (1982), humid climate of forested area encourages the continuous sprouting of perennial grasses and herbs, which could provide sufficient food resources throughout the year for forest inhabiting mammals. Diet quality analysis of Jorgo-Wato buffalo revealed that African buffalo that feed in the forested habitats benefited more, in terms of forage quality, than those feeding in open savanna habitats, where forages dieback over the course of the dry season (Owen-Smith 1982). As revealed by Klaus-Hugi et al. (1999), large herbivores live in more open habitats consume less quality food in bulk and graze less selectively on grasses.

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