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Functional heterogeneity of habitats and dry season forage variability in an Okavango Delta landscape, northern Botswana

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ABSTRACT

The late dry season is a period when forage resources become limited in some African savannas that can induce a strong demographic bottleneck in herbivore populations with limited access to resource heterogeneity. This study determined forage quality and quantity between wetlands and drylands habitats during the late dry season. We subjectively sampled forage characteristics in four habitat types around the distal reaches of the Tsum Tsum floodplains of the Okavango Delta during the late dry season of 2015. The habitat types were mopane and sandveld woodland far from floodplains (two major dryland habitat types), sandveld habitats that receive soil moisture inputs from adjacent floodplains (wet sandveld) and sedgeland habitat within the floodplain. Leaves collected from forage in each habitat type were oven dried, milled and analysed for total nitrogen. Data of greenness, height, biomass and protein were analysed using Kruskal-Wallis test. Forage in wet sandveld had by far the highest protein content (~16%) of all habitat types but forage height and biomass were very low, whereas sedgelands had the highest biomass of adequate-quality forage, while dryland communities had the lowest quantity and quality of forage. Thus, foraging between a higher-biomass, adequate-quality reserve resource (sedgeland) and a high-quality but low-quantity bridging resource (wet sandveld) can help to ensure a balanced protein and fibre intake during the late dry season. Our study demonstrated the importance of wetland habitats for providing green forage with sufficient biomass and protein to sustain herbivores over the late dry season.

1. Introduction

Forage quantity and quality in African savannas may become limiting during the dry season (Sinclair, 1975; Ellis and Swift, 1988; Owen-Smith, 2008; Voeten et al., 2010) because there is no grass growth, so forage becomes depleted and at the same time it dries out resulting in energy and protein content declining below maintenance requirements of herbivores. Dryland ecosystems where there is little soil moisture available for growth over the dry season, grasses will dry out and decline in both biomass and in protein/energy/digestibility content, irrespective of location (Ellis and Swift, 1988). Breman and de Wit (1983) showed this in the Sahel, while Owen-Smith, 2008 shows this using data from areas as far apart as Nairobi NP (Kenya), Masaai Mara GR (Kenya), Botswana, and Nylsvlei, South Africa. It appears, therefore, that the general principle of forage having highest forage quality in the early wet season, highest biomass in the mid wet season and both parameters declining to a low point by the end of the dry season holds from the Sahel to South African savannas. This relationship will not hold if there is soil moisture in the dry season such as in wetlands or in high-rainfall areas that enable regrowth during the dry season. Regrowth of forage during the dry season may have very high forage quality (eg *Panicum repens* lawns in Matusadona NP, Zimbabwe). As the quality and quantity of forage in their preferred wet season habitats declines through the dry season, herbivores may be forced to migrate away to habitats that provide more reliable water (Redfern et al., 2003) and forage during this resource-limited period (Maddock, 1979; Bartlam-Brooks et al., 2011; Bennitt et al., 2014; Fynn et al., 2014; Sianga et al., 2017).

A common feature of functional dry season habitats in African savannas is the availability of soil moisture during the dry season to allow growth and the presence of green forage even during the hottest and driest parts of the dry season. Soil moisture may be provided by sufficient dry season rainfall in high rainfall regions (McNaughton and Banyikwa, 1995; Hopcraft et al., 2010; Fynn and Bonyongo, 2011) or by the presence of shallow water tables in poorly drained regions such as dambos, floodplains and swamps (Hopcraft et al., 2010; Fynn et al.,

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2015). The ability to provide green forage during the dry season is a key functional aspect of dry season habitats because green forage contains above maintenance levels of energy and protein whereas these resources have dropped below maintenance levels in dry forage (Ellis and Swift, 1988; Prins, 1996; Owen-Smith, 2008). Consequently, fires in wet grasslands that provided a green flush during the dry season greatly elevated protein intake of sable antelope (*Hippotragus niger*) relative to years when these wet grasslands were not burned (Parrini and Owen-Smith, 2010). Similarly, buffalo (*Syncerus caffer*) populations in Matusadona National Park (Zimbabwe), which had access to high-quality green forage in lake shore grasslands over the late dry season, had greater reproductive productivity and population growth rates relative to other savanna populations (Taylor, 1985). In addition, the ability of high-rainfall regions and wetlands to provide a higher standing biomass of forage results in a reserve of forage for the dry season (reserve resource) and critical buffer/key resources during drought periods, which can prevent catastrophic herbivore population collapses (Illius and O'Connor, 2000; Owen-Smith, 2002).

A variety of large herbivore species are well known for their use of various wetland habitats over the dry season across Africa: Rukwa Valley Tanzania (Vesey-FitzGerald, 1960), Amboseli ecosystem Kenya (Western, 1973), Gorongosa Ecosystem Mozambique (Tinley, 1977), Matusadona National Park Zimbabwe (Taylor, 1985), Lake Manyara National Park Tanzania (Prins and Beekman, 1989), Marromeu Complex of the Zambezi Delta Mozambique (Beilfuss et al., 2010), Okavango Delta (Bennitt et al., 2014) and during Sianga et al. (2017) we observed three collared buffalo herds to focus their foraging by the late dry season in wetlands (floodplains and swamps) in the Savuti-Mababe-Linyanti ecosystem in northern Botswana. In addition, Fynn et al. (2015) observed that heterogeneity of forage height as determined by flood depth and grazing intensity in these wetland habitats such as the Okavango Delta may play a key role in promoting adaptive foraging options for a variety of herbivores. Impala *Aepyceros melampus* and lechwe *Kobus leche* favour areas of short grass where flood depth and duration are least or areas of regrowth after heavy grazing, whereas zebra *Equus burchelli* will forage in areas of intermediate grass height and buffalo and elephant *Loxodonta africana* on taller grass areas. Even buffalo however will forage between short and tall grass areas to balance their intake of protein vs fibre. At Gorongosa Mozambique, Tinley (1977) showed how shorter grass grazers use the regrowth after buffalo have grazed down the taller grasses. Typical floodplains in the Okavango Delta are not homogenous vegetation units but have a gradient of increasing depth and duration of flooding, which influences plant productivty, composition and quality. The deeper parts of floodplains become increasingly important for forage provision for herbivores as the dry season progresses because they retain soil moisture later into the dry season (Fynn et al., 2015).

In the Okavango Delta, as the depth and duration of flooding increases, floodplains become increasingly dominated by taller more productive sedges and swamp grasses (Murray-Hudson et al., 2014; Fynn et al., 2015). Thus while the deeper parts of floodplains provide more reliable green forage during the late dry season, their tall fibrous grasses and sedges are expected to be of lower digestibility and quality owing to greater cellulose and lignin content (Wilmshurst et al., 2000). Likewise, Mosimane (2015) found that wetland plants in the Okavango Delta have higher silica content which may lower their digestibility. Along the Selinda Spillway and the eastern edge of the Okavango Delta we have observed that where plant communities on deep Kalahari sands (sandveld) directly abut the floodplain, without large rises in elevation away from the floodplain, soil moisture from the river channel/floodplain is able to move laterally and permeate these sandy soils, thereby forming a shallow water table that maintains high-quality dryland grass species such as *Digitaria eriantha* and *Brachiaria nigropedata* (authorities for plant species follows The Herbarium Catalogue, 2017, Royal Botanic Gardens, Kew) in a green state during the late dry season (Fig. 1).

In this paper, sandveld communities on deep Kalahari sands are termed dryland sandveld (occur far from the river channel and thus do not receive soil moisture inputs from lateral below-ground seepage) whereas wet sandveld (abut the river channel and thus receive soil

Fig. 1. Wet sandveld showing regrowth of *Brachiaria nigropedata* during the late dry season along the Selinda Spillway (northern Botswana). The taller sedgeland community can be seen in the background, associated with the deeper parts of the floodplain. The photo was taken in the favored late dry season range of buffalo (see Fig. 2 for location) and the heavy utilization of *B. nigropedata* by buffalo is apparent (photo credit Andrew Zinn, 19th October 2015).

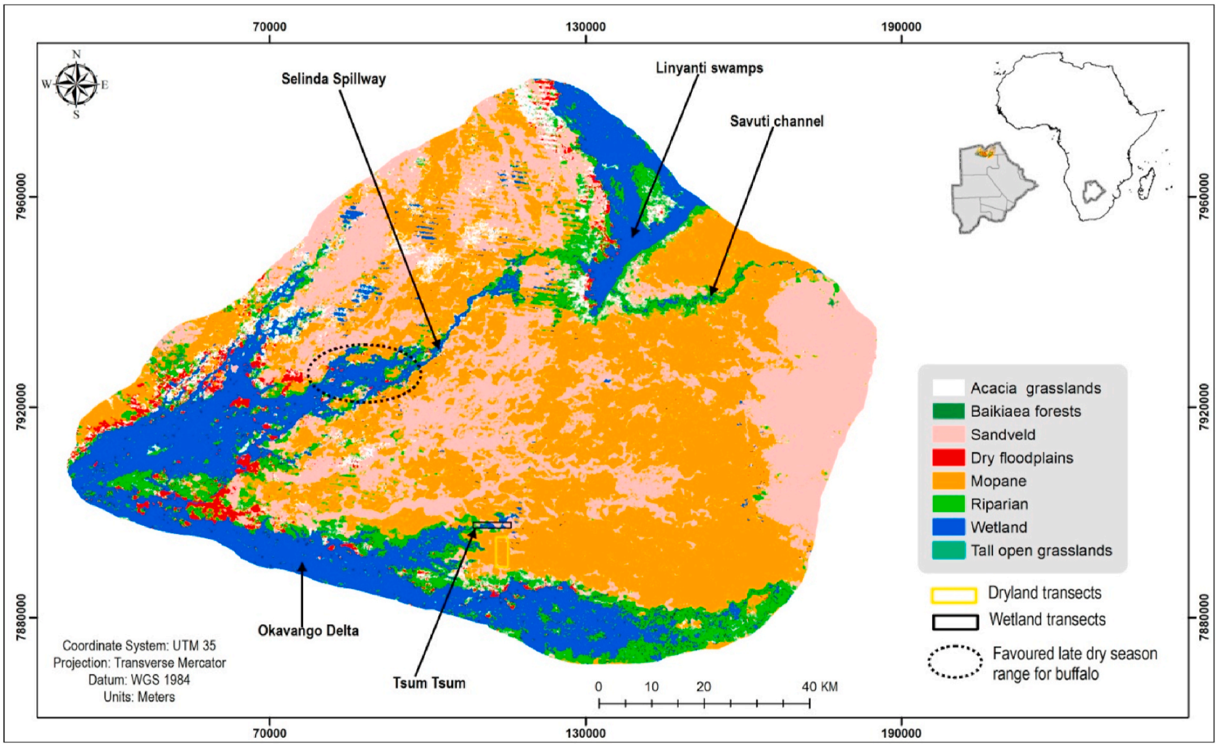

Fig. 2. A map of the study area within the Savuti-Mababe-Linyanti ecosystem, northern Botswana (adapted from Sianga and Fynn, 2017).

moisture inputs from lateral below-ground seepage – but are never inundated by floodwaters). The various channels of the western reaches of the Selinda Spillway (an eastern branch of the Okavango Delta linking to the Linyanti Swamps) have extensive areas of this wet sandveld habitat greening up during the late dry season (Fig. 1), which appears to attract many buffalo herds during this resource-limited time of the year (Naidoo et al., 2014; Sianga et al., 2017).

This paper reports on a study of heterogeneity of forage quantity and quality in various habitats of a landscape of the eastern edge of the Okavango Delta, northern Botswana and how this may relate to seasonal herbivore use of these habitats. Our hypothesis was that during the late dry season, the deeper-flooded sedge zone of wetlands would have higher biomass (sedges and grasses) than the adjacent wet sandveld grasses but that the wet sandveld grasses would have higher quality owing to being dryland species with lower silica, cellulose and lignin contents than more productive wetland grasses and sedges (Wilmshurst et al., 2000; Mosimane, 2015). Owing to the fact that grasses in sandveld and mopane woodland communities far from floodplains (dryland sandveld and mopane) have no access to soil moisture during the late dry season, we hypothesized that these dry grasses would have lower quality (protein content) during the late dry season than green grasses in wet sandveld communities adjacent floodplains and sedges of the sedge zone.

2. Materials and methods

2.1. Study area

Our study was located in the Tsum Tsum region of the Savuti-Mababe-Linyanti ecosystem (SMLE) of northern Botswana between the Okavango Delta and the Linyanti Swamps (Fig. 2).

Detailed descriptions of the hydrology, ecology and vegetation of the ecosystem can be seen in Fynn et al. (2014) and Sianga and Fynn (2017). One key feature of relevance to this study is the Selinda Spillway - a channel connecting the Okavango Delta and the Linyanti Swamps (Fig. 2). The floodplains of the western section of the Selinda Spillway have extensive areas of wet sandveld communities adjacent the various channels of the Spillway (Fig. 1). Similarly, the nearby Tsum Tsum floodplains on the eastern edge of the Okavango Delta extend out into the woodlands (Fig. 2) and thus intersect with sandveld communities, thereby giving rise to wet sandveld. Thus, both the Selinda Spillway and the Tsum Tsum were favored by several collared buffalo herds during the dry season, which moved between these areas (Naidoo et al., 2014; Sianga et al., 2017). Owing to their easier access than the western region of the Selinda Spillway we used the Tsum Tsum floodplains as our study area (Fig. 2). The climate is semi-arid with rainfall around 500 mm per annum (Fynn et al., 2014). Seasons may be divided into a wet season (December–April), cool early dry season (or flooding season) and hot late dry season (September–November), where maximum daily temperatures range between 35 and 40 °C (Fynn et al., 2014).

Another key feature of the region is the long time taken for the flood pulse to reach the Okavango Delta from the distant high-rainfall Angolan highlands, resulting in the flood levels peaking during the early dry season (hence the term flooding season) and receding over the late dry season (Mendelsohn et al., 2010). This exposes the floodplains during the late dry season and provides sufficient soil moisture input to support green forage production during this resource-limited period (Fynn et al., 2014).

2.2. Measurement of heterogeneity of forage quality and quantity

We subjectively selected four habitat (plant community) types around the distal reaches of the Tsum Tsum floodplains of the Okavango Delta for the study (Fig. 2): sandveld woodland on deep Kalahari sands and mopane woodlands on alluvial soils, both far from floodplains (two major dryland habitat types of the region), a wet sandveld community on deep Kalahari sands abutting the floodplains and a sedgeland community within the parts of the floodplain flooded at intermediate depth and duration (4–6 months, Murray-Hudson et al., 2014).

Sampling was conducted in 2015 during the late dry season (September and October) because this is the time of the year when forage quantity and quality is most limiting to herbivores in African savannas habitats (Sinclair, 1975; Ellis and Swift, 1988; Owen-Smith, 2008) and thus when the functional nature of dry season habitats is most relevant to herbivores (green forage production during the most resource limited time of the year). Thus, forage quantity and quality were sampled only during the late dry season, a time when resources are limiting in most habitats in African savannas including some parts of the dryland woodlands of the Okavango Delta. Forage resources of variable quality are abundant during the wet and early dry seasons in the study area. Within walking distance (<2 km) to the only access road to the distal end of the Tsum Tsum floodplains, we subjectively located four different sites where deep Kalahari sands intersected the floodplains (sandveld occurs in paleo-river channels filled with aeolian sand deposits and is thus patchy in its distribution) thus providing four spatially-blocked replicates as sampling sites for wet sandveld and adjacent sedgeland habitats (Fig. 2). The dryland communities (mopane and sandveld) were sampled at four sites along the access road where it passed through the dryland woodlands between the main edge of the Okavango Delta (between Splash and Kwara Lodges) and the distal reaches of the Tsum Tsum floodplains where they extend out into the woodlands (Fig. 2). These dryland woodlands consist of alternating patches of sandveld communities on deep Kalahari sands and mopane communities on alluvial soils enabling us to select four patches of sandveld and four patches of mopane as spatially blocked sampling sites. At each of the four sampling sites per habitat type a 40 m tape measure was laid down subjectively to ensure that it passed through a representative section of the habitat in question. Thus, we sampled four 40 m transects per habitat type (wet sandveld and sedgelands) on the Tsum Tsum floodplains and 4 transects per habitat type in the dryland woodlands (sandveld and mopane) yielding a total of 16 transects.

Forage (grasses and sedges) greenness (quality), height (quality and quantity) and biomass (quantity) were sampled at every 5-m mark on the tape measure (transect) using a one x one metre quadrat (five quadrats per transect). A 5-m mark was selected to yield a reasonable representation per sampling sites. Forage height was determined by measuring the leaf table height of grasses and sedges at the centre of the quadrat using a 30 cm measuring ruler (adapted from Stewart et al., 2001). Greenness of forage was estimated as percentage cover of green grasses and sedges rooted within the quadrat, while forage biomass was estimated by clipping all grasses and sedges at ground surface level in the quadrat. The clipped samples were air-dried in the field and then oven dried for 48 hours at 60 °C at the Okavango Research Institute laboratory (Maun, Botswana), followed by weighing on an electric balance for biomass. We also collected leaves (no stems) from dominant sedges and grasses in each habitat type. The major dominant in the sedgeland was *Cyperus esculentus* while *D. eriantha*, *B. nigropedata*, *Schmidtia pappophoroides* and *Eragrostis* spp were dominant in sandveld (wet and dry) and *Heteropogon contortus*, *Eragrostis rigidior* and *Digitaria milanjiana* were dominant in mopane. These samples were oven dried, milled (Okavango Research Institute, Maun, Botswana) and analysed for total nitrogen (N) following Kjeldahl procedures at Bemlab (Western Cape, South Africa). Crude protein content was calculated as % N x 6.25 (Crampton and Harris, 1969).

2.3. Data analysis

Data of grass greenness, height, biomass and protein were analysed using a Kruskal-Wallis test ('kruskalmc' function in the pgirmess package) after failing assumptions of normality (Shapiro-Wilk Test) or homogeneity of variance (Levene Statistic) in R (RCore-Team, 2013).

3. Results

The sedgeland habitat and the wet sandveld woodlands had plants of higher greenness, height and protein content than dryland habitats far from floodplains (mopane and sandveld woodland). For example, protein content in sedgelands and wet sandveld was about 9% and 16% respectively whereas protein content was 6% and 4.5% in dryland sandveld and mopane respectively ($P < 0.05$, Fig. 3; Table 1). Similarly, forage greenness in sedgelands and wet sandveld was 49% and 37% respectively whereas greenness was 0.5% and 1% in dryland sandveld and mopane respectively ($P < 0.05$, Fig. 3; Table 1). Despite their excellent protein content during the dry season, plant height and biomass in wet sandveld woodland was much less than that in sedgelands ($P < 0.05$, Fig. 3; Table 1) but similar to that of sandveld and mopane woodland ($P > 0.05$, Fig. 3; Table 1).

4. Discussion

Our study shows that dryland habitats are likely not able to meet the energy and protein intake requirements of buffalo during the late dry season, whereas wetland habitats likely will meet their requirements in this season. During the late dry season forage quantity was limiting in dryland sandveld and mopane because forage biomass was 25 g m^{-2} and 20 g m^{-2} for sandveld and mopane respectively, which is far below the optimal forage biomass for an adult buffalo, where the optimal forage biomass of a 450 kg buffalo is estimated to be 156 g m^{-2} (Wilmshurst et al., 2000). Forage quality was also limiting because greenness was about 1% and 0.5% while protein content was well below the 6% protein content respectively (Robbins, 1993) required for maintenance. By contrast, wetlands were neither limiting in both quantity nor quality during this season. For example, biomass of the sedgelands was about 200 g m^{-2} which is well above optimal biomass levels for buffalo while protein sedgelands was near maintenance levels (~9%) and protein content of wet sandveld was well above maintenance level (~16%). High-quality grasses such as *D. eriantha* and *B. nigropedata*, which are dominants in both wet and dry sandveld woodlands had high leaf protein levels (~16%) during the late dry season in the wet sandveld habitat where soil moisture inputs from adjacent floodplains enabled these grasses to produce green leaves at a time when grasses and sedges in dryland habitats have dried out. Thus, these wetland habitats appeared to be functional dry season habitats for herbivores because they provide sufficient green forage to meet intake requirements even on a large bodied herbivore like a buffalo and extremely high protein resources in the wet sandveld. As found in the Masai Mara Reserve (Kenya), buffalo generally avoid short grass because of their large body size combined with a tongue sweep strategy for maximizing bite size (e.g. Bhola et al., 2012) and, therefore, their intake rates on short grass are likely to be strongly constrained whereas smaller-bodied short grass grazers such as gazelles, impala and wildebeest are able to meet their intake requirements on short grasses (Illius and Gordon, 1987; Wilmshurst et al., 2000). Small bodied herbivores can therefore, likely find sufficient biomass in the wet sandveld without the need to forage in the sedgeland, whereas a buffalo can forage adaptively between the very high-quality short grass wet sandveld and the adequate quality of the taller sedgeland. This demonstrates important functional heterogeneity even within the wetland, which allows herbivores to forage adaptively between the short and tall states to meet their intake requirements. For example, Prins and Beekman (1989) showed that buffalo were able to achieve sufficient protein intake as well as overall bulk (fibre) intake by foraging adaptively between short, high-quality *Cynodon dactylon* lawns around Lake Manyara (Tanzania) and taller sedgelands within the lake. The heterogeneity in forage structural states in our study system (wet sandveld versus sedgelands), appears therefore to provide a very similar scenario to the Lake Shore grasslands versus sedgelands of the Lake Manyara system. The sedgeland could be referred to as a reserve resource or key resource as it provides sufficient adequate-quality forage to prevent large declines in body condition or even mortality over the late dry season but its lower quality will not contribute much to growth or optimal foetus development (Illius & O'Conner, 2000; Owen-Smith, 2002). The short high-quality grasses of the wet sandveld could be referred to as a high-quality resource (Owen-Smith, 2002) because they are likely to be able to elevate protein intake during this highly resource

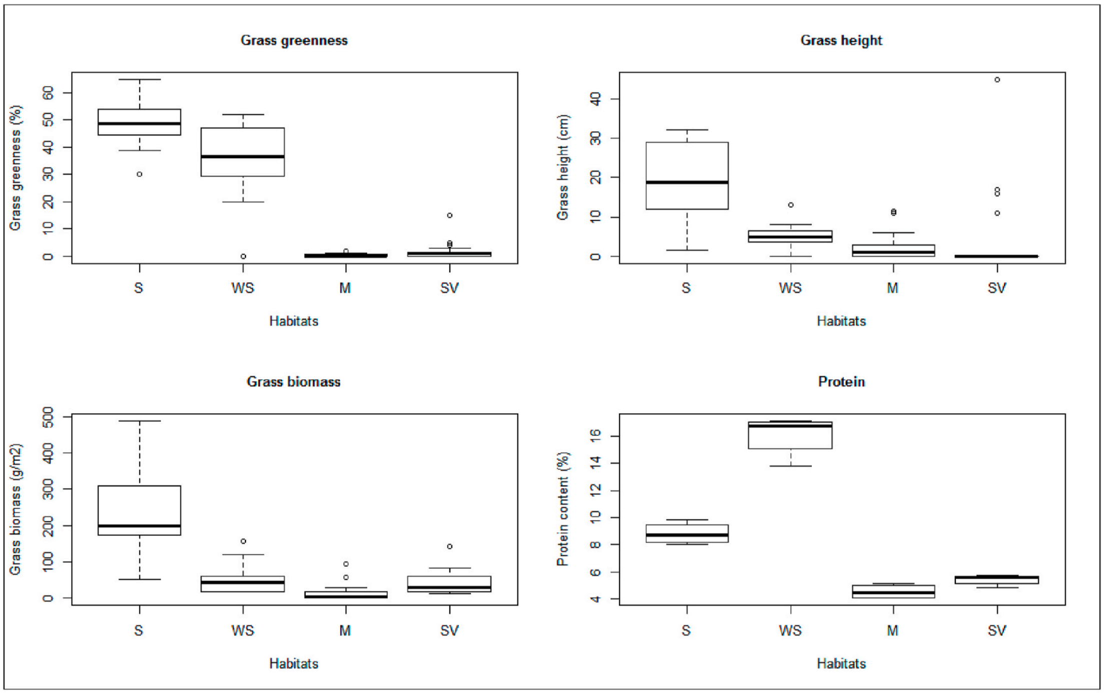

Fig. 3. Forage characteristics across the four habitats sampled in the Savuti-Mababe-Linyanti ecosystem, northern Botswana (S - sedgelands, WS - wet sandveld, SV – dryland sandveld and M – dryland mopane).

Table 1
Kruskal Wallis Multiple Comparison Test (*. Significant difference at the 0.05 level) on forage characteristics in the SMLE.

Habitat characteristics	Habitat	Habitat	Test statistic	P value
Grass greenness (%)	Mopane	Sedgelands	−48.98	.000*
	Mopane	Wet sandveld	−34.75	.000*
	Mopane	Sandveld	−6.58	1
	Wet sandveld	Sedgelands	14.23	0.297
	Sandveld	Sedgelands	42.4	.000*
	Sandveld	Wet sandveld	28.18	.001*
Grass height (cm)	Mopane	Sedgelands	−37.2	.000*
	Mopane	Wet sandveld	−14.95	0.235
	Mopane	Sandveld	5.15	1
	Wet sandveld	Sedgelands	22.25	.013*
	Sandveld	Sedgelands	42.35	.000*
	Sandveld	Wet sandveld	20.1	.033*
Grass biomass (g m^{-2})	Mopane	Sedgelands	−52.95	.000*
	Mopane	Wet sandveld	−23.9	.007*
	Mopane	Sandveld	−19.95	.039*
	Wet sandveld	Sedgelands	29.05	.000*
	Sandveld	Sedgelands	33	.000*
	Sandveld	Wet sandveld	3.95	1
Protein (%)	Mopane	Sedgelands	−48.98	0
	Mopane	Wet sandveld	−34.75	0
	Mopane	Sandveld	−6.57	1
	Wet sandveld	Sedgelands	14.23	0.297
	Sandveld	Sedgelands	42.4	0
	Sandveld	Wet sandveld	−28.175	0.001

limited period when forage is dry and depleted in drylands. However, Owen-Smith (2002) referred to relatively high-quality green forage during the late dry season as a bridging resource because it provides a bridge of green forage over the late dry season. Prins and Beekman (1989) referred to the short cynodon grasslands as a restricted intake resource for buffalo because their dry matter intake rate is strongly restricted on short grasslands. For impala, however, these short grasslands would not be restricted.

This may explain why many buffalo herds concentrate on the western end of the Selinda Spillway during the late dry season (Naidoo et al., 2014; Sianga et al., 2017, Fig. 2), which support some of the highest concentrations of buffalo in northern Botswana at this time (Mike Chase pers. com.) because wet sandveld habitats appear to be more extensive in this region of the Selinda Spillway than elsewhere in the ecosystem, allowing buffalo to forage adaptively between these wet sandveld areas and adjacent sedgelands (Fig. 1). In addition, apart from the reliable water source for drinking (Redfern et al., 2003), the higher quality and quantity offered by the various habitats in and adjacent wetlands than in drylands during the dry season explains why buffalo and other herbivores switch from dryland woodland habitats during the wet season to wetland habitats during the dry season (Taylor, 1985; Fynn et al., 2014; Sianga, 2014; Sianga et al., 2017).

While the dryland sandveld and mopane woodland was not functional for herbivores during the late dry season, when rains arrive during the wet season, they green up and produce very high-quality forage. For example, Taylor (1985) showed at Matusadona National Park (Zimbabwe) that while Lake Shore grasslands had the highest protein content during the late dry season, during the wet season woodland grasslands had the highest protein content. Similar findings were recently observed from the Eretsha region of the Okavango Delta (Keemekae, unpublished data). Dryland woodlands become highly functional for herbivores during the wet season. For example, in the Selinda and Linyanti region of northern Botswana, buffalo were observed to leave floodplains and move out into the woodlands as soon as the first rains of the wet season fell, suggesting that forage quality was more appealing to buffalo in the woodlands during the wet season (Sianga et al., 2017).

5. Conclusion

In conclusion, our study demonstrated the importance of wetland habitats for providing green forage with sufficient biomass and protein to sustain herbivores over the late dry season. Importantly, we demonstrated that the functionality of wetland is not only related to the ability to provide greenery in the late dry season but also in the heterogeneity in forage biomass and quality related to the degree of flooding and inundation. Thus, the deeper flooded areas provide taller but less digestible forage that act as a reserve of forage for the dry season whereas less inundated areas provide high quality forage but where intake rates are likely to be limited by forage quantity. Structural heterogeneity within the wetlands therefore provides adaptive foraging options between high quality and more reliable quantity which can also provide important niche for different body sized herbivores. Dryland woodlandss likely only become functional when new high quality emerges following the onset of the rains. Structural and compositional heterogeneity is, therefore, likely to be a key factor determining population productivity and stability in herbivore populations by providing important adaptive foraging options over the annual cycle (Owen-Smith, 2002, 2004; Hopcraft et al., 2010).

Ethical standards

The research involved in this manuscript followed the journal's Code of Conduct for authors contributing articles and was conducted in accordance with regulations outlined in the research permit (EWT 8/36/4 XXV (16)) issued by the Ministry of Environment, Wildlife and Tourism and The Department of Wildlife and National Parks (Botswana).

CRediT authorship contribution statement

Keoikantse Sianga: Conceptualization, Methodology, Data curation, Writing – original draft, Visualization, Investigation, Supervision, Validation. **Richard W.S. Fynn:** Conceptualization, Methodology, Data curation, Writing – original draft, Visualization, Investigation, Supervision, Validation.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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