# 8 · *The Environments of the African Buffalo, with Different Selection Forces in Different Habitats*

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## Introduction

Every first-year text book in ecology informs students that every species has its own niche. This is sometimes taken further with the assertion that every species also has its own function (whatever that means). In this chapter, we ask what the 'niche' is of the African buffalo *Syncerus caffer*. However, 'the African buffalo' is not a homogeneous species because there is much morphological variation within the species. This variation is to some extent geographically restrained, and hence scientists have distinguished 'subspecies'. Due to the recent proliferation of 'recognized' subspecies and species, the reader should be aware that the recognizing and naming of taxa, which used to be safely in the hands of systematicists and taxonomists, has become politicized (see O'Brien and Mayr, 1991; Gippoliti and Amori, 2007). Under U.S. legislation, there may be a need to recognize and name taxa because any *named* taxon that may deserve protection can get it, but unnamed taxa cannot. Indeed, the U.S. Endangered Species Act considers any subspecies of fish or wildlife or any distinct population segment as an entity available for protection (Schwartz and Boness, 2017). To our knowledge, this does not apply to legislation in African buffalo range states, and so there is no conservation need for distinguishing many or few subspecies of African buffalo.

In the scientific literature, there are currently five recognized forms or subspecies of African buffalo, namely, *matthewsii*, *aequinoctialis*, *brachyceros*, *caffer* and *nanus* (Prins and Sinclair, 2013). Confusingly, the Safari Club International trophies system (SCI) also recognizes five subspecies, but they are not the same (see below). Ecologically speaking, we know next

to nothing about *matthewsii*; this subspecies occurs in mountainous areas to the north of Lake Kivu as far as the Virunga Mountains. Whether it is justified to separate it from *caffe*r is unclear (Prins and Sinclair, 2013); there is no scientific literature available to state whether this form has special ecological requirements, except if we consider the buffalo of Virunga National Park (a.k.a. Albert NP) in the Democratic Republic of the Congo (DRC) and of Parc National des Volcans in Rwanda as *matthewsii* too. In that case, the ecological literature does not provide clues to see it as functionally different from *caffer* (see e.g. Mertens, 1985; Mugangu et al., 1995; Plumptre, 1995; Treves et al., 2009).

Another blank spot in our knowledge on buffalo ecology concerns *aequinoctialis*. This subspecies occurs north of the Congo rainforest between the Chari River in the west and the Nile in the east. Phenotypically it looks very much like *caffer*, but on the basis of mitochondrial DNA clustering it resembles *nanus/brachyceros* (Smitz et al., 2013). One study on the diet of this subspecies has been published (Hashim, 1987) and does not give reason to think it is different from the diet of *caffer*.

Further to the west, from Senegal to the Chari River in southwest Chad, to the north of the Guinea rainforest, roams the third form, namely *brachyceros* (the West African bush cow). Again, we do not know much about this subspecies ecologically speaking save for the information provided in the PhD thesis of Cornélis (2011). This subspecies may grade into the *aequinoctialis* form east of Lake Chad, noting that the buffalo is nearly extinct within the Lake Chad Basin with the exception of some incursions from elsewhere (Chardonnet and Lamarque, 1996); genetically speaking, it intergrades with *nanus* (the forest buffalo) of both the Guinea rainforest and the Congo rainforest. Of this latter subspecies we have reasonable knowledge. The SCI system does not recognize *matthewsii* and splits the West African bush cow into two subspecies, namely, *S. c. brachyceros* and *S. c. planiceros*.

And finally there is *caffer* (the Cape buffalo), of which much is known. Its karyotype suggests that it is the most recently derived form. It is the only subspecies with a fusion between chromosomes 5 and 20 (2n = 52), and it lacks the polymorphism for a 1;13 fusion, as observed in *Syncerus caffer nanus* (2n = 54–56; Wurster and Benirschke, 1968; Anon., 2004; Pagacova et al., 2011). Hybrids between *nanus* and *aequinoctialis* have been produced in zoos (Gray, 1972; Anon., 2004), as well as between *nanus* and *caffer* (Cribiu and Popescu, 1980).

There are gradual changeovers but also sharp boundaries between the different forms. By and large, three types can be recognized based on

body mass, namely, the small *S. c. nanus* (adults 265–320 kg), the intermediate *S. c. brachyceros* plus *S. c. aequinoctialis* (adults 300–600 kg) and the massive *S. c. caffer* (adult cows up to 500 kg, adult bulls from 650 kg to 900 kg; Cornélis et al., 2014).

The unclear allocation of individuals to these five forms (*matthewsii*, *aequinoctialis*, *brachyceros*, *caffer* and *nanus*) is well illustrated by comparing Smithers (1983 – who only recognizes '*caffer*' and '*nanus*'), the Rowland Ward trophies system (Smith, 1986 – with a northern savanna buffalo, a southern one and the forest buffalo; basically the same as Grubb, 1972), Ansell's (1972) system (which does not recognize '*matthewsii*') and finally the exuberance celebrated by Groves and Grubb (2011), who elevated every form to its own species, thus revelling in the same super species-splitting that was witnessed 100 years ago (Prins, 1996). Would these different forms then have different niches?

Now, what is a 'niche'? Confusingly, there are three niche concepts in ecology, to wit, the Grinellian niche concept, the Eltonian one and the Hutchinsonian one (see Prins and Gordon, 2014, p. 7ff.). The Grinellian niche concept reflects the habitat in which an organism lives, the Eltonian one stresses the functional attributes of the species and its position in a food web, while the Hutchinsonian niche is defined by the resources and environmental requirements of an individual of a species to live and reproduce. In this chapter, we lean towards the Hutchinsonian niche concept, but we use the 'niche' concept loosely.

It thus would be reasonable to believe that if there are different subspecies of the African buffalo because they are morphologically distinct, then they have different 'niches'. An alternative explanation could be that environmental history 'accidentally' led to vicariance, thus resulting in phenotypically different forms that were isolated long enough to be genetically sufficiently distinct to justify 'subspecies status', but they (still) have the same 'niche'. Yet the null hypothesis should not be forgotten, namely, that the (normally) morphological characters that systematicists use to distinguish species or subspecies have no functional meaning (Gould and Lewontin, 1979).

## An Ultrashort Recapitulation of the Evolutionary History of These Forms

The most direct ancestor of *S. caffer* was S. *acoelotus*; Geraads et al. (2009) state that it was as large as the modern *S. caffer*. *S. acoelotus* was a Plio-Pleistocene species in Africa that disappears from the fossil record about

600,000 years ago (see Kullmer et al., 1999: Late Pliocene; Bunn et al., 2010; cf. Bibi et al., 2017: Early Pleistocene; O'Regan et al., 2005: Middle Pleistocene; Chaix et al., 2000: Middle Pleistocene). This may coincide with the expansion of the present-day species between 1,000,000 and 500,000 years ago as deducted by genetics (Chen et al., 2019; de Jager et al., 2021). *S. acoelotus* may have led to a second *Syncerus* species too, namely *S. antiquus*. This latter species went extinct only about 2000 years ago, and may have been a more drylands-adapted species (see Chapter 2). The other species, namely, *S. caffer*, is extant. In the Lake Turkana basin, the last record of *S. acoelotus* was about 1.6 Myr ago, and the first *S. caffer* about 1.2 Myr ago (Bobe and Behrensmeyer, 2004). The genetics and palaeontology of *S. caffer* shows that it apparently could expand its range to southern Africa when *S. antiquus* went extinct. *S. antiquus* also was able to cross the Sahara Desert, most likely in periods when the desert was much greener, and may even have entered the Middle East (for details see Chapter 2). The first occurrence of *S. c. caffer* is from Melkbos, South Africa, from the Upper Pleistocene (Hendey, 1969; see Groves, 1992). However, there is the possibility that *Syncerus caffer* and *S. acoelotus* were both derived from an earlier genus, namely *Ugandax* (see Chapter 2).

Genetics shows that 'subspeciation' may have arisen as long as about one million years ago (de Jager et al., 2021) or as recently as 200 kyr (Smitz et al., 2013; de Jager et al., 2021), but does not provide evidence (yet) whether *S. c. nanus* is more ancestral than the other *Syncerus* forms (*pace* Van Hooft et al., 2002; Smitz et al., 2013, even though they suggest that *nanus* is the derived form). The observations that the older *S. acoelotus* had the same size as the present *S. caffer*, and that the older forms that looked like S. *caffer* are known from the Lake Turkana Basin (Bobe and Behrensmeyer, 2004) nearly overlapping with the present-day range of *S. c. aequinoctialis*, thus allow for the scenario that the present-day buffalo with the simplest horns (*S. c. aequinoctialis*) is genetically closest to the ancestral form. On the basis of genetic analyses, this was already suggested by Smitz et al. (2013), and prior to that by Groves (1992 – slightly confusingly, he put forward that this was spp. *brachyceros*, but he did not distinguish spp. *aequinoctialis* from spp. *brachyceros*). Groves (1992) puts this transition from *S. acoelotus* to *S. c. aequinoctialis* at 130 kyr. The observation that (pure?) *nanus* buffalo have one pair of chromosomes less than at least *aequinoctialis* and *caffer* (we could find no evidence for *brachyceros*) due to a recent fusion (Anon., 2004) also points towards the derived status of the forest buffalo.

In such a scenario, *S. c. nanus* could be the result of dwarfing (as has been observed on islands with the Asian buffalo and humans in the rainforest, e.g. pygmies). Additionally, it cannot be ruled out, we think, that *S. c. brachyceros* represents a hybrid of *S. c. nanus* and *S. c. aequinoctialis* (a pattern that is very well known from Asian bovines). Indeed, the genetic distances between these three subspecies are very small (Van Hooft et al., 2002; Smitz et al., 2013). However, there is no evidence for two separated lineages of dwarf buffalo and large buffalo that were separated for a very long time as has been put forward (for a discussion see Chapter 2).

On the basis of the above, different storylines can be constructed, namely: (1) there was a large buffalo species ('*acoelotus*') that evolved into '*caffer*' and '*antiquus*'. *Antiquus* was a species adapted to dry conditions and could outcompete *caffer* under these conditions. When *antiquus* went extinct, *caffer* took over parts of its range but is nowadays limited by the isohyet of 350 mm. It could not cross the Sahara, and along the Nile it encountered the aurochs (*Bos primigenius*), which prevented *caffer*'s establishment to the north of Khartoum. Storyline (2) is different, with the original large buffalo *acoelotus* able to infiltrate the rainforest (perhaps at times when the forest was reduced to gallery forest only). There, secondary dwarfing took place. At times when the rainforest nearly disappeared (e.g. during the Last Glacial Maximum), the range of the buffalo was probably restricted to one or two refuges in present-day CAR, northern Congo and Uganda (Smitz et al., 2013). In such a small area, possibly no more than 1500 km across, hybridization could easily have taken place with *aequinoctialis*, thus leading to the form *brachyceros*. The further west one travels, the lesser is the expected imprint of *aequinoctialis*, thus leading to a possible cline. Alternatively, storyline (3) narrates that after *S. caffer* evolved into a form that looked like *S. c. aequinoctialis*, it developed into the large Cape buffalo (*S. c. caffer*), but also expanded into the Congo Basin where dwarfing took place, producing *S. c. nanus*. Storyline (4) is different. It narrates that there was a large buffalo species ('*acoelotus*') that evolved into '*antiquus*'. However, there was an even older species (so, not *acoelotus*), say, *Ugandax* (see Chapter 2) that evolved into *Syncerus acoelotus* and also into *S. caffer*, which was much smaller and looked like *S. c. nanus*. Note that this putative predecessor has not been unearthed. This *S. c. nanus* than lived in the ancestral rainforest, from which it radiated into the north to form *S. c. brachyceros* and *S. c. aequinoctialis*, and into the east to form *S. c. caffer* (which then expanded towards the Cape).

Storylines (1), (2) and (3) make the point that the forest buffalo are the product of dwarfing; storyline (4) emphasizes that the northern and eastern savanna buffalo became adapted to $C_4$ grasses in their diet and had to adapt to a large new predator, namely the lion (*Panthera leo*), because its descendants moved into the savanna after they had evolved in the rainforest (see below on the different 'niches'). On purpose we do not use the word 'hypothesis' but 'storyline' because too much is unknown. However, the ramifications are startling, because these storylines result in very different insights into the buffalo's 'adaptations'. Thornhill's is nonetheless a stark reminder of the difficulties one faces in deriving notions about adaptation from present-day niche occupation:

A Darwinian adaptation is an organism's feature that was functionally designed by the process of evolution by selection acting in nature in the past. Functional design rules out explanations of drift, incidental effect, phylogenetic legacy and mutation. Elucidation of the functional design of an adaptation entails an implicit reconstruction of the selection that made the adaptation. Darwinian adaptations and other individual traits may be currently adaptive, maladaptive or neutral. (Thornhill, 2007)

## The Environmental Envelopes of African Buffalo

For the present discussion, we discern three environmental envelopes (an important part of the Hutchinsonian niche) for the three major forms of the buffalo, namely, the forest buffalo (*nanus*), the northern savanna buffalo (*brachyceros* and *aequinoctialis*) and the Cape buffalo (*caffer*) (Table 8.1). Judging from distribution maps of the different forms of buffalo, we generally know at which altitudes they occur or once occurred. Altitude is the main determinant of ambient temperature. For the forest buffalo, we assume that they generally occur below 500 m altitude. However, there may be forest buffalo on the slopes of Mt Cameroon (an isolated volcano of 4000 m altitude) and they do or did occur on Mt Nimba (a 1750-m high mountain on the border between Ivory Coast and the Republic of Guinea; the area is now overrun by refugees) and perhaps in the Masisi Region (eastern DRC; dominated by civil war and resource extraction; P. Chardonnet, personal communication). The northern savanna buffalo also is a lowland form, but it occurs up to 1000 m above sea level in, for instance, the Bouba Njida area (northern Cameroon; P. Chardonnet, personal communication). Yet, this is below the $C_3$-grass zone (see Van der Zon, 1992).

On the basis of the environmental envelope parameters of Table 8.1, we posit that forest buffalo run the real risk of getting overheated when

Table 8.1 *Approximate climate envelopes of the three main forms of African buffalo; we have taken S. c. aequinoctialis and S. c. brachyceros together as 'northern savanna buffalo'. The lethal zones (based on what we know of cattle) may be reached due to a combination of temperature and air humidity; for the forest buffalo; for the northern savanna buffalo the lethal temperatures can be reached during heatwaves with dry air. Cape buffalo have been known to freeze to death, but we do not know of the heat index being excessed.*

| | Elevation range (m a.s.l.) | Minimum temperature and cold waves bracketed (°C) | Maximum temperature and heatwaves bracketed (°C) | Radiation heat flux | Rainfall regime (mm yr$^{-1}$) | Air humidity | Wind/ moving air |
|---|---|---|---|---|---|---|---|
| Forest buffalo | 0–700 | 18 | 32 (35) | Very low | 1000–9000 | 70–95 | Absent |
| Northern savanna buffalo | 100–1000 | (6) 30 | 42 (52) | Very high | 400–1000 | 15–70 | Present |
| Cape buffalo | 0–5000 | (–5) 10 | 38 (47) | Very high | 400–1000 | 50–80 | Present |

| Relative Humidity % | Air temperature°C | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | 21 | 24 | 27 | 29 | 32 | 35 | 38 | 41 | 43 | 46 | 49 |
| 0 | 18 | 21 | 23 | 26 | 28 | 31 | 33 | 35 | 37 | 39 | 42 |
| 10 | 18 | 21 | 24 | 27 | 29 | 32 | 35 | 38 | 41 | 44 | 47 |
| 20 | 19 | 22 | 25 | 28 | 31 | 34 | 37 | 41 | 44 | 49 | 54 |
| 30 | 19 | 23 | 26 | 29 | 32 | 36 | 40 | 45 | 51 | 57 | 64 |
| 40 | 20 | 23 | 26 | 30 | 34 | 38 | 43 | 51 | 58 | 66 | |
| 50 | 21 | 24 | 27 | 31 | 36 | 42 | 49 | 57 | 66 | | |
| 60 | 21 | 24 | 28 | 32 | 38 | 46 | 56 | 65 | | | |
| 70 | 21 | 25 | 29 | 34 | 41 | 51 | 62 | | | | |
| 80 | 22 | 26 | 30 | 36 | 45 | 58 | | | | | |
| 90 | 22 | 26 | 31 | 39 | 50 | | | | | | |
| 100 | 22 | 22 | 33 | 42 | | | | | | | |

Serious risk to health – heatstroke imminent

Prolonged exposure and activity could lead to heatstroke

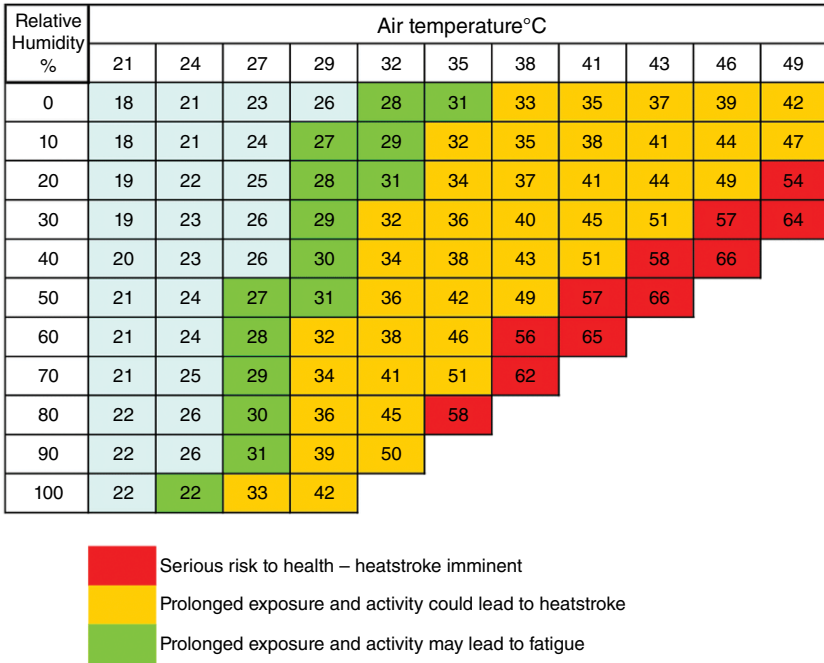Prolonged exposure and activity may lead to fatigue

*Figure 8.1* Heat risk assessment for people. The figures inside the cells are the temperatures (°C) as experienced. Thousands of cattle have died from heat stroke in India and Australia. The combined effect of relative air humidity and temperature is slightly different for cattle and people, but as we do not know the exact relationship in buffalo, we use this for illustrative purposes. From Diffey (2018) © 2018 John Wiley & Sons A/S. Published by John Wiley & Sons Ltd. For more on this issue, see for example Du Preez et al. (1990), Hubbard et al. (1999) or Allen et al. (2013).

the temperature is high and air humidity is very high (thus preventing evaporative heat loss; see Figure 8.1). Buffalo do not have much sweating or panting abilities. In the much more unvarying warm circumstances of a tropical lowland rainforest, wallowing offers much fewer cooling opportunities (because of the higher temperature of standing water but also because of the windless circumstances) than in a savanna where water bodies can cool at night, and more breeze occurs. The northern savanna buffalo can take shelter against high heat loading through direct sunshine by finding places with a breeze and/or shade. Yet these buffalo, we posit, also run a high risk of dying from heat stress during heat waves (Figure 8.1).

Finally, the Cape buffalo runs the risk of being exposed to cold and frost. This is especially important in its southern range, but also high in the mountains of the volcanoes of East Africa.

From this, it follows that it is likely that there is selection pressure for buffalo (and humans, elephants and hippos) to be as small as possible in the tropical lowland rainforest, but in the savanna it would be advantageous to be large (see Table 8.6). The reasons are that in a tropical lowland rainforest where evaporative heat loss is often impossible, heat loss must be achieved through radiation. A large body surface to mass ratio (typical for small animals) is then advantageous; heat can barely dissipate at night because there can be no radiation towards the sky (and thus outer space) due to dense foliage and clouds. In a savanna, however, evaporative loss is possible and body heat can dissipate at night, while a large body mass prevents rapid overheating. Indeed, in areas where there is no hunting, buffalo can be seen resting and grazing during the middle of the day in the full sun even when it is 32°C. Central African rainforest pygmies also separated only recently (i.e. about 70 kyr: Perry and Verdu, 2017; to 190 kyr: Hsieh et al., 2016) from Bantu. Yet, the adaptive significance of small stature in humans in rainforests is far from clear (see e.g. Hsieh et al., 2016; Bergey et al., 2018; Patin and Quintana-Murci, 2018). It is also unclear as to whether the African forest elephant (*Loxodonta africana cyclotis* a.k.a. *L. cyclotis*), genetically perhaps distinct from the African savanna elephant (*L. a. africana*, a.k.a. *L. africana*; but see Debruyne, 2005), is a similar case of dwarfing. Grubb et al. (2000) consider the forest form to be more primitive than the savanna form, which, if correct, would mean that the dwarfing was not recent. There is, by the way, insufficient evidence for the existence of the pygmy elephant ('*L. pumilio*'; Debruyne et al., 2003), so it is unclear whether parallels may be drawn between the case of the African elephant and the emergence of the forest buffalo. The pygmy hippo (*Choeropsis liberiensis*) also is not a dwarfed form of the large *Hippopotamus amphibius*, but is a descendant of a much older, original form that is hardly related to the modern mega-sized hippo (Boisserie, 2005). True dwarfed hippos did occur on Mediterranean islands (Petronio, 2014). The idea could be entertained that dwarfing of buffalo in the rainforest took place because of poorer quality food. Yet food quality in the rainforest of Cameroon, judging by its species composition (Bekhuis et al., 2008) was about equal to or better than that of savanna buffalo (Prins, 1996), and generally it is assumed that larger ruminants (because they have a slower throughput rate) can cope with poorer-quality food. In other words, it is not plausible that a

dwarfing of African buffalo after broadening their niche into the tropical rainforest was a reaction to food quality.

It is unlikely that very high amounts of rainfall pose a problem to forest buffalo. They can swim well, and their large splayed hooves offer sufficient movement possibilities in very wet and muddy terrains. Yet we have observed them taking shelters in grottoes in Cameroonian rain forests (H. Prins, personal observation).

## The Food of the African Buffalo Subspecies

For the diet of the different forms of the African buffalo, one must pay attention to differential occurrence across its range of $C_3$ grasses versus $C_4$ grasses because of their impact on digestibility and intake. Moreover, there appear to be differences in the inclusion of browse (including forbs) for the different buffalo forms. The main difference between the subspecies is that the northern savanna forms have a diet comprised of $C_4$ grasses; they take also 10–15 per cent browse in the dry season (de Iongh et al., 2011; this is nearly completely in the form of the buds and fruits of Caesalpineacea in Benoué NP, Cameroon: Erik Klop, personal communication). Indeed, the range of *S. c. brachyceros* is typically below 500 m altitude, and that of *S. c. aequinoctialis* between 200 and 800 m a.s.l. The Cape buffalo also takes about 10 per cent browse (mainly in the dry season: Prins, 1996) while in the non-montane areas below 2000 m altitude, the grasses they forage on are also of the $C_4$ type. However, above 3000 m and in wetlands, the grasses are of the $C_3$ type in East Africa (Tieszen et al., 1979); further south this shift occurs at about 2800 m (Morris et al., 1993). An estimated 10 per cent of the original range of *S. c. caffer* is higher than 3000 m a.s.l., and about 30 per cent above 2500 m, so a substantial proportion of the diet of buffalo before the expansion of human agriculture may have been comprised of $C_3$ grass (see altitude maps in SEDAC n.d.). Note that the map of the ratio of $C_3$ over $C_4$ plants in Africa proposed by Shanahan et al. (2016) cannot be used for this comparison because it includes trees and shrubs (most of which use the $C_3$ photosynthetic pathway). The rainforest grass species that comprise the diet of the forest buffalo are mainly the $C_3$ type (Bocksberger et al., 2016). The digestibility of $C_3$ grasses is much higher than that of $C_4$ grasses. In other words, diets of the different subspecies are subtly different (Table 8.2).

In East and South Africa, probably all terrain higher than 1500 m but lower than 3500 m has been taken over by agriculture since the

Table 8.2 *The different subspecies of buffalo basically have different diets. The different photosynthesis pathways of $C_3$ and $C_4$ grasses have major repercussions for digestibility of the food and intake rates (see text). A sizeable proportion of the original distribution area of the Cape buffalo was above 3000 m altitude before agriculture displaced them.*

|  | Percentage browse | Type of grass |
| --- | --- | --- |
| Forest buffalo | ~30% (Bekhuis et al., 2008) | $C_3$ photosynthetic pathway |
| Northern savanna buffalo | ~10% (de Iongh et al., 2011) | $C_4$ photosynthetic pathway |
| Cape buffalo | ~10% (Prins, 1996) | Below 2000 m altitude: $C_4$ photosynthetic pathway Above 3000 m altitude: $C_3$ photosynthetic pathway |

start of the Iron Age up until the present. These are so-called Tropical Highlands (see for a map: IFPRI, 2015). On the basis of this, we posit that before the current fragmentation of the range of the African buffalo due to human expansion, some populations of the subspecies *caffer* could easily have moved up to areas with $C_3$ grasses during the dry season, while other populations could have used that type of grass year-round. These buffalo must thus have been buffered against the negative effects of a pronounced dry season. The northern savanna buffalo (*aequinoctialis* but especially *brachyceros*), on the other hand, would have suffered much more from droughts and the dry season in general. Indeed, a migration centred on rivers would have been a good 'evolutionary answer' to that challenge (as was found by Cornélis, 2011, for *S. c. brachyceros*). Proper migratory behaviour of *S. c. caffer* has not been reported, although there is a hint of it from the early 1960s in northern Tanzania's Lake Manyara region, where a migration may have been centred on the Tarangire River (Prins, 1996). Short-distance migrations of *S. c. caffer* have also been reported from woodlands at a relative short distance from the Okavango Delta and from the Linyanti Swamps, both in Botswana (see Chapter 5 for details). It is not known to the present authors whether buffalo forage on $C_3$ grasses in these riverine systems or swamps. Altitudinal seasonal migration (still) occurred between the Rift Valley bottom lands and adjacent high-altitude areas (volcanoes and Ngorongoro Crater highlands) of northern Tanzania in the 1970s and 1980s (P. Chardonnet, personal observations and personal communication). These higher areas abound(ed) in $C_3$ grasses (see Clayton, 1970; Clayton et al., 1974).

The intake of $C_3$ grasses has two very important advantages over $C_4$ grasses: first, the digestibility of $C_3$ grasses is considerably higher, and second, intake is determined to a large extent by rumen fill, which appears to be mainly determined by NDF (neutral detergent fibre). $C_4$ grasses are more fibrous than $C_3$ grasses (see e.g. García et al., 2014 for a review). The throughput rate also is much lower if the fibre content (as in $C_4$ grasses) is higher (Blaxter, 1962, p. 196). In other words, everything being equal, it is easier for *S. c. caffer* and *S. c. nanus* to acquire energy for lactation and growth than for *S. c. brachyceros* or *S. c. aequinoctialis*. However, for *nanus* there may be a disadvantage to forage of highly digestible grass because the heat of digestion could be higher than if foraging on food that is slower to digest (see Blaxter, 1962).

## The Competitors of the African Buffalo Subspecies

Because the different forms of African buffalo live in such different environments (habitats), the animal species they (potentially) share resources with are very different. A little is known already about the habitat requirements of the enormous array of African herbivores, but a striking pattern is that the habitat requirements of these many species coupled with historical processes (and chance) has led to a spatially very variable distribution of these species (see Prins and Olff, 1998). The African buffalo has (together with the leopard *Panthera pardus* and the African elephant) the widest of all distributions of African large mammals, thus overlapping with a very variable suite of other herbivores. This insight leads to the conclusion that possible competition with most species can hardly have shaped the evolutionary pathway of African buffalo because the population of African buffalo is characterized by relatively small genetic distances, particularly within subspecies (Smitz et al., 2013), and has been vast for hundreds of thousands of years (Chen et al., 2019; de Jager et al., 2021). In Table 8.3 we present a non-exhaustive overview of the 'constant' (i.e. occurring everywhere) potential competitors for the three African buffalo forms, and the 'variable' ones (i.e. large herbivorous species that do not occur everywhere in the range of a particular subspecies).

While we posit that the 'variable competitors' on a species level do not exert particular selective pressure, as an ensemble they could do so because in no habitat is a particular 'subspecies' of buffalo free from these variable competitors. Their omnipresent competitor is the African elephant in its two forms (*Loxodonta* [*a.*] *africana* and *L.* [*a.*] *cyclotis*). Adults

Table 8.3 *African buffalo are large grazers with a variable admixture of browse (from woody species and from herbs) in their diet. Some herbivore mammalian species share resources with them, which we tabulated only for those species heavier than 50 kg and with some grass in their diet. Of these, the 'constant competitors' co-occur with African buffalo (or did so in the recent 5000 years or so) nearly everywhere (species names in bold). Other potentially competing species, which we termed the 'variable competitors', co-occur with buffalo only here and there. In this table we split the 'northern savanna buffalo' in to* S. c. aequinoctialis *and* S. c. brachyceros. N = *number of species that may show overlap in resource use with a particular form of buffalo. Species are arranged alphabetically.*

| | Adult mass 50–100 kg | Adult mass 100–200 kg | Adult mass 200–400 kg | Adult mass >400 kg | N |
|---|---|---|---|---|---|
| Forest buffalo (250–300 kg) | **Bushbuck** Sitatunga | | Bongo Okapi | **African elephant Hippopotamus** | 6 |
| Northern savanna buffalo: *brachyceros* (300–600 kg) | **Bushbuck** Kob Sitatunga | Hartebeest Topi (korrigum) Roan antelope Waterbuck | Bongo Giant eland | **African elephant Hippopotamus** | 11 |
| Northern savanna buffalo: *aequinoctialis* (400–700 kg) | **Bushbuck** Kob Nile lechwe Sitatunga | Greater kudu Hartebeest Roan antelope Topi (Tiang) Waterbuck | Bongo Giant eland | **African elephant Hippopotamus** Northern white rhino | 14 |
| Cape buffalo (500–800 kg) | Blesbok Bohor reedbuck **Bushbuck** Grant's gazelle Gerenuk Hirola Impala Mountain nyala Nile lechwe Nyala Puku Sitatunga Southern lechwe Lesser kudu Southern reedbuck | Black wildebeest Bontebok greater kudu Hartebeest Roan antelope Sable antelope Topi Waterbuck | Blue wildebeest Common eland Grant's zebra Mountain zebra Plains zebra | **African elephant Hippopotamus** Southern white rhino | 32 |

are always much heavier (respectively, 3000–6000 kg and 2700 kg) and have much more browse in their diet. So this may suggest that buffalo would encounter a negative selection pressure against increasing in size. Their main 'constant' competitor may be or has been the hippo (*Hippopotamus amphibius*). They are true grazers and twice as heavy as buffalo, thus preventing buffalo from getting heavier (see Olff et al., 2002). All of their other competitors are smaller or do not compete over most of the range of the populations of the three forms (Table 8.3). Outside of the rainforest, their most important potential competitor would be the two species of eland. The giant eland is a browser over nearly the entire year, while the common eland is a browser during the dry season when food is scarce. From this we conclude that the other herbivores would exert stabilizing selection on the body mass of the different forms of African buffalo (see also Prins and Olff, 1998). They potentially have a very important facilitatory role for the species mentioned to the left of the column in which the different buffalo subspecies are located (cf. Prins and Olff, 1998; Olff et al., 2002). This is especially the case for the Cape buffalo.

## The Predators of the African Buffalo Subspecies

The three main types of African buffalo, namely the forest buffalo, the northern savanna buffalo and the Cape buffalo, live in very different worlds, or, better expressed, cohabited until very recently before the collapse of nature conservation in West Africa in very different worlds. The main difference is that adult forest buffalo are basically predator-free (except for man). Lions (*Panthera leo*) are absent from the tropical rainforest proper. The African golden cat (*Caracalla aurata*) with its maximum body mass of only 16 kg is no match, but a 90-kg leopard is. Leopard density may be approximately equal in rainforest and savanna environments (e.g. Jenny, 1996 for rainforest versus Balme et al., 2007, for savanna), but spotted hyaena (*Crocuta crocuta*), a formidable predator in savannas, are absent from rainforests proper (see map in Varela et al., 2009), as are wild dogs (a.k.a. painted dog, *Lycaon pictus*; Woodroffe et al., 1997). The forest buffalo may encounter African dwarf crocodiles (*Osteolaemus tetraspis*), which are likely to be insignificant predators, like the West African slender-snouted crocodile (*Mecistops cataphractus*), the Central African one (*M. leptorhynchus*) or even the sacred crocodile (*Crocodylus suchus*).

The northern savanna buffalo had to deal with lions until this large predator basically went extinct, as the Cape buffalo still must do. Lions

Table 8.4 *The different subspecies of African buffalo share their habitat with different predators. We have taken* S. c. aequinoctialis *and* S. c. brachyceros *together as 'northern savanna buffalo'. The subspecies with the biggest horns, namely, the Cape buffalo seems to live in the most dangerous environment.*

|  | Predator of adults | Predator of calves |
|---|---|---|
| Forest buffalo | None | Leopard, African python |
| Northern savanna buffalo | Lion | Leopard, spotted hyena, African wild dog, African python |
| Cape buffalo | Lion, Nile crocodile | Leopard, spotted hyena, African wild dog, African python |

are large predators (adult females about 115 kg and adult males about 220 kg). Wild dogs are now next to extinct nearly anywhere in West and Central Africa (Woodroffe et al., 1997). We do not think the sacred crocodile was much of a threat to the northern savanna buffalo, nor were African wild dogs before they went functionally extinct in West and Central Africa. The much larger Nile crocodile (*C. niloticus*) appears to be a predator for the Cape buffalo. Finally, the African python (*Python sebae*) may perhaps be an occasional threat to calves of all buffalo subspecies. Spotted hyena and African wild dogs prey on buffalo calves and juveniles in the northern, eastern and southern savannas, but are rarely a threat to adult buffalo (Table 8.4). The different jackal species are insignificant.

From this it follows that there has been a selection pressure for becoming big in the savannas to escape predation from lions and perhaps Nile crocodiles. In the rainforest we believe that the predation pressure has not been high, and buffalo would only have run a risk of major predation if they had attained the size of duiker antelopes.

## Are the Subspecies of the African Buffalo Functionally Different?

Currently, maximally five subspecies are considered to be relevant for a discussion on what the African buffalo 'is'. These are *Syncerus caffer caffer* (the Cape buffalo), *S. c. nanus* (the forest buffalo), *S. c. brachyceros* (the West African bush cow), *S. c. aequinoctialis* (the Nile buffalo) and *S. c. matthewsii* (the mountain buffalo). The last one is morphologically not well distinguishable from the nominate subspecies, and functionally ecological research does not provide any clue as to why it would be different if we take the

Table 8.5 *The relationship with other mammals of the African buffalo depends on the subspecies (we have taken* S. c. brachyceros *and* S. c. aequinoctialis *together in this table). Data on predatory species are from Table 8.4, data on species that can be facilitated or species that can be competitive are from Table 8.3. We use the term 'embeddedness' instead of 'connectedness' because the latter is local food-web–dependent while ours is based on major regions (i.e. West African Guinea and Sudan savanna, West and Central rainforest and the whole region from Ethiopia to the Cape).*

|  | Predatory species of adults | Predatory species of calves | Large mammal species that can be competitive | Large mammal species that can be facilitated by buffalo foraging | Embeddedness |
|---|---|---|---|---|---|
| Forest buffalo | 0 | 2 | 4 | 2 | 8 |
| Northern savanna buffalo | 1 | 4 | 4 | 4 | 13 |
| Cape buffalo | 2 | 4 | 8 | 7 | 21 |

Virunga buffalo as *matthewsii*. If not, and the subspecies must be found closer to Lake Tanganyika, then it comprises a blank spot in our knowledge.

The forest buffalo *S. c. nanus* of the rainforests of Central Africa and West Africa are functionally very different from the nominate subspecies. Actually, they are morphologically and functionally so different that most ecologists would not reject species status. Genetics, however, shows how intrinsically they are related to the nominate subspecies (Van Hooft et al., 2002; Smitz et al., 2013). Their difference does not show up as much in their habitat use (see Korte, 2008; Bekhuis et al., 2008: they mainly use the small savannas in the forest, logging roads and open marshes) than in their relationship with other species of the assemblage, while their morphology adheres to a common pattern of 'forest species'. They have a more reddish coat colour, conspicuous white ear fringes (like the riverine bush pig *Potamochoerus porcus*), small body size, smaller incisor width, more 'streamlined' and smaller horns, and live in much smaller group sizes.

The two forms of the northern savannas pose more problems because so little is known of the ecology of this species in these areas (but see Cornélis, 2011). Yet the role of the different forms is well illustrated in Table 8.5. Cape buffalo appear to be located in the richest web (they

show the highest degree of 'embeddedness'), while the forest buffalo is perhaps only loosely connected to the other species in the rainforest, possibly indicative that it only recently entered the forest.

## The Different Subspecies of the African Buffalo in a Human Context

Humans evolved in Africa; the genus to which we belong is about three million years old (nicely summarized in Dunsworth, 2010). The genus *Syncerus* is likely younger (Chapter 2). If the ancestral species of *Syncerus caffer* was *S. acoelotus*, then there is no convincing evidence that it was hunted by humans (Bobe and Behrensmeyer, 2004). *Homo* may have started controlling fire some 1.2 Myr ago (James et al., 1989), as long as the oldest record of *S. caffer* (see above).

The *Homo–Syncerus* relationship has thus been a long-standing one. In the pre-Modern, this interaction was comprised of one that benefited buffalo when fire modified the vegetation to their benefit, producing more palatable grass, perhaps less tsetse flies and less shrubbery or even forest. Buffalo suffered from humans when they became better at killing large game. Different ways of killing became available over time, for example throwing stones to stampede a herd over a cliff (which can only be done if cliffs are available, for example in the Drakensberg region or some places along the coast in Transkei for instance). We do not think that spears ever made much of an impact on the level of populations even though we are aware that some men single-handedly killed a buffalo bull with a spear (Mr ole-Konchella as young warrior of the Masai did long before he became the Director of Tanzania National Parks; H. Prins, personal communication). Running prey to ground with weapons is an unlikely strategy for killing buffalo (Bunn and Pickering, 2010). Bow-and-arrow technology is perhaps 300 kyr old (Lombard and Haidle, 2012). We are not aware of successful bow-and-arrow hunting with traditional bows, in contrast to European-style long-bows or modern crossbows. Using poisons on arrows, however, is a successful strategy, as was demonstrated by traditional Hadza-hunters near Lake Eyasi (H. Prins, personal observation; cf. O'Connell et al., 1988). Bambote hunters of Zambia successfully kill buffalo with this technique (Terashima, 1980). Indeed, when a good market developed for ivory, Kamba started elephant hunting with poisoned arrows (Steinhart, 2000). The oldest written description of buffalo refers to a similar hunting technique:

[In the Kingdom of Mali] there are undomesticated buffalo which are hunted like wild beasts, in the following fashion. They carry away little calves such as may be reared in their houses, and when they want to hunt the buffaloes they send out one of these calves to the place where the buffaloes are so that they may see it, make towards it, and become used to it because of the unity of the species which is a cause of association. When they have become used to it the hunters shoot them with poisoned arrows. Having cut out the poisoned place, that is, where the arrow has struck and round about it, they eat the flesh. (al-Umari ~1347 CE, translated by Levitzion and Hopkins, 2000, p. 264)

Netting is a viable strategy to capture game, for instance in a rainforest, but needs large groups of cooperating people (H. Prins, personal observation; Abruzzi, 1979) and the largest prey thus taken may be bushbuck *Tragelaphus sylvaticus* (Terashima, 1980; Sato, 1983). Traditional spring traps can catch prey as heavy as bushbuck and yellow-backed duiker *Cephalophus silvicultur* (H. Prins, personal observation; Sato, 1983). Pre-Modern hunting techniques were likely to be sustainable (Hitchcock, 2000).

We posit that it is really with the invention of steel wire (by Wilhelm Albert in 1834), the gin trap and the shotgun that buffalo started directly suffering from people. Leg traps made of steel wire attached to long lines of hundreds to thousands of metres of steel cable can play havoc with buffalo (for a description see Sinclair, 1977, p. 25). In some hunting concessions, concessionaires removed tens of thousands of steel wire snares in northern Tanzania (Hurt and Ravn, 2000). The impact of using snares on a population can be severe (cf. Mduma ert al., 1998). The old-fashioned shotgun basically eradicated buffalo from South Africa, and even just before the independence of Mozambique, the Portuguese shot some 50,000 buffalo for potential gain. Storehouse rooms filled with hooves and dried scrota skins were still a macabre reminder in 1993 (H. Prins, personal observation).

Through agriculture, humans started domineering the landscape. Instead of simply a supply of proteins and fat, buffalo started becoming a nuisance when they damaged crops. Because browse is unimportant in their diet (see above), they would hardly have been an issue to beans, peas or yams. However, even native species such as sorghum would not be very attractive to buffalo because many varieties are high in prussic acid and lignin. Millet, on the other hand, is a good fodder source. Agriculture and associated iron smelting only became important in West Africa around 500 BCE, around 500 CE in the Great Lakes area, around 1000 CE in small mountainous pockets in East Africa, and even later in South Africa. In the rainforest zone, the savanna environment

slowly but surely disappeared during the Holocene, and agriculture even disappeared (e.g. Tutin and White, 1998). Slash-and-burn cultivation, so important in western Africa, enabled the expansion of the Guinea savanna and the Sudan savanna, allowing the expansion of buffalo habitat. In other words, African buffalo may have benefited from humans perhaps until the advent of Modern days. In contrast to East and southern Africa, the West African kingdoms all used cavalry since about 1000 CE, indicative of well-developed grasslands (Fisher, 1972; Ukpabi, 1974; Sayer, 1977), but how much buffalo hunting on horseback took place is not known even though they used stirrups. Plains Indians in North America were only able to have a devastating impact on American bison when they adopted horseback hunting.

The Cape buffalo, however, may have started suffering from humans more than the northern savanna buffalo (which benefited from forest conversion). The advent of pastoralism from the Sudan towards the Cape was a slow process (at a rate of about 5 km per generation; Prins, 2000), but as cattle and buffalo largely use the same resources, and as people are able to monopolize water sources, pastoralists can outcompete grazers like buffalo (Prins, 1992; Prins and de Jong, 2022).

## Speculation on Further Subspeciation of the African Buffalo

Table 8.6 summarizes of the selection forces on the different forms of buffalo that we envisage.

What would the consequences be of *S. c. nanus* becoming smaller? We would not be amazed that it might be able to cope better with climate warming, and become much smaller before encountering serious negative effects from bushbuck and sitatunga (*T. spekii*; both as potentially competing species) or leopards (as major predator).

Yet in a world where people allowed the northern savanna buffalo to continue to live in protected areas, the reality of the West African context would perhaps be that the absence of sufficient shade or wallowing holes would make their lives unbearable, but the extreme scarcity or even absence of predators and competing species would not hinder further evolution towards bigger sizes. Indeed, in West Africa today the lion is nearly extinct, and potentially competing species (Table 8.3) are very rare. The east and southern savanna buffalo, if well-protected, could also well become bigger under natural selection (Table 8.6).

Table 8.6 *Putative selection forces on body mass of the different forms of the African buffalo in the different habitats where they live.*

| | Heat management | Food management | Competitor management | Predator management | Overall selection |
|---|---|---|---|---|---|
| Forest buffalo | Selection to become smaller | Selection to become smaller | Stabilizing selection | **No** selection | Become smaller |
| Northern savanna buffalo | Selection to **become bigger** | Selection to **become bigger** | Stabilizing selection | Selection to **become bigger** | Become bigger |
| Cape buffalo | Selection to **become bigger** | Selection to **become bigger** | Stabilizing selection | Selection to **become bigger** | Become bigger |

We started this attempt to understand the differences between the forms or subspecies of the African buffalo with three storylines. We did not want to use the term 'hypothesis' because in science a hypothesis is a strong presumption preferably based on theory or a set of coherent observations. Too much is missing from the palaeontological records to formulate a proper hypothesis concerning the evolutionary (in contrast to genetical) relationship between the subspecies or forms of the African buffalo. The Popperian instrument of falsifying also is not in our toolkit, so we have to fall back on the concept of plausibility instead of falsifiability. We do this to stimulate research into the question of whether subspecies are ecologically (not classificatory) speaking meaningful entities without claiming 'proof' (see Walton, 1988, 2001), yet the concept of 'plausibility' may become more important in science than it was before (see Sinatra and Lombardi, 2020).

Storyline 2 is of importance here. It states that the original large buffalo *Syncerus acoelotus* was able to infiltrate the rainforest (perhaps at times when the forest was reduced to only gallery forest during one of the Glacial Periods; about 150 kyr; de Jager et al., 2021). Indeed, present-day forest buffalo mainly use small savannas in the rainforest, which savannas have been shrinking in size during the Holocene (Tutin and White, 1998). Secondary dwarfing took place there and the subspecies *S. c. nanus* arose. At times when the rainforest nearly disappeared (e.g. during the Last Glacial Maximum), hybridization took place with *S. c. aequinoctialis* leading to the form *S. c. brachyceros*. The further west one travels, the lesser the imprint of *S. c. aequinoctialis* is expected to be visible in *S. c. brachyceros*, leading to a cline. So, how plausible does it sound that dwarfing of the descendants of *S. acoelotus* took place in the rainforest but not in the savanna? Table 8.6 summarizes our feeling that dwarfing (or better stated: miniaturization) would be under positive selection. The genetics of both dwarfing (Boegheim et al., 2017) and miniaturization (Bouwman et al., 2018; see also Boden, 2008) are well understood in cattle and other species. 'Dwarfing' is often associated with negative effects, but miniaturization much less so. Miniaturization has been observed in Asian buffalo (weighing only 200 kg: Anilkumar et al., 2003) and in cattle (mini zebu's weighing only 150–250 kg: Boden, 2008; Porter et al., 2016). Selection can result quickly in small forms (Miniature Texas Longhorns, n.d.).

Why would we posit the notion that *Syncerus caffer brachyceros* could be viewed as a 'hybrid (sub-)species'? There are a number of reasons to think so. The first is that when the present-day Sahara was a savanna,

other species of buffalo existed there, namely *S. antiquus*, where it lived with the now extinct *Equus mauritianum* and the white rhino (*Ceratotherium simum*). Because no fossil material of *S. c. brachyceros* (or *S. c. aequinoctialis*) is available, we do not know whether there was a zone to the south with *S. c. nanus*, a zone to the north with *S. antiquus*, and in between a zone with the two present-day subspecies (*brachyceros* and *aequinoctialis*). We do not find this very plausible because it assumes quite a lot. Intriguingly, the West African Guinea Savanna (between isohyets 1200 and 900 mm) and Sudan Savanna (between isohyets 900 and 600 mm), presently the habitat of *S. c. brachyceros* and *S. c. aequinoctialis*, appears to be largely man-made and rather recent due to people bringing slash-and-burn cultivation and fire management to this zone (Klop and Prins, 2008). If we are correct, then *S. c. brachyceros* especially, and to a lesser extent *S. c. aequinoctialis*, can be viewed as hybrid 'species' similar to the European wisent (or European bison, *Bison bonasus*). Indeed, based on mitochondrial DNA, the European wisent nests more strongly with *Bos taurus* than with *Bison bison* (Bibi, 2013; Zuranoa et al., 2019); similar results were found using nuclear DNA (Druica et al., 2016). The scenario in this case is that wisent arose as a hybrid between the aurochs (*Bos primigenius*) and the Steppe bison (*Bison* [*Bos*] *priscus*; see Verkaar et al., 2004), even though not all geneticists agree. The modern *B. bison* may also be the result of hybridization between two subspecies of *B. antiquus*, namely, *B. a. antiquus* and a subspecies that evolved from *B. antiquus* into *B. a. occidentalis* (McDonald, 1981, p. 82). Presently, hybridization takes place between the lowland anoa (*Bubalus depressicornis*) and the mountain anoa (*B. quarlesi*) even though they are characterized by a very large divergence time of some 2 Myr (Kakoi et al., 1994; Tanaka et al., 1996) after they putatively immigrated into Sulawesi independently of each other (Takenaka et al., 1987). Similarly, a hybrid zone exists between the two different species of Asian water buffalo, namely, the 'river form' *B. bubalis* and the 'swamp form' *B. carabenensis* (Mishra et al., 2015; Kumar et al., 2020). Microsatellite data seem to show that these two buffalo 'species' were already separated some 1.6 million years ago (Ritz et al., 2000), while cytochrome-b data indicate a separation between 1.7 and 1 Myr (Schreiber et al., 1999). Nuclear data, underpinning their separation, also shows much introgression between these two forms (MacEachern et al., 2009). In other words, much precedent exists for thinking that hybridization can result in new forms or species in large buffalo-like animals, strengthening the plausibility of its occurrence at the root of the existence of the bush cow (*S. c. brachyceros*).

An important consideration here is that the Guinea Savanna and Sudan Savanna are to a very large extent man-made environments due to shifting agriculture, slash-and-burn cultivation and intense use of fire (see Sankaran et al., 2005; Klop and Prins, 2008; Laris, 2008). Grasses become quickly unpalatable when growing during the wet season, reaching heights of 2 m or more (see Penning de Vries and Djitèye, 1982; Olff et al., 2002). Further north lies the Sahel, but that is too dry for buffalo, and does not offer enough food for buffalo in the dry season (or for many of the East African grazers such as zebra; cf. Klop and Prins, 2008). To describe the influence of human-induced habitat changes on the incidence of hybridization, the botanist Edgar Anderson (1948) coined the phrase 'hybridization of the habitat'. Indeed, numerous hybridization events are the outcome of anthropogenic actions (Ottenburghs, 2021). In general, novel environments – whether induced by human actions or not – can offer opportunities for the evolution of hybrid plant species, as has already long been put forward regarding the recolonization of deglaciated areas after a glacial period (see e.g. Daubenmire, 1968; Young, 1970; Kallunki, 1976; Fredskild, 1991; Gussarova et al., 2008). A notable example involves the Arunachal macaque (*Macaca munzala*), a presumed hybrid between *M. radiata* and a member of the *M. assamensis/thibetana* group, which occupies a specialized ecological niche in mountain forests (Chakraborty et al., 2007). Similarly, the transgressive phenotype of the hybrid rodent species *Lophuromys melanonyx* allowed it to invade a new habitat zone (Lavrenchenko, 2008). These examples and additional cases of rapid hybrid speciation in other taxonomic groups (Comeault and Matute, 2018; Ottenburghs, 2018; Nevado et al., 2020) indicate that the hybrid origin of the *brachyceros* is a plausible storyline.

## Conclusion

O'Brien and Mayr (1991) provide guidelines to help think about subspecies: 'Members of a subspecies share a unique geographic range or habitat, a group of phylogenetically concordant phenotypic characters, and a unique natural history relative to the subdivisions of the species.' We believe that we have made the case that this applies to *S. c. nanus* and *S. c. caffer*. We are less convinced about a distinction between *S. c. brachyceros* and *S. c. aequinoctialis*; although they fall into two mtDNA clades, their nuclear DNA does not reveal distinction (Chapter 3). We do not believe that *S. c. matthewsii* should be maintained as a possible subspecies because phenotypically it is not very different from *S. c. caffer*

and it also does not have a unique natural history. O'Brien and Mayr (1991) continue with 'Because they [the subspecies] are below the species level, different subspecies are reproductively compatible … are normally allopatric.' Indeed, evidence of genetic barriers between *nanus* and *caffer* is insufficient, which thus precludes independent species status for these two forms. There is in effect gene flow between *nanus* and *caffer* because there are mtDNA haplotypes that are characteristic in *nanus* found in *caffer* and vice versa (Smitz et al., 2013), and there is thus successful hybridization. O'Brien and Mayr (1991) end by stating that 'most subspecies will be monophyletic, however they may also derive from ancestral subspecies hybridization'. We believe that this is happening and has happened with *nanus* and *brachyceros*, but also with *aequinoctialis*. This then would be our motivation to lump the northern savanna buffalo into one subspecies like Smith (1986) has done previously. In our weighing, we included not only genetic but also ecological and historical reasoning as advocated by O'Brien and Mayr (1991). Because the Syrian Mameluke geographer Ibn Fadl Allah al-Umari was the first to write about these buffalo around 1337 CE (737 AH) (Levitzion and Hopkins, 2000, p. 264), we propose to name it in his honour *Syncerus caffer umarii*, but will leave a formal decision of course to a taxonomist.

The selection forces for the forest buffalo appear to be very different than for the savanna buffalo; the former are expected to further dwarf if that is genetically possible, while the latter would benefit under natural conditions to increase in size. The critical environmental factor is that they should continue having access to sufficient water for cooling. The human impact had been negligible on all forms of buffalo until the relentless expansion of arable agriculture, monopolization of water resources and the widespread availability of steel for snares and gin traps. Indeed, if humans were to go extinct, there would be a bright future for buffalo.

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