Part III

Species accounts

Chapter

20

African buffalo *Syncerus caffer* (Sparrman, 1779)

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Names

Genus: *Syncerus* Hodgson, 1847

Species: African buffalo *Syncerus caffer* (Sparrman, 1779)

Subspecies: Cape buffalo *Syncerus caffer caffer*

Names in other languages: **French**: Buffle du Cap; **German**: Kaffernbüffel; **Spanish**: Búfalo cafre; **Italian**: Bufalo cafro.

Subspecies: West African savanna buffalo *Syncerus caffer brachyceros* (Gray, 1837)

Names in other languages: **French**: buffle de savane d'Afrique de l'Ouest; **German**: Savanne Westafrika Büffel; **Spanish**: Búfalo de Sabana de África Occidental; **Italian**: Bufalo di savana dell'Africa Occidentale

Subspecies: Central African savanna buffalo *Syncerus caffer aequinoctialis* (Blyth, 1866)

Names in other languages: **French**: buffle de savane d'Afrique Centrale; **German**: Savanne Zentralafrika Büffel; **Spanish**: Búfalo de Sabana de África Central; **Italian**: Bufalo di savana dell'Africa Centrale, Bufalo equinoziale.

Other common names: Nile buffalo.

Subspecies: Forest buffalo *Syncerus caffer nanus* (Boddaert, 1785)

Names in other languages: **French**: buffle de forêt; **German**: rotbüffel; **Spanish**: bùfalo de bosque; **Italian**: Bufalo di foresta; **BaAka**: Mboko; **Swahili**: Nyati.

Other common names: dwarf buffalo, red buffalo.

Ecology, Evolution and Behaviour of Wild Cattle: Implications for Conservation, ed. M. Melletti and J. Burton. Published by Cambridge University Press.

Taxonomy

The name *Bos caffer* was attributed by Sparrman in 1779. Since then, 92 species names have been given to the African buffalo. Taxonomists initially thought that each buffalo form represented a distinct species. Brooke (1873, 1875), who established the first classification of the African buffalo, reduced the number to three. Later, Blancou (1935) described up to 12 subspecies of buffalo.

Haltenorth (1963), Ansell (1972) and Grubb (1972) summarized the first classifications of Christy (1929), Schouteden (1945) and Blancou (1935, 1954), concluding that all forms should be considered as monospecific. Although there are considerable morphological variations in body size, fur colour, horn shape and size throughout the range of distribution, the African buffalo is currently considered as a single species by various authorities (IUCN 2013; Prins & Sinclair 2013), with a subdivision into four subspecies: Cape buffalo (*S. c. caffer*), forest buffalo (*S. c. nanus*), West African savanna buffalo (*S. c. brachyceros*), and Central African savanna buffalo (*S. c. aequinoctialis*). Additionally to those four subspecies, a mountain form (*S. c. mathewsi*) was also described in East Africa and may be distinct (Kingdon 1982).

A recent work of Groves & Grubb (2011), based on morphological measures, separates the African buffalo into four species, including the *mathewsi* form. In contrast, recent work of Smitz *et al.* (2013) conducted over the whole geographical range of the African buffalo, analysing mitochondrial D-loop sequences, revealed the existence of two lineages in the species, matching with the *caffer* subspecies of East and South Africa, and the *nanus* subspecies of West and Central Africa. These lineages seem to have diverged between 132and 286 kya (for further insight into the evolutionary history of the African buffalo, see Chapters 1 and 25). On the basis of the evolutionary history of both lineages, the authors suggest that the most prudent treatment of the African buffalo would be a subdivision into two subspecies, or management units, namely *S. c. caffer* (East-Southern Africa's lineage), and *S. c. nanus* (West Central Africa's lineage), which then should be extended to comprise *S. c. brachyceros* and *S. c. aequinoctialis* subspecies following standard nomenclature rules (*S. c. nanus*: Boddaert 1785; *S. c. brachyceros*: Gray 1837; *S. c. aequinoctialis*: Blyth 1866; for more details see Chapter 25). Further investigation using microsatellites may reveal finer-scale population structuring in West-Central and East-Southern Africa, which may be attributed to evolutionary significant units (ESUs) appropriate in terms of conservation management (Moritz 1994).

Hybrids *caffer* x *nanus* have been described in captivity (Cribiu & Popescu 1980). Although the different forms seem to be able to interbreed, the existence of hybridization in wild populations has yet to be conclusively demonstrated by molecular work. The occurrence of red calves in, for instance, the Queen Elizabeth National Park is often quoted as evidence for hybridization, but proof has never been provided. In Lake Manyara National Park, some 800 km further to the east, about 30% of the calves are red when young.

Subspecies and distribution

Historical distribution

Rainfall is the main biophysical factor limiting the distribution and abundance of African buffalo at a large geographical scale. Prior to the nineteenth century, the range of buffalo extended to most sub-Saharan ecosystems with annual rainfall above 250 mm (thus excluding the Horn of Africa and Namib/Kalahari deserts). The African buffalo is essentially a grazer, so its distribution strongly depends on the availability of herbaceous forage. As a consequence, core areas of the closed rainforests in Central Africa (i.e. areas without herbaceous cover) did not historically provide suitable conditions for buffalo (Sinclair 1977; Mloszewski 1983; Prins 1996; Melletti *et al.* 2007a). Buffalo did not colonize islands such as Zanzibar or Mafia, although they colonized Bioko Island (Equatorial Guinea), where they are now extinct (extirpated from Bioko Island sometime between 1860 and 1910 (Butynski *et al.* 1997)).

There is no palaeontological evidence of the presence of the African buffalo in North Africa or in the Nile Valley to the north of Khartoum (Prins & Sinclair 2013). In North Africa, aurochs (*Bos primigenius*; wild ancestor of domestic cattle) occupied a similar niche (Gautier 1988), perhaps preventing the buffalo's spread to the north (for more details on Bovini evolution, see Chapter 1). Buffalo could have expanded their range in eastern and southern Africa during the last Ice Age due to the extinction of possible competitors, such as *Pelorovis antiquus* and *Elephas recki* (for more details on evolution, see Chapter 1; Klein 1988, 1994; Prins 1996). Drawings of buffalo are rare in cave paintings, although representations can be seen in Kondoa in Northern Tanzania (Leakey 1983).

We present below the distribution and abundance of each of the four subspecies. For consistency and comparison purposes, this presentation is based on the geographical contours of the IUCN (Plate 11). Actually these contours are not defined by geographic boundaries, but are gradual and diffuse. For example, the occurrence of two subspecies (*S. c. caffer* and *S. c. aequinoctialis*) in Ethiopia or in the Democratic Republic of Congo is somewhat arbitrary.

Present distribution

Large discontinuities have emerged in the historical distribution range of African buffalo in areas of high human population densities, such as Nigeria or Central Ethiopia (Plate 11) African buffalo populations have undergone a severe reduction in size and geographical distribution since the nineteenth century, as a result of the combined effects of anthropogenic impacts such as land conversion, poaching, disease outbreaks and climatic events such as droughts. At present, around 70% of the savanna buffalo population is confined to a patchwork of protected areas and well-managed surrounding hunting zones, mostly loosely connected to one another (East 1998). Figure 20.1 shows the distribution of the four buffalo

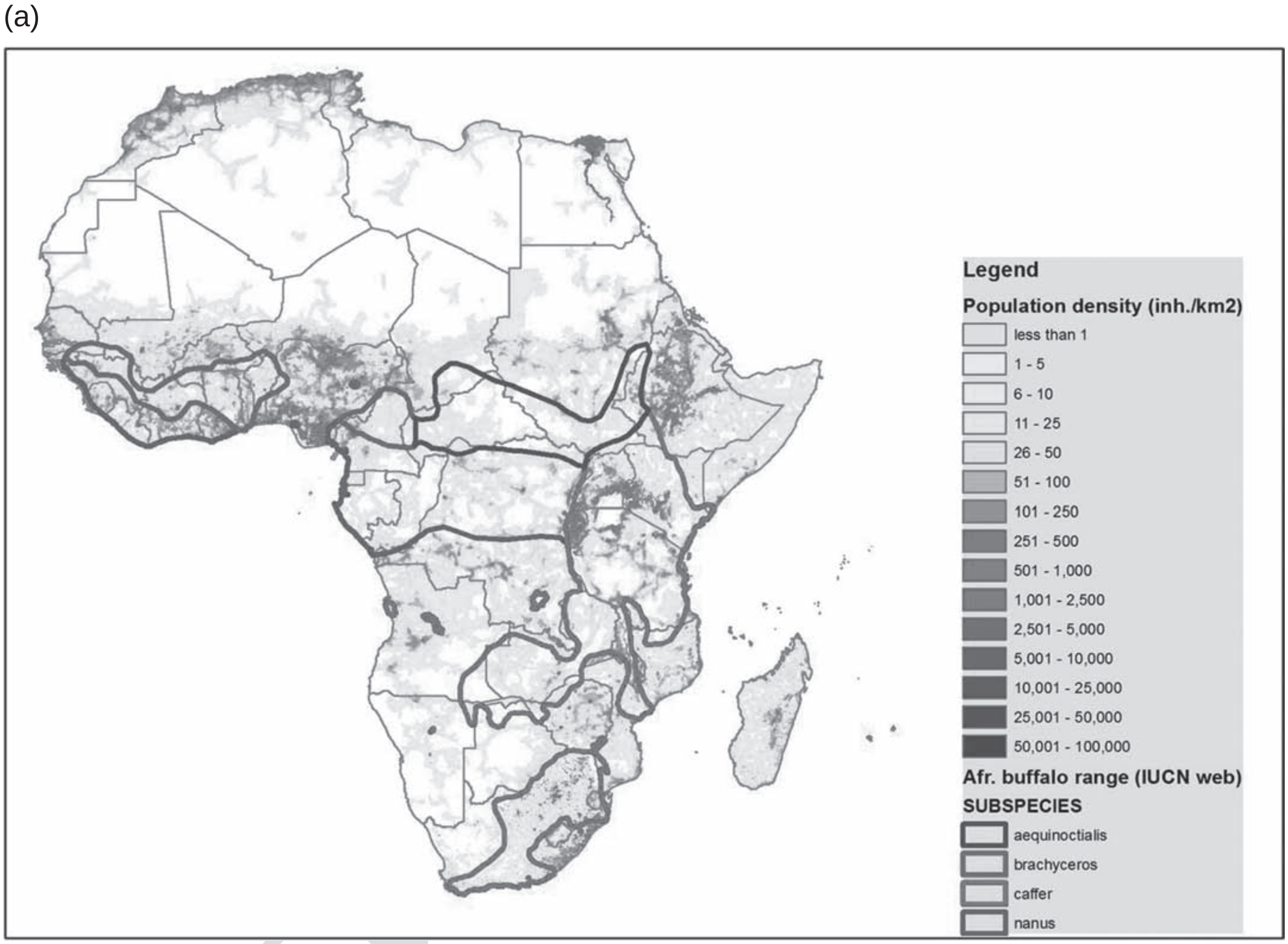

Figure 20.1 Distribution of the four African buffalo subspecies in relation to: (a) human population density; (b) average rainfall and (c) protected areas (source: IUCN SSC 2008). A black and white version of this figure will appear in some formats. For the colour version, please refer to the plate section.

subspecies in relation to human population density, rainfall and protected areas (East 1998; IUCN SSC 2008).

The expansion of livestock production gradually generated direct competition for space and resources and led to large and destructive epidemics in native African buffalo populations. Rinderpest was historically the most devastating disease for buffalo populations throughout Africa, leading to extreme reductions in population densities, and local extinctions. The most severe population collapse occurred in the 1890s, with mortality rates estimated at 90–95% across the continent (Sinclair 1977; Prins & van der Jeugd 1993; Winterbach 1998). This was followed by other episodes throughout the twentieth century. Rinderpest was declared eradicated in Africa by the World Animal Health Organization in 2011. During the twentieth century, the geographic distribution of buffalo has been actively reduced in several countries by large-scale culling operations and veterinary fences, in efforts to limit the transmission of several pathogens, such as foot-and-mouth disease (FMD) and trypanosomiasis, to cattle (Taylor & Martin 1987).

Recent climate fluctuations such as the drought that affected Sahelian and Sudanese regions at the end of the 1960s and Southern Africa in 1992 (Dunham 1994; Mills *et al.* 1995) have also strongly impacted buffalo populations over the past few decades. Last but not least, armed conflicts, the feeding of armies and labourers during peace time, the trafficking of weapons and bushmeat trade have strongly contributed to the reduction of buffalo populations.

Cape buffalo (*S. c. caffer*)

Cape buffalo occurs in southwestern Ethiopia (particularly Omo National Park), southern Somalia and northern Kenya southwards to South Africa. This subspecies is patchily distributed throughout East Africa, southwards to Zambia, Malawi, some parts of Mozambique (small populations south of the Zambezi river with the bulk of it in the north of the country, Niassa Reserve and Cabo Delgado areas; Skinner & Chimimba, 2005), northeastern Namibia (mainly eastern and western Caprivi, Mamili National Park and an introduced population in the Waterberg

(b)

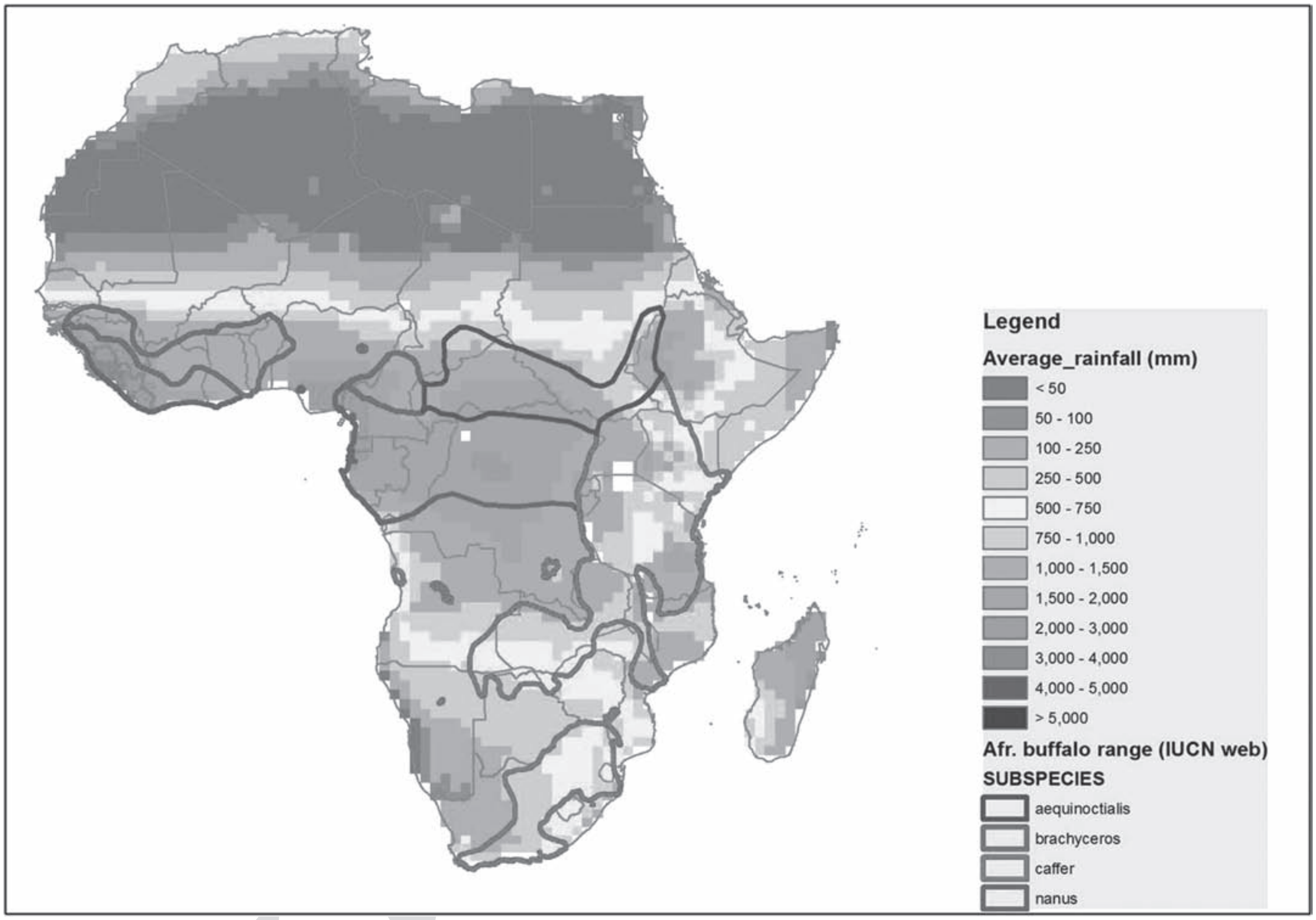

Figure 20.1 *(cont.)*

Plateau Park, central Namibia), Botswana (north of 20° S, Okavango Delta area, Moremi Game Reserve and the Chobe National Park) and Zimbabwe (Hwange National Park; Matabeleland, Zambezi Valley, south Lake Kariba and Gonarezhou National Park; Skinner & Chimimba 2005). Small populations of Cape buffalo still survive in some areas of southeast Angola bordering Zambia and Namibia. In South Africa, Cape buffalo have been reintroduced to some areas from which they were formerly extirpated. They are currently widely distributed in Kruger National Park and smaller populations persist in KwaZulu-Natal (Winterbach 1998) and in many private reserves. The current population in Swaziland was also reintroduced after extirpation.

West African savanna buffalo (*S. c. brachyceros*)

This subspecies still occurs locally in western countries within the Sahelo-Sudanian band (savannas and gallery forests), including southeastern Senegal, northern Ivory Coast, southern Burkina Faso, Ghana, northern Benin, extreme south of Niger, Nigeria (very locally), northern Cameroon and a small part in the Central African Republic (East 1998).

Central African savanna buffalo (*S. c. aequinoctialis*)

This subspecies still locally populates Central African countries within the Sahelo-Sudanian band (savannahs and gallery forests): southeast Chad, northern Central African Republic (East of Chari River), northern Democratic Republic of Congo, southeast Sudan and western Ethiopia (Ansell 1972; East 1998). The subspecies is now extinct in Eritrea.

Forest buffalo (*S. c. nanus*)

This subspecies occurs in two disjoint distribution ranges in West and Central Africa, respectively in the relict coastal rainforest belt and in the large basin of the Congo River. The distribution ranges are mainly located in areas with an annual rainfall of more than 1500 mm, in transition areas between dense tropical forests and savanna ecosystems, for instance in Gabon and Uganda (East 1999). In West Africa, forest buffalo is distributed from Guinea-Bissau to southwestern Ghana. In Central Africa, forest buffalo persist in south Nigeria, south Cameroon, Equatorial Guinea (extinct on Bioko Island), south and southwest Central African Republic, western Uganda,

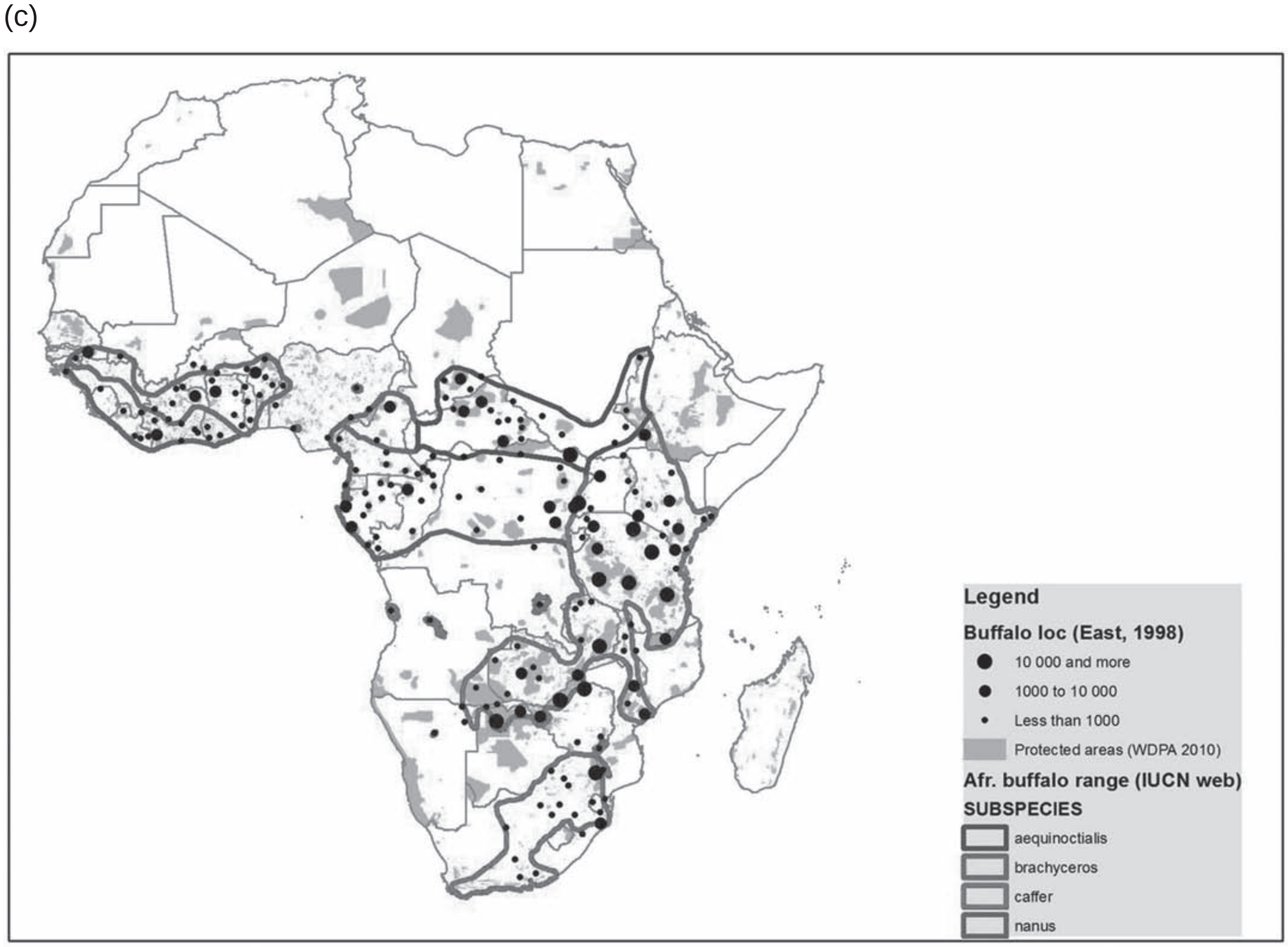

Figure 20.1 *(cont.)*

western Rwanda and possibly northwest Burundi, the Democratic Republic of Congo, the Republic of Congo and Gabon. The greatest part (i.e. 75%) of the population lives in and around protected areas in Cameroon, Central African Republic, Gabon, Democratic Republic of Congo and Republic of Congo (Wilson & Mittermeier 2011). In both distribution ranges, numbers have declined substantially due to poaching and deforestation (East 1999), but their status is generally poorly known (Blake 2002; Melletti *et al.* 2007a, 2007b; Korte 2008a).

Abundance

Over the past 60 years aerial counts have been widely used to estimate population sizes of savanna buffalo. As with any estimation technique, these methods are subject to potentially important biases (Jachmann 2002; Redfern & Viljoen 2002). During aerial counts, significant numbers of animals may be missed due to obstruction by vegetation canopy cover (e.g. high grass, forest galleries), and due to lower probability of detecting small herds. Furthermore, estimates from aerial sampling counts (ASCs) are generally less accurate (especially for small populations and low sampling rates) than aerial total counts (ATCs). Despite these limitations, aerial counts remain the most reliable approach to estimate buffalo populations in savanna ecosystems. We cite the animal numbers from the original reports, in the text, in a rounded-off form, and report to the closest 100 individuals for all figures larger than 200, while we report reserve size to the closest 10 km^2 so as to prevent reporting non-significant digits.

In the following sections and Table 20.1, we present an update of buffalo abundance and distribution per country and protected area, based on the most recent and available census data. The total estimated numbers per country are presented in Table 20.2 and compared with the last update (East 1998) in the section ‘Status in the wild’.

Cape buffalo

In **Ethiopia**, the population of Omo National Park and surrounding buffer zone (7850 km^2) was estimated at 700 individuals, based on an ASC carried out in 2007 (Renaud 2007);

Table 20.1 Abundance and distribution of the four African buffalo subspecies per country and protected area based on the most recent and available census data. Original data are presented.

Subspecies	International PA complex	Country	Protected area/ hunting blocks	Date	Method	Sampling effort[a]	Number obs.	Estimated population	Error	Error statistics	Area (km^2)	Density (ind/ km^2)	Source
S. c. aequinoctialis	/	Central African Republic	Bamingui-Bangoran NP, Manovo-Gounda-St. Floris NP and adjacent PAs	2010	ASC	7%	738	4048	± 27%	CV	94 962	0.04	Bouché 2010
	/	Chad	Zakouma NP	2012	ATC	100%	8091	8091	/	/	3026	2.67	Potgieter *et al.* 2012
	/	Democratic Republic of Congo	Garamba NP	2012	ATC	100%	5980	5980	/	/	4920	1.22	Bolanos 2012
	/	Ethiopia	Gambella NP Akobo block	2010	ASC	6%	91	1378	± 2641	SE	20 000	0.07	EWCA 2010
S. c. brachyceros	WAPOK complex (Burkina Faso, Bénin, Niger, Togo)	Benin	W NP	2003	ATC	100%	21	424	/	/	5872	0.07	Bouché *et al.* 2003
		Benin	Pendjari NP	2003	ATC	100%	124	3421	/	/	2827	1.21	
		Benin	Hunting zones (Djona, Pendjari, Konkombri and Mékrou) + Goungoun Classified Forest	2003	ATC	100%	715	715	/	/	5243	0.14	
		Burkina Faso	W NP	2003	ATC	100%	1400	1400	/	/	2412	0.58	
		Burkina Faso	Arli NP	2003	ATC	100%	399	399	/	/	485	0.82	
		Burkina Faso	Hunting zones (Tapoa djerma, Kourtiagou, Koakrana, Pagou-Tandougou, Ougarou, Pama, Singou and Konkombouri)	2003	ATC	100%	3031	3031	/	/	8124	0.37	
		Niger	W NP and Tamou Reserve	2003	ATC	100%	1170	1170	/	/	3083	0.38	
		Togo	Keran NP & Oti-Mandori Reserve	2003	ATC	100%	0	0	/	/	2886	0.00	
		Burkina Faso	Comoé-Léraba complex	2005	ATC	100%	90	90	/	/	1847	0.05	Bouché 2005
		Burkina Faso	Ponasi Complex (Nazinga GR, Kabore-Tambi NP and adjacent hunting zones)	2004	ATC	100%	145	145	/	/	3105	0.05	Bouché *et al.* 2004

Table 20.1 *(cont.)*

Subspecies	International PA complex	Country	Protected area/ hunting blocks	Date	Method	Sampling effort[a]	Number obs.	Estimated population	Error	Error statistics	Area (km^2)	Density (ind/ km^2)	Source
		Cameroon	Bouba Ndjida, Faro, Benoue NPs + hunting blocks	2008	ATC	100%	630	(4000)	/	/	22 137	0.18	Omondi *et al.* 2008
		Ghana	Mole NP	2006	ATC	100%	700	700	/	/	4500	0.16	Bouché 2006
		Ivory Coast	Comoé NP	2010	ASC	6%	56	899	± 905	SD	11 945	0.08	N'Goran *et al.* 2010
		Nigeria	Yankari NP	2011	ATC	100%	174	174	/	/	2244	0.08	Bergl *et al.* 2011
		Senegal	Niokolo Koba NP	2006	ASC	40%	15	457	± 447	SE	9130	0.05	Renaud *et al.* 2006
		Senegal	Niokolo Koba NP	2003	ASC	7%	68	957	± 864	95% IC	9130	0.10	Mauvais & Ndiaye 2004
S. c. caffer		Botswana	North country (Moremi GR, Chobe National NP, Makgadikgadi Nxai Pan NP and surrounding WMAs in the Ngamiland, Chobe and Central districts)	2010	ASC	14% [5–22]	7958	39 579	± 27%	95% CI	73 478	0.54	Chase 2011
		Democratic Republic of Congo	Virunga NP	2010	ASC	?	?	2154	?	?	7823	0.28	Plumptre *et al.* 2010
		Ethiopia	Chebera Churchura NP	2005–2006	Pedestrial (LT)	5%	130	2617	± 426	SE	1215	2.15	Megaze *et al.* 2012
		Ethiopia	Omo NP and buffer zone	2007	ASC	40%	330	675	± 31%	SE (%)	7853	0.09	Renaud 2007
		Kenya	Laikipia/Samburu ecosystem	2002	ATC	100%	2012	2012	/	/	10 000	0.20	Omondi *et al.* 2002
		Kenya	Masai Mara NR/ community areas	2010	ATC	100%	4649	4649	/	/	4716	0.99	Kiambi *et al.* 2010
		Kenya	Meru Conservation Area	2007	ATC	100%	2288	2288	/	/	12 000	0.19	Mwangi *et al.* 2007
		Kenya	Nasolot/south Turkana/Rimoi/ Kamnarok	2010	ATC	100%	0	0	/	/	4551	0.00	Edebe *et al.* 2010
		Mozambique	Chipanje Chetu	2011	ASC	11%	10	/	/	/	6641	/	Craig 2011b
		Mozambique	Niassa Reserve	2011	ASC	10%	644	6214	[3462–8967]	95% CI	42 296	0.15	Craig 2011a

Mozambique	East Musengezi River (south Lake Cabora Bassa)	2010	ASC	25%	41	143	± 177%	95% CI	13 962	0.01	Dunham 2010
Mozambique	West the Musengezi River (south Lake Cabora Bassa)	2010	ASC	12%	587	4483	± 107%	95% CI	2621	1.71	Dunham 2010
Mozambique	Banhine NP	2009	ASC	19%	16	/	/	/	1192	/	Stalmans & Peel 2009
Mozambique	Quirimbas NP	2011	ASC	10%	0	0	/	/	20 834	0.00	Craig 2011c
Mozambique	Marromeu Complex	2010	ATC	100%	10 300	10 300	/	/	11 270	0.91	Beilfuss *et al.* 2010
Mozambique	Zinave NP and surrounding area	2010	ASC	15.2% [6–21]	0	0	/	/	9 231	0.00	Dunham *et al.* 2010
Namibia	Caprivi River Systems	2007	ATC	100%	5971	5971	/	/	1778	3.34	Chase 2007
Rwanda	Akagera National Park	2010	SRF		?	?			1120		Viljoen *et al.* 2010
South Africa	Kruger NP	2011	ATC	100%	40 922	40 922	/	/	20 000	2.05	Ferreira *et al.* 2012
Tanzania	Selous ecosystem	2002	ASC	?	?	280 701	± 61 278	SE	94 009	2.99	Debonnet & Wilson 2008
Tanzania	Selous ecosystem	2006	ASC	?	?	113 463	± 25 613	SE	80 883	1.40	Debonnet & Wilson 2008
Tanzania	Selous-Niassa Wildlife Corridor	2006	ASC	5%	94	1456	± 949	SE	9096	0.16	Tawiri 2006
Tanzania	Selous-Niassa Wildlife Corridor	2009	ASC	10%	418	4095	± 2116	SE	9096	0.45	Tawiri 2009
Tanzania	Serengeti Ecosystem (Serengeti NP, Maswa and Ikorongo-Grumeti GRs, Ngorongoro CA, Liliondo GCA and adjacent areas)	2009	ATC	100%	32 068	32 068	/	/	26 827	1.20	Tawiri 2010
Tanzania	Katavi-Rukwa ecosystem	1988–2002	ATC	?	?	39 557	?	?	8 494	4.65	Caro 2008
Uganda	Murchison Falls PA (Murchison Falls NP, Bugungu & Karuma WRs)	2010	ATC	?	356	9192	± 3789	SE	5044	1.82	Rwetsiba & Nuwamanya 2010
Uganda	Kidepo NP	2008	ATC	100%	3643	3643	/	/	1128	3.23	WCS Flight Programme 2008

Table 20.1 *(cont.)*

Subspecies	International PA complex	Country	Protected area/ hunting blocks	Date	Method	Sampling effort^a	Number obs.	Estimated population	Error	Error statistics	Area (km^2)	Density (ind/ km^2)	Source
		Uganda	Queen Elizabeth NP	2010	ATC	100%	10 282	10 282	/	/	2113	4.87	Plumptre *et al.* 2010
		Zambia	Kafue Ecosystem	2011	ASC	3–12%	/	4566	± 687	SE	70 000	0.07	Frederick 2011
		Zambia	Luanga Valley ecosystem	2008	ASC	12%	1540	17 155	± 3,673	95% CI	49 700	0.35	WCS Flight Programme 2009
		Zimbabwe	Gonarezhou complex (Gonarhezou NP, Malipati SA and surrounding CLs)	2010	ASC	15.2% [6–21]	558	2742	± 75.8%	95% CI	7112	0.39	Dunham *et al.* 2010
		Zimbabwe	Sebungwe Region (Chizarira and Matusadona NPs, Chiziza/Chete SAs, P&W Estate, Sajarira FA, North Gokwe, Binga Kariba CLs)	2006	ASC	15%[7–23]	1771	10 395	± 37.6%	95% CI	15 622	0.67	Dunham *et al.* 2006
		Zimbabwe	Hwange-Matetsi complex and adjacent areas (Zakuma NP, Deka SA, Ngamo and Sikumi Forest Areas and Tsholotsho and Maitengwe CL)	2007	ASC	8%[3–15]	1461	24 500	±120%	95% CI	24 570	1.00	Dunham *et al.* 2007
	Amboseli-West Kilimanjaro/ Magadi – Natron (Kenya, Tanzania)	Kenya/ Tanzania	Amboseli NP	2010	ATC	100%	235	235	/	/	8797	0.03	WCS Flight Programme 2010
			Namanga-Magadi	2010	ATC	100%	62	62	/	/	5513	0.01	
			Lake Natron	2010	ATC	100%	37	37	/	/	7047	0.01	
			West Kilimanjaro	2010	ATC	100%	0	0	/	/	3014	0.00	

	Tsavo/ Mkomazi ecosystem	Kenya	Tsavo East and West, Chyulu NP, South Kitui NR, Galana, Taita and Rombo blocks	2011	ATC	100%	7281	7281	/	/	45 126	0.16	Ngene *et al.* 2011
		Tanzania	Mkomazi NP				121	121			3193	0.04	
	Zambezi Heartland (Mozambique, Zambia, Zimbabwe)	Mozambique	Lake Cabora Bassa	2003	ASC	15%	265	1561	± 90%	95% CI	6329	0.25	Dunham 2004
		Zambia	Lower Zambezi NP, Chiawa and Rufunsa GMAs/Tonga-Sikongo CL		ASC		844	6658	± 102%	95% CI	11 954	0.56	
		Zimbabwe	Mana Pools NP, Hurungwe, Sapi, Charara, Dande, Chewore SAs and part of Guruve District		ASC		3537	19 527	± 37%	95% CI	13 373	1.46	
S. c. nanus		Cameroon	Campo Ma’an NP	2000–2002	Pedestrial (LT)	/	/	20	/	95% CI	650	0.01	Bekhuis *et al.* 2008
		Central African Republic	Dzanga-Ndoki NP (Dzanga sector)	2002–2004	Pedestrial (RT)	5%	32	40	/	/	495	0.08	Melletti 2005; Melletti *et al.* 2007a
		Gabon	Lope´ NP (northeast sector)	2002–2004	Ground survey	/	/	342	/	/	72	5	Korte 2008b
		Gabon	Réserve de Faune de Petit Loango	2006	Ground survey	/	/	/	/	/	500	1.70	Morgan 2007
		Republic of Congo	Noubale-Ndoki NP	1993–2000	Pedestrial (LT)	/	/	/	/	/	3920	0.01	Blake 2002
		Republic of Congo	Odzala NP	1990s	Ground survey	/	/	500	/	/	13 600	0.04	Chamberlan *et al.* 1995

ASC: aerial sampling counts; **ATC**: aerial total counts; **CA**: conservation area; **CL**: communal land; **FA**: forest area; **GCA**: game controlled area; **GR**: game reserve; **LT**: line transect; **NP**: national park; **NR**: national reserve; **RT**: recce transect; **SA**: safari area; **SRF**: systematic reconnaissance flight; **WMA**: wildlife management area; **WR**: wildlife reserve.

[a] Sampling efforts generally are weighted means of several block counts sampled at different intensities

Table 20.2 The total estimated numbers of three African buffalo savanna subspecies per country are presented and compared with the last update of East (1998)

		East (1998)	**Cornélis, Melletti, Korte, *et al.* (this study)**
S. c. aequinoctialis		**>59 000**	**>23 000**
	Central African Republic	19 000	4050
	Chad	1020	8090
	Democratic Republic of Congo	39 180	5980
	Eritrea	Ex	Ex
	Ethiopia	x	4380
	Sudan	>100	(8900)
S.c. brachyceros		**>20 000**	**> 17 000**
	Benin	>2000	4560
	Burkina Faso	1620	5070
	Cameroon	3210	4000
	Gambia	Ex	Ex
	Ghana	C	700
	Guinea	V	V
	Guinea Bissau	x	?
	Ivory Coast	8330	900
	Mali	120	Ex?
	Niger	500	1170
	Nigeria	>200	>170
	Senegal	>4000	460
	Togo	U/R	x
S. c. caffer		**> 548 000**	**> 473 000**
	Angola	<500	x
	Botswana	26 890	39 580
	Burundi	500	Uk
	Democratic Republic of Congo	No data	2150
	Ethiopia	2330	3600
	Kenya	>19 560	>16 560
	Malawi	>3150	Uk
	Mozambique	9570	23 310
	Namibia	1000	6000
	Rwanda	1200	R
	Somalia	U	Uk
	South Africa	30 970	>77 800
	Swaziland	U	Uk
	Tanzania	>342 450	>189 230
	Uganda	>20 220	23 120
	Zambia	>40 090	>28 330
	Zimbabwe	50 330	63 000
Total		**>627 000**	**>513 000**

-: absent; **?**: may occur but current presence not confirmed; **Ab**: abundant; **C**: Common; **Ex**: Extinct; **Ex?**: probably extinct; **R**: rare; **U**: uncommon; **Uk**: unknown; **V**: occurs only as a vagrant; **x**: definitely present but abundance unknown

this represents a 64% decrease since an ASC conducted in 1996 (Graham *et al.* 1996). At most 300 individuals are estimated to range within Mago National Park and Tama Wildlife Reserve (respectively 1940 and 1670 km^2, east of Omo National Park; Ludwig Siege, EWCA, personal communication). Further north, in Chebera Churchura National Park (1220 km^2), the buffalo population was estimated (line transect; LT) in 2006 at 2600 individuals (Megaze *et al.* 2012).

In **Uganda**, data from the 2010 ASC of Murchison Falls Protected Area estimated a population of 9200 buffalo within an area of 5040 km^2 (Rwetsiba & Nuwamanya 2010). In Kidepo National Park and surrounding areas (1130 km^2) the last ATC estimated a total population of 3600 individuals, primarily located inside the park (WCS Flight Programme 2008). In Queen Elizabeth National Park (2110 km^2), the most recent ATC reported 10 300 buffalo (Plumptre *et al.* 2010).

In the Akagera National Park (**Rwanda**), the buffalo population was estimated at 7800 individuals in the late 1970s (Monfort 1979). During civil unrest in the 1990s, their population was severely reduced. In 1997 Akagera National Park was reduced in size from more than 2500 km^2 to its current extent of 1120 km^2 (East 1999). An aerial survey (SRF; systematic reconnaissance flight) was carried out in 2010 and small numbers of buffalo were sighted in Akagera National Park (average group size 23; individuals $n = 38$) and Gabiro area (average group size 39; individuals $n = 9$), but no reliable population estimate is available (Viljoen *et al.* 2010).

In Virunga National Park (Democratic Republic of Congo, 7820 km^2), an ASC carried out in 2010 reported 2100 buffalo

(Plumptre *et al.* 2010). In the south of the country (Katanga province), the buffalo population in Upemba National Park (10 000 km^2) and Kundelungu National Park (2200 km^2) is on the brink of extinction with just 15 individuals observed in 2008 surveys (Vanleeuwe *et al.* 2008). In these parks wildlife was abundant throughout the 1980s but then rapidly declined in the 1990s and 2000s due to economic and political instability, and subsequent insecurity (Vanleeuwe *et al.* 2008).

In **Kenya**, the status of buffalo varies with the locality considered. In the northern part of the country (Nasolot, south Turkana, Rimoi and Kamnarok region; 4550 km^2) no buffalo were recorded during an ATC conducted in 2010 (Edebe *et al.* 2010). In Laikipia/Samburu ecosystem (an area covering about 10 000 km^2), 2002 aerial surveys reported 2000 buffalo, with an estimated 30% decrease between 1999 and 2002; the largest reported decline (55%) was in Samburu area (Omondi *et al.* 2002). In Meru Conservation Area (4010 km^2, covering Meru National Park, Kora National Park, Bisinadi, Mwingi and North Kitui National Reserves), there were 1800 individuals (wet season), and 2300 (dry season) (Mwangi *et al.* 2007). In Masai Mara National Reserve and community areas (4720 km^2), the buffalo population was estimated at 4600 individuals in 2010 (Kiambi *et al.* 2010).

In Amboseli-West Kilimanjaro/Magadi-Natron protected areas (Kenya/Tanzania border, 24 370 km^2) an ATC estimated the population at 300 individuals (90% in the Kenya section) (WCS Flight Programme 2010). In Tsavo/Mkomazi ecosystem (Kenya/Tanzania border, 48 320 km^2) the last three ATCs reported estimates of 9400 (2005), 5600 (2008) and 7400 (2011) individuals (Ngene *et al.* 2011). During the last ATC, 98% of the buffalo (7300 individuals) were observed in the Kenyan section of the Tsavo/Mkomazi ecosystem.

Tanzania has the largest African buffalo population, with over 342 000 individuals recorded in the last update (East 1998). Buffalo are common in most of the country's major wildlife areas, e.g. Selous Game Reserve, Serengeti, Tarangire and Katavi National Parks, the Ruaha ecosystem and the Katavi-Rukwa and Kilombero Game Controlled Areas. The Selous ecosystem (over 90 000 km^2, southern Tanzania) certainly has the largest buffalo population in Africa and over half of Tanzania's. Recent ASCs reported a population estimate of 280 700 individuals in 2002 (94 000 km^2) and 113 500 (80 890 km^2) individuals in 2006 (Debonnet & Wilson 2008). In Selous-Niassa Wildlife Corridor (9100 km^2), a region bordering Mozambique, dry season ASCs conducted in 2006 and 2009 reported 1500 and 4100 buffalo, respectively (Tawiri 2006, 2009). In the Serengeti ecosystem (north Tanzania), ATCs conducted in 2008 and 2009 (covering 26 830 km^2) recorded 32 900 and 32 100 buffalo, respectively. The population numbers for 2008 and 2009 surveys were the highest for the Serengeti ecosystem in 14 years (Taiwiri 2010). In Katavi-Rukwa ecosystem (8500 km^2, Tanzania) the buffalo population was estimated at 39 600 individuals (surveys 1988–2002; Caro 2008). A review of aerial census data collected during the late 1980s to early 2000s in eight large census zones of Tanzania suggests that buffalo populations globally remained stable in Tarangire census zone, but declined in Burigi Biharamulo, Greater Ruaha, Katavi and Moyowosi-Kigosi census zones during the time period considered (Stoner *et al.* 2006).

In **Mozambique**, buffalo populations occurred throughout the country until the 1970s, but suffered greatly from the former civil conflict (1977–1992). In Niassa Reserve (42 300 km^2) buffalo were successively estimated at 2300 (2006), 6800 (2009) and 6200 (2011) individuals (Craig 2011a). In Quirimbas National Park and adjacent areas, an ASC undertaken in 2011 over 20 830 km^2 reported no buffalo observations (Craig 2011c). In Chipanje Chetu area, an ASC conducted in 2011 (area surveyed: 6640 km^2) reported the observation of a single herd (ten individuals; Craig 2011b). In southern Cabora Bassa region (northwest Mozambique), an ASC undertaken in 2010 estimated the buffalo population at 4600 individuals (area surveyed: 16 590 km^2) (Dunham 2010). In Gilé National Reserve, no buffalo observation was reported by the ASC conducted in 2007 (Mesochina *et al.* 2008), but a reintroduction programme is currently ongoing (20 buffalo reintroduced from Gorongosa National Park in 2012). Central Mozambique hosts residual populations of buffalo, except the open floodplains of the Marromeu Complex (11 270 km^2), with an estimated population >10 300 individuals (Beilfuss *et al.* 2010). Buffalo were extinct in Gorongosa National Park (4000 km^2) and the population (360 individuals; 2010 estimate) was restocked (2006–2011) with 186 buffalo from Kruger and Limpopo National Parks (Carlos L. Pereira, personal communication). In south Mozambique, 16 individuals were recorded by ASC in Banhine National Park (1190 km^2) in 2009 (Stalmans & Peel 2009). In the Limpopo National Park (11 230 km^2) an ASC conducted in 2007 estimated the buffalo population at around 200 (Swanepoel 2007).

In **Zambia**, aerial surveys were conducted in the Kafue ecosystem (Kafue National Park and surrounding game management areas combined). In 2008, 6300 buffalo were recorded in an area of 48 000 km^2, and in 2011, 4600 individuals were recorded in an area of 70 000 km^2. The 2011 survey used a combination of total and sample counts and was more accurate than the previous 2008 survey (Frederick 2009, 2011). In Luanga Valley ecosystem (49 700 km^2; eastern Zambia), an ASC conducted in 2008 reported an estimation of 17,200 buffalo (WCS Flight Programme 2009).

A transfrontier ASC conducted in 2003 in the Zambezi Heartland between Lakes Kariba and Cabora Bassa (Zimbabwe, Mozambique and Zambia; 31 660 km^2) estimated the buffalo population at 27 700 individuals (Dunham 2004). In Zimbabwe, the buffalo population estimate was 19 500 (13 373 km^2, including Mana Pools National Park, Hurungwe, Sapi, Charara, Dande, Chewore Safari Area and part of Guruve District). In Mozambique the estimate was 1 600 (6330 km^2; communal lands south and north of Lake Cabora Bassa and east of the Luangwa River). No buffalo were observed north of Lake Cabora Bassa. In Zambia the buffalo population estimate was 6700 (11 950 km^2, including Lower Zambezi National Park, Chiawa and Rufunsa Game Management Areas and Tonga-Sikongo communal land).

In **Zimbabwe**, an ASC conducted in 2006 in the Sebungwe region (15 620 km^2, including Chizarira and Matusadona National Parks, Chiziza and Chete Safari Areas, P&W Estate, Sajarira Forest Area and North Gokwe, Binga Kariba communal lands) reported an estimate of 10 400 buffalo (Dunham *et al.* 2006). A 2007 ASC conducted in Hwange-Matetsi complex and adjacent areas (24 570 km^2, including Zakuma National Park, Deka Safari Area, Ngamo and Sikumi Forest Areas and Tsholotsho and Maitengwe communal lands) estimated 24 500 buffalo (Dunham *et al.* 2007). In Gonarezhou complex (7110 km^2, including Gonarhezou National Park, Malipati Safari Area and surrounding communal lands), an ASC conducted in 2010 reported 2700 buffalo (Dunham *et al.* 2010). Other substantial buffalo populations also occur in several conservancies in southeast Lowveld, among which are Save Valley (3340 km^2, 1900 individuals in 2002), Bubye Valley (3430 km^2, about 3000 individuals) and Nuanetsi Conservancies (1490 km^2, about 1000 individuals) (Chris Foggin, personal communication).

In **Angola**, buffalo have been wiped out by uncontrolled hunting and poaching throughout the country, including Kissama National Park, where East (1998) reported a declining population of the transitional 'red' buffalo. Residual populations may still range in the areas north of Luanda, in Cabinda and Cangandala National Park. In the southeast, typical Cape buffalo may still occur in Quando Cabando (Wouter Van Hoven, personal communication), but the numbers are unknown.

In **Botswana**, buffalo are found only north of 20° S in the Okavango-Chobe region. In 2010, an ASC covering northern Botswana, (73 480 km^2, including Moremi Game Reserve, Chobe National Park, Makgadikgadi Nxai Pan National Park and surrounding wildlife management areas) estimated the population at 39 600 individuals (Chase 2011).

In **Namibia**, buffalo were largely eradicated as part of a veterinary campaign. The construction of the veterinary cordon fences along the international border with Botswana is thought to be a factor responsible for buffalo decline (Martin 2002). An ATC conducted in 2007 on the Caprivi River systems (area covered: 1780 km^2) reported 5900 buffalo (Chase 2007). A small population (about 50 buffaloes) was introduced in Waterberg Plateau Park (400 km^2) between 1981 and 1991 and increased to 200 in 2000, and a relict population of 70 animals still occurs in Bushmanland (Tsumkwe area; 24 km^2; Martin 2002).

In **South Africa**, buffalo were extirpated from their former range except for a few areas such as Kruger National Park (20 000 km^2), where the country's major population now occurs (37 500 in 2009 and 40 900 in 2011; Ferreira *et al.* 2010, 2011, 2012). About 4000 buffalo persist in Hluhluwe-Imfolozi Park (900 km^2; Jolles 2007). Buffalo from Hluhluwe-Imfolozi and Kruger National Park are known carriers of diseases transmissible to cattle and thus cannot be translocated from one region of South Africa to another. The buffalo population in Mokala National Park (270 km^2) was estimated at 400 in 2012. In Addo Complex area (1640 km^2) 300 were counted in 2011. In Karoo National Park (770 km^2) only four individuals were observed from 2010 to 2012. In Mountain Zebra National Park (280 km^2) 77 individuals were counted in 2012. Mount Camdeboo Game Reserve (140 km^2) presented stable numbers at 30–36 in 2010–2011 surveys (Ferreira *et al.* 2012). There are approximately 32 000 disease-free buffalo in South Africa. Six thousand of these are in national or provincial parks, while the remaining 26 000 are privately owned and resident on approximately 2700 private game ranches or reserves (South African Private Buffalo Owners Association, personal communication).

West African savanna buffalo

In West Africa, buffalo numbers have declined alarmingly during the last decade. Since East's (1998) assessment, populations larger than 1000 individuals persist in only two of five sites. In West Africa, more than anywhere else in Africa, savanna buffalo populations are restricted within the borders of a limited number of protected areas.

In **Senegal**, the last buffalo population is located in Niokolo Koba National Park (9130 km^2). This population was estimated by ASC at 1000 and at 500 in 2003 and 2006, respectively (Mauvais & Ndiaye 2004; Renaud *et al.* 2006). An estimation dating from the early 1990s by pedestrian sampling count (PSC) was of 11 000 individuals (Galat *et al.* 1992).

This subspecies is now extinct in the **Gambia** (Jallow *et al.* 2004).

In **Mali**, the buffalo is extinct in the Boucle de la Baoulé National Park, but a relict population may still occur along the border with Senegal in the riverine forest of the Faleme Hunting Zone, and maybe in Bafing National Park (Bourama Niagate, personal communication).

In **Guinea Conakry**, Sudanian savannas still locally host small populations in protected areas (Kankan Forest reserve, Bakoun classified forest or Bakoy sector), but no population estimate is available (Brugière 2012).

In **Ivory Coast**, savanna buffalo still range in Comoé National Park (11 950 km^2), where the population was estimated (ASC) at 900 individuals in 2010, representing an 80% decline since the 1970s (N'Goran *et al.* 2010).

The largest buffalo population of West Africa is located in WAP Regional Park (28 350 km^2)in **Benin**, **Burkina Faso** and **Niger**. This complex comprises three national parks ('W', Arly and Pendjari) and several hunting zones, containing a buffalo population estimated by ATC in 2003 at 10 600 individuals (Bouché *et al.* 2003). Of these, about one-third (3400) were located in Pendjari National Park (2 830 km^2). Counts have not been repeated for the entire area since 2003. However, recent counts conducted at Pendjari National Park suggest a decreasing trend in population (Sinsin *et al.* 2008), while the 'W' National

Park population has remained fairly stable or increased (Bouché 2012).

In **Burkina Faso**, ATCs conducted on Ponasi (3100 km^2) and Comoé-Leraba (1850 km^2) protected area complexes estimated the buffalo population at 145 and 90 individuals, respectively (Bouché *et al.* 2004; Bouché 2005).

In Mole National Park (4500 km^2, **Ghana**), 500 and 700 individuals were counted in 2004 (ASC) and 2006 (ATC), respectively (Mackie 2004; Bouché 2006), whereas the population was estimated (ASC) at 1700 individuals in 1993 (Wilson 1993), suggesting an overall decline in numbers. The presence of buffalo has been reported in 2013 in Kyabobo National Park along the Togo border (Fazao Malfakassa National Park; D. Brugière, personal communication).

In **Togo** no buffalo were observed during the ATC carried out in Keran National Park (1400 km^2) and in Oti-Mandori Faunal Reserve (1800 km^2; Bouché *et al.* 2003).

In **Nigeria**, the West African savanna buffalo formerly occurred widely in the northern savannas, but has been extirpated from most of its former range. To our knowledge, a relict population remains in the National Parks of Yankari (2240 km^2; 170 individuals) (Bergl *et al.* 2011) and Kainji Lake (not estimated; Aremu *et al.* 2007).

In Northern **Cameroon**, an ATC conducted in 2008 in the complex of protected areas of Faro, Benoue and Bouba Ndjidda National Parks and their adjacent hunting blocks (22 140 km^2 in total) found 600 individuals (Omondi *et al.* 2008). It is likely that this figure is a gross underestimate due to inappropriate transect inter-distance (3–5 km). On the basis of empirical correction factors (effective bandwidth of 200–300 m), the size of the population can be estimated at around 4000 individuals.

Central African savanna buffalo

Most Central African savanna buffalo populations declined alarmingly during the last decades, and few protected areas still encompass significant ($>$1000) numbers. However, in contrast to West Africa, the savannas of Central Africa are less degraded overall, and still host diffuse (low density, small size) populations of buffalo in many areas.

One of the largest populations is located in **Chad** (Zakouma National Park; 3030 km^2), where the ATC carried out in 2012 reported an estimate of 8100 individuals (Potgieter *et al.* 2012). Interestingly, the Zakouma population is still increasing (due to intense conservation efforts), with a mean annual growth rate of 8% during the four last years.

A second important population is located in the northeast of the **Central African Republic**, in a complex of protected areas (94 960 km^2) comprising Bamingui-Bangoran National Park, Manovo-Gounda-St. Floris National Park and protected areas of diverse statuses. This complex includes a population estimate in 2010 (ASC) of 4000 individuals (Bouche 2010). The comparison with prior ASCs emphasized a population decline of 31% between 1985 and 2005 (Douglas Hamilton *et al.* 1985) and a drastic decline (76%) between 2005 and 2010 (Renaud 2005). In 2010 most herds were found in hunting zones, while the national parks and reserves were occupied by transhumant cattle. No information currently exists from Bangassou Forest Reserve (12 080 km^2) where East (1998) reported a population greater than 1000 individuals.

In **South Sudan**, ASCs carried out in 2007 (Fay *et al.* 2007) in an area larger than 150 000 km^2 revealed sizeable buffalo population estimates (8900), mainly located in Boma National Park (22 800 km^2), but these figures may be inferred from very few sightings and thus strongly overestimated. However, comparison with an ATC conducted over the same area (using the same methods) in 1981 indicates that buffalo populations declined by at least 80% in 25 years. No buffalo were observed in 2007 in Southern National Park (23 000 km^2) although 60 000 were counted in 1981. In northern **Democratic Republic of Congo**, ATCs carried out in Garamba National Park (4 920 km^2) in 2007 and 2012 reported estimates of 5200 and 6000 buffalo, respectively (Bolanos 2012). In **Ethiopia**, an ASC conducted in 2010 in Gambella National Park (20 000 km^2) and adjacent areas reported 1400 individuals (EWCA 2010), but this inference was based on very few observations and is to be taken with precaution. Roughly 3000 buffalo are estimated to range in Dati area, north of Gambella (EWCA, unpublished).

Forest buffalo

Forest buffalo population estimates are available for only a few sites. At Lopé National Park (**Gabon**), the population is using a mosaic landscape of forest and equatorial savanna (70 km^2) in the northeast corner of the park, and is estimated to be 300 individuals, organized into 18 herds (Korte 2008b). In Odzala National Park, **Republic of Congo**, the population is estimated to be 500 buffalo subdivided mainly into three large herds (Chamberlan *et al.*, 1995).

Bekhuis *et al.* (2008) estimated a population of 20 buffalo in an area of 650 km^2 in **Cameroon** at Campo-Ma'an National Park. At the Dzanga sector of Dzanga-Ndoki National Park, **Central African Republic**, the population is estimated between 32 and 40 individuals in two herds in 500 km^2 of rainforest (Melletti 2005; Melletti *et al.* 2007a).

Density

Buffalo density is dependent on many factors, including the spatiotemporal distribution of resources (water, forage quality and quantity), and also in conjunction with epidemiological, conservation and management contexts.

Cape buffalo may locally reach very high densities (20 individuals/km^2) in optimal habitats such as Lake Manyara National Park (Tanzania), where both high-quality forage and water are available year-round (Prins 1996). In contrast, in the woodlands of the nearby Serengeti National Park, lower densities were reported (8 individuals/km^2; Sinclair 1977). In the northern section of Akagera National Park (Rwanda), high

Table 20.3 Main differences between the four African buffalo subspecies

African buffalo subspecies	Syncerus caffer caffer	Syncerus caffer brachyceros	Syncerus caffer nanus	Syncerus caffer aequinoctialis
Main habitat	Different types of woodland and open arid savannas, montane grassland	Different types of woodland and open savannas	Rainforest, natural forest clearings, equatorial savanna, forest logging roads, coastal forest	Different types of woodland and open savannas
Home range size (km^2)	Range 0.5–1537 [1]	Range 172–620	Range 2.3–8.0	
Herd size (individuals)	Range 10–1654 2000–4000 [2]	Range 19–150	Range 3–24	Range 2–800 Mean 24.8 [5]; 7.7 [4]
Density (individuals/km^2)	Range 0.7–20	Range 0.8 [4]–1.19 [5]	Range 0.01–7.4	Range 2.55 [5]; 1.75 [4] Mean 2.15
Daily movement (km)	Range 1–15 [1]	Range 5–15 [3]	Range 1–4 [3]	
Calving interval (months)	Range 12–36	~24	~24	~24
Herd structure	Many males in mixed herds; bachelor groups; lone males; fission–fusion patterns	Many males in mixed herds; bachelor groups; lone males; fission–fusion patterns	Only 1–2 males in mixed herds; no bachelor groups; few lone males; fission–fusion patterns	Many males in mixed herds; bachelor groups; lone males; fission–fusion patterns
References	Prins & Sinclair 2013; Bennitt 2012; Naidoo *et al.* 2012; Chase 2011; Ryan *et al.* 2007; Hunter 1996; Prins 1996, 1989b; Funston *et al.* 1994; Prins & Douglas-Hamilton 1990; Conybeare 1980; Sinclair 1977; Cobb 1976	Cornelis *et al.* 2011; Sinsin *et al.* 2008; Stark 1986	Korte 2008a, 2008b; Melletti 2008; Bekhuis *et al.* 2008; Melletti *et al.* 2007a; Morgan 2007; Van Der Hoeven *et al.* 2004; Tutin *et al.* 1997	

[1] Migratory subpopulation combined for different areas
[2] Possible temporary associations of two or more herds
[3] Mixed herds
[4] Dry season (Stark 1986)
[5] Wet season (Stark 1986)

densities were also reported (13 individuals/km^2) until the 1990s. To date, in well-managed protected areas such as Selous reserve (South Tanzania), Kruger National Park (South Africa), or Hwange National Park (Zimbabwe), the average density of Cape buffalo ranges between 1 and 3 individuals/km^2.

West and Central African savanna buffalo range on soils poorer in nutrients than those of Cape buffalo habitats and display lower densities (0.5–1.5 individuals/km^2) in the well-managed protected areas (e.g. within WAPOK complex). Historically, higher densities were observed in several large floodplains (e.g. South Sudan, north Central African Republic), but these areas are now dominated by cattle and crop production, or were heavily poached. At present, high buffalo densities are still observed in the floodplains of Zakouma National Park (Chad; 2.4 individuals/km^2).

In Campo Ma'an National Park (Cameroon) the density of forest buffalo is 0.01–0.04 individuals/km^2 in 650 km^2. Most of this forest has a closed canopy without grass in the understory (Bekhuis *et al.* 2008), leading to low buffalo densities. The same holds for Nouabalé-Ndoki National Park in adjacent Republic of Congo (Blake 2002) and the coastal rainforests of Gabon (Prins & Reitsma 1989). In Dzanga-Ndoki National Park (Dzanga sector, 490 km^2) in Central African Republic the density is between 0.06–0.08 individuals/km^2 (Melletti 2005). In Lopé National Park (Gabon), buffalo density is locally high (5 individuals/km^2; 70 km^2 of the northeast corner of the park) in the forest–savanna mosaic, but lower (0.4 individuals/km^2) in the surrounding forest (White 1992; Korte 2008b). In the Réserve de Faune de Petit Loango (Gabon) the density was locally estimated at 1.7 individuals/km^2 in a coastal habitat (Morgan 2007).

More details on density in different areas are summarized in Tables 20.1 and 20.3.

Descriptive notes

Among African mammals, the buffalo has (with the African elephant) a very marked polymorphism across its range. The size, pelage colour and shape of horns differ greatly by region.

The African buffalo is the largest and most massive bovid of the African continent, with a broad head and short, thick legs and neck. Horns are present in both sexes. The front hooves are larger than the hind to support the heavy weight of the trunk and the head. The muzzle is wide, with a wet nose, large eyes, and drooping fringed ears. Females have a small, rounded udder with two pairs of inguinal mammae. Adult males have a tufted penis. Buffalo have sweat glands but no specialized olfactory skin glands. The tail is tufted with dark hair, and adult males sometimes appear to have a beard. The sense of smell in the buffalo is highly developed. Buffalo also seem to have good eyesight, and can spot predators from a great distance (Prins & Sinclair 2013).

The deciduous dentition is: I 0/3, C 0/1, P 3/3 = 20; by the ninth month of age the temporary teeth have erupted. Crown height and enamel ridge pattern, together with stages of tooth eruption, can be used for ageing buffalo and results are identical for populations of Western, Eastern and Southern Africa (Grimsdell 1969, 1973a; Spinage & Brown 1988; Taylor 1988). The permanent molars erupt at about 3.5 years of age. The lower canines erupt between 4.5 and 5.5 years old. Each year, one cementum line develops, making dental analysis a useful tool for ageing buffalo. Dental formula is: I 0/3, C 0/1, P 3/3, M 3/3 (× 2) = 32. The structure and adaptation of the stomach is described in Chapter 6.

Cape buffalo

Body measurements: **Shoulder height**: 140–160 cm (Ansell 1972); **Head and body length**: 210–300 cm; **Tail length**: 75–120 cm; Body mass: females up to 500 kg, males from 650 kg (Ansell 1972) to 900 kg. Their skin can be thicker than 2–3 cm. The main morphological differences between the four buffalo subspecies are shown in Figure 20.2.

The world trophy record (horn span) comes from Lake Manyara (Tanzania): 165 cm (bull) and 150 cm (cow). The mean live mass of Southern African adult bulls is 753 kg. Muscular tissues represent 40.6% of the live mass and fat 5.6% of carcass mass (Du Toit 2005).

The Cape buffalo is the largest subspecies, heavily built, with the biggest horns, including strong development of bosses in the horns of the males (Prins & Sinclair 2013). Bulls have a hump above the shoulders that supports the heavy head and horns. The pelage colour varies from black to reddish-brown. Horns are large in both sexes. The body is covered by short hair, with some areas where it is absent. Juveniles have a denser coat than adults and may go through colour changes from yellowish-brown to dark brown before they attain the typical adult black. Red calves are also present up to 30% in some Cape buffalo populations (Prins 1996). Colour mutations have been described in two individuals from Luangwa valley (Zambia), with a white band around the body (Skinner & Chimimba 2005), considered partial albinism.

Cape buffalo males have laterally extending curved horns, large bosses, and when adult, little or no hair between the horns. Females have more slender horns, also laterally extending, with hair on the skin between the horns. The tips of the horns often show signs of breakage. Bosses are very variable in size and do not develop until males are 3–5 years old. There is no relation between the age of an adult male (older than five years) and the size of the boss (Prins & Sinclair 2013). Male's horns become conspicuously roughened after some 4–5 years. In particular in the southern savanna males, the basal horn sheaths expand medially and anteposteriorly across heavily roughened frontals that are up-arched to form prominent bosses (Klein 1994). These bosses are not formed in females. When bulls are sparring, they place their bosses against each other and push. Extensive bossing is a recently derived feature that developed only in the Late Quaternary (Gentry 1978, 1990). It does not occur in the *nanus* subspecies, where fights are infrequent (Kingdon 1997; Van Hooft *et al.* 2002). Since extensive bossing only occurs in adult males, it probably evolved through sexual selection; it occurs particularly in Cape buffalo in east and southern Africa, which are characterized by large group sizes. This suggests that bossing has evolved in the context of a complicated male hierarchy (for details see the section on behaviour; Prins & Sinclair 2013). The frontal bones under the bosses have a honeycomb structure. The height of the bony walls of the cells is about 15–20 mm, while cell diameter is about 7 mm. It is thought to be an adaptation to absorb strong hits and for moving the head in any direction to face attack. While the average weight of a dry skull (including horns) is 8 kg in Lake Manyara National Park, the heaviest skulls were 16 kg (Prins & Sinclair 2013). Horn size was studied as an indicator of health status in male and female Cape buffalo (Ezenwa & Jolles 2008). In both sexes, horn size was significantly negatively correlated with the number of different parasites infecting an individual. These findings support the idea that horn condition plays a role as an indicator of health in both sexes. In particular, Ezenwa & Jolles (2008) suggest that this is a possible role for sexual selection in the maintenance of horns in female ungulates; however, this hypothesis needs further research.

West and Central African buffalo

Body measurements: **Shoulder height**: 120–145 cm; **Head and body length**: 200–245 cm; **Tail length**: 55–70 cm; **Body mass**: 300–600 kg. Smaller than Cape buffalo and bigger than forest buffalo, these intermediate subspecies also have widely spread horns, but these are not curved down as are those of Cape buffalo. Horn span measures 56–103 cm and horn length along the curve is 53–94 cm. The skull measures 43–60 cm.

There are also populations that appear to be intermediate between *brachyceros* and *nanus* subspecies in South Nigeria, Central African Republic and North Cameroon (Wilson & Mittermeier 2011). The red forms of savanna buffalo may be found from Guinea to Chad until North Uganda in the Sahel-Soudan savanna (Grubb 1972; Mloszewski 1983; R. Kock, personal communication).

Forest buffalo

Body measurements: **Shoulder height**: 100–130 cm; **Head and body length**: 170–220 cm; **Tail length**: 60–90 cm; **Body mass**: 265–320 kg. Among the four *Syncerus* subspecies, forest buffalo is the smallest, at around half the size of Cape buffalo

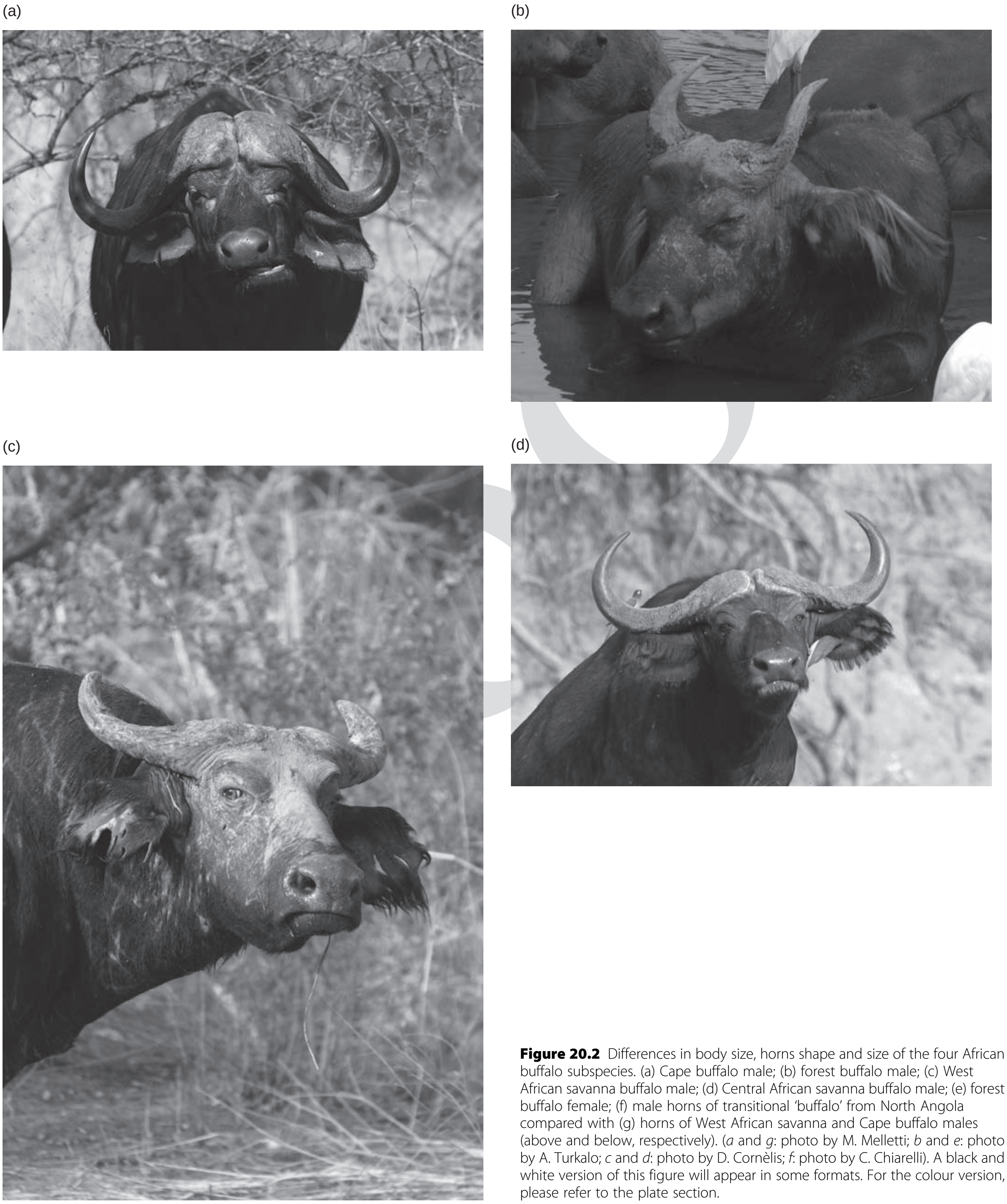

Figure 20.2 Differences in body size, horns shape and size of the four African buffalo subspecies. (a) Cape buffalo male; (b) forest buffalo male; (c) West African savanna buffalo male; (d) Central African savanna buffalo male; (e) forest buffalo female; (f) male horns of transitional 'buffalo' from North Angola compared with (g) horns of West African savanna and Cape buffalo males (above and below, respectively). (*a* and *g*: photo by M. Melletti; *b* and *e*: photo by A. Turkalo; *c* and *d*: photo by D. Cornèlis; *f*: photo by C. Chiarelli). A black and white version of this figure will appear in some formats. For the colour version, please refer to the plate section.

Figure 20.2 *(cont.)*

(Sinclair 1977; Mloszewski 1983; Prins 1996; Wilson & Reeder 2005; Figure 20.2).

Horns are oriented towards the rear in the same plane as the forehead. Horns span ranges of 34–65 cm and horn length along the curve is 41–69 cm and 35–63 cm, in Central and West African populations, respectively (Wilson & Mittermeier 2011). The skull is smaller than that of a savanna buffalo, but still short and wide. The skull length ranges between 39 cm and 49 cm (Wilson & Mittermeier 2011).

Morphological differences within forest buffalo populations are less pronounced than within other subspecies. In addition, the sexual dimorphism (e.g. horn shape and body size) is much less pronounced in the forest buffalo than in the other subspecies. In forest buffalo, the horns are much smaller, back swept and with no boss. These characteristics may reflect the infrequency of fighting, and instead, adaptation to dense rainforest (Kingdon 1997). It has been suggested that horn size tends to increase from West Africa to East and Southern Africa (Grubb 1972); this remains to be tested empirically.

The pelage colour ranges from shades of red and brown to black. Calves and juveniles can have a denser and redder coat than adults, although they may also display dark patterns. Adult bulls show variability in colour patterns even within the same herd. They may be almost all black or completely reddish-brown, with many intermediate shades possible. Females are generally red brown with different shades and show a less pronounced colour gradation than males, but can sometimes be black (L. Korte, personal observation). Another characteristic are the tufted hairs of the ears.

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. They appear not to be bounded by elevation constraints, and their altitudinal distribution ranges from coastal to the boundaries of forests on the highest mountains, except areas with annual rainfall less than 250 mm (e.g. Namib and the Sahara deserts). African buffalo persist in semi-arid environments, as long as surface water is available within 20–40 km, year-round (Naidoo *et al.* 2012; Prins & Sinclair 2013).

The carrying capacity of savanna ecosystems for large grazers such as buffalo is positively correlated with mean annual rainfall and the soil quality (Sinclair 1977; Grange & 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 rich soils (Breman & De Wit 1983; Le Houérou 2008). The low carrying capacity 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; Hibert 2007).

Most of what we know today about the behavioural ecology of savanna buffalo comes from monographs focused on the Cape buffalo (e.g. Grimsdell 1969; Sinclair 1977; Mloszewski 1983; Prins 1996; Ryan 2006). To date, the ecology of West and Central African savanna buffalo remains poorly investigated and comes from sporadic publications (Boy 1958; Gillet 1969, Stark 1986; Cornelis *et al.* 2011). For this reason, and because several behavioural traits are similar within savanna buffalo subspecies, we present all savanna subspecies in one grouping.

Savanna (Cape, West and Central African) buffalo

Savanna buffalo are mainly found in habitats with a high herbaceous biomass. In the distribution range of Cape buffalo (Eastern and Southern Africa) suitable grasses are found in several types of woodland, such as mopane (*Colophospermum mopane*), miombo (*Brachystegia* spp.), Acacia (*Acacia* spp.) and *Baikiaea* spp. West and Central African 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*).

The availability of surface water and cover are commonly cited as the main constraints on habitat use of savanna buffalo. Buffalo must drink at least every two days, taking in about 45 litres daily; they are unable to survive on the moisture content of their food alone (Prins 1996; Prins & Sinclair 2013). They have not evolved any water-saving mechanisms (buffalo sweat profusely, and their faeces comprise approximately 80% water (Taylor 1970; Prins 1996)).

This constraint of access to water is manifest in studies of buffalo habitat use. For example, a GPS-tracking protocol undertaken in West Africa showed that buffalo herds spend 95% of their time within 5.3 km of permanent water areas and around 50% of their time within 1.4 km (Cornelis *et al.* 2011). Many studies showed a preference for riverine habitats, at least during the dry season. These lowland areas (e.g. riparian galleries and surrounding grasslands) provide water, green grass and cover against climatic extremes and predators, simultaneously (Sinclair 1977; Redfern *et al.* 2003; Ryan *et al.* 2006; Cornelis *et al.* 2011). At first rains, the water constraint relaxes and buffalo generally (but not systematically) leave the depleted areas of the dry season and move to habitats located higher in the toposequence (e.g. plateaus), where both water and new green grass are temporary available (Sinclair 1977; Cornelis *et al.* 2011).

It is worth noting that buffalo are also good swimmers, and can forage underwater in floodplains (Chobe River, Okavango, Botswana; Prins & Sinclair 2013). Finally, savanna buffalo may also ascend and descend steep slopes, up to about 50° and may be found at high elevations (Prins & Sinclair 2013). They are known to regularly reach the alpine belt on Mount Kenya and are observed on Kilimanjaro, throughout the forest belt on the northern and western slopes, and tracks were observed up to 4200 m (Grimshaw *et al.* 1995).

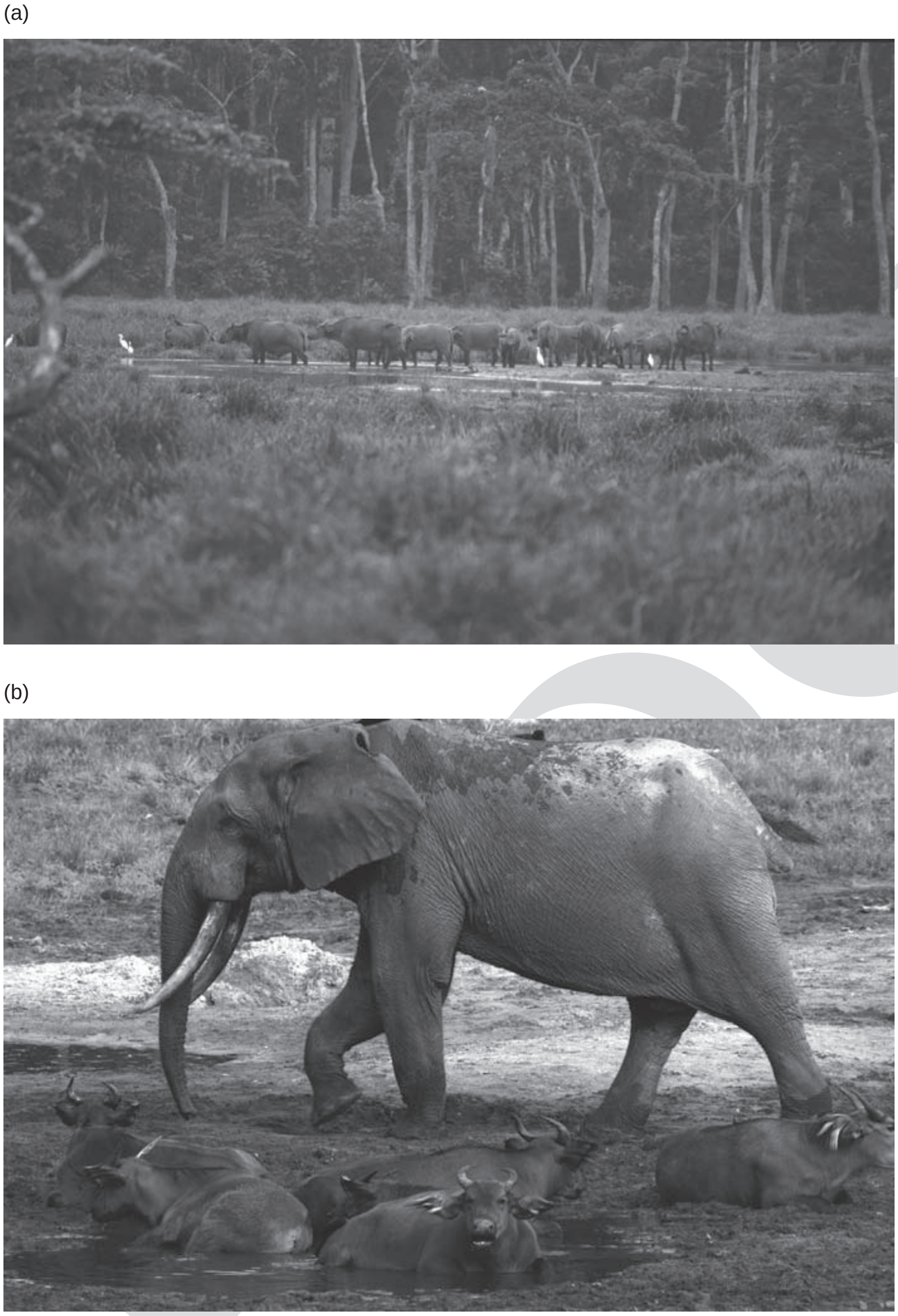

Figure 20.3 Forest buffalo are forest dwellers, inhabiting different habitats with: (a) grassy glades and watercourse areas in rainforest (photo by M. Melletti); (b) forest muddy areas (photo by A. Turkalo); and (c) coastal and equatorial savannas (photo by Mathieu Bourgarel, Cirad). A black and white version of this figure will appear in some formats. For the colour version, please refer to the plate section.

Forest buffalo

Forest buffalo are forest dwellers, inhabiting rainforests with grassy glades, watercourse areas and mosaics of equatorial forests and savannas (Figure 20.3). This subspecies is absent (or present at very low densities) in continuous forests (Prins & Reitsma 1989; Blake 2002; Melletti *et al.* 2007a, 2009; Melletti 2011).

Suitable habitats for forest buffalo are mosaics of forest with equatorial savannas or clearings, which consist of grassy vegetation and shrubs such as *Palisota* spp. (Reitsma 1988; Blake 2002; Tchouto 2004). Blake (2002) at Noubale-Ndoki National Park found high buffalo abundance close to open grassy areas with low abundance in the closed canopy forest, suggesting it is unsuitable for forest buffalo. Melletti *et al.* (2007a, 2007b, 2008, 2009) also found a significant relationship between buffalo and natural forest clearings at Dzanga-Ndoki National Park, where clearings were the centre of buffalo home ranges and no signs of buffalo presence were recorded more than 500 m from clearings (Figure 20.4; Melletti *et al.* 2007a). Buffalo positively selected these clearings, although the surface area of clearings represented only 1% of the total area. In Cameroon, buffalo rarely penetrated into the forest more than

Figure 20.3 (*cont.*)

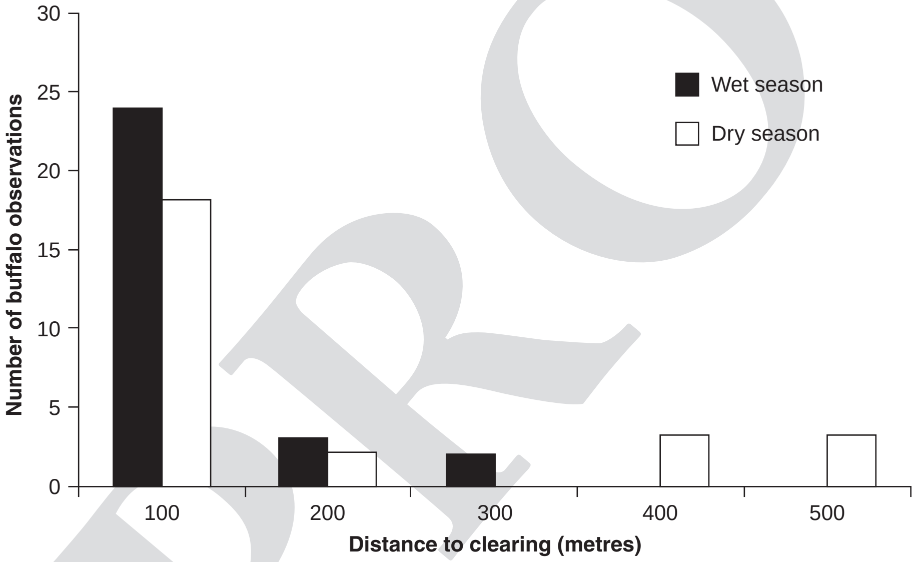

Figure 20.4 Forest buffalo: distribution frequency of the distances to clearings of buffalo observations as revealed by RECCE method in forest habitat during both the dry (from December to February) and wet (from March to November) seasons (Melletti *et al*. 2007a, with kind permission from John Wiley and Sons, *Journal of Zoology*, modified).

300 m from logging roads, which were the main feeding sites for buffalo (Bekhuis *et al*. 2008).

Sites with greater percentages of open areas report high densities of forest buffalo (Morgan 2007; Korte 2008b; Table 20.1). For example, forest buffalo density is 5 individuals/km^2 in the forest–savanna mosaic at Lopé National Park, but only 0.4 individuals/km^2 in the adjacent continuous forest (White 1992). In the coastal area of the Réserve de Faune de Petit Loango (Gabon), Morgan (2007) reports densities of 1.75 individuals per km^2, whereas sites with forest clearing have low densities (Van Der Hoeven *et al*. 2004; Melletti 2005; Bekhuis *et al*. 2008).

At Lopé National Park, Korte (2008a) used radio-tracking data of nine adult females from different herds to quantify habitat preference. Buffalo select proportionally more open habitat (marsh and savanna) and use forest less than would be expected based on available habitat at the landscape level. Habitat use within home ranges varied with season (Figure 20.5). Between March and August >60% of locations of individuals were in forest habitats that represented <50% of home range area. In addition, between the June and August dry season buffalo moved into burned savanna to feed on new grass. These results suggest that forest buffalo use forest fragments, galleries and corridors more often than continuous forest, and habitat preference changes with season based on food availability. Buffalo remained close to the forest clearing areas and did not penetrate deep into the forest, as confirmed

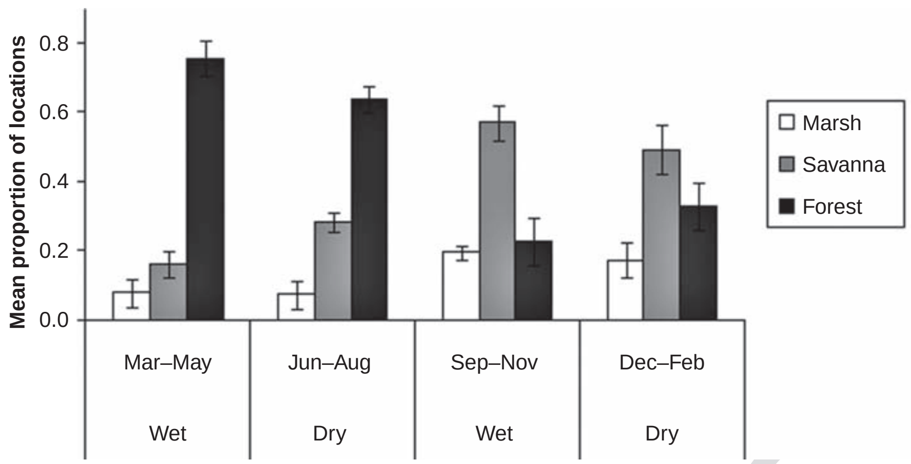

Figure 20.5 Mean proportion of locations (± SE) during daylight hours in each habitat by season for seven radio-collared adult female forest buffalo at Lopé National Park, Gabon, December 2002–December 2004 (Korte, 2008a; with kind permission of the American Society of Mammalogy, Allen Press, Inc).

by studies in other localities (Blake 2002; Melletti *et al.* 2007a; Bekhuis *et al.* 2008; see also Figure 20.4).

Very little information is available on foraging technique. At Dzanga-Ndoki National Park, buffalo use every place within a clearing for feeding, with intermediate areas between the forest edge and the centre of glades used more frequently (Melletti *et al.* 2007b; Melletti 2011). While feeding was mainly within the clearings in Dzanga-Ndoki National Park and in Noubale-Ndoki National Park (Maisels *et al.* 2002; Blake 2002; Melletti *et al.* 2007a; Melletti 2011), sites that lack of clearings in Cameroon and Ivory Coast report signs of feeding on the edges of roads and river banks (Hoppe-Dominik 1992; Bekhuis *et al.* 2008).

Differences in habitat use between age and sex classes are not pronounced. Males are generally permanent members of the herd and share the same habitat and home range with females. Finally, forest buffalo have been found making use of dry caves in the rainforest of Cameroon for resting (C. A. van der Hoeven *et al.*, personal observation).

Movements and home range

The African buffalo is generally considered a sedentary species. In buffalo, both home range (HR) size and movements (either seasonal or daily) are related to habitat and to the spatiotemporal distribution of key resources. As pointed out previously, buffalo habitat use tends to be largely constrained by access to water in most study locations. Small HRs are generally observed in forested or high-rainfall regions, and large ones in open, drier habitats.

Savanna (Cape, West and Central African) buffalo

Large seasonal movements approaching migrations were reported by several authors. Large herds in the Serengeti National Park were shown to undertake seasonal movements (Sinclair 1977). Before the fencing in the 1960s, buffalo in Kruger National Park ranged westward in the dry season to take advantage of wetter areas with persistent forage (Witkowski 1983; Ryan 2006). Using GPS-tracking on Cape buffalo in the Caprivi Strip (northeastern Namibia), Naidoo *et al.* (2012) showed that part of the buffalo population undertook seasonal migrations (‘partial migration’). The GPS-tracked animals moved up to 115 km from permanent rivers. This study also emphasized that some individuals behaved as dispersers. Variation in migratory behaviour was explained by a large set of factors: environmental conditions (rainfall, fires, woodland cover, vegetation, biomass), distance to the nearest barriers (rivers, fences, cultivated areas) and social factors (age, herd size). Buffalo in larger herds moved greater distances than those in small ones. A similar study undertaken in the south-eastern part of the Okavango Delta (Botswana) also emphasized contrasting movement strategies (Bennitt 2012). Buffalo formed two subpopulations with divergent migratory strategies (resident in the west of the study area and migrant in the east). According to the author, this contrast was probably driven by differing resource availabilities and levels of anthropogenically induced spatial restriction. Finally, in West Africa (WAP Regional Park), most GPS-tracked herds were shown to perform a large (35 ± 10 km) omnidirectional movement at the onset of the monsoon in response to a large-scale gradient of primary production (Cornelis *et al.* 2011).

At a daily scale, Cape buffalo may transit long distances between different grazing areas and often walk single-file. Buffalo herds can cover distances up to 8 km in a 24-hour period (Sinclair 1977; Stark 1986). Daily average distances of 3 km and 6 km have been reported in Zimbabwe (Conybeare 1980; Taylor 1985), and of 3.35 km in Kruger National Park (Ryan & Jordaan 2005). In contrast, bachelor herds were reported to move 1–2 km/day (Taylor 1985). While moving in the mixed herds, adult bulls are often located in the front and at the rear of the herd, but do not make decisions about where to move (Prins 1996).

Savanna ecosystems generally display strong spatial and temporal variations of resources (Estes 1991). As a result, savanna buffalo herds exhibit variable HR sizes across their continental distribution range. A compilation of the literature reveals that annual HR areas generally range between 50 km^2 and 350 km^2, but sometimes can exceed 1000 km^2 (Table 20.4). Buffalo living in wetter areas appear to have smaller HRs than those in drier habitats (Ryan *et al.* 2006). The larger ranges are generally observed in areas where resources are spatially segregated, which forces buffalo to undertake seasonal movements

(Cornelis *et al.* 2011; Naidoo *et al.* 2012). As in many ungulate species, sexual segregation occurs in herds, and some of the adult and subadult bulls temporarily leave the mixed herds to form bachelor groups (see the Behaviour section). Several studies suggest that bachelor groups form smaller (0.5 km^2 and 4 km^2) HRs (Grimsdell 1969; Sinclair 1977; Taylor 1985; Naidoo *et al.* 2012).

Seasonal differences in home range sizes also varied across studies. For example, in Serengeti National Park (Tanzania), the HR size of mixed herds was smaller in the dry season because space is constrained around water points at this point in the year (Sinclair 1977). In contrast, the opposite was observed in Benoue National Park (Cameroon), with an increase in HR size during the early dry season fires (61 km^2 versus 46 km^2) (Stark 1986).

Long-term longitudinal studies undertaken on buffalo mixed herds have suggested that HRs are stable over time (Sinclair 1977; Prins 1996). Interestingly, studies investigating space sharing between neighbouring mixed herds reported contrasting results. In the Cape buffalo, a tendency to use exclusive HRs was observed by Prins (1996), Halley *et al.* (2002) and Ryan *et al.* (2006), whereas Grimsdell (1969), Conybeare (1980) and Mloszewski (1983) reported overlaps between neighbouring HRs. Cross *et al.* (2005) found considerable exchange of individuals between apparent herds, and a flexible structure over time, suggesting that herd definition itself may vary. In West Africa, (WAP Regional Park), the GPS-tracking of adult females emphasized a marked spatial segregation between neighbouring herds (Cornelis *et al.* 2011). The quasi-absence of direct contacts in this study suggests that HRs were not actively defended. These herds found a way to exploit exclusive HRs without spending substantial energy in their defence. Several ongoing GPS-tracking studies implemented in different places (e.g. Zimbabwe, Mozambique, Botswana, South Africa, Namibia), should soon lead to a better understanding of the strategies of exploitation and sharing of space by this species.

Forest buffalo

Few studies investigated HRs and movements of forest buffalo. In Dzanga-Ndoki National Park (Central African Republic), a study of a single buffalo herd over two years identified a stable HR size of 8 km^2 (Melletti *et al.* 2007a). In this herd, daily distances travelled by buffalo were generally very short (i.e. 500–1500 m) and were mainly restrained to clearings and surrounding areas (Table 20.3). The maximum distance travelled during a 24-hour tracking period was about 4000 m (Melletti 2008). Forest buffalo males are permanent members of the herd and their HRs thus overlap completely with those of females range: 2–8 km^2; Melletti *et al.* 2007a).

In the mosaics of savanna and forest of Lopé National Park (Gabon), the average HR size was estimated at 5 km^2 (range: 2–8 km^2; $n = 7$ radio-collared adult females) and herds were shown to maintain stable HRs from year to year (Korte 2008a). In this area, the HR overlap was small between radio-collared buffalo belonging to neighbouring herds, suggesting a strong spatial segregation (Figure 20.6).

Table 20.4 Home ranges size in different African buffalo populations

Study area	Home range size (km^2), mixed herds	Reference
Okavango Delta (Botswana)	359–1537 [1]; 159–818 [2]	Bennitt 2012
Caprivi strip (Namibia)	50–448 (0.6–125 male herds)	Naidoo *et al.* 2012
Klaserie Private Nature Reserve (South Africa)	170–327	Ryan *et al.* 2006
Botswana	920–1455	Hunter 1996
Lake Manyara National Park, Tanzania	50	Prins 1996
Sabi Sand Game Reserve (South Africa)	40–120	Funston *et al.* 1994
Matusadona National Park, Lake Kariba (Zimbabwe)	60–110 (0.5–3.0, male herds)	Taylor 1989, 1985
Kenya, Zambia (Busanga swamp), Zimbabwe	126–1075	Mloszewski 1983
Sengwa Wildlife Research Area (Zimbabwe)	207–286	Conybeare 1980
Hwange National Park (Zimbabwe)	286	Conybeare 1980
Akagera National Park (Rwanda)	35–60	Monfort 1980
Serengeti (Tanzania)	222	Sinclair 1977
Momella Lakes, Arusha National Park (Tanzania)	10.9	Vesey-Fitzgerald 1974
Rwenzori National Park (Uganda)	9.4–9.6	Eltringham & Woodford 1973
Tsavo National Park (Kenya)	85–350	Leuthold 1972
W Regional Park (Niger, Burkina Faso, Benin)	172–620	Cornélis *et al.* 2011
Benove National Park (Cameroon)	46–61	Stark 1986
Lopé National Park (Gabon)	2–8	Korte 2008a
Dzanga-Ndoki National Park (Central African Republic)	2–8	Melletti *et al.* 2007a

[1] Migratory population
[2] Resident population

Long-term observations in the Central African Republic and in the Republic of Congo support the assumption that the same herds occupy the same clearings for long periods (Turkalo & Fay 2001; Blake 2002; Breuer 2008; Geßner 2008).

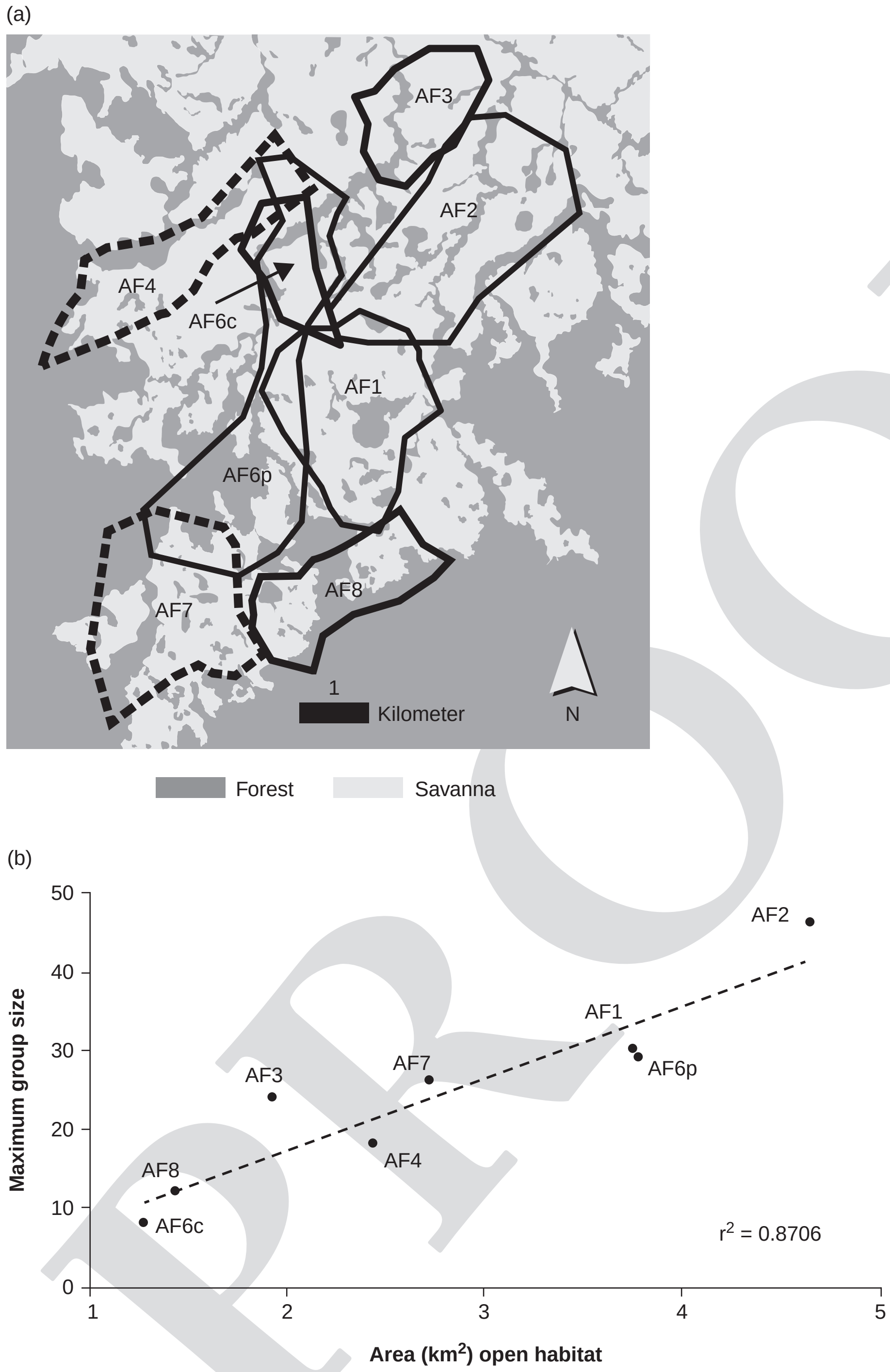

Figure 20.6 (a) Home range of each radio-collared buffalo in the study area at Lopé National Park, Gabon (December 2002 to December 2004); (b) maximum size of group based on observations that included a radio-collared adult female (AF) forest buffalo in relation to the area of open habitat in the home range of those females. Each data point represents maximum group size ($n = 8$) defined by the presence of radio-collared buffalo. Positive correlation between maximum group size and area of open habitat is significant (Korte, 2008b; with kind permission from John Wiley and Sons, *Journal of Zoology*).

Forest buffalo HRs are much smaller than those of the typical savanna subspecies. It is likely that this pattern, common to all studies, primarily results from the spatial arrangement of suitable resources in dense tropical forest, but also to less pronounced seasonality of the environment. Accessible and palatable food for buffalo is scarce in dense tropical forest, except in ecotone areas (e.g. forest clearings, glades, marshes, included savannas, logging roads, etc.: see Bekhuis *et al*. 2008), which often are small in size, patchily distributed and distant from each other (i.e. beyond the locomotion capacity of buffalo). The forest buffalo may thus have adapted several ecological traits to this environment, such as HRs small in size centred on ‘islands’ of profitable resources, small herds and a lower body mass.

Activity patterns

African buffalo display a large array of activity modes, including feeding, resting/ruminating, relocating between foraging areas (transit), checking for predators (vigilance), wallowing

Table 20.5 Percentages of daytime grazing, resting and ruminating activities for different populations of Cape buffalo

Study area	Grazing	Resting	Ruminating	Reference
Chebera Churchura National Park (Ethiopia)	50%	39%		Megaze *et al.* 2012
Okavango Delta (Botswana)	~40%	~30%		Bennitt 2012
Huhluwe-Umfolozi Game Reserve (South Africa)	21–28% adult females 14–28% adult males	66% adult females 70% adult males		Turner *et al.* 2005
Kruger National Park (South Africa)	37%	26%	29%	Ryan & Jordaan 2005
Willem Pretorius Game Reserve, Free State (South Africa)	40%	34%	34%	Winterbach & Bothma 1998
South Africa	48%			Whyte 1996
Lake Manyara National Park (Tanzania)	22–56%	25% adult females 29% adult males	10–50%	Prins 1996; Prins & Iason 1989
Matusadona National Park (Zimbabwe)	51% bachelor males[1] 47% herds[1]		25% bachelor males[1] 41% herds[2]	Taylor 1989
Western Zambia- Zimbabwe	44–52%[2]	53%[1]	36%	Mloszewski 1983
Serengeti (Tanzania)	38–44%			Sinclair 1977

[1] Mean for dry and wet seasons
[2] Dry season
Males, females and mixed herds are indicated. The range of percentage represents minimum and maximum values.

and drinking. Their respective proportion in both daily and seasonal activity budgets is mainly influenced by spatiotemporal changes in resources quality and availability, interspecific competition, weather conditions and predation pressure (Sinclair 1977; Prins 1996; Ryan & Jordaan 2005; Valeix *et al.* 2009a; Owen-Smith *et al.* 2010). Ruminant ungulates such as buffalo spend large proportions of their time feeding, and must additionally allocate time to ruminating, which results in an overall total time (feeding plus ruminating) of 70–80% (Beekman & Prins 1989; Prins 1996).

Savanna (Cape, West and Central African) buffalo

In Cape buffalo, most studies report feeding time accounting for 35–45% of the 24-hour activity budget (Table 20.5; Grimsdell & Field 1976; Sinclair 1977; Mloszewski 1983; Prins 1996; Winterbach & Bothma 1998; Ryan & 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 National Park (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 & Iason 1989; Ryan & Jordaan 2005). At a seasonal scale, most authors reported a trend toward more time spent feeding in the dry season than the wet 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% of the 24-hour activity budget (Sinclair 1977; Prins 1996; Winterbach & Bothma 1998; Ryan & 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. Buffalo must drink at least every two days, but when they drink appears to vary by study site. 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 that buffalo drank in the early afternoon, and Grimsdell and Field (1976) found that they 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.* 2009b). To our knowledge, no seasonal trend in drinking frequency was reported in literature. Mud wallowing is frequent in buffalo males, contrary to females and young. Males generally wallow during the hottest

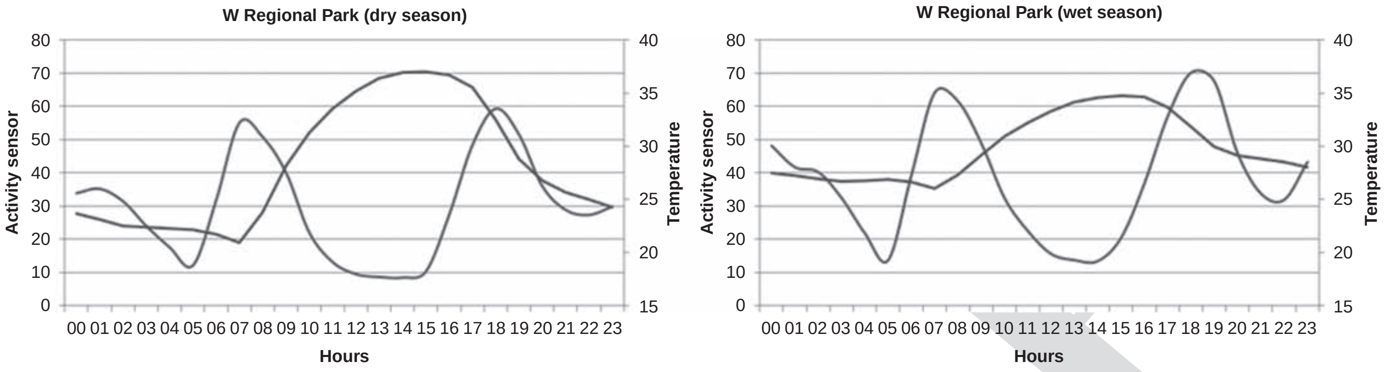

Figure 20.7 Daily bigeminus activity pattern of a buffalo cow tracked in WAP transfrontier conservation area (Burkina Faso, Benin, Niger) from March 2007 to February 2008 (using temperature and activity sensors). The first peak of activity started at dawn and the second finished after dusk, both lasting on average about 3–4 hours. This daily bigeminus pattern was particularly marked during the dry season, with the occurrence of a major resting period between 09:00 and 15:00, corresponding to the hottest hours of the day (Cornelis, 2011).

period of the day for periods lasting up to three hours. This practice is less effective in temperature regulation than the use of shade, which mixed herds generally seek at this time of the day (Sinclair 1977).

Fewer studies investigated the activity patterns of West and Central African buffalo. In Central Africa (Benoue National Park, Cameroon), observations over a 24-hour period conducted during the dry season suggested that buffalo graze approximately 33% of the time, with temporal patterns similar to those of Cape buffalo. In West Africa (WAP Regional Park), the seasonal and daily activity patterns of buffalo herds were explored using biorhythm indices derived from GPS location data and activity sensors (Cornelis 2011). Results suggest that the herds moved faster and were more active when food conditions were most favourable (beginning of the wet season). At a daily scale, herds were equally active during night and day, and were mostly crepuscular, with two main active periods per day (Figure 20.7). However, one herd locally facing a risk factor (daytime human disturbance) clearly switched to a nocturnal activity mode.

Forest buffalo

Observations of forest buffalo activity show similar patterns to those recorded for savanna buffalo: both usually alternate periods of grazing with resting/ruminating throughout the day and the night. At Dzanga-Ndoki, Melletti *et al.* (2007b) recorded higher figures of resting and ruminating time in the dry season than in the wet season and, for this activity, the differences between seasons were statistically significant. At Dzanga-Ndoki, around 50% of the time spent in the clearings by buffalo was dedicated to resting and ruminating activities (both sexes). Observations performed in clearings also suggest than females spent more time feeding (50%) than males (20%). The proportion of grazing individuals increased with increasing group size. Forest buffalo do not show an increase in grazing during the dry season, suggesting that season does not influence grazing activity. A decrease in grazing rate followed by resting in the middle of the day, when temperatures were highest, was observed both in CAR (Melletti *et al.* 2007b) and in Gabon (Molloy 1997).

Korte (2008a) observed similar patterns of feeding activity at Lopé National Park, where buffalo spent >30% of the time feeding. Feeding varied with the habitat and time of the day. Buffalo were most active in savanna habitat during the late morning (09:30–12:30). Periods of inactivity also varied with habitat and period of the day (Korte 2008a). Inactive behaviours were most often observed in marshes in the late afternoon. During daylight hours, the herds spent >38% of their time inactive. Buffalo were relatively inactive during the day between March and August, when >60% of their locations were recorded in forest habitat. Korte (2008a) found that the proportions of time spent in different behaviours did not differ between years or among seasons. However, activity varied significantly among individuals. Forest buffalo wallow in mud and water during the hottest daylight hours mainly in the dry season (December–March; Melletti *et al.* 2007a). Korte (2008a) recorded similar mud and water wallowing within marsh habitat, especially between September and February. Buffalo feed in the savanna areas in the early morning, retire to a wallow and rest in marsh areas until sunset.

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% 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 (adapted dentition and mobile tongue allowing the ingestion of high quantities of grass in a short 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 (Estes 1991; Prins 1996). Their primary competitors are cattle, *Bos taurus*, African elephant, *Loxodonta africana*, plains zebra, *Equus quagga*, and wildebeest, *Connochaetes taurinus* (Sinclair 1977; De Boer & Prins 1990; Plumptre 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 & Sinclair 2013). Detailed diet studies conducted in Eastern and Southern Africa indicate that buffalo are resource-limited and constrained by a minimum dietary protein concentration of 7–8% to make fermentation in the rumen possible (Sinclair 1977; Prins 1996). In such a situation, buffalo thus face a tradeoff 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 constrained 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 1989b; 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 on the one hand ('bottom-up regulation') and a control by predation ('top-down' regulation) on the other (Hunter & 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 (Sinclair 1977). Usually species that are avoided contain low nutritious quality or 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 & Sinclair 2013). Buffalo prefer grasses such as *Cynodon dactylon*, but may also eat broadleaved grasses such as *Panicum maximum*. Sinclair (1977), in the Serengeti, reported that buffalo preferred soft, nutritious grass such as *Digitaria macroblephora*. Although there is little information on seasonal changes of 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 National Park, Zimbabwe). In Cape buffalo, the diet of the different age and sex classes does not appear to differ, and dry matter food intake ranges between 1.2% and 3.5% of body mass, similar to other ruminants, but subject to food quality (Sinclair 1977; Prins & Beekman 1989).

Few studies have 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*; Cornelis *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% threshold. At Benoue National Park (Cameroon), Stark (1986) similarly reported a very high proportion of grasses in the diet, particularly *Andropogon gayanus*, which represented 51% of the volume ingested in the dry season, versus 40% in the wet season. At Zakouma National Park (Chad), Gillet (1969) noted a preference for *Setaria anceps* (particularly new shoots after fire) and *Andropogon gayanus*, but also *Vetiveria nigritana*. In the dry season, the unburned straws of *Echinochloa obtusiflora* appeared to be preferred.

For more details on grass species eaten by savanna buffalo in different locations, see Table 20.6.

The 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% of the total diet, but higher figures were reported in several sites (e.g. 26% in the dry season in Cameroon; Stark 1986). A wide range of species of shrubs and trees are consumed throughout the African savanna, including *Grewia* spp., *Heeria* spp., *Combretum* spp., *Capparis* spp., *Piliostigma* spp. (Field 1968; Pienaar 1969; Jarman 1971; Graaff *et al.* 1973; 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% 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 National Park 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 elephant at Lake Rukwa, Tanzania (Vesey-FitzGerald 1960) or hippopotamus in Uganda (Eltringham 1999) and Benoué National Park in central Cameroon (H. H. T. Prins, personal observation).

Geophagy has been reported at several sites, where clay or substrates rich in iron also may explain this preference. On

Table 20.6 Main grass species recorded in the diet of savanna buffalo in different locations

Okavango Delta, Botswana[15]	**Serengeti, Tanzania[1]**	**Lake Manyara National Park, Tanzania[2,5]**	**Tsavo NP, Kenya[3]**	**Gonarezhou National Park, Zimbabwe[4]**	**Mount Meru, Tanzania[1]**	**Ruwenzori Uganda[6]**	**Kafue National Park, Zambia[4]**	**Zambezi Valley, Zimbabwe[4]**
Aristida. adscensionis	*Cynodon dactylon*	*Chloris gayana*	*Digitaria macroblephora*	*Cenchrus ciliaris*	*Cynodon dactylon*	*Capparis tomentosa*	*Andropogon gayanus*	*Eragrostis rigidior*
Cenchrus ciliaris	*Panicum coloratum*	*Cynodon dactylon*	*Panicum coloratum*	*Chloridum cameronii*	*Cyperus laevigatus*	*Cynodon dactylon*	*Cenchrus ciliaris*	*Hyparrhenia filipendula*
Cynodon dactylon	*Panicum maximum*	*Cynodon plectostachyus*	*Panicum maximum*	*Colophospermum mopane*	*Themeda trianda*	*Hyparrhenia filipendula*	*Chloridum cameronii*	
Dactyloctenium giganteum	*Panicum infestum*	*Cyperus laevigatus*		*Eragrostis rigidior*		*Sporobolus pyramidalis*	*Cynodon dactylon*	
Eragrostis rigidior	*Setaria chevalieri*	*Leptocarydion vulpiastrum*		*Heteropogon* sp.			*Heteropogon contortus*	
Panicum repens	*Sporobolus spicatus*	*Sporobolus spicatus*		*Hyparrhenia filipendula*			*Hyparrhenia filipendula*	
Panicum maximum	*Sporobolus pyramidalis*	*Sporobolus helvolus*		*Panicum maximum*			*Panicum maximum*	
Stipagrostis uniplumis	*Themeda triandra*	*Sporobolus cordofanus*		*Schizachyrium sanguineum*			*Parinari capensis*[a]	
Sporobolus fimbriatus		*Sporobolus pyramidalis*		*Schmidtia bulbosa*			*Sporobolus pyramidalis*	
Tragus berteronianus		*Urochloa mosambicensis*					*Themeda trianda*	
Urochloa trichopus							*Vossia cuspidata*	

Kruger National Park, South Africa[7,13,14]	**Hwange National Park, Zimbabwe[8]**	**Lake Kariba, Zimbabwe[9]**	**Sabi Sand Wildtuin, South Africa[10]**	**Akagera National Park Rwanda[11]**	**Huhluwe-Umfolozi G.R. South Africa[12]**	**Zakouma National Park, Chad[16]**	**Benoue National Park, Cameroon[17]**
Andropogon gayanus	*Andropogon gayanus*	*Panicum repens*	*Panicum maximum*	*Chloris gayana*	*Panicum deustem*	*Andropogon gayanus*	*Andropogon gayanus*
Cenchrus ciliaris	*Cynodon dactylon*		*Themeda trianda*	*Cynodon dactylon*	*Panicum maximum*	*Echinochloa obtusiflora*	*Andropogon tectorum*
Digitaria eriantha	*Cyperus laevigatus*			*Hyparrhenia filipendula*	*Themeda trianda*	*Setaria anceps*	*Chloris robusta*
Euclea sp.	*Schizachyrium sanguineum*			*Panicum maximum*		*Vetiveria nigritana*	*Digitaria* spp.
Heteropogon contortus				*Sporobolus pyramidalis*			*Echinochloa* spp.
Panicum coloratum				*Themeda trianda*			*Hyparrhenia* spp.
Panicum maximum							*Loudetia* spp.
Schmidtia bulbosa							*Panicum* spp.
Themeda trianda							
Urochloa mosambicensis							

[1] Sinclair 1977; [2] Prins 1996; [3] Leuthold 1972; [4] Mloszewski 1983; [5] Vesey-Fitzgerald 1969; [6] Field 1968; [7] Pienaar 1969; [8] Wilson 1975; [9] Taylor 1985; [10] Funston *et al.* 1994; [11] Monfort 1979; [12] Perrin & Brereton-Stiles 1999; [13] Macandza *et al.* 2004; [14] Bowers 2006; [15] Bennitt 2012; [16] Gillet 1969; [17] Stark 1986

[a] Fruit also eaten

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 forest buffalo feeding ecology because direct observations are rarely feasible in rainforest habitats. Blake (2002) and Melletti (2008) observed buffalo feeding mainly on Poaceae and Cyperaceae within clearings, in particular on *Rhyncospora corymbosa*, *Kyllinga* sp. and *Cyperus* sp., in Noubale-Ndoki National Park and in Dzanga-Ndoki National Park. Blake (2002) also recorded several species of Marantaceae, including *Marantochloa purpurea*, *M. cordifolia*, *M. filipes* and *Halopegia azurea*. In addition, species of Commelinaceae family such as *Commelina diffusa*, *Palisota brachythyrsa* and a species of algae (*Spirogyra* sp.) were recorded. Melletti (2008) also found indirect signs of feeding activity on *Commelina* 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 National Park (southern Cameroon). They found that the most important part of the diet was composed of graminoids (43%, with *Leptochloa caerulescens* representing 15% of the total diet), non-graminoid monocots (21%, mainly Commelinaceae such as *Palisota* spp.), dicotyledonous plants (33%, mainly leaves) and cryptogamous plants (3%). The composition of the diet suggests that buffalo fed mainly along logging roads and river banks (Bekhuis *et al.* 2008). Using a similar method at Lopé National Park (Gabon), Lustenhouwer (2008) and Van der Hoek *et al.* (2012) found that the majority of plants consumed by forest buffalo were monocotyledons, primarily grasses (*Poaceae*) and sedges (*Cyperaceae*), with a low proportion of dicotyledonous plants in the diet. In the same study area, Van der Hoek *et al.* (2012) emphasized the importance of savanna habitat, noting that controlled burning is a key tool for maintaining open areas.

Details of forage species composition and percentage identified in buffalo dung are shown in Table 20.7.

So 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 National Park (L. Korte and M. Melletti, personal observations).

Table 20.7 Major diet categories of forest buffalo (Campo Ma'an National Park, Cameroon)[1]

Major categories[2]	Percentage
Graminoids	42.9
Leptochloa	15.1
Other graminoids	27.8
Non-graminoid monocots	21.3
Commelinaceae	18.2
Other non-graminoid monocots	3.1
Dicotyledons	32.1
Dicotyledon leaves	26.5
Dicotyledon stems	6.2
Cryptogamous plants	3.1

[1] Bekhuis *et al.* (2008)
[2] Data refers to April–May 2002
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Reproduction and growth

Savanna (Cape, West and Central African) buffalo

In most of the Cape buffalo range there is a birthing peak during the wet season; however, in the more mesic conditions of Lake Manyara National Park (Tanzania) such a peak is not apparent (Prins 1996). In Matusadona National Park (Zimbabwe), conceptions occurred between December and May, with births between November and April, of which almost two-thirds of them were in January/February (Taylor 1985). These patterns have also been observed in northern Botswana (Carmichael *et al.* 1977), Kruger National Park and neighbouring Klaserie Private Nature Reserve in South Africa (Fairall 1968; Pienaar 1969; Ryan *et al.* 2007). In the Serengeti there is a clear calving peak, with about 50% of all calves born within seven weeks (Sinclair 1977). This peak may be tied to differences in social organization among bulls (see above). In Klaserie Private Nature Reserve, South Africa, births were quite highly synchronized, and the birthing peak was found to be correlated to the highest protein content of grass, which mostly coincided with the month of January (Ryan *et al.* 2007).

Experiments on captive buffalo males in South Africa showed a seasonal cycle in testosterone levels, endocrine function and seminal quality; but this pattern is not clear enough to explain a breeding or calving season (Brown *et al.* 1991). More recently Skinner *et al.* (2006) found a calving period in January for captive buffalo, similar to what was observed in wild populations (Ryan *et al.* 2007). Pro-oestrus may last two or three days and oestrus one day in captive Cape buffalo, and the oestrous cycle from 18 to 22 days (Knechtel 1993). The gestation period is about 340 days (Vidler *et al.* 1963; similar in captivity; Knechtel 1993). Buffalo give birth of a single calf, which weighs 30 kg, and twins are extremely rare. Suckling bouts of calves last about ten minutes when they are four weeks old, decreasing to five minutes when they are six months old (Prins 1996). Calves suckle from the rear; when the female starts walking with the herd the calf can continue receiving milk and the mother does not lose the protection of the herd. The age of weaning depends on many factors, including population density and intraspecific competition. In Lake Manyara National Park, where the buffalo density was high and the population stationary, many calves were still not weaned at

18 months old, while in Serengeti, where the density was much lower and the population increasing, fast weaning took place at the age of ten months. The calving interval in Manyara was therefore about 36 months (Prins 1996) and in Serengeti only 15 months (Sinclair 1977). Considering these patterns, birth rates seem to be density dependent.

Buffalo young are called 'calves' until they reach the inguinal fold at its highest point on the flank of the cow (Pienaar 1969). Juveniles are defined as weaned, but younger than three years (if testicles are not observable it is difficult to sex a juvenile in the field). Subadults begin to show secondary sexual characteristics and horn shape begins to diverge in males and females. For example, in Cape buffalo, the horns of cows start extending laterally whereas those of males curve strongly, upwards, and bosses start to develop. Subadult savanna buffalo bulls still have skin covered with hairs between the bosses, while adult bulls normally do not. Ovulating in females starts after three years of age, and the age at first breeding is five years (Grimsdell 1973b; Sinclair 1977; Taylor 1985). Males reach sexual maturity at 5–6 years of age, but usually do not breed until seven years or older, at which time the horns are fully developed.

Foetal sex ratio is approximately 1:1 in Kruger National Park and Lake Manyara National Park, Tanzania, and appears to be independent of rainfall, maternal lactation status or density (Visscher *et al.* 2004). In Manyara National Park, with increasing age, the sex ratio in herds becomes increasingly slanted in favour of females (Prins 1996). Van Hooft *et al.* (2007, 2010) found that during dry years, calves are sired by bulls with haplotypes that differ from bulls that sire calves during wet years (Van Hooft *et al.* 2007 2010). Bulls spend considerable amounts of time outside herds, which may partly explain the differentiation in fatherhood of calves. Life tables show that mortality patterns across ages in males and females are similar (Grimsdell 1969; Sinclair 1977); the average age of death (excluding calf mortality because remains of calves are too rare to find) is about 12 years. Maximum longevity in the wild is about 20 years and in captivity 29.5 years (Jones 1993).

Forest buffalo

What is known on reproduction and growth in forest buffalo is largely based on incidental observations during field studies of habitat, home range or behavioural activities rather than comprehensive studies focused on reproduction or growth. These initial observations give an indication of trends, but we lack long-term data on forest buffalo reproduction and growth.

It is difficult to ascribe a breeding season to forest buffalo because observations of mating are rare and births do not, so far, seem seasonally limited (Melletti *et al.* 2007a, 2007b; Korte 2008a, 2008b). At Lopé National Park in Gabon, Korte (2008a, 2008b) reported just one observed mating among nine radio-collared buffalo during a two-year study. The mating was observed in August 2003, with a calf born in June 2004. This June birth preceded the September through November wet season, when the lactating female would have access to a seasonal flush of new grass. Other collared females were also observed with new calves during this period, suggesting a possible calving season in the June through August dry season. Two of the buffalo had calves with them when collared in December 2002, two other animals birthed in July 2004, and a fourth female birthed in August 2004. In 1996 at Lopé, new calves were reported in August, September and December, during a six-month study of three herds. However, Korte (2008a, 2008b, 2008c) observed new calves in March 2003 and April 2003, ruling out a definitive calving season.

Sites in the Central African Republic and Cameroon report births during the wet season (Melletti 2008; Geßner 2008). At the Dzanga-Ndoki National Park, Melletti (2008) observed mating three times between June through August in 2002 and 2003. Although the same months as observations at Lopé National Park (Korte 2008a, 2008b), at Dzanga this period is the wet season with a light decreasing of rainfall. Also during the April through August wet season, Melletti (2008) reported new calves; however, no new calves were reported during the December through February dry season. Two births, one on 20 April and a second on 25 June, were reported at Ikwa Bai in Cameroon during a four-month study between 2 April and 6 July 2007 (Geßner 2008). Although calves were born during the wet season when food availability is probably at its peak, small sample size and short study period limit conclusions for calving seasons in Cameroon.

To the best of our knowledge, the literature reports births of only a single calf. During two years of observation of a population of about 342 buffalo at Lopé National Park in Gabon, no multiple births were observed (Korte 2008b). Melletti *et al.* (2007b) report a herd growing from 16 to 24 individuals with the addition of eight calves over a two-year period with no twins. Calving intervals are about two years, with a gestation of at least ten months (Melletti *et al* 2007b; Korte 2008b). Calves remain with cows for at least two years (Korte 2008b). Only adult female buffalo are observed with calves, suggesting that age of first reproduction is at least three years of age, if not older (Melletti *et al.* 2007b; Korte 2008b).

Studies of forest buffalo have followed guidelines developed for Cape buffalo to age individuals (i.e. calves: <12 months; juveniles: 12–36 months; subadults: 3–5 years; adults: >5 years; Pienaar 1969; Sinclair 1977). Little has been done to develop methods for ageing forest buffalo using cementum lines, tooth wear or tooth eruption sequences, to validate or calibrate ageing methods. Tooth wear is not found to be constant within species, differing with factors such as heredity, nutrition, habitat and the severity of the seasons (Hillson 1986). Thus, forest buffalo may have a different tooth wear pattern than Cape buffalo, given their very different habitat, i.e. forest versus savanna. Although horn size can be used as an indication of sex for individuals, visual observation of testicles is the most reliable method to determine a male individual. Adult females can have similar horns and body size to subadult males, so it is best to not rely solely on horn size and/or shape to sex individuals (Molloy 1997). When herds are observed over several months, it is possible to identify distinct individuals using horn morphology, scars and pelage characteristics to consistently record individuals (Prins 1989a; Melletti *et al.* 2007b; Korte 2008a, 2008b; Geßner 2008).

Behaviour

Savanna (Cape, West and Central African) buffalo

African savanna buffalo are gregarious animals living in mixed 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 certainly 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 (and occasionally earlier), the males temporarily leave the herd to form bachelor groups. The elder males (from about ten years) sometimes permanently leave the herd, but this behaviour is not systematic (Sinclair 1977; Prins 1996).

Herd size in Cape buffalo 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 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 (Cornelis *et al.* 2011). Similar figures were reported for Central African savanna buffalo, except in floodplain areas such as Zakouma National Park (Chad), where herds of up to 800 individuals were observed. Within savanna buffalo populations, differences in herd sizes were also observed, and herd sizes tend to be smaller where food resources are poor (Winnie *et al.* 2008).

Mixed herds were shown to be long-lasting social structures displaying a high degree of fidelity to their home range (Sinclair 1977; Prins 1996). The herd as a social unit has a much longer life span than any individuals, and recognizable herds were known to have existed for over 50 years (Prins 1996). Although adult females generally exhibit a high degree of philopatry to their native herd, herd switching was reported by a telemetry study in northern Botswana, where 7 of 45 adult cows switched herds, covering distances up to 133 km (Halley *et al.* 2002). In Cape buffalo, the migration rate per generation between herds was estimated by a genetic approach to be 5–20% for females and close to 100% for males (Van Hooft *et al.* 2003).

Fusion–fission group dynamics operate within mixed herds, meaning that herds may temporarily split into sub-herds and then merge again. Contrasted patterns of splitting and merging were described across studies. In the Serengeti, Sinclair (1977) reported that mixed herds tend to split into sub-herds when resources are fragmented, i.e. during the dry season. In contrast, Bothma (2002) reported that the herds tend to congregate during the dry season in areas where water and forage are abundant, and split into sub-herds during the wet season to exploit the available habitat more efficiently. Halley *et al.* (2002) made the same observation in Chobe National Park (Botswana), where buffalo were shown to range in herds of more than 1400 individuals during the dry season. Such large herds might in fact be temporary associations of two or more mixed herds.

At Lake Manyara National Park (Tanzania), where herds are less constrained by resources, the pattern of fusion–fission appears related to herd size: large herds split more frequently than smaller ones (Prins 1996). In Kruger National Park, South Africa, a longitudinal monitoring of multiple radio-collared individuals showed that herds were far less discrete than in previous studies (Cross *et al.* 2005). New herds may arise from these fusion–fission processes, comprising mixed subsets of previous herds, or single subsets.

As described above, bulls can be found within herds or smaller groups called 'bachelors' (Sinclair 1977; Prins 1989a, 1996). This sexual segregation operated by males is related to the energy cost of reproduction activities, which occur at the expense of the time normally allocated to foraging. Males competing for females are forced to leave the herd once their body condition decreases (Prins 1996; Turner *et al.* 2005). Individuals living in bachelor groups thus can spend more time foraging, but also utilize patches of habitat too small for the herd. The temporal patterns of sexual segregation appear contrasted between study areas. In Serengeti, where buffalo display a clear peak in calving, males join the mixed herds during the wet season (about eight months) and form stable bachelor groups during the dry season (Sinclair 1977). Bachelor herds in Serengeti comprise, on average, 5–10 individuals, the largest ones up to 50 (Sinclair 1977). They have a stable membership and there is evidence of linear dominance hierarchies in both bachelor and herd males (Sinclair 1977). In contrast, in more profitable areas such as Manyara (Tanzania), where buffalo are able to cover maintenance costs year-round, calving (and thus rutting) does not show a clear seasonal pattern, and adult males move in and out of mixed herds at a higher frequency (the so-called 're-entrant consecutive polygyny system'; Prins 1996). In this situation, buffalo males do not form stable associations, do not show fidelity to the same herd and do not have a particular home range. In the re-entrant consecutive polygyny system, the average size of bachelor groups is 3.5 individuals, and the largest groups comprise as many as 50 individuals (Prins 1996). These differences in patterns of sexual segregation depend on the seasonal patterns in resources availability. These two reproductive states may also explain the great differences in testosterone level between bulls during a season (Brown *et al.* 1991).

Cows, juveniles and calves stay together in large to very large herds, and even subadults of both sexes stay within their maternal herd. When the herd moves between feeding areas one or more adult males may precede it. However, adult cows are quite often in the lead as well. Buffalo leaders may stop an entire herd by not moving on or by giving a stopping signal, which involves standing and blocking the direction of movement. These 'individuals' are not to be viewed as 'true leaders' – for example, taking the decision of where to drink. It seems to be a communal decision taken by the adult cows in a procedure that has been called 'voting' (Prins 1996). Communal decision making seems to take place also in other mammals, and may be linked to information exchange. 'Voting' in buffalo takes place after a long resting bout, typically at the end of the afternoon when almost all individuals lie down. In this case females rise and elevate their head as if staring in a particular direction. Prins (1996) describes the voting posture as when the head position is halfway between a resting position and full alert, when the individual has the head elevated at a height as if gazing over its nostrils. The voting posture is maintained for a few minutes, after which the cow beds down again. We can distinguish two patterns of voting postures: (1) when we have a short vector that implies little consensus within the herd of voting females; and (2) where a long vector means a high degree of consensus (i.e. all heads were pointing in the same direction). Little consensus is often followed by a splitting of the herd and the resulting sub-herds then merge again after a few days (Prins 1996).

Social interactions between subadult cows are quite rare and restrained. Subadult bulls show intense sparring behaviour, similarly to adult bulls. During sparring, horns, and especially the bosses, are placed against each other, after which the animals start pushing. The 'winner' often is able to hook the other buffalo. Sparring may function as testing dominance between individuals, although it looks as if both contestants enjoy the game. Most interactions between adult bulls appear to be limited to evaluating the size of each other, often observed by other bulls. A more intense form of 'sizing each other up' is the parallel walk. Fights only happen when both contestants are equally strong and large. They are exceptionally rare and can result in fatal injuries to both bulls. Buffalo calves seldom play.

Females and their offspring have a rather fixed location inside a herd, which may vary with age and sex classes. Such a location may be inherited, because female offspring stay with their mothers up to maturity (Prins 1989b). Aggressive (agonistic) behaviour may also play a role in determining position within the herd. Agonistic behaviour consists of hooking and butting with the horns; among females this is typically aimed at the flanks or the rump of other adult females (Prins & Sinclair 2013; a summary of the main behaviours recorded are shown in Table 20.8).

Among males there is a distinct ritualized threat and submissive behaviour. Dominant males threaten by standing with the head up but muzzle pointing down, thus emphasizing the shoulders, a posture characteristic also of other bovine species, including the gaur (*Bos gaurus*), banteng (*Bos javanicus*) and bison (*Bison bison*, *B. bonasus*). A submissive male, when threatened, approaches the dominant with head held low and parallel to the ground and will often place the muzzle between the hind legs of the dominant one. At the same time the subordinate animal utters a loud and long bellow, sometimes continuing for the entire duration of the submissive display. The behaviour is similar to that of small calves when suckling or searching for their mother. This ritualized submission seems unique to African Buffalo; it is not shown by water buffalo. Buffalo are generally silent. They occasionally grunt, especially when a cow is hooked by another animal. They snort and cough when alarmed and when they start running. Bulls that are injured or about to die can make very loud bellows. Other bulls may or may not react to the sound. In about one-third of the instances that a bull is wounded by lions or hunters another adult bull will try to help him. Buffalo that are badly wounded may also seek the protection of the herd. They do not have an alarm call, but have a very efficient warning system, especially at night, by becoming silent (Prins & Sinclair 2013).

Mating depends on degree of willingness of a cow to be mounted. When the female is receptive, bulls show extensive tending behaviour ('consorting'); only adult bulls exhibit tending. Bulls show flehmen when testing urine of receptive females. When receptiveness increases the bull tries to lay his chin on her tail base. In general she then walks away, after which the bull tries again. When the cow is willing to stay put, the tending bull is often supplanted by a more dominant one who then mates with the cow. Other bulls may attempt intromission during mating, but females start running away, making copulation impossible. Mounting and ejaculation usually take a few seconds only. Females mating with more than one male has not been reported, but given the interrupted tending behaviour described above, this is a possibility (see Van Hooft *et al.* 2010). The cow remains with the herd to calve, although if the herd moves the females and their calves may be left behind temporarily. Calves may associate with age mates, and these associations are especially noticeable in females and may last for many years (Prins 1996), similarly to zebu cattle (Reinhardt 1983). Sometimes these coalitions result in coincident death at a much older age, when both 'friends' perish in so-called 'multiple kills' by lions; in Lake Manyara National Park multiple kills comprised about 6% of kills (H. H. T. Prins, personal observation).

Buffalo exhibit quite aggressive behaviour when attacked by predators, chasing and sometimes killing lions. In particular, they may respond to calf distress calls by chasing off the predators (Sinclair 1977). Buffaloes can reach 48–55 km/hr at top speed, and they can jump about 1.5 m in height. They also defend themselves against lions quite well in dense thickets, standing with their hindquarter to trees and bushes. Buffalo in open habitats adopt the antipredator strategy of forming large herds – predator swamping (Sinclair 1977; Melletti *et al.* 2007b; Prins & Sinclair 2013).

Lions use terrain features as cover to stalk buffalo herds (Prins & Iason 1989; Mugangu *et al.* 1995). Lions may take buffalo from the middle of a herd, sometimes without other

Table 20.8 Main behaviours recorded in the African buffalo

Agonistic behaviour	Vocal communication	Sexual behaviour	Parent/juvenile behaviour	Antipredator behaviour
High horn presentation[1]	Signal to move[9]	Urine testing by bulls	Calf croaking[19]	Alert posture[20]
Submissive bellow[2]	Direction giving signal[10]	Licking vulva by bulls[18]	Pushing off calf	Head tossing[4]
Wallowing[3]	Water call[11]	Cow head on bull rump		Wheeling and flight
Circling[4]	Position signal[12]	Cow pushing belly of bull		Individual/herd attack
Rolling (mud/dust)	Warning call[13]			
Horning (vegetation)[4]	Aggressive call[14]			
Head tossing[4]	Mother to calf call[15]			
Rubbing face and neck in mud[4]	Calf distress call			
Lateral display[5]	Danger call[16]			
Head low posture[6]	Grazing vocalizations[17]			
Flight/alarm posture				
Charging – chin raised[7]				
Front-pressing[7]				
Sparring[8]				

[1] The head is held at shoulder level, associated with head tossing
[2] Mouth is opened and the tongue is curled
[3] Mud and dust baths mainly carried out by dominant males (social significance)
[4] Dominance, threat and aggressive displays
[5] Head is held at or above shoulders, chin pulled, tossing and hooking movements, means of asserting dominance
[6] Defensive and submissive displays performed by a low-ranking male
[7] During fighting
[8] No charge, milder exercise, little horn-tangling and half-hearted pushing, mainly performed by subadults
[9] Call given for herd coordination during movements
[10] Intermittent sound given by leaders at the beginning of herd movement
[11] Call emitted many times during movement to drinking places
[12] Sound emitted by a high-ranking buffalo within a herd that announces its presence and location
[13] Sound given to an encroaching submissive individual
[14] Grunt given by a dominant bull after a stampede
[15] Croaking call emitted by cows seeking their calves
[16] When lions are detected
[17] Variety of sounds during grazing
[18] Bulls can prompt cows to urinate
[19] Call emitted when losing contact with mothers
[20] Advancing to investigate the presence of a possible predators, etc. Alert behaviour mainly performed by adult females in forest buffalo
Sources: Sinclair 1977; Mloszewski 1983; Estes 1991; Prins 1996; Melletti *et al.* 2007b

buffalo paying attention, while in other instances buffalo chase lions and sometimes kill them. It seems that large numbers make buffalo safer, and adult bulls seem invulnerable when in prime condition. However, lions often kill males in bachelor groups (Schaller 1972). In the Serengeti, predation by lions accounted for 44 males, versus six females, six young and six indeterminate sex (Wilson & Mittermeier 2011). Usually, two or more lions attack from the rear, and they have to take the buffalo down quickly, otherwise he can drive them off. Lions unable to take down a standing buffalo have been seen perched on top of the standing buffalo (H. H. T. Prins, personal observation). Sometimes buffalo will try to push lions against *Acacia* thorns. If lions successfully put down the buffalo they try to suffocate it by holding the muzzle because they cannot break the neck.

The main predators of Cape buffalo are lions, but predation by spotted hyena (*Crocuta crocuta*) and leopard (*Panthera pardus*), has been recorded, usually targeting young animals (Kruuk 1972; Schaller 1972; Prins & Iason 1989; Ruggiero 1991; Funston *et al.* 2003). In forest areas such as Mount Meru, Tanzania, predation is insignificant. In the Serengeti National

Park, predation by lions accounts for only 25% of mortality (Sinclair 1977). In Lake Manyara National Park lion predation is very high, up to 85%, in the absence of major diseases. Thus, the population regulatory effect of predation depends strongly on location. Other infrequent (less than 5%) causes of natural mortality include getting stuck in mud, falling down cliffs or fights with other buffalo (Prins & Sinclair 2013). Mass mortality of buffalo has been reported in Zambia when they were stampeded over cliffs by lions on two occasions (63 and 42 buffalo, respectively), and also by mass entanglement in floating grass while trying to cross a lagoon (Prins & Sinclair 2013).

Forest buffalo

Forest buffalo herds are small, stable groups with relatively little switching between herds (Melletti *et al.* 2007b; Geßner 2008; Korte 2008b, 2009). Adult cows and their offspring live in herds that vary between about 3 and 25 individuals in the forest buffalo (Happold 1973; Melletti *et al.* 2007a; Korte 2008a, 2008b). Herds comprise several adult females with their young and with one or two bulls (Dalimier 1955; Blake 2002; Melletti *et al.* 2007a; Korte 2008a). This may be the best reproductive strategy when females occur in small herds that are widely scattered in grassy patches within a rainforest that is otherwise unsuitable to forest buffalo. The ratio of adult males to adult females at Lopé National Park in Gabon is 1:6, with an overall ratio of 1:2 for adults and subadults to juveniles and calves (Korte 2008a). At Bai-Hokou of the Dzanga-Ndoki National Park in the Central African Republic, a herd of 24 individuals included one adult male, nine adult females, six juveniles and eight calves (Melletti *et al.* 2007b). Geßner (2008) reported a stable herd of at least 23 buffalo, including an adult male, at least one subadult male, two subadult females and ten adult females with at least three juveniles and four calves at Ikwa Bai at Nki National Park in Cameroon. Forest buffalo herds split into smaller subgroups and not all individuals are together at all times.

Herd size appears stable within herds, but can vary widely across herds (Korte 2008b). During a two-year study at Lopé National Park in Gabon, the mean group size for 18 herds was 12 (range of means 3–24), considerably smaller than Cape buffalo herds. Although mean group size varied little with time of day, across season or between savanna and marsh habitat, herd size varied widely across herds, from fewer than ten individuals in the smallest herds to more than 20 in the largest herds. Melletti *et al.* (2007b) also report that herd size did not vary with season or food availability. This herd at Dzanga-Ndoki National Park in the Central African Republic increased from 16 to 24 due to the birth of eight calves during the two-year study, with no immigration or emigration. Although the herd remained small, individuals split into smaller subgroups with fission patterns lasting 1–3 days before the herd merged again (Melletti *et al.* 2007b; Melletti 2008). This trend seemed more frequent when the herd grew to 24 individuals at the end of the study period (Melletti 2008). Melletti *et al.* (2008) also report that group size was smaller and individuals were more dispersed within the same forest clearing during the wet season.

Although this subspecies is forest-dwelling, forest buffalo are dependent on open areas adjacent to continuous forest (Melletti *et al.* 2007a, 2007b; Bekhuis *et al.* 2008; Geßner 2008; Korte 2008a, 2008b). At a local level, the quantity and dispersion of food resources appear to influence group size (figure 20.6a,b from Korte 2008b). For eight radio-collared buffalo at Lopé National Park there was a significant positive correlation between maximum group size and the area of open habitat in each collared animal's home range. These open habitats are savannas and marshes, where food resources are abundant. Thus, aggregation patterns appear to be linked to food resources. At other forested sites, buffalo depend on forest clearings or grassy areas along roads, where food resources are present (Hoppe-Dominik 1992; Melletti *et al.* 2007a; Bekhius *et al.* 2008; Geßner 2008; Korte 2008b).

Antipredator strategies in forest buffalo seem to consist of moving and resting together (Melletti *et al.* 2007b). At Dzanga-Ndoki National Park, buffalo were closer to each other when moving compared to distance between individuals when grazing. In addition, an adult female always led the group in flight with the adult male often (i.e. in over 90% of cases) the final individual, possibly an antipredator strategy. Melletti *et al.* (2007b) also report larger group size when buffalo are a greater distance from forest edges, noting that every individual was surrounded by other buffalo, probably indicating an antipredator strategy. In addition, the adult male was commonly closer to the females than to juveniles (Melletti *et al.* 2007b). Melletti *et al.* (2007b, 2008) also report observations of the herd standing in alert postures for a few minutes and then fleeing a few hundred metres within the same clearing (i.e. when the herd smelled the observers or a predator), but on some occasions the buffalo moved to another clearing, with an adult female always leading the group.

Leopard predation on buffalo is rarely observed in the rainforest; however, at Lopé National Park, Gabon, where buffalo density is high in the savanna areas, buffalo make up over 10% of the biomass consumed (Henschel *et al.* 2005).

Geßner (2008) reports that forest buffalo displayed increased vigilance at the start of her three-month study when an observation mirador was constructed at the forest clearing. Vigilance decreased during the study as animals adjusted to the presence of observers; however, levels of vigilance increased when a non-herd subadult female visited the clearing and at the births of two calves. At Dzanga-Ndoki National Park levels of vigilance increased when buffalo were approached by lowland gorillas feeding in the same clearing (Melletti 2008).

Forest buffalo are more often observed as part of a herd than as individuals (Melletti *et al.* 2007b; Korte 2008b; Geßner 2008). For example, solitary males and females are observed at Lopé National Park, but the majority of observations are of two or more buffalo (Korte 2008a, 2008b). Although solitary adult males are observed more often than solitary adult females, adult males were not observed leaving herds to form bachelor groups, and males consistently stayed with the same herds. During two years of field work, Melletti *et al.* (2007b) encountered neither solitary adult males nor bachelor groups. Solitary adult females and juveniles were observed on a few occasions, but they joined the herd after a few days. Geßner (2008) reports a solitary subadult male at the Ikwa Bai in Cameroon, but did not observe bachelor herds. Thus, so far, field studies have produced little evidence for bachelor herds in forest buffalo, unlike Cape buffalo studies.

Forest buffalo herds usually include more than one generation of young. Calves stay with their mothers for at least two years and juveniles will often stay with their mothers after the birth of the next calf (Melletti *et al.* 2007b; Korte 2008a, 2008b). Calves stay close to the females after birth and integrate into the herd with little attention from other herd members (Geßner 2008). Melletti (2008) observed females leaving their herd for a few days at the time of birth, returning to the herd when the new calves are able to walk properly. During these periods, females remained apart from the herd and concealed their calves in tall grass or bushes when grazing. Cape buffalo can display similar behaviour when calves are born (Sinclair 1977; Mloszewski 1983; Prins 1996). Forest buffalo are attentive to calves, but the literature reporting on births of calves does not describe specific care of calves by females (Melletti *et al.* 2007b; Geßner 2008; Korte 2008c).

Few observations of agonistic behaviours are reported for forest buffalo (Molloy 1997; Melletti *et al.* 2007b; Geßner 2008; Korte 2008a, 2008b). Geßner (2008) defined the sequence of a buffalo placing it nose between the hind legs of a second individual and jumping away as a submissive behaviour. This is similar to the appeasement ceremony observed in Cape buffalo (Estes 1991). At Ika Bai in Cameroon, subadult buffalo males displayed submissive behaviour to the adult male of the group; adult females from different subgroups also displayed submissive behaviour when the subgroup joined; and juveniles displayed submissive behaviour to adult buffalo, establishing hierarchy within the group. Geßner (2008) also reports a peak of chasing between the adult male and subadult male in June, when the adult male is establishing his position in the herd. Melletti (2008) also reports submissive behaviour when a subadult or juvenile approached the herd. Defensive displays are rare, with Melletti *et al.* (2007b) reporting the most frequent interaction as adult females displacing juveniles from resting areas at Bai-Hokou (Dzanga-Ndoki National Park) in the Central African Republic. Despite distinct home ranges and the occasional encounters of different herds, territorial defence was not observed at Lopé National Park (Korte 2008a). Field studies report a limited number of behavioural displays among forest buffalo. Melletti (2008) at Bai-Hokou in the Central African Republic observed the only adult male performing urine testing just before copulation on a few occasions. He also reported short vocal signals when the herd was moving from one clearing to another, during grazing, while resting and with all activities associated with the displacement of young by adults at Dzanga-Ndoki National Park.

There are few data on intraspecific and interspecific competition for food resources in forest buffalo. This buffalo lives in smaller herds than savanna buffalo, which could facilitate better inter-individual tolerance and reduce competition for food resources. However, this hypothesis is not supported by the strong spatial segregation of home ranges observed at all study sites (see above). Melletti *et al.* (2007b) observed that most frequent interaction between the members of the herd during feeding and resting was the driving off of other individuals, mainly initiated by adult females and usually directed towards a juvenile. The authors conclude that this kind of interaction could be due to competition for the best feeding and resting spots. Within a clearing these social interactions between buffalo were relatively common. Moreover, several other large mammals use this habitat type and can congregate in the same clearing. During feeding, buffalo, sitatunga, red river hogs, gorillas, bongos and even forest elephants may tolerate each other even within a few metres. Among these, sometime elephants are less tolerant, mainly towards buffalo, driving them off or simply annoying them.

Spatial aggregation patterns in forest buffalo have been studied by Melletti *et al.* (2008, 2010) at 45 resting sites of a single herd in Dzanga-Ndoki National Park, where both habitat structure and season influenced these patterns. In open habitats such as clearings, groups cover a larger area when resting and are more rounded in shape compared to group properties noted in forest during the wet season. Forest buffalo also have a more aggregated spatial distribution when resting in clearings than when in the forest. Individual positions within the herd in the clearing habitat varied with age and sex. In the clearings, the adult male was on most occasions located in the centre of the herd ($n = 20/24$ observations). In contrast, females occupied intermediate ($n = 57/80$), peripheral ($n = 14/80$) and central positions ($n = 9/80$) within the group. Juveniles also occurred in intermediate ($n = 64/77$) and peripheral positions ($n = 13/77$). Although these results are limited by small sample size (one herd), it can give an indication that habitat characteristics and social behaviour can have relevant effects on the spatial distribution of animals within a group.

Parasites and diseases

Savanna (Cape, West and Central African) buffalo

The savanna buffalo is susceptible to several infectious diseases of importance in Africa. Some diseases (hereafter referred to as indigenous) originated in Africa and co-evolved with African buffalo populations while others (hereafter referred to as alien) have been introduced by imported cattle breeds. The savanna buffalo is known to be a reservoir for foot-and-mouth disease (FMD), corridor disease (theileriosis), bovine tuberculosis (BTB) and bovine brucellosis. The role of savanna buffalo in the epidemiology of pathogens such as anthrax, Rift Valley fever and lumpy skin disease is still unclear and requires more investigation (Prins & Weyerhaeuser 1987; de Garine-Wichatitksy *et al.* 2012; Caron *et al.* 2013).

The transmission of infectious diseases between individuals can occur though different routes, including direct inter-individual contact (e.g. sperm, milk, aerosols), indirectly by contaminated material (e.g. faeces, saliva) released on food and in water, or by haematophagous vectors (e.g. ticks, mosquitoes). In buffalo, several ecological traits (e.g. highly gregarious behaviour, fusion–fission group dynamics, dispersal and mating strategies) are conducive to the transmission and the diffusion of pathogens.

Rinderpest, an alien disease imported in the Horn of Africa in the 1890s, had a devastating effect on many African cloven-hoofed ungulate species and is thought to have caused up to 95% mortality of savanna buffalo populations throughout Africa in the early twentieth century. Subsequent rinderpest epizootics caused major die-offs throughout the twentieth century (until the mid 1980s), but the disease was recently declared eradicated (Morens *et al.* 2011). The extreme pathogenicity of rinderpest and high mortality prevented the development of a wildlife reservoir (De Vos & Bengis 1994). In contrast, BTB and bovine brucellosis successfully established themselves in buffalo, which act as a maintenance host. Bovine tuberculosis is a chronic, progressively wasting disease with prevalence rates up to 60% in buffalo herds (Jolles 2004). Although BTB-infected buffalo can suffer declines in body condition (Caron *et al.* 2003), adult survival and fecundity (Jolles *et al.* 2005), longitudinal studies undertaken in a high-prevalence area such as the Kruger National Park (South Africa) suggest little demographic impact (Cross *et al.* 2009). Similarly, current knowledge of the impact of bovine brucellosis (a chronic disease also known as 'contagious abortion') does not indicate an immediate threat to buffalo survival at the population level (Michel & Bengis 2012). However, the impacts of these chronic diseases may be a non-linear function of environmental conditions such that they are only detectable in stressful periods (e.g. prolonged droughts) (Cross *et al.* 2009). For example, anthrax outbreaks were locally shown to cause mass mortalities in buffalo during drought periods (Prins & Weyerhaeuser 1987; De Vos & Bryden 1996).

Indigenous diseases (e.g. FMD, corridor disease and African trypanosomiasis) generally do not pose a threat to the survival of buffalo populations because of the evolutionary development of unique coping mechanisms (Michel & Bengis 2012). These diseases are generally carried asymptomatically by buffalo, which act as biological reservoirs of transmission to cattle, thus posing particularly severe problems at wildlife–domestic interfaces (Miguel *et al.* 2013; see Chapter 26 for more details). In Southern Africa, diseases transmitted from buffalo to cattle have contributed greatly to the eradication of buffalo from cattle production areas and to the confinement of buffalo to well-fenced areas, thus strongly limiting their movements and distribution range (Laubscher & Hoffman 2012). Due to their known or perceived role in the epidemiology of many infectious diseases, buffalo populations have been the target of control measures by veterinary services to protect cattle populations, crucial livelihood assets for most African national economies, but also for poor small-scale farmers living in the periphery of protected areas.

Finally, savanna buffalo are known to be hosts of a long list of endoparasites, including trematodes, cestodes, nematodes and pentastomids (Penzhorn 2000; Belem & Bakoné 2009). These infections do not normally result in pathogenic symptoms or mortality, although co-infection by gastrointestinal worms and bovine tuberculosis was shown to generate synergistic effects (increased mortality) (Jolles *et al.* 2008).

Forest buffalo

The susceptibility of forest buffalo to infectious diseases is expected to be similar to the savanna buffalo due to their phylogenetic relatedness. However, forest buffalo have not been reported to be infected by diseases of importance such as FMD and BTB. Forest buffalo sustain little exposure to alien infectious diseases compared to savanna buffalo because habitat within its distribution range is not suitable for cattle production. Interspecific contacts are thus rare. However, the recent increase in human encroachment in rainforest habitat (e.g. the logging industry) is currently boosting cattle production along the forest block of the Congo Basin, thus potentially leading to higher risks of disease transmission.

Ectoparasites in the forest buffalo have been recorded from an adult male found dead in the Nouabale-Ndoki National Park, Republic of Congo (Deem *et al.* 2005). This individual was affected by ticks of genus *Amblyomma* sp., *Rhipicephalus* sp., trematodes *Carmyerius gregarius* and oocysts of *Eimeria* spp. Intestinal schistosomes can also heavily infest buffalo, especially old bulls that spend considerable time around water. At Lopé National Park in Gabon, Lustenhouwer (2008) reported that forest buffalo used moist areas despite the risk of exposure to endoparasites. A genus of rumen fluke, *Paramphistomum* sp., was the most common parasite based on dung sampling.

Status in the wild

IUCN: Least Concern

African buffalo is considered a species of Least Concern according to the IUCN Red List (IUCN SSC 2008), not qualifying for Critically Endangered, Endangered, Vulnerable or Near Threatened status; buffalo are not a listed CITES species (UNEP-WCMC 2012). Though African buffalo appear to be widespread and abundant, many countries recognize the need to protect forest buffalo at the national level (Djeukam 2007). For example, buffalo are a protected species in Gabon, with no hunting allowed, and in Cameroon buffalo are a partially protected species with regulations on hunting (Kamdem-Toham *et al.* 2003; Djeukam 2007).

Savanna (Cape, West and Central African) buffalo

Savanna buffalo populations are likely to be impacted by a large array of factors, among which are land use changes, competition with livestock, poaching, drought and disease. Buffalo numbers suffered their most severe collapse during the great rinderpest epidemic of the 1890s, and subsequent outbreaks that have spread from cattle to wildlife during the twentieth century (Winterbach 1998). As above mentioned ('Parasites and diseases' section), local eradication programmes, corridor barriers and fencing of protected areas have further fragmented the initial meta-population.

During the last decades, civil wars (e.g. Angola, Sudan, Ivory Coast, Central African Republic, Mozambique, Democratic Republic of Congo, etc.) and national policies allowing armies to exploit bushmeat largely contributed to locally decimate buffalo populations. Opening roads through natural ecosystems facilitates uncontrolled hunting, fragments populations and generates barriers to dispersal (Blom *et al.* 2004). Poaching is not only conducted to support a local demand, but is often carried out by informal but well organized market channels delivering meat to towns (Dublin *et al.* 1990; FitzGibbon *et al.* 1995; Mduma *et al.* 1998). Increasing agricultural activities, high livestock numbers, deforestation (e.g. charcoal production) and increasing human population densities progressively contribute to the degradation of areas suitable for buffalo. In many locales, livestock overgrazing makes the habitat unsuitable for the buffalo and other large mammals, both through straightforward competition and due to impacted soils and erosion. Protected areas thus increasingly become isolated and disconnected, and buffalo subpopulations are left vulnerable to local extinction due to disease outbreaks, hunting or fires. In much of rural Africa, programmes for livestock vaccination have come to a complete standstill. In many regions a combination of disease and lawlessness is likely to present a major threat to the future survival of buffalo populations (Prins & Sinclair 2013).

Buffalo have a high commercial value as trophies throughout Africa, a value enhanced by their reputation of being one of the most dangerous African animals. For example, in 2013 the price of a two-week safari including the opportunity to shoot one buffalo globally amounts to €7000–35 000 (depending on the region, quality of service, trophy size, etc.; for more details on buffalo hunting, see Table 20.9). In Southern Africa, many private ranches and communal 'game conservancies' have been stocked with disease-free buffalo and make a good profit (e.g. Hearne & McKenzie 2000; Du Toit 2005 – see also the section 'Status in captivity'). Most hunting areas, if well managed, play an important role in conserving habitats, species richness, employment and income for local people around protected areas. Buffalo also have an unrealized potential value due to their resistance (both apparent and inherent) against many tropical diseases compared to livestock.

The conservation prospects of the three savanna subspecies of buffalo are quite different. Summation of the country estimates given above (Tables 20.1–20.2) gives a total population of >513 000 for the three subspecies of savanna buffalo, a figure slightly lower than the last global estimate (627 000; East 1998). As mentioned above, these estimates are likely to be conservative, for two main reasons. The first is that aerial surveys tend to underestimate buffalo populations due to detection bias from the air. The second is that population estimates are unavailable for some parts of these subspecies' ranges. Although comparisons between estimates are complex in areas presenting a dissimilar level of information (e.g. Sudan), global trends emerge from this exercise. The Cape buffalo (*S. c. caffer*) population globally appears stable and even increasing in countries such as Mozambique or South Africa. The slight decrease in the overall number of Cape buffalo mainly results from an apparent decrease of the total estimate in Tanzania, the country hosting the largest population. The situation of the West African savanna buffalo (*S. c. brachyceros*) also appears globally stable at the scale of the distribution range, but marked contrasts appear by country. In Burkina Faso, Niger and Benin, sustained efforts brought to several protected areas by the international community (e.g. the European Commission) during the last decade seem to bear fruit. In contrast, the West African savanna buffalo population of Senegal (Niokolo National Park) and Ivory Coast (Comoe National Park) has alarmingly dropped by 90%. Most worrying is the future of the Central African savanna buffalo (*S. c. aequinoctialis*) population, which has faced an estimated decrease of 60% during the last 15 years. Although uncertainties remain about the status of the population in Sudan, the large population previously observed in Democratic Republic of Congo and the Central African Republic fell sharply due to internal problems of governance (civil war, civil unrest).

Forest buffalo

The forest buffalo is declining across its geographic range (IUCN SSC 2008). Based on only a few population estimates, East (1999) estimated a total population of 60 000 forest buffalo with about 75% of the population in nominally protected areas, including Lobeke National Park (Cameroon), Dzanga-Ndoki National Park (CAR), Nouabalé-Ndoki-Kabo (Congo-Brazzaville), Lopé National Park, Wonga-Wongue and Gamba (Gabon), Odzala National Park (Congo-Brazzaville) and Maiko National Park (Congo-Kinshasa).

The future of this subspecies depends on well-managed protected areas and hunting zones with special attention to forest clearings and mosaics of forest and savannas, where critical food resources are abundant (Blake 2002; Melletti 2008; IUCN SSC 2008). In addition to habitat loss, poaching is a major threat to forest buffalo populations (IUCN SSC 2008). Buffalo are hunted for their meat and many rural populations depend on bushmeat for protein (Foerster *et al.* 2012). For example, in the Gamba Protected Areas Complex, Gabon, forest buffalo is a target species in the bushmeat trade, and is the fourth highest species present in the markets (Thibault & Blaney 2003). Thus, appropriate hunting regulations

Table 20.9 The range of costs for a single buffalo hunt in different African countries where the species is legally hunted

	Guinea[1]	**Burkina Faso**	**Benin**	**Cameroon**	**Central African Republic**	**Ethiopia**	**Uganda**	**Tanzania**	**Mozambique**	**Zambia**	**Zimbabwe**	**Botswana**	**Namibia**	**South Africa (RSA)**
Trophy fees	1120	€430–480	€600	800–1800 €1500–2000[1]	€800–2000	1000–3300	2000–4000[2]	2500–3900	3000–5000	3000–3500	2600–4500	5000	3250–8500	6500–30 000[3]
Daily rates	?	€850	€1000–1300	944–1300 €2230[1]	€1900	1950–3584	1200–1500	2000	1000–1550	1000–1500	850–1250	3900	1650–2000	200–640
Total hunter days	8	7–10	7	7–13	7–10	16	10	10	7–10	7–10	10	10	8	5–10
All-inclusive hunting cost per buffalo	10 000	€6380–8930	€7600–9700	7408–10 900 ~€17,110[1]	~€14 100	~17 950	~14 000	15 000–22 000	10 000–14 500	10 000–18 500	10 000–17 000	~14 000	11 500–14 000	9750–48 000

Buffalo are a key species in the safari hunting industry. The economic activity that can be generated around a buffalo hunt is much higher than only the buffalo trophy fee. This activity creates also jobs, recruiting people from local communities such as drivers, trackers, skinners, cooks, cleaning ladies, etc.

All hunts are considered to be carried out by a single hunter, with one buffalo bull included.

All prices are in US dollars unless otherwise specified.

The trophy fees and daily rates listed come from the websites of the main hunting outfitters. These values may change by a small percentage from year to year.

Daily rates depend on the kind of accommodation, service, quality of hunting areas, logistics and so on and vary from country to country.

A buffalo hunt starts from a minimum of five to a maximum of 16 days.

A percentage of trophy fees and total hunting cost go to local communities and to the government. This percentage varies from country to country.

[1] Trophy and daily fees and total hunting cost are related to the forest buffalo (*Syncerus caffer nanus*).

[2] 75% of trophy fees goes to local communities and 25% to the Ugandan government (source: Uganda Wildlife Authority).

[3] The trophy fees are determined by trophy size (horns size measured in inches) and location. This is mainly applied in private, fenced reserves.

Both the government reserves and private fenced lands are included.

and enforcement of these regulations are also critical for maintaining forest buffalo populations (Wilkie *et al.* 2011).

Status in captivity

Savanna (Cape, West and Central African) buffalo

In South Africa, numerous disease-free buffalo breeding projects have been supported by the government since 1996, with the objective of restocking areas where buffalo populations were not viable anymore, or disappeared due to disease or exclusion by cattle farmers (Laubscher & Hoffman 2012). Disease-free animals were produced using calves taken at birth from captive mothers and fostered by surrogate disease-free dairy cows (mainly Jersey cows due to their good mothering abilities and high milk yield). The initial stocks were built from the Kruger National Park population, offering the best gene pool, but animals (record-class trophies) were also imported from Tanzania. These projects rapidly had a snowball effect through the involvement of the private sector (mainly driven by trophy hunting businesses) and buffalo breeding is now part of a wholly commercial system. Around 26 000 buffalo are privately owned and resident on approximately 2700 private game ranches or reserves in 2013 (South African Private Buffalo Owners Association, personal communication). In recent years, the increasing demand for disease-free buffalo has gradually led to an increase of their price in South Africa. In 2008 disease-free buffalo were being sold for just over ZAR 160 000 (ZAR 1 ≈ \$0.11), while in 2010 this price increased to over ZAR 325 000 per buffalo at the same farmers' auctions (Cloete 2011). In 2012, ZAR 20 million was paid for a buffalo cow and her bull calf, as well as a record price of ZAR 26 million for a buffalo bull (Laubscher & Hoffman 2012). The buffalo cow that fetched the 2012 record price had a horn spread of 109 cm, making it the biggest of any cow in captivity. In this buffalo breeding system, bulls are selected on temperament and semen quality as well as horn length, and cows are primarily selected on reproductive performance. Although game farmers argue that selective breeding is restoring what years of culling has eliminated, a selection process based on specific traits (here trophy quality) and implemented at an industrial scale may have unexpected consequences for the genetic integrity of the species.

In 2012 there were 166 Cape buffalo in captivity across five regions of the world. In Africa, 48 (22 males, 24 females, 2 unknown) are kept in different zoos (ISIS: www2.isis.org/Pages/Home.aspx). Furthermore in Africa there are hundreds of Cape buffalo that are sold as game annually. For example, if we only look at the data from www.gamefarmnet.co.za/veiling.htm in 2012, about 350 Cape buffalo were sold.

Europe has 62 (17 males, 45 females), North America 26 (7 males, 19 females), Asia 18 (9 males, 9 females) and Latin and Central America report 12 (4 males, 8 females) (ISIS: www2.isis.org/Pages/Home.aspx; see also Chapter 27 and, in particular, Table 27.1). These numbers reflect individuals managed in cooperation with zoological breeding collections, and therefore are likely an underrepresentation of the total number of buffalo in captive collections.

Forest buffalo

In 2012 there were 135 forest buffalo in captivity across four regions and 26 institutions of ESB (EAZA) (see also Chapter 27). In Africa, six buffalo (two males, four females) are in two zoological gardens. In Australia there are four males and one female forest buffalo in two institutions. Europe has the greatest number of forest buffalo with 32 males, 84 females and 4 undetermined housed across 20 institutions. In the United States there are just four females in two different institutions. San Diego Zoological Society reports high calf mortality and a decision to no longer maintain forest buffalo due to little hope for maintaining high genetic diversity (G. P. Carmi & R. G. Rieches, personal communication).

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