Home range and habitat use of roan antelope *Hippotragus equinus* in northern Botswana

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HIGHLIGHTS

- First study to investigate the home ranges and habitat use of roan antelope in northern Botswana.
- Study area is relatively unhindered by human intervention (i.e. no water provision, fences), providing a useful model system for understanding natural roan antelope habitat use through seasons.
- Importance of 'back-country' habitats away from permanent water is highlighted for persistence of the species.
- Management actions for conserving heterogeneity should not ignore 'marginal' habitats or those reflecting low abundance as these may be critical for maintaining rare species.

ABSTRACT

Studies investigating animal movement and habitat use are essential for wildlife management and conservation. Northern Botswana represents some of the least modified landscapes in Africa. Studying the seasonal habitat use of herbivores in these landscapes provides important baseline information with which to compare the behavioural responses of similar species occurring in anthropogenically modified landscapes. We report on the home range extent and habitat use of roan antelope (*Hippotragus equinus*) in a region of northern Botswana unaffected by artificial water and fences. We deployed Global Positioning System (GPS) collars on individuals in four roan antelope herds in northern Botswana, three herds in the drier northern section of Botswana and one herd in the wetter Okavango Delta. Herds in the drier northern section occupied larger home ranges (>50km^2) than did herds in the wetter Okavango Delta (<50km^2). All herds preferred specific core areas (all smaller than 20 km^2) within their home ranges. All herds had similar location and size of home range between the wet and dry season (non-migratory). All herds occurred in back-country sandveld areas dominated by either Kalahari apple-leaf (*Philenoptera nelsii*) or silver cluster-leaf (*Terminalia sericea*) woodlands with low densities of competitors and predators. In Botswana, the long-term persistence of free-roaming roan antelope herds likely depends on the preservation of these unmodified back-country habitats away from permanent water.

GRAPHICAL ABSTRACT

Keywords: Roan antelope, home-range, habitat use, Botswana

1. INTRODUCTION

Ungulates respond dynamically to their environment, choosing suitable habitat and moving within a defined home range (Viana *et al.* 2018). When choosing habitats, ungulates trade-off between selecting areas that increase reproductive effort and energy intake and avoiding predators and competitors (Viana *et al*. 2018; Ofstad *et al.* 2019). Long term studies of home range size and shape provide valuable insight into a species' population density, habitat preferences and foraging behaviour (Harris *et al*. 1990; Boitani & Fuller, 2000). While a home range describes the area traversed by an individual, studying seasonal changes in habitat use within these home ranges provides additional ecological information.

The requirements of animals, as well as the features of their habitats, vary spatially and temporally, resulting in individuals distributing themselves in relation to changing parameters (Fritz *et al.* 1996; Dörgeloh, 1998). Seasonal changes in temperature and rainfall influence the availability of water, affecting the growth cycle and senescence of many plant species which determines the nutritional quality available to herbivores (Owen-Smith, 2008; Macandza *et al*. 2012). Many herbivore species adapt to these changes in resource availability by using different habitat types during the wet and dry seasons (Fynn *et al*. 2014). While some species migrate to access these seasonally functional habitats, others can switch from grass to browse during the dry season, thereby maintaining access to green forage over the annual cycle (Selebatso *et al*. 2018; Weber *et al*. 2020). To conserve these species, we need to consider how populations respond to changing habitats, especially if habitat change is driven by anthropogenic activities.

The influence of humans is evident, even in large protected areas in Africa (Jones *et al*. 2018; Kendall *et al*. 2018). The borders of protected areas are facing growing pressure from surrounding communities (Jones *et al*. 2018). Within national parks, the erection of fences and artificial water provision (AWP) can greatly modify landscapes (Peel & Smit 2020). Fences restrict animal movements and providing permanent drinking water at fixed points changes the seasonal habitat use of herbivores (Peel & Smit, 2020). With no need to track ephemeral water sources, herbivores may stay in the same area permanently, eventually homogenizing herbivore distributions. The increased pressure from herbivores further negatively affects the regeneration of vegetation and disrupts grassland structural heterogeneity on distance to water gradients (Sianga *et al*. 2017a). Large groups of herbivores staying in the same area also attract predators, which may increase the predation risk for non-migratory herbivores (Harrington *et al*. 1999). One of the best examples of this was the decline of roan antelope, from 450 to approximately 45 animals, in the Kruger National Park over a 13-year period. The population crash was attributed to the provision of artificial water points attracting large herbivores such as zebras (*Equus quagga*) and wildebeest (*Connochaetes taurinus*), which prevented the grass layer from regenerating and attracted lions (*Panthera leo*) to the area (Harrington *et al.* 1999). Narrow mouthed herbivores such as roan cannot forage efficiently on short grasses, so loss of their favoured medium height grasses would have negative impacts on their resource intake (Schuêtte *et al*. 1998; Arsenault & Owen-Smith 2008).

Roan antelope (*Hippotragus equinus*) are one of Africa's largest antelope species. Although they appear to be widely distributed across Africa, they are considered rare and locally endangered in many range states (Martin 2003). Roan can be found in a wide range of habitats but seem to be limited by climatic conditions, availability of vegetation types within home ranges, availability of water and the distribution of competitors and predators within the area (see Havemann *et al*. 2016). Roan antelope are unusual among African grazing ruminants in that they favor areas where soils are predominantly infertile (Heitkönig & Owen-Smith, 1998), with few competitors and predators (Tyowua *et al.* 2012). Roan antelope tend to avoid closed canopy woodlands, closed stands of vegetation and short grass areas and prefer open and wooded grasslands (Martin, 2003; Kimanzi, 2011). Roan antelope select lightly wooded savannas with relatively high rainfall and low-nutrient soils and are well adapted to open areas of medium to tall grasses up to 1.5 metres in height (Joubert, 1976; Harrington *et al*. 1999; Perrin & Taolo, 1998; Schuêtte *et al*. 1998; Martin, 2003; Kimanzi, 2011; Tyowua *et al*. 2012). Roan antelope herds are also usually found within 5 km of a water source (Martin, 2003; Kimanzi, 2011) but this may be an artefact of studies in modified landscapes, which emphasizes the importance of studies in unmodified landscapes. Throughout Africa, roan antelope appear to use open 'dambo-like' grasslands and floodplains possibly due to the increased availability and density of high green leaf vegetation, which has higher sodium content and is of better quality (Heitkönig & Owen-Smith, 1998). These habitats seem to be more important towards the end of the dry season (Afolayan & Ajayi, 1980; Tchamba & Elkan, 1995; Caro, 1999; Knoop & Owen-Smith, 2006; Scholte *et al*. 2007).

Roan antelope occur naturally in Botswana (Havemann *et al*. 2016), with an estimated population of 833 individuals (Chase *et al.* 2018). The roan antelope populations are largely confined to the drier north-east section of the country in the Ngamiland and Chobe districts (DWNP, 2012), with a few isolated populations in the Okavango Delta (Havemann *et al.* 2016).

Compared to many conservation areas in Africa, northern Botswana's conservation and wildlife management areas are largely unfenced without artificial water points. As a result, the distribution of both water and food resources are influenced by local seasonal precipitation and seasonal floods (Fynn *et al*. 2014). Permanent water sources are very far apart (>20 km) and back country woodlands have no water during the dry season, which influences the distribution of herbivores and predators (Sianga *et al*. 2017a). Being mostly free of human influence, northern Botswana provides an ideal site for studying natural habitat use of roan antelope. We predicted that herds will adjust their home range size and habitat use in response to seasonal climatic conditions, most notably water availability.

Few studies have described the natural home range and habitat use of roan antelope (Havemann *et al* 2016) with most of these focussing on introduced or heavily managed populations or populations at the edge of their distribution (Joubert, 1976; Erb, 1993; Perrin & Taolo, 1998; Kimanzi, 2011; Havemann *et al*. 2016). These studies indicate that breeding herd home ranges varied from 2-100 km^2 in size and showed distinct wet and dry season ranges, with seasonal preferences dictated by grass composition and topography (Joubert, 1976; Wilson & Hirst, 1977; Erb, 1993; Perrin & Taolo, 1998; Martin, 2003; Kimanzi, 2011). In this study, we determine the home range extent and habitat use of roan antelope in two unfenced, largely undisturbed concessions in northern Botswana that have different climates and vegetation composition. We use roan antelope as a model to better understand interactions of water availability, home range size and habitat use in large ungulates in variable environments across a seasonal gradient.

2. MATERIAL AND METHODS

2.1. Study Area

The study was conducted in the unfenced NG15 (Linyanti Wildlife Reserve) and NG26 concessions between January 2010 and November 2013. The NG15 is a private concession of approximately 1 210 km^2 extent situated in northern Botswana, on the western boundary of the Chobe National Park (Figure 1). The climate is semi-arid and is characterized by a prolonged dry season (April/May–October/November). The rainy season usually starts at the end of October and lasts until April and is characterised by thunderstorms (McCarthy *et al*. 1998). The NG15 is considered as being a much drier habitat compared to the NG26, as it is not influenced by the annual flooding event of the Okavango Delta, the latter occurring annually between February and September. Vegetation in the NG15 concession is dominated by dry mopane (*Colophospermum mopane*) and sandveld woodland, with the Linyanti River and Swamps on the north-western side and the Savuti Channel bisecting the southern part of the concession (Figure 1).

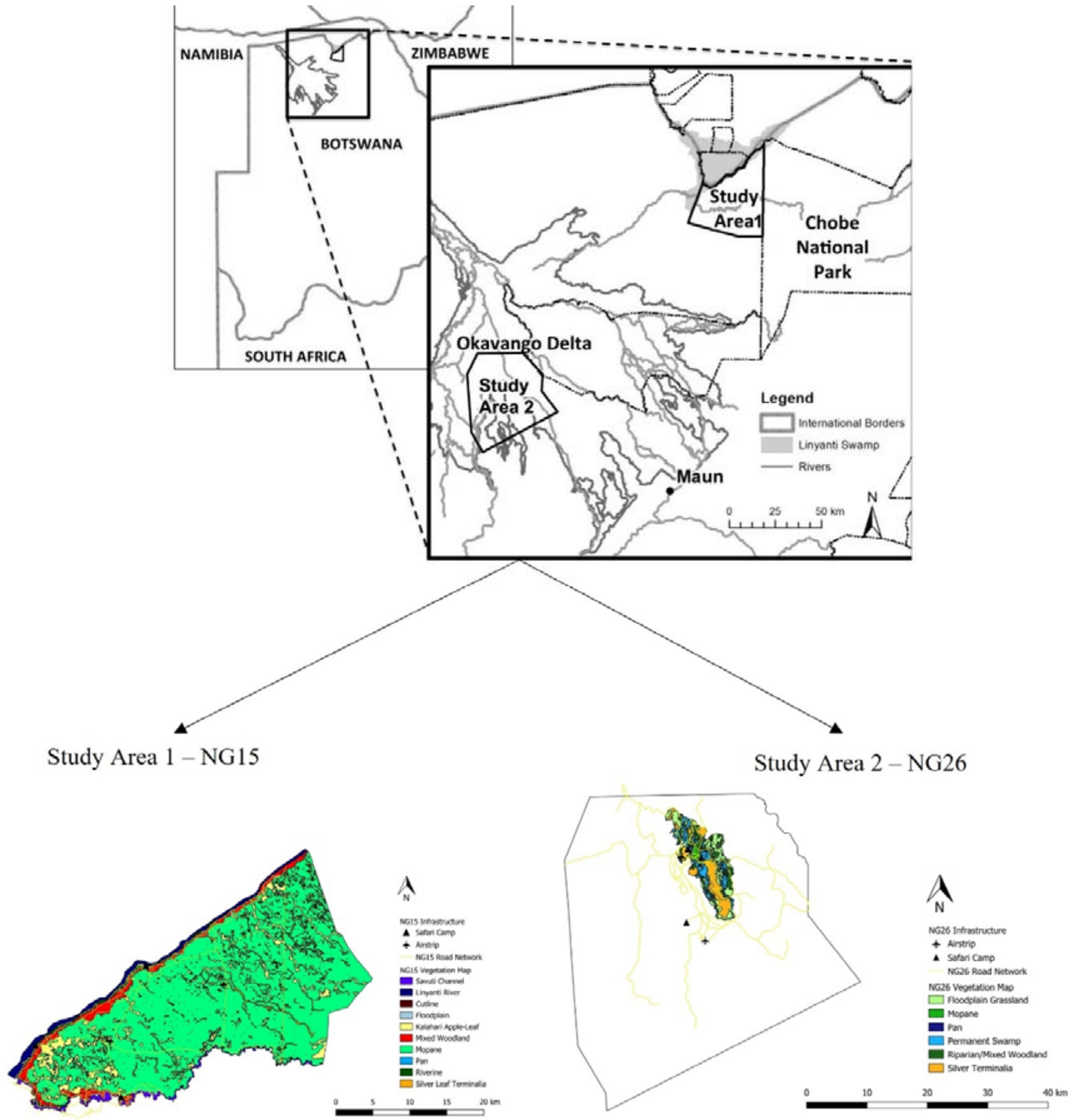

Figure 1. Study area and location of the vegetation maps constructed for the NG15 concession (study area 1) and NG26 concession (study area 2) in northern Botswana.

The NG26 concession is approximately 1 853 km^2 in extent and is situated in the upper-central portion of the Okavango Delta in northern Botswana, on the western boundary of the Moremi Game Reserve (Figure 1). The vegetation dynamics of the NG26 concession are partly driven by the delta flooding event, which results in significant annual and seasonal changes. Flooding normally begins between February and May when floodwaters arrive from the Angolan highlands, peaking in June/July (McCarthy *et al.* 1998; van Bommel *et al*. 2006) and lasting until August/September (Gumbricht *et al.* 2004). The forage is of poor quality due to the sandy, infertile soils that dominate the region (Mendelsohn *et al*. 2010). Table 1 shows the habitat types found in both NG15 and NG26 concessions.

Table 1. Characteristics of different vegetation types found in the Linyanti (NG15) and NG26 concessions (adapted from Hensman 2011 and Fynn *et al.*. 2014).

Vegetation Type	**Defining Characteristics**	**NG15**	**NG26**
Mopane woodland (MOP)	Dominated by mopane (*Colophospermum mopane*) that varies between dense scrub woodlands, open woodlands and tall closed canopy woodlands. Generally found on alluvial sand, silt and clay soils. Depressions in the clay soils capture and hold rainwater until late in the dry season. Grass cover is sparse (particularly during the late dry season) and grass species present are generally unpalatable.	**X**	**X**
Mixed woodland (MW)	Open deciduous woodland found on drier soils with relatively high clay content. Typically found adjacent to riparian woodlands. Dominated by trees such as apple-leaf (*Philenoptera violacea*), camelthorn (*Acacia erioloba*), leadwood (*Combretum imberbe*) and shepherd's tree (*Boscia albitrunca*) with an understory typically containing wild sage (*Pechuel-loeschea leubnitziae*), knobbly creeper (*Combretum mossambicense*) and Kalahari star apple (*Diospyros lycioides*). In the wet season, broad-leafed palatable grass species are abundant but quickly disappear as the dry season progresses. Large densities of herbivore and associated predator species are found in this habitat type.	**X**	
Silver cluster-leaf woodland (SLT)	Occur on deep aeolian sand deposits and usually dominated by silver cluster-leaf (*Terminalia sericea*) trees. Predominantly contains tall grass species such as giant three-awn (*Aristida meridionalis*), long-three awn (*Aristida stipitata*) and broom love grass (*Eragrostis pallens*). Kalahari apple-leaf (*Philenoptera nelsii*) is also often found in this habitat type.	**X**	**X**
Kalahari apple-leaf woodland (KAL)	Found in deep, low-nutrient aeolian sand deposits with predominantly Kalahari apple-leaf (*Philenoptera nelsii*) trees. Usually contains tall grass species such as giant three-awn (*Aristida meridionalis*), long-three awn (*Aristida stipitata*) and sand quick (*Schmidtia pappophoroides*).	**X**	
Riparian woodland (RW)	Small stretch of tall evergreen woodland situated on deep soils with a high water table, usually directly adjacent to permanent rivers. Dominated by tall trees such as sycamore fig (*Ficus sycomorus*), jackal berry (*Diospyros mespiliformis*), African mangosteen (*Garcinia livingstonei*) and bird plum (*Berchemia discolor*). Understory dominated by large fever-berry (*Croton megalobotrys*) and knobbly creeper (*Combretum mossambicense*).	**X**	
Mixed mopane/Kalahari apple-Leaf woodlands (MOP/KAL)	Usually found on the boundary between mopane and Kalahari apple-leaf woodlands, on alluvial sand, silt and clay soils, which vary between open wooded areas to dense stands of vegetation. Dominated by *Digitaria eriantha* and *Schmidtia pappophoroides* grass species.	**X**	

Cathedral mopane woodland (CATH MOP)	Open area dominated by tall mopane (*Colophospermum mopane*) trees, with very little understory growth. Usually occurs in isolated patches within the dominating dense mopane woodlands. Contains grass species such as *Digitaria eriantha*, *Aristida adscensionis* and *Sporobolus panicoides*.	**X**	
Floodplain grassland (FG)	Usually adjacent to permanent water and found on alluvial sand, silt and clay deposits. Seasonal fluctuations in flood water gives rise to medium height green grasslands when floodwaters recede and shallow wetlands during the floods. Area dominated by sedge and grass species, such as *Cynodon dactylon*, and contains very few tree species due to the high water table.	**X**	**X**
Riparian/Mixed woodland (RW/MW)	Typified by tall evergreen trees such as jackalberry (*Diospyros mespiliformis*), sausage tree (*Kigelia africana*), real fan palm (*Hyphaene petersiana*) and rain tree (*Philenoptera violacea*). With an understory typically containing confetti bush (*Gymnosporia senegalensis*), Kalahari star-apple (*Diospyros lycioides*) and magic guarri (*Euclea divinorum*). In the wet season, broad-leafed palatable grass species are abundant but quickly disappear as the dry season progresses.		**X**
Permanent swamps (PS)	Inundated by water all year round. Typified by beds of papyrus, islands rimmed with forests, lagoons and deep water channels.		**X**

2.2. DATA COLLECTION

2.2.1. Home Range and Habitat Use

We collared an adult female roan antelope in each of three herds in the NG15 concession (referred to as the SAV, BDF and CBE herds) and one adult female was collared in the NG26 concession (referred to as the ABU herd). The number of roan antelope herds utilizing the NG26 concession at the time of the study was unknown. Based on reports from guides, only one herd was known to be utilizing the area quite frequently. The ABU herd was also located towards the end of the study period, which is why only one collar was deployed in this concession. Initially only combined Global Positioning System-Ultra High Frequency (GPS-UHF) collar transmitters were deployed, although these were later replaced with satellite collars (African Wildlife Tracking, Pretoria, South Africa, www.awt.co.za) (Table 2). The GPS-UHF transmitters were programmed to take an hourly GPS location and the satellite collars were programed to record a GPS location every two hours. Data were either remotely downloaded via a satellite uplink (satellite collars) or were manually downloaded when the collar was retrieved (GPS-UHF collars). A veterinarian registered with the government of Botswana conducted all darting operations in accordance with the research permit (EWT 8/36/4 XVII [23]) and the corresponding collaring permit (WP/RES/15/2/2 XXII [10]) issued by the Ministry of Environment, Wildlife and Tourism and the Department of Wildlife and National Parks (Gaborone, Botswana). Initial darting and the removal of collars were done from a vehicle and a helicopter, respectively, and all collars were successfully removed at the completion of this project. The study had ethical clearance from the University of Pretoria Animal Ethics Committee (project no. AEC062-12).

Table 2. Seasonal Minimum Convex Polygon (MCP) home range sizes, as well as 95% and 50% Kernel Density Estimate (KDE) home range sizes calculated using the smooth crossed validation bandwidth (SCV). The number of seasonal GPS locations recorded by each collar and the number of days over which the GPS locations were recorded are also reported. *Collar was a GPS/UHF collar, whereas all the other collars were satellite collars.

Herd ID	Season	Period of GPS functioning (dd/mm/yy)	No. of days	No. of GPS positions	MCP (km^2)	95% KDE (km^2)	50% KDE (km^2)
BDF	Wet	01/11/2011–17/12/2011	47	574	125.02	64.84	14.25
		24/01/2012–30/04/2012	97	1175			
		01/11/2012–14/01/2013	75	198			
	Dry	22/09/2011–31/10/2011	40	482	154.39	68.6	13.86
		01/05/2012–31/10/2012	184	2162			
CBE	Wet	07/11/2011–26/01/2012	81	963	103.34	66.17	15.52
SAV*	Wet	07/12/2010–17/01/2011	42	924	72.44	47.17	10.48
		01/11/2011–30/11/2011	30	705			
	Dry	12/06/2011–31/10/2011	142	3269	89.74	60.21	14.12
ABU	Wet	29/04/2012–30/04/2012	2	2	90.74	35.05	7.15
		01/11/2012–30/04/2013	182	1581			
	Dry	01/05/2012–31/10/2012	184	1972	45.94	34.03	8.1
		01/05/2013–19/05/2013	19	19			

Location data (Table 2 and 3) and direct observations (362 sightings in NG15 and 11 sightings in NG26) of roan antelope herds were used to determine home range and habitat use during the wet (November–April) and dry seasons (May–October).

Spatial analyses were conducted in the software program Geospatial Modelling Environment (GME) Version 0.7.2.0 (www.spatialecology.com) and the results projected in ArcGIS 10.0. Detailed vegetation maps, including the location of pans, were generated for both concessions using Google Earth (CNES/SPOT imagery 28/6/2013; Figure 1) with ground-truthing for accuracy. The roan antelope herds within the NG15 concession were usually wary of vehicles and were only followed when they appeared relaxed to avoid unnessessary stress on the animals and to prevent "chase" data (whereby the individuals were constantly moving in order to move away from the researchers) being recorded by the collar instead of natural movement patterns.

When a relaxed herd was encountered, the habitat utilization of roan antelope in both the NG15 and NG26 concession was determined by direct observations made of both the collared females and various roan antelope herds sighted opportunistically during the study period. When a roan antelope herd was sighted, the habitat type, habitat class, GPS location and herd activity (i.e. resting, feeding, socializing etc.) were recorded.

Table 3. Annual Minimum Convex Polygon (MCP), 95% and 50% Kernel Density Estimate (KDE) home range sizes of roan antelope (*Hippotragus equinus*) estimated using the smooth crossed validation bandwidth (SCV) in northern Botswana. The number of GPS locations recorded for each herd as well as the number of days over which the GPS positions were recorded is also reported. *Collar was a GPS/UHF collar, whereas all the other collars were satellite collars.

Herd ID	Herd size when collared	No. of days	No. of GPS positions	MCP (km^2)	95% KDE	50% KDE
BDF	12	443	4592	161.51	73.21	18.65
CBE	4	80	963	103.34	66.17	15.52
SAV*	7	214	4898	94.01	59.12	14.81
ABU	14	386	3574	96.33	35.45	8.21

Habitat physiognomy was classified into four categories based on vegetation density: 1 = open grassland with no or few scattered trees; 2 = relatively open woodland with spaces of approximately 3 m between individual trees; 3 = relatively dense stands of vegetation with stem diameters of <20 cm; 4 = extremely dense stands of vegetation with stem diameters of >20 cm.

We conducted vegetation plots at 178 randomly selected collar locations within the two concessions. At each plot the habitat type, habitat class and grass species were recorded. Using the advanced Daubenmire method (Bonham *et al.* 2004), grass species were recorded at each site by placing a 0.5 x 0.5 m quadrat at 0, 10, 20, 30 and 40 m intervals along a transect. Within each quadrat, aerial cover proportion and greenness were estimated for all grass species rooted within the quadrat, with greenness estimated using Walker's (1976) eight-point greenness scale (0%; 1–10%, 11–25%, 26–50%, 51–75%, 76–90%, 91–99% and 100%). Grass height was measured by placing a 20 x 10 cm brown paper bag on top of the grass swards at the centre of the quadrat and measuring the perpendicular height from the soil surface to the top of the bag.

2.3. DATA ANALYSIS

2.3.1. Home Range and Habitat Utilization

For each herd, we used Minimum Convex Polygons (MCP) and Kernel Density Estimates (KDE) to determine annual and seasonal home range extent. For the KDE analyses, 95% isopleths approximated annual and seasonal home ranges, excluding occasional outliers, and 50% isopleths indicated core home ranges.

For each collared herd, locations were overlaid onto vegetation maps and the number of locations within each habitat type counted. Using the GME package, we calculated the total area of each habitat type, excluding pans, perennial water and permanent water. Jacobs index (Jacobs, 1974) was used to calculate the degree of positive or negative selection for a specific habitat type in each concession. Jacobs index minimizes problems associated with many preference indices (Hayward *et al*. 2006) and is based on the formula $D = \frac{r-p}{r+p-2rp}$; where r is the proportion of location events within a specific habitat type and p is the proportional area of that habitat type within the study area. Values between 0 and -1 indicate negative selection and values between 0 and +1 indicate positive selection for a given habitat type. A value of 0 indicates that a habitat type is used in proportion to its availability (Grignolio *et al*. 2003; Fynn *et al*. 2014). For direct observations, the number of sightings within each habitat type was calculated and presented as a proportion of the total number of observations.

We calculated the number of vegetation plots conducted within each habitat type and expressed these as a proportion of the total number of vegetation plots. The proportional aerial cover of each grass species was averaged across each transect to calculate a single value per transect. The proportional cover of each grass species was averaged across all samples within a habitat type to yield the sample mean and associated standard error. The results for grass species composition were then separated by habitat type, herd and season.

3. RESULTS

3.1. Home Range:

GPS collars transmitted locations for 80–443 days, representing 963–4 898 locations (Table 2). Minimum convex polygon home ranges varied between 94.01–161.51 km^2, while 95% and 50% KDE varied between 35.45–73.21 km^2 and 8.21–18.65 km^2, respectively (Table 3). The ABU herd had similar seasonal 95% kernel home ranges, with the wet season home range being slightly larger than the dry season home range (Table 3). The ABU herd had a larger core home range, with two core areas during the dry season, while several smaller core ranges were recorded during the wet season (Table 3, Figure 2).

The three NG15 herds occupied adjacent home ranges, and importantly all three core home ranges were situated away from permanent water sources (Figure 3). Transmitter failure resulted in less data for the SAV and CBE herds. Both the BDF and SAV herds showed similar seasonal home ranges, with dry season home ranges being slightly larger than the corresponding wet season home ranges (Table 3). The core home ranges of both the SAV and BDF herds were more clustered and situated further away from permanent water during the wet season, whereas during the dry season core home ranges became less clumped and shifted closer to permanent water sources (Figure 3).

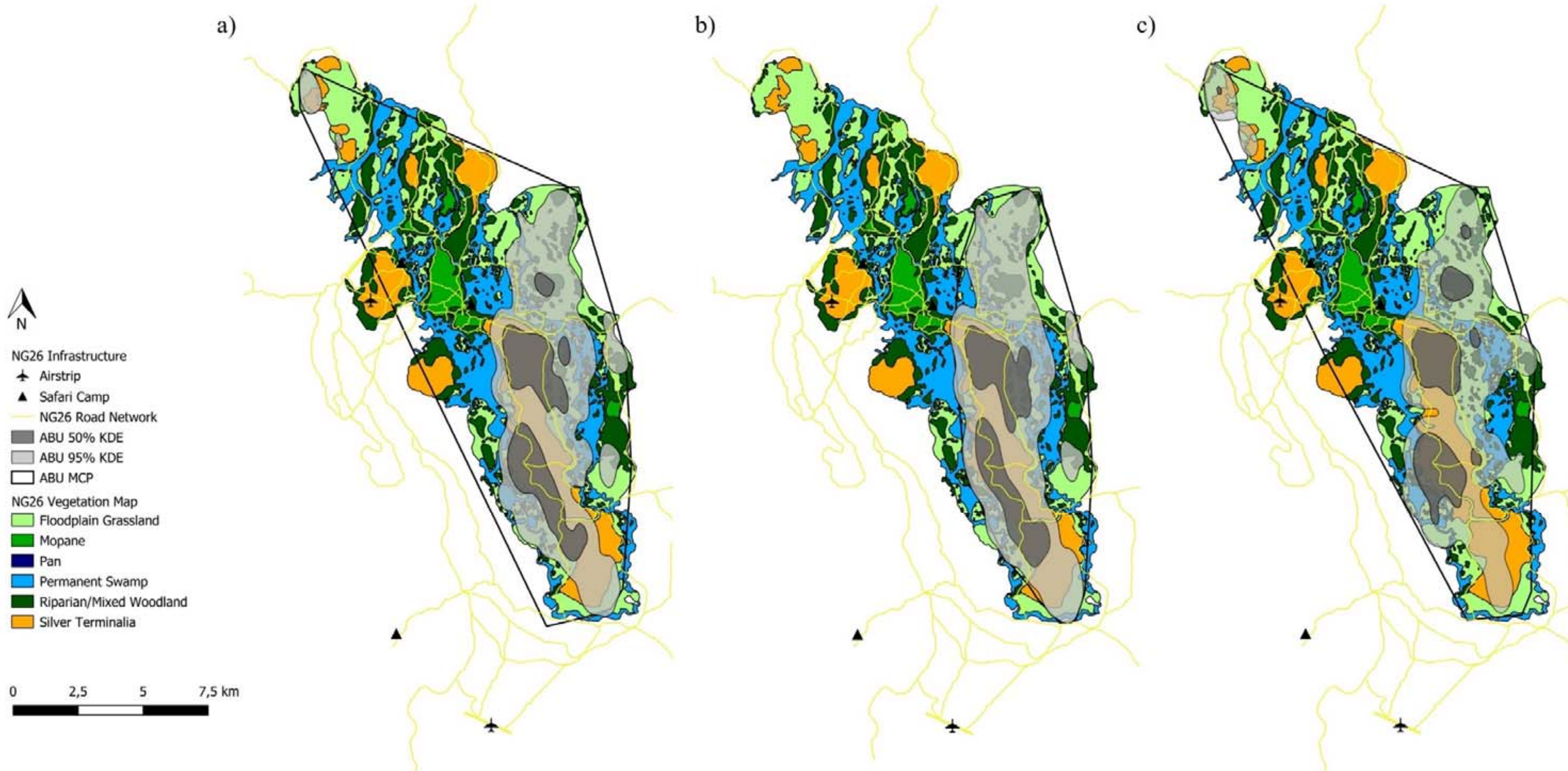

Figure 2. The a) annual, b) dry season and c) wet season Minimum Convex Polygon (MCP) and 95% and 50% Kernel Density Estimate (KDE) home ranges of the ABU roan antelope (*Hippotragus equinus*) herd in the NG26 concession, northern Botswana.

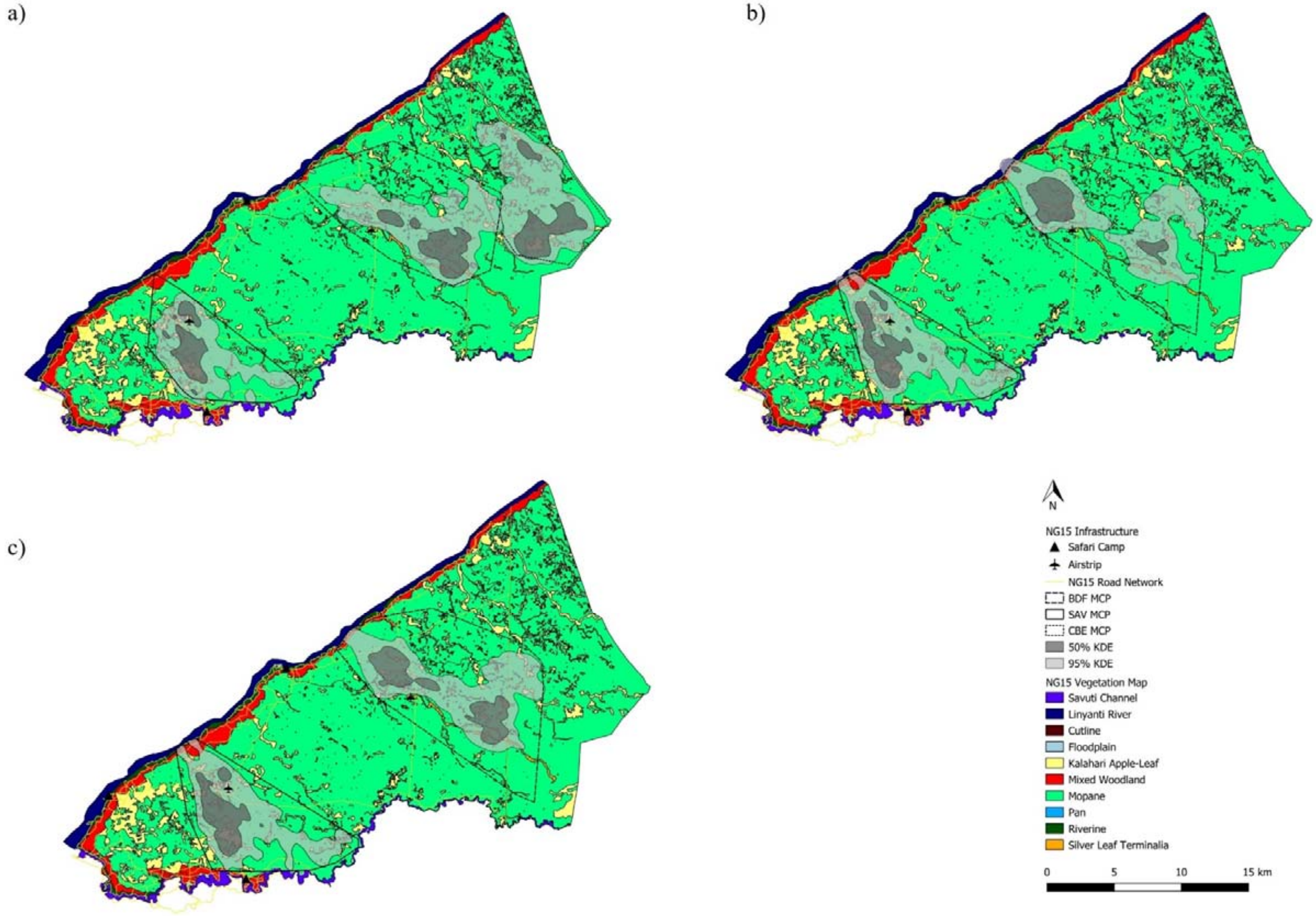

Figure 3 The a) wet season, b) dry season and c) annual Minimum Convex Polygon (MCP) and 95% and 50% Kernel Density Estimate (KDE) home ranges of the SAV, BDF and CBE roan antelope (*Hippotragus equinus*) herds in the NG15 concession, northern Botswana. The cutline separates the NG15 concession to the west from the Chobe National Park to the east.

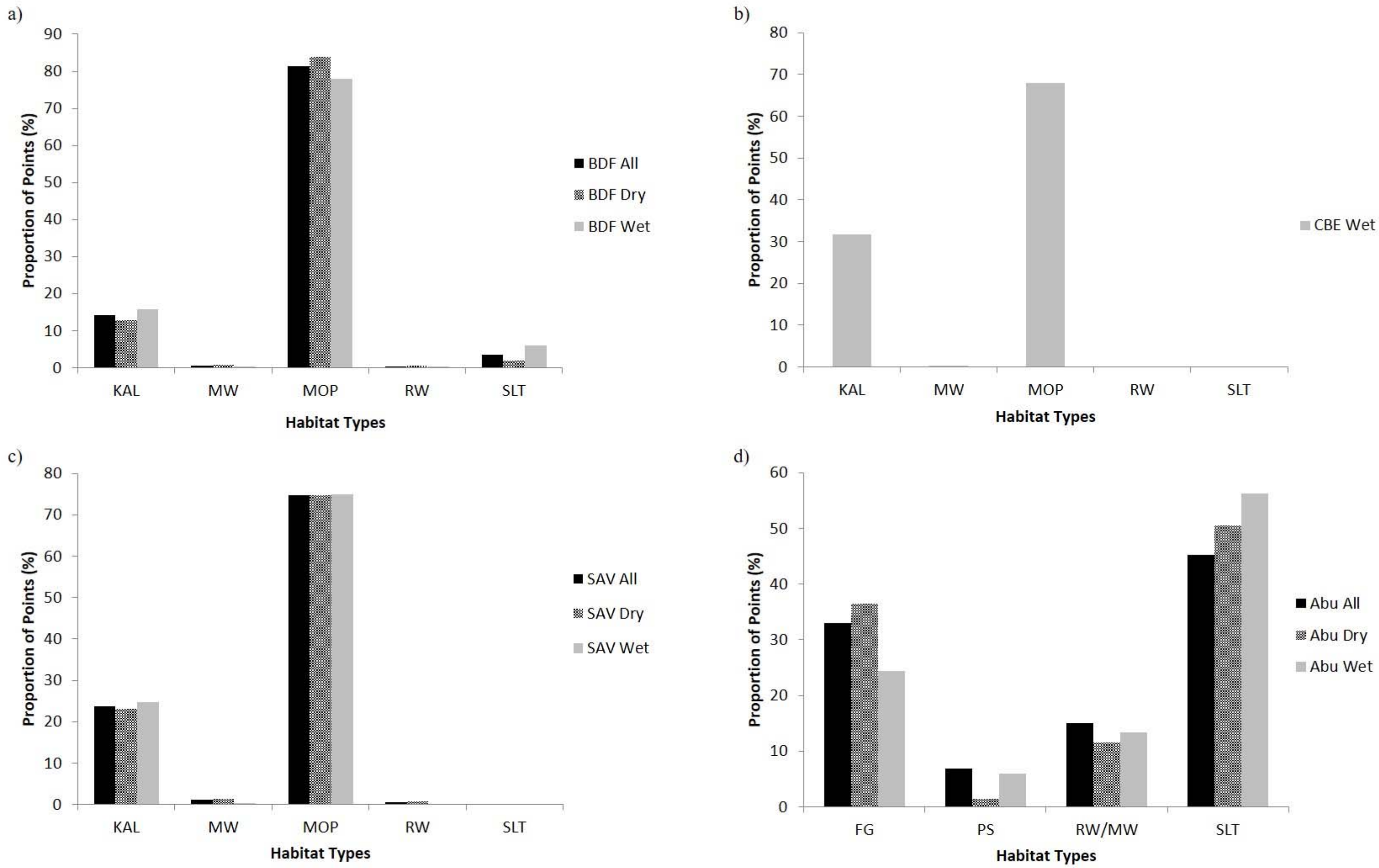

Figure 4 Proportion of Global Positioning System (GPS) collar points situated within the habitat types utilized by a) the BDF herd; b) the CBE herd; c) the SAV herd; and d) the ABU herd, during the wet (November–April) and dry (May–October) seasons between January 2010 and November 2013. Habitat types are: FG = Floodplain grassland; KAL = Kalahari apple-leaf (*Philenoptera nelsii*) woodland; MOP = Mopane (*Colophospermum mopane*) woodland; PS = Permanent swamps; RW = Riparian woodland; MW = Mixed Woodland; RW/MW = Riparian/Mixed Woodland; SLT = Silver cluster-leaf (*Terminalia sericea*) woodland.

3.2. Habitat utilization:

The ABU herd (NG26) predominantly used silver cluster-leaf (*Terminalia sericea*) and floodplain grassland vegetation types (Figure 4). Most of vegetation plots for the ABU here occurred in *T. sericea* woodland. Jacob's index results indicated that the ABU herd had a strong positive selection for *T. sericea* woodland during both the wet (J.I.: 0.71) and dry (J.I.: 0.65) seasons (Table 4). We frequently observed the ABU herd in floodplain grassland and the Jacobs index showed a low negative selection for this habitat type for both seasons, indicating that this habitat is being used in proportion to its availability.

Table 4. Jacob's index of habitat types selected by the ABU roan antelope (*Hippotragus equinus*) herd in the NG26 concession, northern Botswana overall and in the wet and dry seasons, respectively. Values in bold indicate positive selection for that particular habitat type.

Vegetation Type	Annual	Dry Season	Wet Season
Floodplain grassland	-0.10	-0.02	-0.30
Permanent swamps	-0.60	-0.90	-0.64
Riparian/mixed woodland	-0.16	-0.31	-0.23
Silver cluster-leaf woodland	**0.58**	**0.65**	**0.71**

NG15 herds were sighted on 362 occasions in nine habitat types, including the airstrip and cutline. The NG15 herds were never seen in the floodplain grasslands. Most sightings occurred in *C. mopane*, Kalahari Apple-leaf (*Philenoptera nelsii*) and mixed *C. mopane*/*P. nelsii* woodland. The *C. mopane* woodlands in which roan antelope herds were sighted consisted of dense stands of vegetation (habitat class 3), whereas most of the herds seen in *P. nelsii* and mixed *C. mopane*/*P. nelsii* occurred in more open habitats (habitat class 2) (Figure 5). All three NG15 herds showed positive selection for the *P. nelsii* woodland throughout the year (Table 5). The *Terminalia sericea* woodland only occurred in the home range of the BDF herd, which showed a very strong positive selection for this habitat type overall (J.I.: 0.83), as well as in the dry (J.I.: 0.69) and wet (J.I.: 0.89) seasons. Although the sightings data suggest that the NG15 herds selected *C. mopane* woodlands, all three herds showed a negative selection based on the Jacobs index (Table 5), probably due to the availability of large expanses of *C. mopane* woodlands. The riparian and mixed woodland were the least preferred habitat types within the NG15 concession (Table 5).

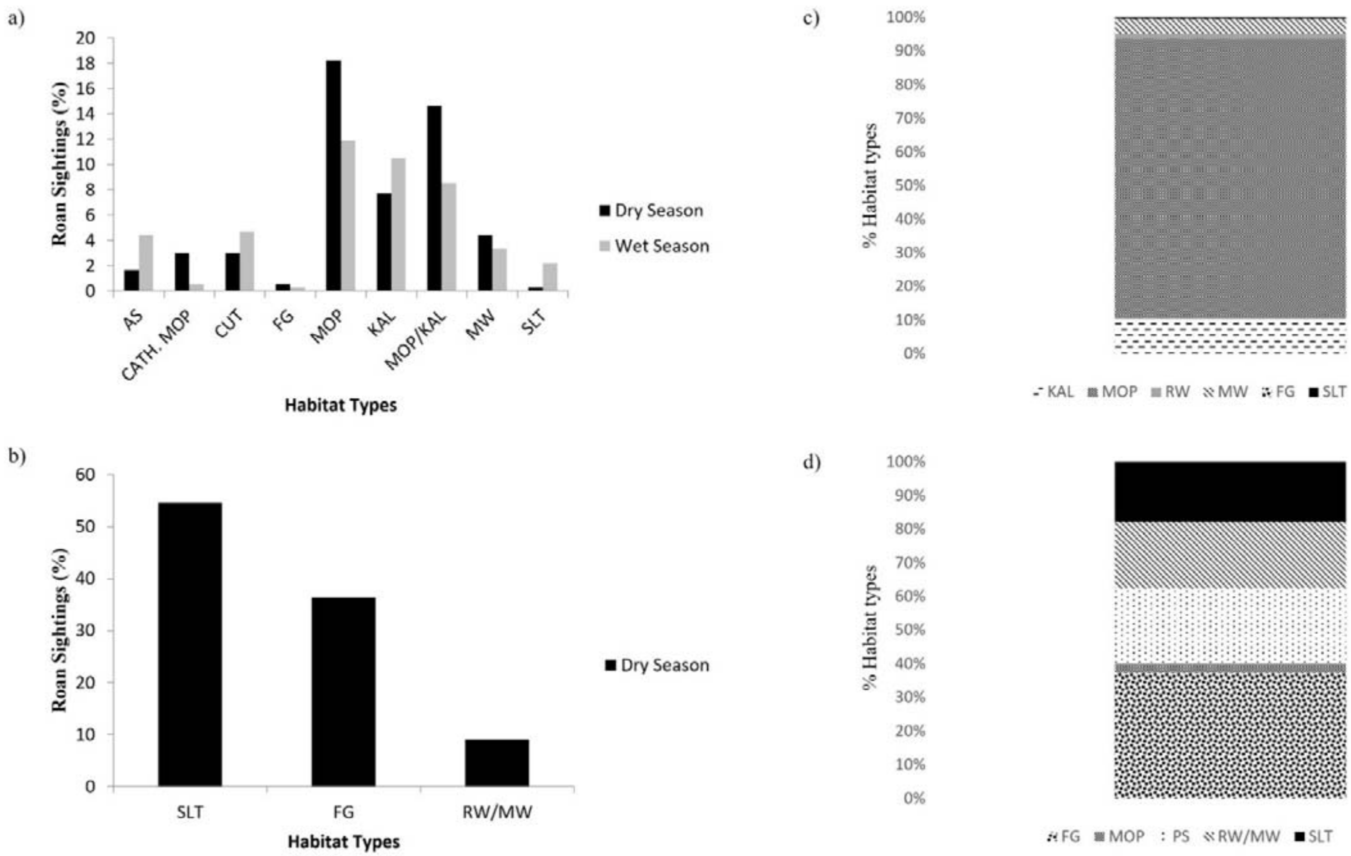

Figure 5 Percentage of roan antelope (*Hippotragus equinus*) sightings in different habitat types in a) the NG 15 concession (362 sightings) during the wet and dry season and b) the NG 26 concession (11 sightings) during the dry season. c) and d) represent the % habitat types available within each vegetation map. Habitat codes are: CATH MOP = Cathedral mopane (*Colophospermum mopane*); FG = Floodplain grassland; KAL = Kalahari apple-leaf (*Philenoptera nelsii*) woodland; MOP = Mopane (*Colophospermum mopane*) woodland; MOP/KAL = Mixed mopane (*Colophospermum mopane*)/Kalahari apple-leaf (*Philenoptera nelsii*) woodland; RW/MW = Riparian/Mixed woodland; RW = Riparian woodland; SLT = Silver cluster-leaf (*Terminalia sericea*) woodland; MW = Mixed Woodland; PS = Permanent Swamps; CUT = Cutline; AS = Airstrips.

Table 5. Jacob's index of habitat types selected by the BDF, CBE and SAV roan antelope (*Hippotragus equinus*) herds in the NG15 concession, northern Botswana. MOP = mopane woodland (*Colophospermum mopane*); KAL = Kalahari apple-leaf (*Philenoptera nelsii*) woodland; SLT = silver cluster-leaf (*Terminalia sericea*) woodland; MW = mixed woodland; RW = riparian woodland; NIH = Not in habitat. Values in bold indicate positive selection for the particular habitat type.

	BDF Herd			CBE Herd	SAV Herd		
Vegetation Type	Annual	Dry Season	Wet Season	Wet Season	Annual	Dry Season	Wet Season
KAL	**0.17**	**0.12**	**0.24**	**0.60**	**0.46**	**0.44**	**0.48**
MW	-0.78	-0.70	-0.91	-0.83	-0.62	-0.52	-0.87
MOP	-0.07	0.01	-0.18	-0.41	-0.26	-0.26	-0.26
RW	-0.60	-0.41	-0.93	NIH	-0.51	-0.34	-1
SLT	**0.83**	**0.69**	**0.89**	NIH	NIH	NIH	NIH

Twenty-seven vegetation plots were conducted in the NG26 concession (ABU herd) and 151 in the NG15 concession (80 for the SAV herd, 65 for the BDF herd and six for the CBE herd). Twenty-one grass species were identified in habitats utilized by the ABU herd, with the dominant species in the *T. sericea* woodland being *Digitaria eriantha* and *Brachiaria brizantha*. Average greenness was highest in the *P. nelsii* woodland in concession NG15 and the riparian/mixed woodland in concession NG26, respectively, while grass height was higher in summer than in winter. Twenty-nine grass species were identified in the NG15 concession, of which only five species (*Aristida adscensionis*, *D. eriantha*, *Eragrostis rigidior*, *Pogonarthria squarrosa* and *Schmidtia pappophoroides*) occurred within the habitat types utilized by all three NG15 herds. The greatest greenness and grass height were recorded during the wet season in all habitat types in the NG 15 concession.

4. DISCUSSION

We quantified the home ranges and core ranges of roan antelope in a core region of their distribution, which was unfenced and had minimal management intervention. When compared to more intensively managed populations elsewhere, the Botswana herds in this study did not show distinct seasonal home range variation, as has been observed elsewhere (Erb, 1993; Perrin & Taolo, 1998; Kimanzi, 2011). In this undisturbed population of large antelope it is likely that the dispersion of herds responds to seasonal changes, with herds spreading out in the dry season and becoming more clumped in the wet season. What remains unclear, is whether the roan antelope herds are responding to predation pressure, interspecific competition or resource availability.

4.1. Home range:

Our results suggest that the home range size of roan antelope was not solely driven by the availability of water as the ABU herd had access to water year-round and the NG15 herds were always within 12km of a permanent water source. The availability of surface water has been shown to be an essential requirement for roan antelope herds, which are usually found within 2–5 km of water (Wilson & Hirst, 1977; Martin, 2003; Kimanzi, 2011). Despite marked fluctuations in seasonal water availability, roan antelope herds in both concessions had similar home ranges in the wet and dry seasons, preferring specific core areas away from permanent water. In the NG15 concession, herds spent most of their time in areas dominated by *C. mopane* and *P. nelsii* woodlands in both the wet (> 4km) and dry (>2km) season, thus falling within the 2-5km distance to water described in previous studies. In the NG15 concession, the SAV herd home range was bounded by the Linyanti River and Savuti Channel, preventing them from moving further away from permanent water. The BDF herd was less restricted by physical barriers and had core home ranges that were further away from permanent water. All three NG15 herds had their wet season home range located midway between the two water sources. These results suggest that when possible they will set up their home range >5km from permanent water. The NG15 concession is not influenced by an annual flooding event as seen in the NG26 concession, but is dominated by a strong seasonal climate with a prolonged dry season (May–October) when the availability of food and water becomes extremely limited. In the dry season, roan herds are forced to move over larger areas to obtain sufficient resources when compared to the same or similar species in wetter environments (Fennessy, 2006). Due to the annual flooding event, the ABU herd occurs in a much wetter environment, contributing to this herd having a comparatively smaller home range. In the NG15 concession, we identified 660 seasonal pans in the *C. mopane* woodlands during the wet season, providing herds with water and facilitating slightly smaller core range sizes. The pans dry up during the dry season forcing herds to find sufficient water at either the Linyanti River (used by all three NG15 herds) or the Savuti Channel (used by the SAV herd). If water was the main factor influencing home range size, it would be expected that the NG15 herds would shift their core ranges to within 2 km of permanent water, which was not the case. Instead, roan antelope herds were often seen walking >10 km to and from the permanent rivers in the NG15 concession during the dry season, after which they would return to the back-country *C. mopane* and *P. nelsii* woodlands (C.P. Havemann Pers. Obs.).

The seasonal flooding in the NG26 concession limits the area available for movement and foraging during the peak flooding months but also induces grass regrowth when the floodwaters recede. This flooding has a profound effect on the movement of many animal species (Bartlam-Brooks *et al.* 2013). The core home ranges of the ABU herd were all confined to drier *T. sericea* woodlands, and the number of core areas increased during the dry season when flood waters receded and more grazing became available.

4.2. Habitat utilization:

In this study, roan antelope herds seem to be influenced by site specific factors, although some of these factors do conform to known species requirements (Joubert, 1976; Schuêtte *et al*. 1998; Kimanzi *et al*. 2013; Havemann *et al.* 2016). Roan antelope are considered highly selective feeders, with two or three plant species generally comprising the bulk of their diet (Martin 2003). They obtain most of their food through grazing; although they may include a small amount of browse during the dry season (Schuêtte *et al*. 1998; Martin, 2003). None of the herds in the NG15 concession showed any drastic seasonal variation in their use of habitat types indicating that forage quality may not be the main factor driving roan antelope habitat use. highly palatable grass species *D. eriantha, S. pappophoroides* and *E. rigidior.* Even during the dry season when the greenness and height of many grass species became severely reduced, roan antelope herds still used these habitat types and survived by supplemental browsing (C.P. Havemann & T.A. Retief, *pers. obs.*; Staver & Hempson, 2020). Browsing on the green leaves of trees during the dry season may allow roan herds to avoid the floodplains where there is also a higher density of predators. Schuêtte *et a*l. (1998) and Knoop & Owen-Smith (2006) showed that roan antelope's narrow mouth facilitates efficient bite size on woody species leaves and taller grasses by accurately selecting green leaves and soft stems and avoiding tough stems and dead leaves. During the dry season, the NG26 concession, where the ABU herd foraged, had greener and taller grasses compared to the NG15 concession, which was probably facilitated by the annual flooding event.

Roan antelope in both concessions actively selected *P. nelsii* and *T. sericea* woodlands, regardless of the presence of permanent water. These woodlands were relatively open and contained good grazing grass species (e.g. *D. eriantha* and *B. brizantha*). Sianga *et al*. (2017a) found that *P. nelsii* and *T. sericea* woodlands in northern Botswana (>20 km from permanent water) generally had a taller and denser grass layer than habitat types closer to water (>5 km) suggesting fewer herbivores. The roan antelope herds in our study may be selecting these woodlands because there is less interspecific competition and/or fewer predators. The presence of tall grass species (e.g. *Aristida stipitata* and *A. meridionalis*) may also contribute to increased calf survival (Martin, 2003). Heitkönig & Owen-Smith, (1998) also showed that roan antelope were most abundant in savannas with infertile soils. These habitats often contain high abundances of highly palatable medium-height grass species such as *D. eriantha* and low abundances of short, palatable grasses such as *Urochloa trichopus*, which occur closer to water in mixed and riparian woodlands (Sianga *et al.* 2017a). Many grazers, such as plains zebra and common wildebeest prefer shorter grasses and usually frequent short-grass areas. High densities of short-grass grazers may competitively exclude herbivore species that prefer taller grasses by keeping grasses short (Knoop & Owen-Smith, 2006, Fynn *et al.* 2014, Sianga *et al*. 2017b). Low densities of herbivores in medium-tall grass areas may also facilitate lower predator densities (Fynn *et al*. 2014). Aside from selecting for taller grasses, roan antelope can remain in back-country areas by selecting grass species (e.g. *A. stipitata*) that produce more green leaf in the dry season (C.P. Havemann & T.A. Retief, *pers. obs.*). The compositional and structural heterogeneity of grass minimizes competition between herbivore species (Sianga *et al.* 2017b) and allows different species to occupy different niches, where medium and tall-grass grazers such as roan and sable antelope (*Hippotragus niger*) can occur far from water, and short-grass grazers can occupy habitats closer to water (Fynn *et al*. 2014).

Roan antelope in the NG15 concession also frequented *C. mopane* woodland habitats. In northern Botswana, the *C. mopane* woodland provides drinking water in the form of pans and key minerals (Ca, Na, P) in very saline soils that are required by pregnant and lactating herbivores (Dye & Walker 1980; Romanens *et al*. 2019; Vittoz *et al.* 2020). Highly mobile herbivores (e.g. zebras) obtain their minerals by migrating to saline paleolake systems, such as Makgadikgadi and Mababe Depression, during the wet season, whereas non-migratory herbivores (e.g. roan and sable) obtain their minerals in saline stunted *C. mopane* patches (Vittoz *et al.* 2020). Thus, because back-country woodlands in this region consist of a fine scale mosaic of sandveld paleo-river channels among a matrix of *C. mopane* woodland (Sianga *et al*. 2017a, b; Vittoz *et al.* 2020), they provide important functional heterogeneity for sedentary herbivores; sandveld channels support favoured medium height leafy grasses, such as *D. eriantha* and *P. maximum*, while mopane provides drinking water and salinity.

Floodplains are an important habitat for roan antelope throughout Africa (Havemann *et al*. 2016), although this habitat was not actively selected by the herds in this study. In the NG26 concession, rising floodwaters during the early dry season result in the grasslands being inundated with shallow water limiting the area available for foraging. When the floodwaters recede, the regrowth of green grass is stimulated, providing resources in the dry season (van Bommel *et al.* 2006; Fynn *et al*. 2014). The flooding event had little or no effect on the ABU herds' movements as they used floodplains equally during the dry season when the water level is at its highest (36.4%), , and the wet season when water level is at its lowest (24.5%). In our study, the ABU herd used floodplain habitats in proportion to availability and mostly through necessity as they had to move through this habitat to access drier sandveld areas and to drink. In the dry season, mature leaves often lose energy and protein concentration (Sinclair 1975; Ellis & Swift 1988; Owen-Smith 2008). Not being able to maintain their energy requirements, most herbivores will move to alternative habitat types that offer better quality resources. In the NG15 concession, African buffalo (*Syncerus caffer*), plains zebra, common wildebeest and common impala (*Aepyceros melampus melampus*) herds move to floodplain grasslands with green grass during the dry season (Fynn *et al*. 2014; Sianga *et al.* 2017b). In contrast, roan antelope in the NG15 concession completely avoid floodplains during the dry season (this study). Similarly, sable antelope herds south-west of the Linyanti avoid floodplains during the dry season (Hensman *et al.* 2013). Sable and roan antelope may employ a different seasonal foraging strategy to many other herbivores, which may be driven by avoiding predators and competitors.

5. CONCLUSION

Northern Botswana offers great heterogeneity in functional seasonal habitats providing exceptional niche diversity for wildlife to thrive and coexist (Fynn *et al.* 2014). Ours is the first study to investigate the home ranges and habitat use of roan antelope in northern Botswana, a region central to their distribution and relatively unhindered by anthropogenic influences. For roan antelope, the presence of back-country mosaic of sandveld (*Philenoptera nelsii* or *Terminalia sericea*) and *C. mopane* woodlands that are more than 15km away from permanent water seem to be an important factor defining suitable habitat for this species (Sianga *et al*. 2017a). These sandveld woodlands also provide suitable forage and serve as a refuge where vegetation is spared from excessive impact and degradation by large herbivore populations that congregate close to water and the associated high predator densities. Furthermore, they provide niches for other rare herbivores such as sable antelope and common eland (*Tragelaphus oryx*) (Sianga *et al*. 2017a).

The long-term survival of roan antelope in Botswana likely depends on the preservation of these habitat types. Conservation strategies for roan antelope should focus on the preservation of back-country areas without artificial water sources to reduce grazing pressure from other grazers especially in the dry season, which will further reduce predation pressure for this locally rare species.

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