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Seasonal habitat selection by African buffalo *Syncerus caffer* in the Savuti–Mababe–Linyanti ecosystem of northern Botswana

Authors:
Keoikantse Sianga[1]
Richard W.S. Fynn[1]
Mpaphi C. Bonyongo[1]

Affiliations:
[1]Okavango Research Institute, University of Botswana, Botswana

Corresponding author:
Keoikantse Sianga,
keosianga@gmail.com

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This study aimed to establish seasonal movement and habitat selection patterns of African buffalo *Syncerus caffer* in relation to a detailed habitat map and according to seasonal changes in forage quality and quantity in the Savuti–Mababe–Linyanti ecosystem (Botswana). Two buffalo were collared in November 2011 and another in October 2012. All three buffalo had greater activities in the mopane–sandveld woodland mosaic during the wet season, which provided high-quality leafy grasses and ephemeral water for drinking, but moved to permanent water and reliable forage of various wetlands (swamps and floodplains) and riverine woodlands during the dry season. Wetlands had higher grass greenness, height and biomass than woodlands during the dry season. Buffalo had similar wet season concentration areas in the 2011–2012 and 2012–2013 wet seasons and similar dry season concentration areas over the 2012 and 2013 dry seasons. However, their dry season location of collaring in 2011 differed dramatically from their 2012 and 2013 dry season concentration areas, possibly because of the exceptionally high flood levels in 2011, which reduced accessibility to their usual dry season concentration areas. The study demonstrates that extremely large and heterogeneous landscapes are needed to conserve buffalo in sandy, dystrophic ecosystems with variable rainfall.

Conservation implications: This study emphasises the importance of large spatial scale available for movement, which enables adaptation to changing conditions between years and seasons.

Introduction

African buffalo (*Syncerus caffer*) have a large distributional range across the savannas of Africa. Their habitat selection and foraging ecology have been relatively well studied (Landman & Kerley 2001; Macandza, Owen-Smith & Cross 2004; Sinclair 1979; Taylor 1985). Because of their large body size and large groups, buffalo are able to fend off predators (Sinclair, Mduma & Brashares 2003), thereby enabling them to forage in wooded vegetation with relatively low visibility and high predation risk. The large absolute food demands of buffalo, which is a function of their large body size (Illius & Gordon 1987; Wilmshurst, Fryxell & Bergman 2000), combined with their inability to efficiently crop short grass (use of tongue to increase bite size cannot work on short grass) constrain them to foraging in vegetation with sufficient height and biomass of forage (Codron et al. 2008; Illius & Gordon 1987). Buffalo generally avoid heavily grazed regions of short grassland (Bhola et al. 2012; Jarman & Sinclair 1979; Traill & Bigalke 2007), preferring woodlands dominated by tufted and leafy perennial grasses during the wet season and often relying on more productive riverine vegetation during the dry season (Bell 1970; Bennitt, Bonyongo & Harris 2014; Fynn, Chase & Roder 2014; Macandza, Owen-Smith & Cain 2012; Sinclair 1979).

While drylands often support less productive but higher quality forage than wetlands over the wet season (Fynn et al. 2014; Taylor 1985), their moisture-limited position in the landscape results in forage drying out and declining in forage quality and quantity over the dry season (Ellis & Swift 1988; Owen-Smith 2008; Taylor 1985). Thus, wetlands, where permanent water is easily accessible and perennial grasses continue to produce green forage over the dry season, would be expected to be favoured by many herbivores at this time with drylands being favoured over the wet season (Bell 1970; Fynn et al. 2014; Maddock 1979; Taylor 1985).

In contrast to more mobile species such as zebra (*Equus burchellii*) and wildebeest (*Connochaetes taurinus*), which often migrate between distinct wet- and dry season ranges (Bartlam-Brooks, Bonyongo & Harris 2011; Maddock 1979), most buffalo studies have found strong overlap between wet- and dry season ranges (Macandza et al. 2012; Ryan 2006; Ryan, Knechtel & Getz 2006; Venter & Watson 2008). Many studies, however, were conducted in small reserves (Landman & Kerley 2001; Ryan et al. 2006; Tshabalala, Dube & Lent 2009) where opportunity for large seasonal movements are limited or in larger reserves where functional heterogeneity of resources may be well developed at the landscape (catena) scale (Bell 1970; Macandza et al. 2012; Perrin & Brereton-Stiles 1999; Sinclair 1979), thereby reducing the need for large seasonal movements (Hopcraft, Olff & Sinclair 2010). However, in large, relatively unfragmented ecosystems and where landscape scale functional heterogeneity may be poorly developed relative to regional-scale heterogeneity (Fynn et al. 2014), larger buffalo movements may be expected (Naidoo et al. 2012; Skarpe et al. 2004).

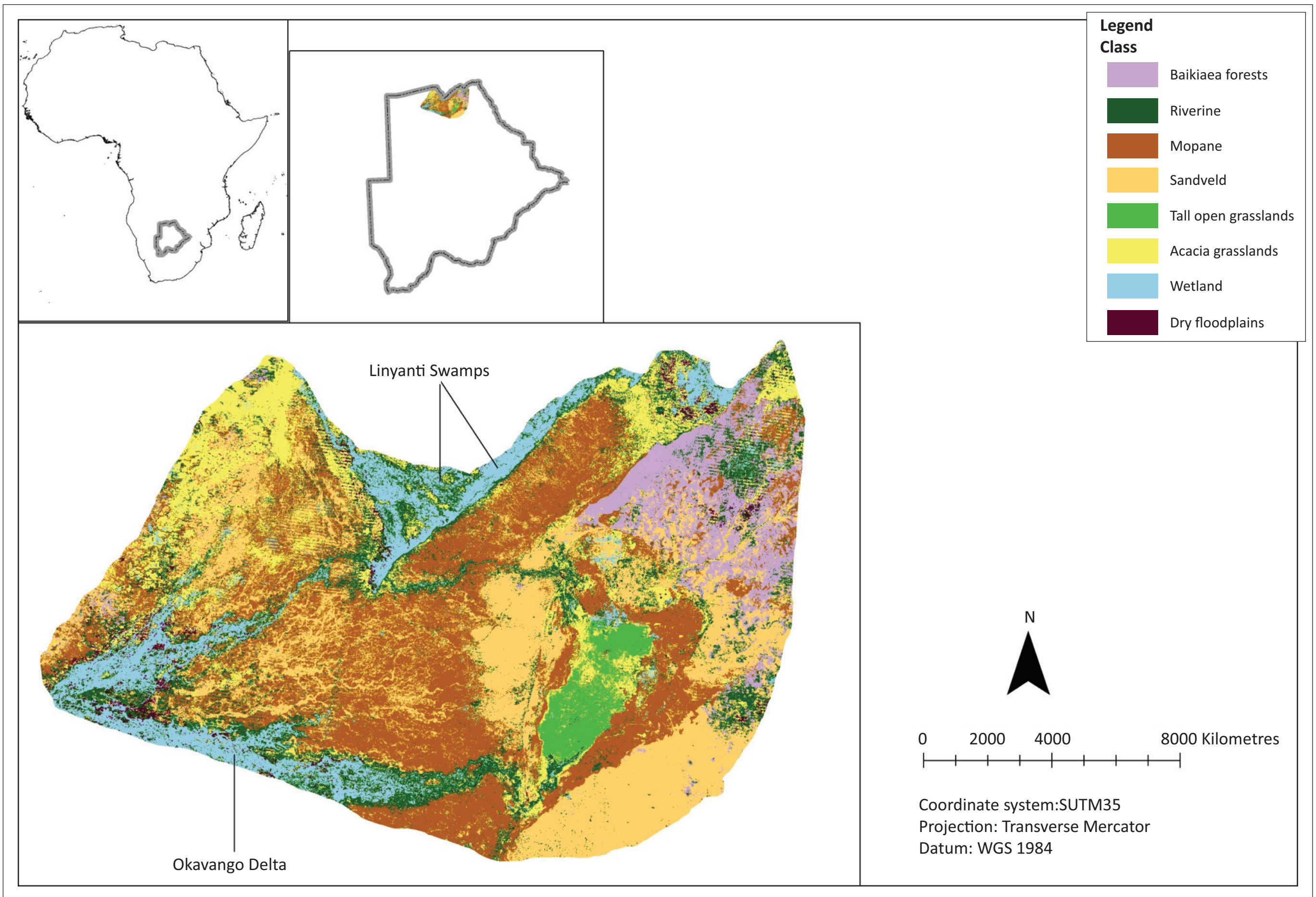
The Savuti–Mababe–Linyanti ecosystem (SMLE) is part of the > 80 000 km^2 northern conservation area of Botswana, one of the largest relatively unfragmented wildlife regions in Africa (Fynn & Bonyongo 2011). Despite several studies on buffalo in the SMLE (Fynn et al. 2014; Patterson 1972), detailed seasonal movement and habitat selection patterns of buffalo in the region have not been fully identified and established, especially seeing that no detailed habitat map has been available until this year (2016). Considering their non-specialised mouth anatomy and their large body size–mediated demands for absolute food intake, we expected buffalo in the SMLE to favour vegetation where tufted, leafy grasses provided sufficient height and biomass of grass to enable food intake requirements to be satisfied (Illius & Gordon 1987; Wilmshurst et al. 2000) (Hypothesis 1 – H1).

The strongly developed regional-scale distribution (rather than landscape scale) of functional heterogeneity of wet- and dry season vegetation types in the SMLE (Fynn et al. 2014) is likely to promote extension of buffalo home ranges beyond the landscape scale (Hopcraft et al. 2010). Consequently, we expected seasonal movement patterns of buffalo in the SMLE to match the scale at which functional seasonal vegetation types are distributed in the ecosystem, which is strongly regional (Fynn et al. 2014) (Hypothesis 2 – H2). The objectives of this study were to (1) to examine seasonal movements and habitat selection of buffalo in the SMLE of northern Botswana and (2) to link seasonal movements to the quality and quantity (grass greenness, height and biomass) of vegetation in favoured seasonal regions of the landscape.

Methods

Study area

This study was conducted in the SMLE (northern Botswana, Figure 1). Climate in the study area is described as semi-arid



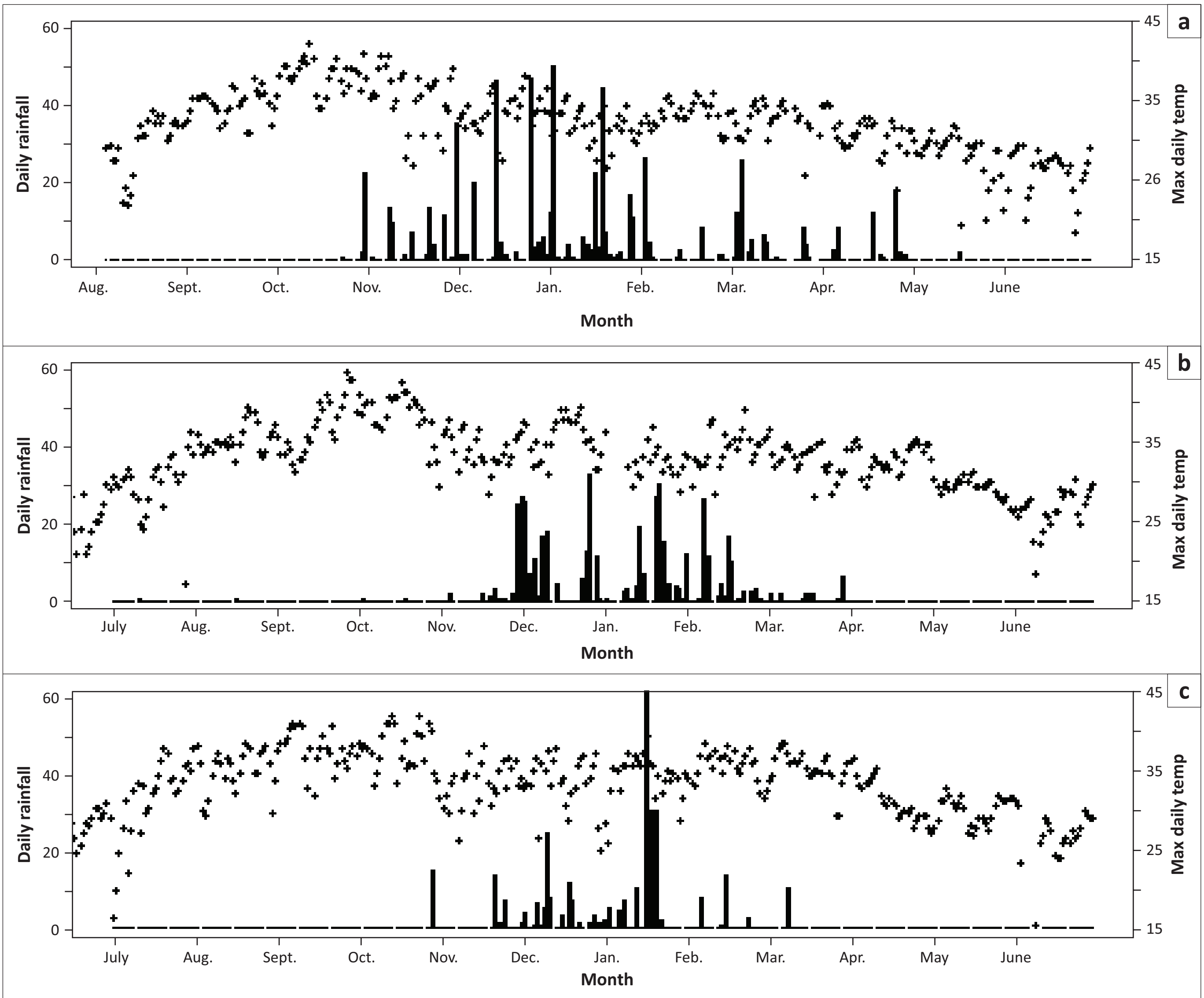
Source: Adapted from Sianga, K. & Fynn, R., 2017, 'The vegetation and wildlife habitats of the Savuti-Mababe-Linyanti ecosystem, northern Botswana', *Koedoe* 59(2), a1406. https://doi.org/10.4102/koedoe.v59i2.1406

FIGURE 1: Savuti–Mababe–Linyanti ecosystem vegetation.

with mean annual rainfall ranging from around 500 mm in the Okavango region (western boundary of the SMLE) to over 600 mm in the Chobe Enclave (eastern boundary of the SMLE), most of which is received between November and April (Botswana Meteorological Services). Seasons may be functionally separated into a wet season (December–April), a cool early dry season (May–August) and a hot late dry season (September–November), where daily maximum temperatures are between 35 °C and 40 °C (Figure 2, adapted from Fynn et al. 2014). The SMLE is defined by a variety of vegetation types from swamps, floodplains and riverine in wetter areas to vast dryland woodland systems away from permanent water comprising a mosaic of mopane woodland on alluvial soils and sandveld woodland on Kalahari sands (Figure 1; Sianga & Fynn 2017; Wolski & Murray-Hudson 2006). In addition, very heavy clay soils formed under sedimentation in a paleolake system known as the Mababe Depression (Teter 2007) give rise to open grassland and sparse savanna in the eastern section of the SMLE (Figure 1). Another key feature are the dambo grasslands of the Chobe Enclave, which are seasonally flooded shallow, linear depressions (flooded by runoff from upslope regions) supporting tall grassland.

Buffalo habitat use

Single cows in three buffalo herds were fitted with satellite collars (Africa Wildlife Tracking, Pretoria, South Africa). Buffalo 1 (BH1) and Buffalo 2 (BH2) were collared in the Savuti Channel floodplains and near the Savuti Marsh, respectively, at the end of the late dry season in November 2011. Buffalo 3 (BH3) was collared in the Savuti Marsh in the late dry season (October 2012). Anaesthetic *M3080 Xylazine* was used to immobilise cows during capturing and later reversed using *naltrexone* after fitting collars. Collars were programmed to take a global positioning system (GPS) position of the animal every 4 hours. Every fix obtained by the satellite collars was downloaded and plotted in ArcGIS 10.1 (ESRI 2010) for various analyses. For analyses relating to seasonal differences in movement patterns and habitat



Source: Adapted from Fynn, R.W.S., Chase, M. & Roder, A., 2014, 'Functional habitat heterogeneity and large herbivore seasonal habitat selection in northern Botswana', *South African Journal of Wildlife Research* 44, 1–15. https://doi.org/10.3957/056.044.0103

FIGURE 2: Rainfall and temperature patterns between 2010 and 2013. (a) 2010/2011, (b) 2011/2012 and (c) 2012/2013 rainfall season.

selection, we defined six seasonal periods to which each GPS fix could be allocated. The seasonal periods were early wet season (mid-November to end of December), mid wet season (January and February), late wet season (March and April), early dry season (May and June), mid dry season (July and August) and late dry season (September to mid-November). For visual presentation of seasonal movements and locations for each buffalo, we plotted the home ranges of each buffalo (colour coded for each of the six seasonal periods) in a local convex hull (a-LoCoH, 95% isopleths) (Getz et al. 2007) in R (RCore-Team 2013) and later displayed as a shapefile on a habitat map of the region. The habitat map was developed from a detailed vegetation classification and mapping study of the SMLE funded by Southern African Science Service Centre for Climate Change and Adaptive Land Management (SASSCAL); a detailed account of the vegetation communities and habitat map can be seen in an accompanying paper in this special issue on Botswana (Sianga & Fynn 2017). LoCoH has been found to be an appropriate tool in GPS studies (Getz et al. 2007).

Vegetation sampling

GPS data from satellite collars were used to locate sites where buffalo have been during the wet and dry seasons. Sampling of buffalo's wet season vegetation types was conducted in the 2012–2013 wet season, while their dry season vegetation types were sampled in the 2012 dry season. A total of 124 samples (grass greenness, height and biomass) were collected from sites where the buffalo have been. Seventy-five samples (20 and 55) were collected for BH1 during the early and late dry season of 2012, while 20 samples were collected for BH2 in the late dry season of 2012. At each site, five 0.25 m^2 quadrats were set-up at the GPS position obtained from the collar. The first quadrat was set at the 0-m position on the hand-held GPS (Garmin GPS Map 62s) and the other four quadrats 5 m each side of the first (central) quadrat. Greenness was estimated visually as the percentage of green tissue of grasses and sedges rooted within the quadrat. Grass height was measured by lowering a brown paper sample bag at the centre of each quadrat, and the height above the soil surface was measured. All grasses rooted within the quadrats were clipped at ground surface level and air-dried during the field exercise. The air-dried grasses were oven-dried at 60 °C for 48 hours and weighed for biomass at the Okavango Research Institute Laboratory (Maun, Botswana). In addition, to determine the vegetation type, we noted grasses and trees common within approximately a 10-m radius around the central quadrat.

Statistical analyses

Home ranges and habitat selection

For analysis of habitat selection, we determined seasonal minimum convex polygons (MCPs) in ArcGIS 10.1 (ESRI 2010) and local convex hulls in R (Getz et al. 2007; RCore-Team 2013) using seasonal location data of each collared buffalo. Seasonal habitat selection indices of each buffalo were determined by dividing the proportion of use of each habitat by the proportion of availability of each habitat following Jacobs Index (J.I) = $(r - p)/(r + p - 2rp)$, where r is the proportion of habitat used, and p is the proportion of habitat available (Jacobs 1974). J.I ranges between –1 (selected against) and +1 (selected for). To consider the effects of scale on resource availability (Gustine et al. 2006), we calculated habitat selection at second and third order. Second-order selection (Johnson 1980) was determined by comparing the availability of various habitat types in the individual buffalo MCPs against availability in the overall population MCP (Thomas & Taylor 1990), while third-order selection (Johnson 1980) was determined by comparing the availability of various habitat types in the individual buffalo local convex hulls to availability in the respective individual buffalo MCPs (Thomas & Taylor 1990). Owing to having only three collared individual buffalo, there was insufficient replication to effectively statistically test habitat selection. Thus, the J.I merely provides a guide to readers on potential habitat selection.

To determine home-range overlaps between seasons, we used Intersect Tool (Universal Transverse Mercator, ESRI 2010) to estimate area percentage overlaps, where % overlaps = area overlap of two seasons/(area of season 1 + season 2) × 100. To examine how buffalo moved in relation to distance from perennial water sources differed seasonally, we determined the distance to the nearest perennial water source of every GPS location of all buffalo throughout the study period using Near Tool in ArcGIS 10.1 (Universal Transverse Mercator, ESRI 2010).

Vegetation data

Data of grass greenness, height and biomass were subjected to Shapiro–Wilk test (test of normality) and Levene statistic (test of homogeneity of variance) in R version 2.15.2

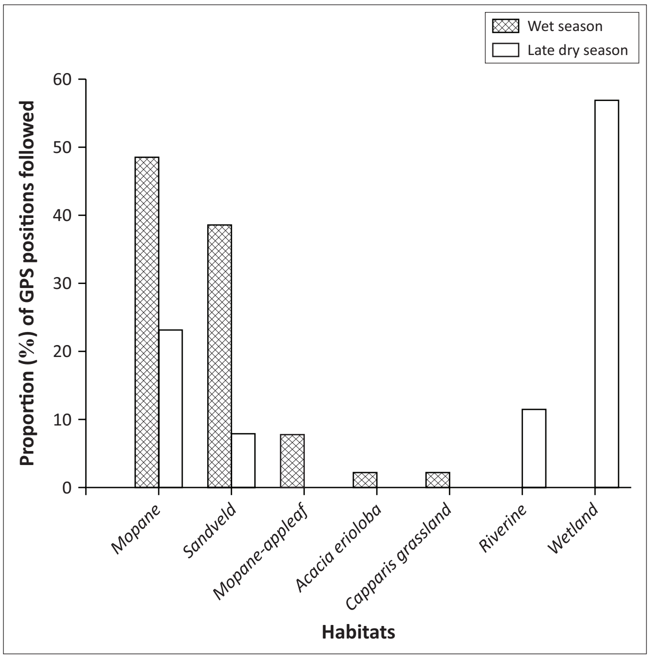


FIGURE 3: Percentage of various vegetation types observed in the follow-ups of GPS collar locations during the wet season and late dry season.

(RCore-Team 2013). Data sets that failed assumptions of normality or homogeneity of variance were natural log transformed, and failure to meet these assumptions after transformation led to the use of non-parametric tests (Kruskal–Wallis test). Multiple comparison tests (kruskalmc's function) in 'pgirmess' package in R (RCore-Team 2013) was used to analyse data sets.

Results

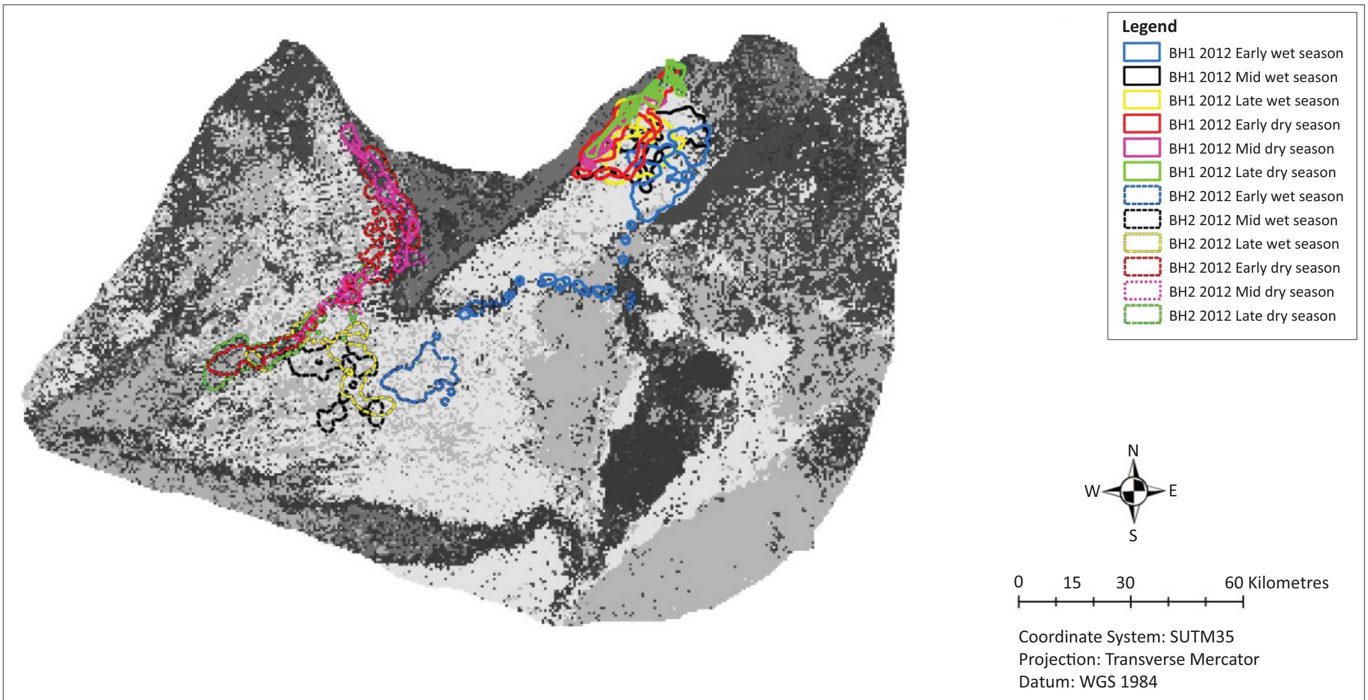
All three buffalo had much greater activities in sandveld and mopane woodlands during the wet season and various wetland systems during the dry season (Figure 3). BH1 and BH2 had greater separation of their wet and dry season concentration areas than BH3 (quantified by percentage overlap of their wet and dry season 95% local convex hull isopleths – Table 1; also see Figure 4 vs. Figure 5). BH1 and BH2 demonstrated distinct wet and dry season concentration areas, returning to these respective seasonal locations in successive years (Table 1; Figure 6).

TABLE 1: Percentage overlaps of home ranges by buffalo in different seasons over the 2012 and 2013.

Season	% overlap† (BH1)	% overlap† (BH2)	% overlap‡ (BH3)
Early wet to mid wet	12.2	0.0	13.6
Early wet to late wet	9.8	0.0	29.7
Early wet to early dry	1.4	0.0	12.9
Early wet to mid dry	0.0	0.0	18.4
Early wet to late dry	0.0	0.0	-
Mid wet to late wet	22.3	15.5	22.0
Mid wet to early dry	11.1	0.0	1.9
Mid wet to mid dry	0.6	0.0	1.8
Mid wet to late dry	0.6	0.9	-
Late wet to early dry	17.9	6.5	14.1
Late wet to mid dry	11.1	2.5	19.8
Late wet to late dry	11.1	13.2	32.6
Early dry to mid dry	26.6	23.3	-
Early dry to late dry	26.6	21.1	-
Mid dry to late dry	0.5	8.8	-
Mid wet to mid wet¶	23.4	6.6	-
Mid dry to mid dry¶	4.5	0.0	-

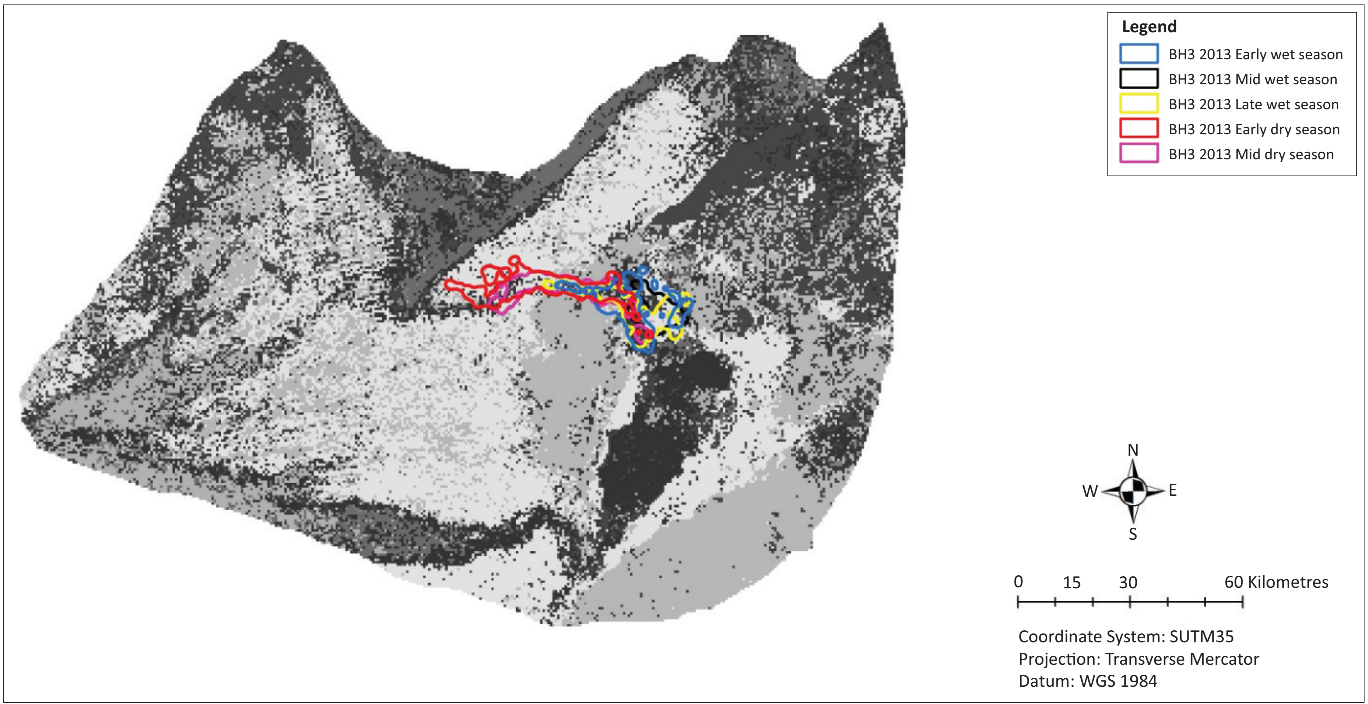
†, Year 2012; ‡, year 2013; ¶, year 2012 and 2013.

For second-order habitat selection, the buffalo selected mopane and sandveld woodlands over the wet season, whereas riverine and wetland habitats were selected over the dry season (Table 2); for third-order habitat selection, the buffalo selected mopane woodlands over the wet season and acacia grasslands, whereas riverine and wetland habitats were selected over the dry season (Table 3). For more details of the plant species composition and classification of these plant communities and for details of the habitat map development, see a parallel paper in this special issue (Sianga & Fynn 2017). Over both dry seasons, BH1 concentration areas were in wetland and adjacent woodlands where it focused on the Linyanti Swamp in increasing proportions (and regularly across the international border with Namibia) as the dry season progressed (Figure 4). The concentrations of BH2 were in the Selinda Spillway and Kwando River wetland (floodplains) and adjacent woodlands in the 2012 and 2013 dry seasons (Figures 4 and 6). Interestingly, BH2 concentrated its activities in the Tsum Tsum wetlands (floodplains) of the Okavango Delta in the late wet season of April 2013 (which it did not do in 2012) before moving to the Selinda Spillway later in the dry season (Figure 6). BH3 had the wetland habitats of the Savuti Channel and Savuti Marsh at the core of its range, which it focused on during



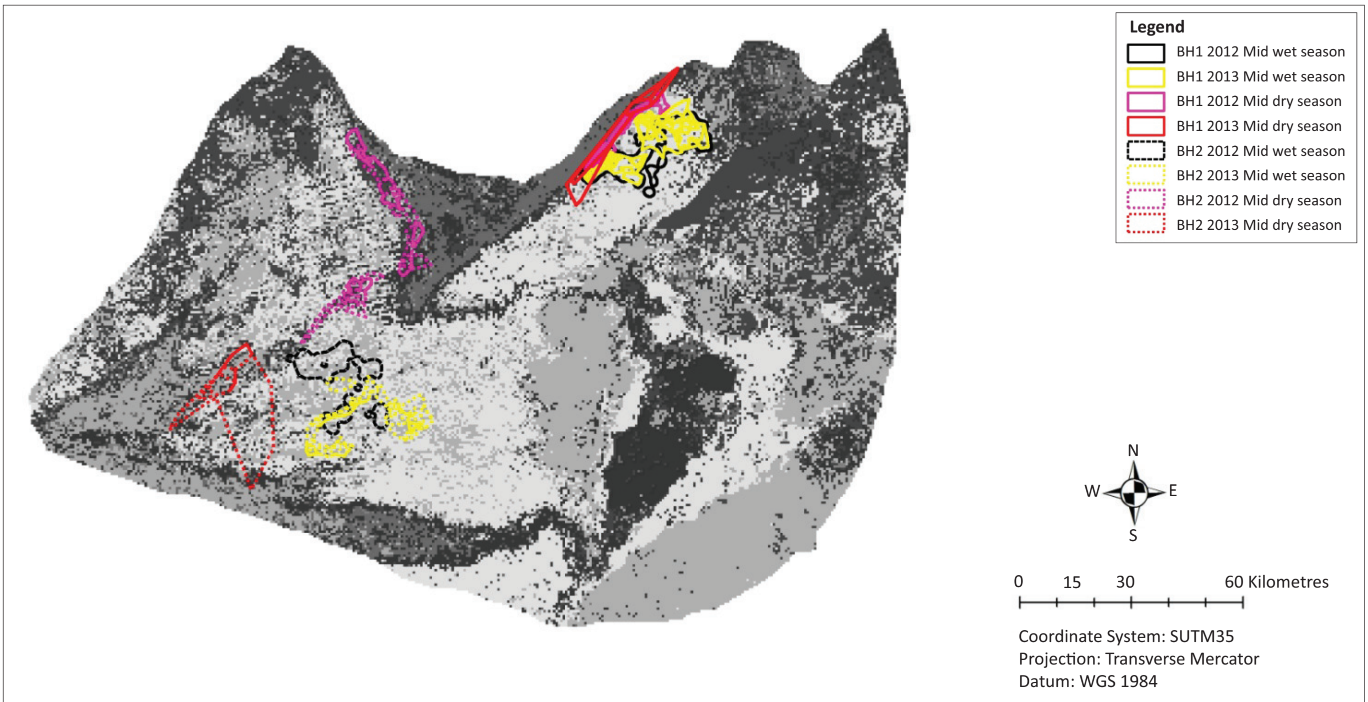
See details of vegetation types and habitat map development in a paper in this special issue (Sianga & Fynn 2017).

FIGURE 4: Movement patterns of buffalo 1 (BH1) and buffalo 2 (BH2) over the 2011/2012 annual cycle, in relation to vegetation.



See details of vegetation types and habitat map development in a paper in this special issue (Sianga & Fynn 2017).

FIGURE 5: Movement patterns of buffalo 3 (BH3) over the 2012/2013 annual cycle, in relation to vegetation.



See details of vegetation types and habitat map development in a paper in this special issue (Sianga & Fynn 2017).

FIGURE 6: Movement patterns of buffalo 1 (BH1) and 2 (BH2) in the mid wet and mid dry season of 2012 and 2013, in relation to vegetation.

the dry season, and utilised adjacent woodlands on the peripheries of the home range during the wet season (Figure 5).

During the early and late dry season of 2012, wetland habitats (floodplain not sampled in the early dry season) had higher grass greenness, height and biomass than mopane, sandveld and riverine habitats, respectively ($p < 0.05$; Figure 7), while mopane, sandveld and riverine habitats were not significantly different in grass greenness, height and biomass, respectively ($p > 0.05$; Figure 7).

Ethical considerations

A veterinarian registered with the government of Botswana conducted all darting operations in principle with the research permit (EWT 8/36/4 XVII [31]) and the supplementary collaring permit (EWT 8/36/4 XVII [41])

TABLE 2: Second-order habitat selection (annual minimum convex polygons vs. wet or dry seasons minimum convex polygons) by three buffalo in the Savuti–Mababe–Linyanti ecosystem (northern Botswana).

Habitats	Mean ± SE (annual MCP vs. herds MCP_W)	Mean ± SE (annual MCP vs. herds MCP_D)	Mean ± SE (annual MCP vs. herds MCP_EW)	Mean ± SE (annual MCP vs. herds MCP_MW)	Mean ± SE (annual MCP vs. herds MCP_LW)	Mean ± SE (annual MCP vs. herds MCP_ED)	Mean ± SE (annual MCP vs. herds MCP_MD)	Mean ± SE (annual MCP vs. herds MCP_LD)
Acacia grasslands	-0.12 ± 0.29	-0.07 ± 0.14	-0.06 ± 0.28	-0.27 ± 0.40	-0.19 ± 0.30	-0.11 ± 0.15	-0.07 ± 0.16	-0.01 ± 0.14
Baikiaea forests	-0.65 ± 0.19	-0.78 ± 0.20	-0.67 ± 0.20	-0.99 ± 0.01	-0.94 ± 0.04	-0.77 ± 0.21	-0.72 ± 0.26	-0.97 ± 0.01
Dry floodplains	-0.46 ± 0.23	-0.33 ± 0.36	-0.41 ± 0.27	-0.50 ± 0.37	-0.44 ± 0.28	-0.44 ± 0.33	-0.38 ± 0.38	-0.27 ± 0.61
Mopane	0.10 ± 0.22	0.00 ± 0.11	0.07 ± 0.22	0.32 ± 0.17	0.12 ± 0.25	0.04 ± 0.13	-0.13 ± 0.16	-0.14 ± 0.03
Riverine	-0.01 ± 0.21	0.12 ± 0.05	0.02 ± 0.21	-0.27 ± 0.30	-0.01 ± 0.24	0.08 ± 0.08	0.18 ± 0.06	0.28 ± 0.06
Sandveld	0.03 ± 0.11	0.03 ± 0.15	0.02 ± 0.11	-0.15 ± 0.25	-0.03 ± 0.14	0.05 ± 0.15	0.11 ± 0.18	-0.29 ± 0.05
Tall open grasslands	-0.09 ± 0.42	-0.53 ± 0.25	-0.09 ± 0.42	-0.24 ± 0.39	-0.41 ± 0.45	-0.50 ± 0.23	-0.47 ± 0.26	-0.83 ± 0.16
Wetland	-0.64 ± 0.01	-0.29 ± 0.20	-0.62 ± 0.08	-0.91 ± 0.04	-0.54 ± 0.04	-0.38 ± 0.15	-0.28 ± 0.21	0.35 ± 0.01

MCP, minimum convex polygons; D, dry season; ED, early dry; EW, early wet; LW, late wet; LD, late dry seasons; MD, mid dry; MW, mid wet; W, wet season.

TABLE 3: Third-order habitat selection (annual minimum convex polygons vs. wet or dry season local convex hull) by three buffalo in the Savuti–Mababe–Linyanti ecosystem (northern Botswana).

Habitats	Mean ± SE (annual MCP vs. herds LoCoH-EW)	Mean ± SE (annual MCP vs. herds LoCoH-MW)	Mean ± SE (annual MCP vs. herds LoCoH-LW)	Mean ± SE (annual MCP vs. herds LoCoH-ED)	Mean ± SE (annual MCP vs. herds LoCoH-MD)	Mean ± SE (annual MCP vs. herds LoCoH-LD)
Acacia grasslands	-0.05 ± 0.44	-0.22 ± 0.44	-0.04 ± 0.19	0.06 ± 0.65	0.28 ± 0.22	0.19 ± 0.31
Baikiaea forests	-0.93 ± 0.07	-0.99 ± 0.04	-0.99 ± 0.006	-0.95 ± 0.06	-0.99 ± 0.006	-0.99 ± 0.00
Dry floodplains	-0.64 ± 0.30	-0.35 ± 0.41	-0.38 ± 0.31	-0.24 ± 0.88	-0.25 ± 0.51	0.01 ± 0.70
Mopane	-0.05 ± 0.37	0.31 ± 0.20	0.07 ± 0.22	-0.22 ± 0.43	-0.35 ± 0.19	-0.64 ± 0.19
Riverine	0.11 ± 0.28	-0.35 ± 0.23	0.07 ± 0.25	0.45 ± 0.098	0.56 ± 0.01	0.48 ± 0.09
Sandveld	-0.05 ± 0.05	-0.14 ± 0.29	-0.16 ± 0.19	-0.25 ± 0.11	-0.31 ± 0.03	-0.64 ± 0.14
Tall open grasslands	0.04 ± 0.52	-0.34 ± 0.33	-0.45 ± 0.37	-0.81 ± 0.17	-0.81 ± 0.14	-0.99 ± 0.009
Wetlands	-0.63 ± 0.14	-0.95 ± 0.02	-0.31 ± 0.23	-0.29 ± 0.57	-0.24 ± 0.16	0.49 ± 0.33

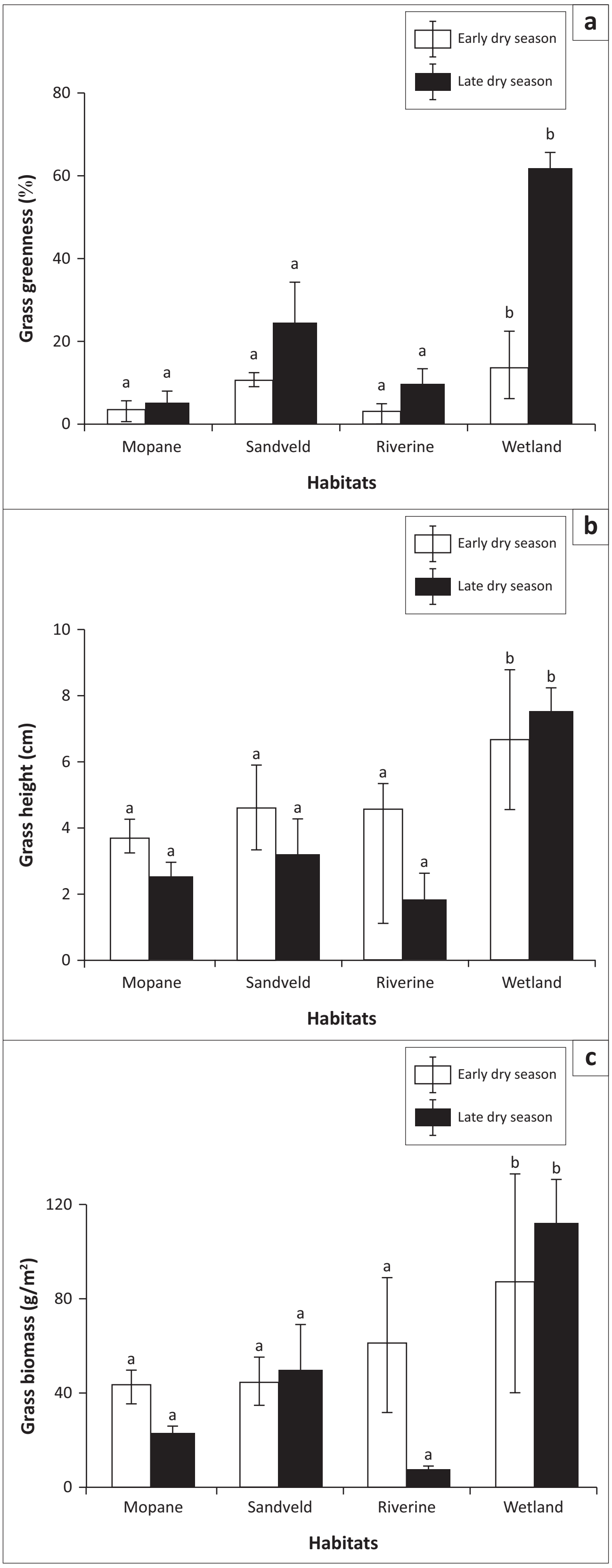
MCP, minimum convex polygons; LoCoH, local convex hull; ED, early dry; EW, early wet; LD, late dry seasons; LW, late wet; MD, mid dry; MW, mid wet.

issued by the Ministry of Environment, Wildlife and Tourism and the Department of Wildlife and National Parks (Gaborone, Botswana). Darting operations or removing collars from cows were done from a vehicle and a helicopter, respectively. Collars were removed successfully after two successive years.

Discussion

Buffalo shifted their seasonal concentration areas between wetlands and woodlands (Figures 3 and 4) as an adaptive strategy to seasonal forage dynamics and water availability over the annual cycle, with BH1 and BH2 having a migratory strategy with little overlap between wet and dry season concentration areas. However, the distance moved from perennial water sources over the wet season varied significantly across the buffalo, with BH3 being more sedentary. Bennitt et al. (2014) and Taolo (2003) reported similar results, noting that buffalo selected contrasting seasonal vegetation types, using woodlands far from permanent water during the rainy season and seasonally flooded vegetation close to permanent water during the early and late flood seasons. As with our findings, several other studies in the region have also found a mix of strategies (migratory vs. sedentary) between buffalo (Bennitt et al. 2014; Bennitt, Bonyongo & Harris 2015; Naidoo et al. 2012, 2014). Cornélis et al. (2011) also noted similar findings where buffalo were observed to range between woodlands and riverine habitats during the wet and dry season, respectively.

A key factor that may influence buffalo concentration patterns during the wet season appears to be the availability of higher quality, soft-leaved grasses (such as *Digitaria eriantha*) in back country woodlands than in wetlands (floodplains), which in contrast support tougher-leaved grasses adapted to shading and litter accumulation under the more productive conditions of wetlands (Fynn & Bonyongo 2011), and where greater biomass dilutes nutrient concentrations (Jarrell & Beverly 1981), while greater silica contents of wetland versus dryland grasses further reduce digestibility (Mosimane 2015). One of the most favoured grasses by buffalo, *D. eriantha*, peaks in abundance beyond 10 km from the permanent water of the Okavango Delta and Linyanti Swamps, whereas shorter grazing lawn–forming grasses such as *Urochloa trichopus* peaked in abundance with 5 km of these extensive wetland systems (Sianga et al. 2017). The medium to tall, leafy high-quality *D. eriantha* would be expected to be optimal in height and digestibility for maximising protein and energy intake rates in buffalo, which explains why buffalo focused their wet season foraging beyond 10 km from wetland systems (Figure 4). By contrast, wildebeest and impala, which favour shorter grasses, focused within 5 km of these wetland systems (Fynn et al. 2014). This suggests that short and tall grass grazers in the SMLE have distinct spatial niche separation during the wet season driven by distance to wetland systems. Similar observations have been made in the Maasai-Mara, where buffalo favour the taller grass areas within the reserve and wildebeest and gazelles the shorter grass areas outside the reserve (Bhola et al. 2012). Thus, a high conception rate of buffalo during the wet season is probably because of the availability of high-quality green forage of optimal height and biomass (Ryan, Knechtel & Getz 2007). Thus, concentration during the wet season by the three buffalo in vegetation types (sandveld and mopane) where tufted, soft-leaved grasses are more abundant supports our first hypothesis (H1). Drying up of ephemeral pans over the



Error bars shows standard error of the mean. Different letters shows significant difference according to Kruskal–Wallis test at α = 0.05.

FIGURE 7: (a) Grass greenness, (b) height and (c) biomass of mopane woodland, sandveld, riverine and wetland used by buffalo herds during the early and late dry season.

dry season forced buffalo to move away from favoured wet season ranges towards permanent water sources (Figures 3 and 4), which included floodplains and swamps (wetlands) and adjacent woodlands within the study area. It is this forced movement away from favoured wet season ranges towards permanent water that likely contributes to reduced grazing pressure in favoured wet season ranges and, therefore, higher abundances of favoured grasses such as *D. eriantha* far from permanent water. This indicates that artificial water provision in back country woodlands far from permanent water may be an unwise management option that could reduce niche diversity in the system leading to declines in taller grass grazers such as buffalo, as well as roan and sable antelope.

These floodplain and swamp (wetlands) systems provided buffalo not only with reliable drinking water during the dry season but also with forage significantly greener than that found in woodlands, as observed in other studies in the region (Bennitt et al. 2014; Fynn et al. 2014; Taolo 2003). More productive wetland areas are likely to provide a critical reserve and critical buffer resources (Owen-Smith 2002) for the late dry season, or elsewhere referred to as key resources (Illius & O'Connor 2000), especially during drought years when more preferred resources have been depleted (Owen-Smith 2002). The ability of wetlands to provide taller green forage with higher energy and protein levels relative to drylands during the late dry season has been shown to greatly elevate buffalo population productivity (Taylor 1985). The taller grass of wetlands is likely to be especially critical for buffalo, which are highly vulnerable to competition for forage (Bhola et al. 2012), owing to their tongue sweep foraging strategy, which cannot deal with short grass.

Thus, our findings of increasing use of swamp, marsh and floodplains (wetlands) as the dry season progressed by our three buffalo together with similar observations in other studies (Prins & Beekman 1989; Taylor 1985; Tinley 1977; Vesey-FitzGerald 1960; Western 1973), demonstrate the importance of wetland systems as dry season key-resource habitat for buffalo, as is the case for cattle and other wild herbivores across Africa (Fynn et al. 2015).

Our collared buffalo migrated at an intermediate scale from wetlands to woodlands rather than from wetlands to the high-quality Mababe Depression grasslands, favoured by a migratory zebra population over the wet season (Sianga 2014) and, thus, our second hypothesis (H2) that buffalo seasonal movements would match the regional-scale distribution of functional seasonal vegetation types was not supported. Though this finding does not support our H2, it does not rule out the possibility of buffalo migrating into the depression during the wet season because not all buffalo herds in the ecosystem were fitted with collars to determine their movements. Also, aerial surveys conducted by Fynn et al. (2014) did not observe any buffalo in the Mababe

Depression at that time, suggesting that buffalo probably do not favour the Mababe Depression during the wet season, unlike the zebra population (Sianga 2014). However, the buffalo appear to show adaptive variation in seasonal presence to changing environmental conditions in different years. For instance, in 2011, BH1 and BH2 avoided floodplains and swamps (wetlands) in their usual dry season concentration areas of the Linyanti Swamps and Selinda Spillway (2012 and 2013) because of the exceptionally high floods of 2011, being forced to use the more elevated floodplains of the Savuti Channel. This shift in location of different dry season concentration areas emphasises the importance of having a large spatial scale available for movement (Fynn et al. 2014), which enables adaptation to changing conditions between years. Finally, the finding of cross-border movements by BH1, together with those of Naidoo et al. (2014) and Patterson (1972), demonstrates the importance of Transfrontier Conservation Areas such as this one (Kavango Zambezi Transfrontier Conservation Area, KAZA), which transcends the borders of Angola, Namibia, Botswana, Zimbabwe and Zambia allowing adaptive foraging to a variety of different functional seasonal resources.

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Competing interests

The authors declare that they have no financial or personal relationships that may have inappropriately influenced them in writing this article.

Authors' contributions

All authors of this research article have directly participated in the planning, execution and analysis of this study.

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