

5 • *Habitat, Space Use and Feeding Ecology of the African Buffalo*

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Introduction

Spatial distribution and movement patterns of wild ungulates are strongly dependent on the spatial and temporal heterogeneity of biotic and abiotic resources (Bailey et al., 1996; Fryxell et al., 2004). In most African ecosystems, feeding, drinking and resting places are subject to high seasonal variability and can be spatially segregated at certain times of the year. In this context, animals adopt space-use, movement and activity strategies that allow them to minimize detrimental effects of the main limiting factors to reach, at different scales, suitable trade-offs between several constraints and needs that must be addressed simultaneously (Godvik et al., 2009; Massé and Côté, 2009).

Ungulates, like the vast majority of higher vertebrates, do not move erratically through the environment, but restrict their movements to sites much smaller in size than their locomotion capabilities allow, and which they mostly exploit over a long period. Based on this, Burt (1943) conceptualized the concept of home range as ‘the area traversed by the individual in its normal activities of food gathering, mating, and caring for young’. The home range is thus the spatial result of the movements and behaviours that an individual (or a social group) expresses at different spatiotemporal scales to survive and reproduce, in other words to maximize its (their) selective value. The home range is a central concept

* The views expressed are solely those of the authors and do not necessarily represent the views of the institutions represented.

in ecology because it materializes a link between the movement of an animal and the resources necessary for its survival and reproduction.

In this chapter, we present the current state of knowledge on the space-use and feeding ecology of the African buffalo. This chapter also introduces some behavioural traits required for the comprehensiveness of this chapter, and which are further developed in other chapters. Most of what we know today about the behavioural ecology of savanna buffalo comes from studies focused on the Cape buffalo. In contrast, the ecology of the West and Central African savanna buffalo remains thus far poorly investigated. For this reason, and because several behavioural traits are similar within savanna buffalo subspecies, we present all savanna subspecies in one section, while the forest buffalo is the subject of a separate section.

Habitat

African buffalo live in a wide range of habitats, from open grasslands to rainforests, including all intermediate vegetation types: scrublands, woodlands and deciduous forests. African buffalo persist in semi-arid environments, as long as surface water is available within 20–40 km, year round (Cornélis et al., 2014).

Biomass or production of savanna ecosystems, such as buffalo populations, is positively correlated with mean annual rainfall and the soil quality (Coe et al., 1976; Sinclair, 1977; Grange and Duncan, 2006; Winnie et al., 2008). In similar water regime conditions, the nutrient content of vegetation and primary production are much lower on poor than on rich soils (Breman and De Wit, 1983; Le Houérou, 2008). The low biomass of wild ungulates in savanna ecosystems of West Africa (compared to those of volcanic areas in East Africa) mainly results from poorer soil conditions (Bell, 1982; East, 1984; Fritz, 1997).

Savanna Buffalo

Savanna buffalo are mainly found in habitats with a high herbaceous biomass. In eastern and southern Africa, suitable grasses for Cape buffalo are found in several types of woodland, such as mopane (*Colophospermum mopane*), miombo (*Brachystegia* spp.), acacia (*Acacia* spp.) and *Baikiaea* spp. In West and Central Africa, savanna buffalo live in a variety of habitats ranging from typical Sahelian shrub savannas (*Combretum* spp., *Terminalia* spp, *Acacia* spp.) to Sudanian woodlands (e.g. *Isoberlinia doka*, *Daniellia oliveri*, *Burkea africana*).

Forest Buffalo

Forest buffalo are forest-dwellers, inhabiting rainforests with grassy glades, watercourse areas and mosaics of equatorial forests and savannas. This subspecies is absent (or present at very low densities) in continuous forests (Blake, 2002; Melletti, Penteriani and Boitani, 2007; Melletti, 2008).

Suitable habitats for forest buffalo are mosaics of forest with equatorial savannas or clearings, which consist of grassy vegetation and shrubs (Reitsma, 1988; Blake, 2002). Blake (2002) at Noubale–Ndoki National Park (NP) found high buffalo abundance close to open grassy areas with low abundance in the closed canopy forest, suggesting it is unsuitable for forest buffalo. A significant relationship between buffalo and natural forest clearings was also reported at Dzanga–Ndoki NP, where clearings were the centre of buffalo home ranges. In addition, no signs of buffalo presence were recorded over 500 m from clearings (Melletti, Penteriani and Boitani, 2007; Melletti 2008). In Cameroon, buffalo rarely penetrated into the forest more than 300 m from logging roads, which were the main feeding sites for buffalo (Bekhuis et al., 2008).

Behaviour

Savanna Buffalo

African savanna buffalo are gregarious animals living in herds, and core members include adult females, subadults, juveniles and calves. Young females are known to maintain post-weaning bonds with their mother until the birth of their first calf, and probably longer. In contrast, young males gradually become independent, and are likely to form subadult male groups within the mixed herd. At the age of about 4–5 years (occasionally earlier), the males temporarily leave the herd to form bachelor groups of 2–20 individuals (sometimes more). The elder males (from about 10 years) sometimes permanently leave the herd, but this behaviour is not systematic (Sinclair, 1977; Prins, 1996). Adult males competing for females leave the herd once their body condition decreases. Bachelor groups spend more time foraging and recover physical condition by foraging on patches of habitat too small and sometimes too risky for the herd, such as dense riparian woodland (Prins, 1996; Turner et al., 2005; see Chapter 6 for more details).

Savanna buffalo herd size varies across their distribution from as few as 20 to as many as 2000 individuals in the floodplains of eastern and

southern Africa (Sinclair, 1977; Prins, 1989, 1996). In West Africa (WAP Regional Park), the mean herd size was about 45 individuals when excluding bachelor males, and the largest herds were estimated to contain about 150 individuals (Cornélis et al., 2011). Similar figures were reported for Central African savanna buffalo, except in floodplain areas such as Zakouma NP (Chad), where herds up to 800 individuals were observed (D. Cornélis, personal observation).

Forest Buffalo

Forest buffalo form small and stable herds of 3–25 individuals (Melletti, Penteriani, Mirabile and Boitani, 2007; Korte, 2008b; Melletti, 2008). Herds generally comprise several adult females with their young and one or two bulls (Dalimier, 1955; Blake, 2002; Melletti, Penteriani and Boitani, 2007). In Lopé National Park, Gabon, the mean group size for the 18 herds was 12 ± 2 (range of means = 3–24; Korte, 2008a). Larger herds were shown to contain a higher proportion of open habitat within their home range.

Although observations of solitary individuals (males and females) were reported, there is no evidence of the occurrence of sexual segregation in herds. Males apparently access profitable resources all year long and do not leave the mixed herds to form bachelor groups.

Home Range and Movements

The African buffalo is generally considered a sedentary species. In buffalo, home range (HR) size and movements (either seasonal or daily) are related to the spatiotemporal distribution of key resources. As pointed out previously, space use tends to be largely constrained by access to water in most study locations.

Savanna Buffalo Subspecies

Savanna buffalo herds exhibit HRs that generally range between 50 and 350 km² (see Table 6.1 in Chapter 6). The larger HRs are generally observed in areas where resources are spatially segregated, which forces herds to undertake seasonal movements (see below). In contrast, males living in bachelor groups use smaller patches of habitat and form smaller HRs (0.5 and 4 km²; Grimsdell, 1969; Sinclair, 1977; Taylor, 1985; Naidoo et al., 2012a).

In some systems, the HR size of mixed herds increases during the rainy season and decreases during the dry season (Naidoo et al., 2012b; Roug et al., 2020). During the rainy season, forage and water are abundant across the landscape and herds can move freely to find productive areas, whereas water availability often limits movement during the dry season, constraining buffalo to areas close to permanent water sources. In other systems that either have abundant natural surface water or extensive man-made water networks, buffalo HR sizes will increase during the dry season as they search for optimal foraging grounds (Ryan et al., 2006).

Some buffalo populations migrate between seasonal HRs (Cornélis et al., 2011; Bennitt et al., 2016; Sianga et al., 2017), although the exact migration pattern is not always consistent across years (Roug et al., 2020). Some buffalo populations were shown to undertake partial migration, meaning that within a group (or subpopulation), some will be migrant and others resident (Cornélis et al., 2011). Some groups exhibiting intermediate or partially migratory behaviour were qualified as ‘expanders’ (Naidoo et al., 2012b).

Naidoo et al. (2014) report several seasonal movements of buffalo from the Kavango–Zambezi Transfrontier Conservation Area (KAZA TFCA) that are the longest documented distances for this species. A female collared on the Kwando River floodplains in Namibia during the dry season moved 87 km west along the Caprivi Strip before returning to her dry season range, a round trip journey of >170 km. The following wet season, she again moved ~87 km south into Botswana, before returning to the same dry season range for a different >170 km journey.

The most frequent pattern of buffalo seasonal movements is the use of extensive upland woodland and savanna systems during the wet season, which support more abundant high-quality grasses. Once grasses and waterholes in wooded savannas have dried out, buffalo move to lowland habitats, such as extensive wetlands, riparian areas and lake shore grasslands where sufficient soil moisture for plant growth and green forage persists into the dry season (Vesey-FitzGerald, 1960; Taylor, 1985; Prins, 1996; Cornélis et al., 2011; Sianga et al., 2017). During drought years, buffalo resort to eating more productive and less digestible forage in the form of tall robust grasses and sedges and even reeds. They will resort to browsing in the absence of sufficient grass (Jarman and Jarman, 1973; Stark, 1986).

For example, in Ruaha National Park (Tanzania), Cape buffalo showed strong association with habitats near dry season water sources,

whereas they were distributed widely across the park during the wet season (Roug et al., 2020). As cool drier seasons advance, herds may move progressively towards localized concentrations of remaining suitable grazing resources and water supplies, with increasing herd size.

In W Regional Park (Burkina Faso, Benin, Niger), the movements of seven West African savanna buffalo breeding herds were monitored using GPS collars (Cornélis et al., 2011). In the dry season, herds were shown to range close (within 5.3 ± 2.0 km, mean \pm SD) to segments of permanent rivers. At the onset of the monsoon rains, all herds but one (which had year-round access to suitable resources along the Niger River) performed a larger (35 ± 10 km) south-west movement in response to a large-scale directional gradient of primary production. Furthermore, the establishment of wet season HRs appears conditioned by a threshold (~ 10 per cent) in the availability of perennial grasses, underlining the key role played by this resource for buffalo.

This was also observed for wet season ranges of buffalo in northern Botswana, where buffalo favoured areas >15 km from permanent water that have the highest cover of high-quality perennial grasses (Sianga et al., 2017). This is likely because leafy perennial grasses facilitate maximum intake for a large-bodied herbivore that relies on a tongue-sweep strategy to increase bite size.

Several recent studies based on GPS tracking have highlighted the occurrence of one-way movements over long distances, akin to dispersion. In the KAZA TFCA, two GPS-tracked females (among 30 females and five males tracked) undertook a long-range (~ 200 km) dispersal from the Kwando and Kavango Rivers in Namibia towards the Okavango Delta (Naidoo et al., 2014). In the Great Limpopo TFCA, a total of 66 GPS collars were deployed during 2008–2013 on females (47 adults, 19 subadults; Caron et al., 2016). Among this sample, three subadults were reported to leave the HR of their herd and disperse over 90 km.

Perhaps the most remarkable long-range movements came from female adult animals tagged in Mahango National Park, Namibia that exited via a break in the park fence in 2011. Numerous sightings of these animals suggest they moved as a group from north-eastern Botswana into Khaudum National Park. From there, the animals split into two groups, with one group observed in Angola near the Kavango River, around 250 km from where they had been ear-tagged. Another ear-tagged animal was eventually shot in an agricultural area in the Otjozondjupa Region in central Namibia. This location was a staggering 500 km from where

she was tagged, far outside what is considered current buffalo range in Namibia (Martin, 2002).

Although the occurrence of large-amplitude dispersions is probably inherent to the spatial behaviour of some buffalo, it cannot be excluded at this stage of knowledge that some of these movements result from disorientation due to the anaesthesia required to fit the GPS collars.

Forest Buffalo Subspecies

HR data are limited for forest buffalo because there are few sites where direct observation is possible due to the forest habitat and the animal's elusive nature (Blake, 2002; Melletti, Penteriani, Mirabile and Boitani, 2007; Korte, 2008b). Melletti, Penteriani, Mirabile and Boitani (2007) report an HR of 8 km² for a herd of 24 buffalo at Danzga-Ndoki NP (Central African Republic). Based on seven radio-collared adult female forest buffalo at Lopé National Park, Gabon, over a two-year period (2002–2004), HRs of female forest buffalo averaged 4.6 km² with little HR range overlap (Korte, 2008b). Space use within HRs varies with season, with a preference for marshes during the wet season (September through February) and for forest in the dry season (March through August).

Forest buffalo HRs are thus much smaller than those of the savanna subspecies. It is likely that this pattern, common to all studies, results from the spatial arrangement of suitable resources in dense tropical forest, but also to less pronounced seasonality of the environment.

Activity Patterns

African buffalo display a large array of activity modes, including feeding, resting/ruminating, relocating between foraging areas, vigilance, wallowing and drinking. The relative proportions of these activity modes are mainly driven by spatiotemporal changes in the quality and availability of resources, interspecific competition, weather conditions and predation pressure (Sinclair, 1977; Prins, 1996; Ryan and Jordaan, 2005; Owen-Smith et al., 2010).

Savanna Buffalo Subspecies

Daily Movements

Previous investigations on the daily movement rates of buffalo herds (based on short-term sampling, radiotelemetry or path retracement) reported

contrasted results. Taylor (1989) reported mean distances moved over a 24-hour period of <4 km compared to >6 km elsewhere (Sinclair, 1977; Conybeare, 1980). These authors reported that proximity of both food and water influence movements, and that bachelor males tend to move much less than herds. In South Africa (Kruger NP), buffalo herds were estimated to move 3.5 km per day during the dry season and 3.1 km during the wet season (Ryan and Jordaan, 2005). In contrast, in Cameroon (Benoué NP), Stark (1986) estimated a buffalo herd to travel on average 7.2 km per day during the rainy season and 5.6 km during the dry season.

More recently, Cornélis et al. (2011) showed that GPS-tracked adult female savanna buffalo ($n = 7$) in West Africa (W Regional Park) travelled on average 6.5 ± 0.5 km (mean \pm SD) per day at an annual scale. Analyses showed no significant differences between herds. In contrast, analyses at a subannual scale globally emphasized interesting trends in movement speed. Daily speed peaked around the dry–wet season transition (8.4 ± 0.5 km), either during the late dry season phases or during the early wet season phases. Minimum daily values (4.8 ± 0.4 km) were observed in most herds during the phases corresponding to the late wet season or just after. The daily movement speed thus followed in all herds a decreasing pattern between dry–wet and wet–dry season transitions.

Similar patterns were reported in Ruaha NP, where daily movements of GPS-tracked herds averaged 4.6 km with the longest distances (mean 6.9 km) travelled during November at the end of the dry season and beginning of the wet season. The shortest daily distances (mean 3.6 km) travelled occurred in the wet season in April–June (Roug et al., 2020).

Grazing and Ruminating

Ruminant ungulates such as buffalo spend a large proportion of their time feeding, and must additionally allocate time to ruminating, which results in an overall total time (feeding + ruminating) of 70–80 per cent (Beekman and Prins, 1989; Prins, 1996). In savanna buffalo, most studies report feeding time accounting for 35–45 per cent of the 24-hour activity budget (Grimsdell and Field, 1976; Sinclair, 1977; Mloszewski, 1983; Stark, 1986; Prins, 1996; Winterbach and Bothma, 1998; Ryan and Jordaan, 2005; Bennitt, 2012).

Grazing most often takes place in the early morning and late afternoon, and during the first half of the night, suggesting that buffalo cease feeding during the hottest part of the day and during the coolest part of the night for thermoregulation purposes. Note that an exception to

this feeding pattern was observed at Lake Manyara NP (Tanzania), with the main grazing bout occurring between 10:00 and 14:00 hours (Prins, 1996). In most studies, buffalo herds appear to spend an equal or greater proportion of time feeding at night than during the day (Sinclair, 1977; Taylor, 1985; Prins and Lason, 1989; Ryan and Jordaan, 2005). At a seasonal scale, most authors reported a trend towards more time spent feeding in the dry than the wet season in response to lower vegetation quality and quantity and decreased intake rates. Other modes of activity such as resting, rumination and vigilance are not mutually exclusive, thus making it hard to individualize ratios and to compare across studies.

Most studies reported average rumination times of around 30–35 per cent of the 24-hour activity budget (Sinclair, 1977; Prins, 1996; Winterbach and Bothma, 1998; Ryan and Jordaan, 2005). Seasonal trends in rumination time are the subject of debate; Sinclair (1977) reported that buffalo spend more time ruminating during the dry season, whereas Beekman and Prins (1989) found the opposite.

Thermoregulation

Buffalo generally cease feeding during the hottest part of the day and during the coolest part of the night for thermoregulation purposes. During the hottest hours of the day, mixed herds generally seek shade (Sinclair, 1977). Contrary to females and young, males generally wallow during the hottest time of the day for periods lasting up to three hours. This practice is more effective in temperature regulation than the use of shade (Sinclair, 1977).

In West Africa (WAP Regional Park), the daily activity patterns of buffalo herds were explored using biorhythm indices derived from GPS location data and activity sensors (Cornélis et al., 2011). At a daily scale, herds were equally active during night and day, and were mostly crepuscular, with two main active periods per day (dawn and dusk). Buffalo rested during the hottest hours of the day, and the duration of the resting bout was particularly marked during the hot dry season (Figure 5.1; Cornélis et al., 2014).

Water Resources and Drinking Activity

In many savanna regions of Africa, pronounced seasonal variability in rainfall results in wildlife being restricted to floodplains and other habitats adjacent to permanent surface water in the dry season. Nearly 100

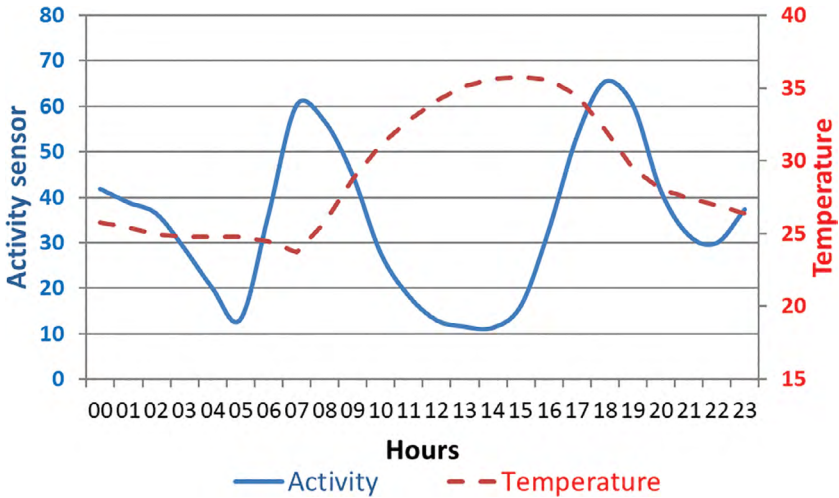


Figure 5.1 Average daily activity of a buffalo cow tracked in the WAP transfrontier conservation area (Burkina Faso, Benin, Niger) from March 2007 to February 2008 (using temperature and activity sensors embedded in the GPS collar). The first peak of activity started at dawn and the second finished after dusk, both lasting on average about 3–4 hours. Source: Cornélis, D. (2011). *Ecologie du déplacement du buffle de savane ouest-africain (*Syncerus caffer brachyceros*)*. PhD, Université de Montpellier 2, Montpellier.

per cent of the biomass density of large water-dependent grazing herbivores has been found within a 15 km radius from surface water (Western, 1975). Nevertheless, while rarely quantified, ephemeral water sources far from permanent surface water also allow wildlife to exploit forage and other resources further afield, influencing their distribution, abundance and movement (Naidoo et al., 2020; Rumiano et al., 2021).

African buffalo are water-dependent: they can sweat profusely (Taylor, 1970), the water content of their faeces is high (about 80 per cent: Prins, 1996) and their body water turnover rate is high (King, 1979). They have to drink at least every two days, taking about 45 litres daily, and they are not able to survive on the moisture content of their food (Prins, 1996).

Previous studies on drinking reported contrasted hourly patterns. In Hwange NP (Zimbabwe), equipped with pumped artificial surface water supplies, Weir and Davidson (1965) found during the dry season that buffalo drank in the late afternoon (16:30–20:00) with a shorter peak early in the morning (08:30–10:30). In Kruger NP (South Africa), Ryan and Jordaan (2005) found two main periods of diurnal drinking

(the early morning and mid-morning) and their observations suggest more time devoted to drinking during the day than at night. In contrast, Winterbach and Bothma (1998) found in Willem Pretorius game reserve (South Africa) that buffalo drank in the early afternoon. Grimsdell and Field (1976) also found that herds in Rwenzori NP (Uganda) drank in the mid-morning. In one study, buffalo were shown to modulate hourly drinking patterns according to the risk of predation by preferentially avoiding waterholes during high-risk hours of the day (dawn and dusk), when lions were likely to be in their vicinity (Valeix et al., 2009).

A detailed analysis of drinking behaviour was reported by Taylor (1989) in Matusadona NP (Zimbabwe), where Lake Kariba provides permanent water supplies for buffalo, in addition to seasonal rivers and pans that hold water in pools. During the hot dry season, herds drank once during the daytime, either around midday or between 16:00 and 19:00. The average drinking time took 20 minutes. In the wet season buffalo herds were a greater distance away from permanent water (mean 2.8 km) than during the dry season, when the mean distance from permanent water was 1.3 km. The converse held for seasonal water supplies. Buffalo herds were closer to these (1.5 km) in the wet season but further away in the dry season (2.4 km). This is to be expected because buffalo disperse during the wet season when abundant food and water resources are widespread, but concentrate on the lakeshore during the dry season where the only readily available food and water resources are present (Taylor, 1989).

For bachelor males, over 50 per cent of drinking bouts occurred between 10:00 and 14:00 with a peak from 11:00 to 12:00. Males drank throughout the day from before 06:00 until 20:00 and in the early morning hours at 02:00–03:00 (Taylor, 1989). During the wet season an individual may drink 2–3 times from the lake's edge, but usually once in the morning and once in the afternoon. During the cooler months, drinking during the day usually occurred only once, either late morning or at midday. As the hot season progressed, the number of drinking bouts increased to two or three in the morning and afternoon. Drinking bouts for individual males were, on average, of 1–3 minutes' duration.

Overall, however, in the literature reviewed, there appears to be no clear seasonal trends in drinking frequency among savanna buffalo.

Forest Buffalo Subspecies

Much less is known about the movement and activity of forest buffalo compared to savanna populations. In Dzanga–Ndoki NP (Central African

Republic), a study of a single buffalo herd showed that daily distances travelled by buffalo were generally very short (i.e. 500–1500 m) and were mainly restrained to clearings and surrounding areas (Melletti, 2008). The maximum distance travelled during a 24-hour tracking period was about 4000 m. Like savanna buffalo, forest buffalo wallow in the late afternoon; however, they spend more time in wallows during the dry season (Melletti, Penteriani, Mirabile and Boitani, 2007; Korte, 2008a).

Feeding Ecology

Buffalo are ruminants, essentially feeding on grass and roughage. This species is capable of subsisting on pastures too coarse and too tall for most other herbivores (Bothma, 2002), and as a ‘bulk grazer’ they ingest around 2.2 per cent of their body mass daily. This represents on average 6.5 kg for a forest buffalo of 300 kg, 11 kg for a West or Central African buffalo of 500 kg and 15 kg for a Cape buffalo of 700 kg.

Buffalo are very efficient grazers (their adapted dentition and a mobile tongue allowing the ingestion of high quantities of grass in a short amount of time). Optimal feeding conditions for buffalo prevail when the grass forms swards and leaf heights reach and exceed 10 cm, as in flood plains or in forest glades (Prins, 1996). However, buffalo cannot cut pastures as short as other species. The African buffalo thus occupies an important niche, opening up habitats that are preferred by short-grass grazers (Prins, 1996; Estes, 1991). Their primary competitors are cattle *Bos taurus*, African elephant *Loxodonta africana*, plains zebra *Equus quagga* and wildebeest *Connochaetes taurinus* (Sinclair, 1977; de Boer and Prins, 1990; Plumptre and Harris, 1995; Prins, 1996).

Savanna (Cape, West and Central African) Buffalo

In savanna buffalo, optimal dietary conditions occur during the rainy season, while the end of the long dry season is a period of food scarcity (both in quantity and quality; Prins and Sinclair, 2013). Detailed diet studies conducted in eastern and southern Africa indicated that buffalo are resource limited and constrained by a minimum dietary protein concentration of 7–8 per cent to make fermentation in the rumen possible (Sinclair, 1977; Prins, 1996). In such a situation, buffalo thus face a trade-off of quality and quantity in obtaining an appropriate protein-to-fibre ratio in their diet (Redfern et al., 2006; Ryan et al., 2012). During the dry season, savanna buffalo are generally forced to become

more selective, and to partially switch their diet to browse (see below). Despite this, buffalo were reported to live at or below nitrogen requirements for prolonged periods, accounting for visibly losing body condition (Prins, 1989; Ryan, 2006; Ryan et al., 2012). In natural ungulate communities, the regulation of populations is driven by two processes: a control by available food resources ('bottom-up regulation') on the one hand, and a control by predation ('top down' regulation) on the other (Hunter and Price, 1992). In the case of savanna buffalo, most authors agree that resources play a dominant role in the regulation of populations (Sinclair et al., 2003; Hopcraft et al., 2010).

There is moderate consensus in feeding studies on Cape buffalo about the preferred grass species. Usually species that are avoided contain low nutritious quality or the presence of aromatic oils (Prins, 1996). During the dry season, usual food resources are of poor quality, due to lignifications and high standing biomass. During this period, floodplain species (e.g. *Leersia hexandra*) and riverine forest species (e.g. *Setaria sphacelata*) become important. In areas with upwelling groundwater, species such as *Cyperus laevigatus* may also form a mainstay in the dry season (Prins and Sinclair, 2013). Buffalo prefer grasses such as *Cynodon dactylon*, but may also eat broad-leaved grasses, such as *Panicum maximum*. Sinclair, in the Serengeti, reported that buffalo preferred soft, nutritious grass such as *Digitaria macroblephora*. Although there is little information on seasonal changes on diet, Sinclair (1977) analysed stomach contents and showed that Cape buffalo select more grass leaf at the end of the rainy season. Finally, Taylor (1985) found that grasslands dominated by *Panicum repens* were the best habitat on the shores of Lake Kariba (Matusadona NP, Zimbabwe). In Cape buffalo, the diet of the different age/sex classes does not appear to differ and dry matter food intake ranges between 1.2 per cent and 3.5 per cent of body mass, similarly to other ruminants, but subject to food quality (Sinclair, 1977; Prins and Beekman, 1989).

Few studies investigated the feeding ecology of West and Central African buffalo. In West Africa (WAP Regional Park), habitat selection analysis emphasized the importance of perennial grasses (e.g. *Andropogon gayanus*; Cornélis et al., 2011). In this study, a gradient in primary production appeared to determine large-scale movements of herds at the onset of the wet season, but its action clearly was modulated by the proportion of perennials available. Buffalo herds were shown to establish early wet season HRs at locations where this proportion reached a 9 per cent threshold. At Benoué NP (Cameroon), Stark (1986) similarly reported a very high proportion of grasses in the diet, particularly *Andropogon*

gayanus, which represented 51 per cent of the volume ingested in the dry season, versus 40 per cent in the wet season. At Zakouma NP (Chad), Gillet (1969) noted a preference for *Setaria anceps* (particularly new shoots after fire) and *Andropogon gayanus*, but also *Vetiveria nigriflora*. In the dry season, the unburned straws of *Echinochloa obtusiflora* appeared to be preferred.

Savanna buffalo are primarily grazers, but partially switch to browse when grasses become tall and lignified (Field, 1972; Leuthold, 1972; Sinclair, 1977; Mloszewski, 1983; Hashim, 1987; Prins, 1996). Shrub and tree leaves have been shown to contain higher protein (nitrogen) content than dry grasses during the dry season (Kone et al., 1990; Prins, 1996). As mentioned above, the contribution of nitrogen from browse facilitates the fermentation of fibrous grass in the rumen, which they eat in high quantities during the dry season. According to Estes (1991), the browse can represent up to 5 per cent of the total diet, but higher figures were reported in several sites (e.g. 26 per cent in dry season in Cameroon; Taylor, 1985). A wide range of species of shrubs and trees are consumed throughout African savanna, including *Grewia* spp., *Heeria* spp., *Colophospermum mopane*, *Combretum* spp., *Capparis* spp. and *Piliostigma* spp. (Pienaar, 1969; Jarman, 1971; De Graaf et al., 1973; Taylor and Walker, 1978; Ryan, 2006). In drier habitats in the Eastern Cape, buffalo appear to be adapted to eat woody species because grassy vegetation is scarce. In this particular habitat, during the dry season, up to 33 per cent of their diet comprises species such as *Acacia* sp., *Plumbago* sp. and *Grewia* sp.

In some areas buffalo can maintain or create 'grazing lawns' if the feeding interval is short enough (Prins, 1996). Evidence of this 'returning' behaviour has also been described for buffalo in Kruger NP and Klaserie Private Nature Reserve in South Africa (Bar-David et al., 2009). They may also create favourable lawns in conjunction with other large herbivores such as elephants at Lake Rukwa, Tanzania (Vesey-FitzGerald, 1960) and Benoué NP in central Cameroon (H. H. T. Prins, personal observation).

Geophagy has been reported at several sites, where clay or substrates rich in iron may explain this preference. On Mount Kenya, geophagy is reported in the bamboo belt (2100–3000 m), where clay soils are rich in iron and aluminium (Grimshaw et al., 1995). This rare activity is carried out mainly by solitary individuals on Mount Kenya (Mahaney, 1987). In Lent Valley in Kilimanjaro, buffalo enter into caves rich in sodium bicarbonate and chew off the soda deposits.

Forest Buffalo

Few data exist on the feeding ecology of forest buffalo because direct observations are rarely feasible in rainforest habitats. Blake (2002) in Noubale–Ndoki NP and Melletti (2008) in Dzanga–Ndoki NP observed buffalo feeding mainly on Poaceae and Cyperaceae within clearings, in particular on *Rhynchospora corymbosa*, *Kyllinga* sp. and *Cyperus* sp. Blake (2002) also recorded several species of Marantaceae, including *Marantochloa purpurea*, *M. cordifolia*, *M. filipes* and *Halopogon azurea*. In addition, species of the Commelinaceae family such as *Commelina diffusa* and *Palisota brachythyrso* and a species of algae (*Spirogyra* sp.) were recorded. Melletti (2008) also found indirect signs of feeding activity on *Commelina* sp and *Palisota* sp. in the understory of *Gilbertodendrum dewevrei* mono-dominant forest.

Bekhuis et al. (2008) used micro-histological faecal analysis in a two-month study to determine the diet of forest buffalo at Campo-Ma'an NP in southern Cameroon. They found that the most important part of the diet was composed of graminoids (43 per cent, with *Leptochloa caerulescens* representing 15 per cent of the total diet), non-graminoid monocots (21 per cent, mainly Commelinaceae such as *Palisota* spp.), dicotyledonous plants (33 per cent, mainly leaves) and cryptogamous plants (3 per cent). The composition of the diet suggests that the buffalo fed mainly along logging roads and river banks (Bekhuis et al., 2008). Using a similar method at Lopé NP (Gabon), Lustenhouwer (2008) and van der Hoek et al. (2013) found that the majority of plants consumed by forest buffalo were monocotyledons, primarily grasses (Poaceae) and sedges (Cyperaceae), with a low portion of dicotyledonous plants in the diet. In the same study area, van der Hoek et al. (2013) emphasized the importance of savanna habitat, noting that controlled burning is a key tool for maintaining open areas.

Thus far, no evidence of the existence of grazing lawns was found in the different studies focused on the feeding ecology of forest buffalo, even in areas of high density such as Lopé NP (L. Korte and M. Melletti, personal observations).

Conclusion

The African buffalo is endowed with an amazing adaptability, which probably explains why this species is one of the most successful large African mammals in terms of geographical distribution, abundance and biomass. On an evolutionary scale, African buffalo have adapted their phenotype across their distribution range, which covers almost all natural

ecosystems south of the Sahara. For example, the mass ratio between the large Cape buffalo and the small forest buffalo is about 2.7 to 1. With the exception of the elephant, few species have an equivalent mass range across their distribution area. The African buffalo has also managed to adapt its behaviour to the different ecosystems in which it lives. For example, in dense tropical forests where food resources are scarce and aggregated, the African buffalo forms small herds of 5–20 animals. In contrast, in the rich pastures of the savanna floodplains, the African buffalo can gather in herds of up to 2000 animals.

The space-use behaviour of buffalo herds also differs strongly according to the spatial arrangement of resources. In areas where buffalo access profitable resources all year long, the herds settle in home ranges of a few square kilometres. In contrast, in areas where resources are spatially segregated, buffalo occupy home ranges of several hundreds of square kilometres. In some regions, buffalo undertake seasonal movements of several dozen kilometres. Such migrations may be only partial within a population, meaning that it is not undertaken by all herds.

At a seasonal and daily scale, buffalo are also able to modulate their social behaviour within the herd according to the availability of resources. The herd splits into subgroups and reforms within the contours of a long-lasting (multiannual) home range, according to mechanisms that remain largely unexplored (Chapter 6). Finally, within their seasonal home range, we also saw that buffalo can regulate their diet and activity patterns according to the quality and quantity of food resources, as well as according to abiotic factors such as temperature.

Thus, despite reported regional declines in buffalo population numbers due, inter alia, to climate change, habitat fragmentation, livestock development and diseases, the species may be flexible enough to adapt to the wide range of challenges it faces and will face in the coming decades.

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