3 · *Taxonomic Status of the African Buffalo*

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Introduction

Because the African buffalo (*Syncerus caffer*) exhibits extreme morphological variability across its range (e.g. body size and weight, coat colouration, horn size and curvature), its taxonomic status has been the subject of many debates over time (reviewed in Chapter 2). The most recent update of the IUCN Red List recognized four African buffalo subspecies: *S. c. nanus*, *S. c. brachyceros*, *S. c. aequinoctialis* and *S. c. caffer*. Two genetic clusters can be identified based on maternally inherited mitochondrial DNA (mtDNA): one cluster encompassing the three subspecies from West and Central Africa (*S. c. nanus*, *S. c. brachyceros*, *S. c. aequinoctialis*); the other cluster consisting of the *S. c. caffer* subspecies from East and Southern Africa. The amount of genetic differentiation between these two clusters is typical of that of subspecies in other African bovids (Smitz et al., 2013). The same picture emerges with the paternally inherited Y-chromosome: three haplotypes (genetic variants) among West and Central African populations and one unique haplotype among East and Southern African populations (Van Hooft et al., 2002). Thus, with both mtDNA and Y-DNA *S. c. caffer* emerges as a distinct genetic cluster. The only exception may be *S. c. caffer* in Angola and Namibia. There, two mtDNA haplotypes and one Y-haplotype typical of West and Central Africa were observed (Van Hooft et al., 2002). However, these latter observations should be taken with caution considering these genotypes were derived from zoo animals.

Nevertheless, the spatial genetic pattern based on microsatellites (polymorphic genetic markers residing on non-sex chromosomes) is different. Among *S. c. caffer* populations, genetic variation is mainly clinal (Van Hooft et al., 2021). This clinal variation is characterized by a linear relationship between genetic distance (pairwise F_{ST}: the proportion

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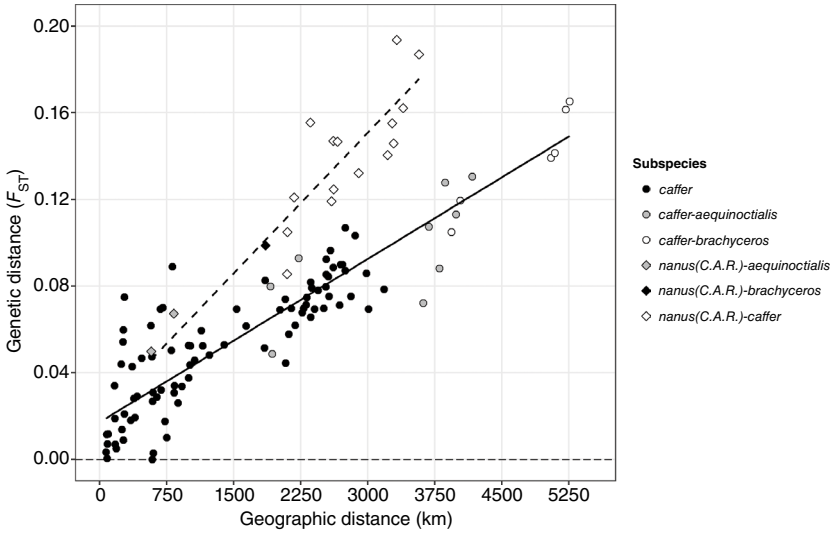

Figure 3.1 Increase of pairwise F_{ST} with geographic distance (isolation-by-distance): among savanna-dwelling populations (i.e. excluding *S. c. nanus*): $R^2 = 0.83$ (solid line), between the *S. c. nanus* population from Central African Republic (C.A.R.) and the savanna-dwelling populations: $R^2 = 0.85$ (dashed line). Regression is weighted by 'square root of number of genotyped individuals per population pair X number of shared genotyped microsatellites per population pair'. Only population pairs are included with weight >102 in case of savanna-dwelling populations and with weight >48 in case pairs including the *S. c. nanus* population from C.A.R. In all cases, sample size per population ≥5 with number of microsatellites per population pair varying between 8 and 18. Data from Van Hooft et al. (2021) and unpublished data from Smitz et al. (2014b). Genotype data came from different laboratories, which when also coming from the same population permitted allele alignment by matching each microsatellite's allele frequencies while preserving size order (Van Hooft et al., 2021).

of the total genetic variation per population pair, that is between the two populations) and geographic distance, a pattern also known as isolation-by-distance, with the latter explaining as much as 78 per cent of the variation. This clinal pattern even extends to the populations of *S. c. brachyceros* and *S. c. aequinoctialis*, which like *S. c. caffer* also occur on savannas ($R^2 = 0.83$, Figure 3.1). Predicted pairwise F_{ST} gradually increases to ~0.15 at 5,300 km. Genetic distances involving the *S. c. nanus* population from the Central African Republic (Ngotto Forest Reserve) are also clinal ($R^2 = 0.85$, Figure 3.1), but twice as large in comparison to those involving only savanna-dwelling populations. This is probably due to a combination of low population density and reduced gene flow

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in rainforests compared to savannas. The only exceptions to these clinal patterns are populations with elevated F_{ST} values ($F_{ST} > 0.2$ beyond 2000 km distance; not shown in Figure 3.1) due to small size, isolation or a bottleneck, as observed with the populations from HiP (Hluhluwe-iMfolozi Park, South Africa; Van Hooft et al., 2019), Nairobi National Park (Kenya; Heller et al,. 2010) and Lékédi Park (Gabon).

Thus, at the level of neutral genetic markers in savanna-dwelling buffalo, neither the subspecies nor buffalo in the contact zones between them appear as distinct genetic clusters. As has been proposed in human genetics (Handley et al., 2007), one should abandon the traditional island model of population differentiation (treating populations as discrete random mating units) when explaining genetic structure in relation to historical gene flow (in the case of African buffalo before 1870). The observed linear relationship between genetic and geographic distance indicates that, historically, the savanna-dwelling buffalo populations constituted one large metapopulation with continuous gene flow over limited distance, in which 'limited' is defined as less than the lifetime dispersal distance.

The clinal pattern of genetic variation seems to be in conflict with studies that describe population genetic structure as discontinuous or clustered (Heller et al., 2010; Smitz et al., 2014a). It is possible that genetic clusters are an artefact of a discontinuous sampling scheme (Pritchard et al., 2000; Kopec, 2014). On the other hand, clinal and clustered depictions of genetic structure are not necessarily mutually exclusive (Handley et al., 2007). Genetic structure may also be described using a synthetic model, in which most population differentiation can be explained by gradual isolation-by-distance, with some discontinuities due to historical or recent geographic barriers (e.g. human-induced population fragmentation). However, clusters probably explain only a small fraction of the variation when there is a strong underlying pattern of isolation-by-distance; a fraction which in case of African buffalo is no more than 0.17 (1 minus R^2) (Handley et al., 2007).

The question of how many subspecies of buffalo can be recognized depends on the subspecies concept to which one adheres. If one merely relies on the notion of heritable geographic variation in phenotype (Patten, 2015), then almost any number of subspecies can be justified, as long the phenotypic traits used in subspecies designation are heritable and confined to specific areas. On the other hand, if one uses partial restricted gene flow and clearly delineated genetic clusters as additional criteria (Haig et al., 2006), then no more than three subspecies may be recognized: (1) *S. c. caffer* of the East and Southern African savannas (a separate cluster with

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mitochondrial and Y-chromosomal markers), (2) *S. c. nanus* of the West and Central African rainforests (restricted gene flow indicated by relatively high F_{ST} values) and (3) the northern savanna buffalo of the West and Central African savannas (currently assigned to two different subspecies: *S. c. brachyceros* and *S. c. aequinoctialis*). Prins et al. (Chapter 2) propose to name the latter *Syncerus caffer umarii*. Considering that *S. c. nanus* is not phylogenetically distinct from the northern savanna buffalo, one may even argue that all of the buffalo from West and Central Africa, irrespective of habitat, should be lumped into one subspecies as suggested in Smitz et al. (2014a). Irrespective of subspecies designation, which appears quite subjective according to the selected criteria and to the interpretation of the obtained results, the West and Central African buffalo should be recognized as a separate Conservation Unit (see next section).

Phylogeography and Evolutionary History of the African Buffalo

Phylogeography is the study of the geographic distribution of genetic lineages (Avise, 2000). As mentioned above, the African buffalo is genetically divided in two main lineages, one encompassing the buffalo distributed in West, Central and possibly southwestern Africa (Angola and Namibia; hereafter called the WC cluster) and another one including buffalo roaming East and southern African savannas (hereafter referred to as the ES cluster). This clear genetic discontinuity has led to the recognition of two management units (Moritz, 1994) deserving specific conservation efforts (Van Hooft et al., 2002; Smitz et al., 2013). Each management unit is characterized by a unique evolutionary history, which can be investigated using molecular tools. In fact, genomes retain records of demographic changes and evolutionary processes that have shaped present-day diversity within the species. Reconstructing the species' evolutionary history allows us to determine the effect of recent and past climatic events, as well as of human activities. Over the last decades, some congruent results were obtained when investigating the signature left in the buffalo genomes by past and recent events using various DNA markers (i.e. mtDNA fragments, Y-chromosomal loci, autosomal microsatellites, mitogenomes and whole genomes). In this section we review the present understanding of the effect of these events in a chronological way (from the past to the recent). However, note that inferring history and linking demographic changes to specific historical events can hardly be achieved with more than some thousand years of certainty.

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The species is widespread in sub-Saharan Africa, physically able to disperse through a wide range of habitats, from sea level to the limits of forests on the highest mountains (Sinclair, 1977; Prins, 1996) and morphologically able to rapidly adapt in evolutionary terms to different ecological conditions (Smitz et al., 2013). Its distribution is limited by the availability of permanent sources of water. Drought is considered to be a major cause of ungulate mortality, with short-term rainfall fluctuations proven to significantly affect both vegetation indices and buffalo dynamics (Dublin and Ogutu, 2015; Abraham et al., 2019; see Chapter 7). Additionally, while it was long believed to be strongly philopatric, forming large aggregations remaining on separate home ranges and with few interchanges (male-biased dispersal; Estes, 1991; reviewed in Chapter 6), according to collaring studies in Botswana, 5 of 75 (7 per cent) female buffalo showed long-distance movement, with distances from 120 km to over 200 km, and 5 of 32 (16 per cent) herd-switching. The latter is supported by a high mtDNA diversity among females within herds in Kruger Nation Park (KNP, South Africa). Consequently, the African buffalo shows high gene flow over evolutionary timescales, reflected by low genetic differentiations between populations within lineages (Simonsen et al., 1998; Van Hooft et al., 2002; Smitz et al., 2013; de Jager et al., 2021) – in fact, the lowest among African mammals studied, as reviewed in Smitz et al. (2013) and Lorenzen et al. (2012).

During the Pleistocene, oscillations in the precipitations governing the physiography of Africa – the major vegetation zones being savannas and tropical forests (Moreau, 1963; Dupont and Agwu, 1992; DeMenocal, 2004; Dupont, 2011; Lehmann et al., 2011; Staver et al., 2011) – are believed to be the main drivers of population expansion in savanna species during cool and dry phases (interpluvials/glacial) and contraction during wet and warm phases (pluvials/interglacials). This is in agreement with the fact that congruent phylogeographical patterns across taxonomic groups and trophic levels have been observed, suggesting similar forces shaped species' evolutionary histories (reviewed in Lorenzen et al., 2012). Repeated shifts of the two major vegetation zones facilitated the emergence and evolution of many bovid taxa (Vrba, 1995; Bobe et al., 2002; Bobe and Behrensmeyer, 2004). These considerable fluctuations have promoted divergence within and between the two buffalo lineages (WC versus ES clusters); the latter north-south structuration has been identified across multiple species associated with savanna ecosystems (Lorenzen et al., 2012). Periodic separation by an equatorial forest belt during moist pluvials could have acted as a barrier to gene

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flow (populations isolated in refugia), with secondary contacts during dry interpluvials (Arctander et al. 1999; Van Hooft et al., 2002; Lorenzen et al., 2012). The overlapping or suture zone between WC and ES buffalo clusters is proposed to be located in East Africa (Smitz et al., 2013), a region identified as a melting pot of long-diverged lineages across many taxa – for example, the kob, *Kobus kob* (Lorenzen et al., 2007, 2012). Despite the lack of contemporary barriers to gene flow (supported by the aforementioned clinal genetic structure at autosomal microsatellites), lineages appear conserved, with female gene flow estimated to be in the order of no more than five mitochondrial genomes per generation since divergence (Smitz et al., 2013).

Some inferred demographic changes shaping the pattern of divergence and distribution of the species could be dated and linked to historical climatic, environmental and/or anthropogenetic events. The most ancient identified expansion pre-dated the above-mentioned divergence between the WC and ES clusters, and started approximatively one million years ago to continue until ~500 kyr (de Jager et al., 2021). This period was marked by a shift between arid and moist conditions toward less extreme cycles leading to the development of a more stable savanna environment, allowing for the expansion of the buffalo ancestor (see Chapter 2). The genetic divergence between the WC and ES clusters was dated to around 130–300 kyr, resulting from populations isolated in allopatry in savanna refugia (Van Hooft et al., 2002; Smitz et al., 2013). These particular core areas were characterized by long-standing savanna habitat enabling the continued survival of savanna-adapted taxa (Lorenzen et al., 2012). Because Pleistocene-dated fossils resemble buffalo of the present-day WC cluster, the ES cluster (or Cape buffalo) might have derived from a stock of savanna buffalo from WC (Gentry, 1978; Kingdon, 1982). Likewise, the forest dwarf buffalo (*S. c. nanus* – WC cluster) turned out to be an advanced form derived from savanna buffalo, rather than being the ancestor of all living African buffalo (Smitz et al., 2013; see Chapter 2). African buffalo refugia were purportedly proposed in present-day Uganda and Central African Republic, where present-day populations display the highest genetic diversities within the species (Smitz et al., 2013). Yet, both sampling size and species distribution coverage in West Central Africa have been limiting factors in all conducted studies, presumably linked to the difficulty of collecting material for DNA-based investigations from these regions. Further efforts are recommended to fill knowledge gaps, based on the use of a new generation of molecular markers made available by technological advances in the field of genome sequencing.

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The aforementioned refugia played an important role in the dispersal of the lineages. A first westward expansion event of the WC cluster after divergence occurred in the late to middle Pleistocene (~100 kyr) along two routes, into the forest belt and the Western Sahel region, hence adapting morphologically to colonize new habitats (Smitz et al., 2013). The latter can be associated with the shift from persistent rainforest in both dry and wet periods before ~220 kyr to its reduction and replacement by savanna after ~220 kyr (Dupont and Agwu, 1992; Dupont et al., 2000; DeMenocal, 2004). Unlike the WC cluster, the southward expansion of the ES cluster occurred after a core was retained in Eastern Africa, probably unable to colonize this part of the continent due to extremely arid conditions between 135 and 90 kyr. A demographic decline in the ES cluster was even identified around 100 kyr, proposed to be a consequence of a series of mega-droughts registered in East Africa around that time, to which the African buffalo is especially sensitive (de Jager et al., 2021). After aridity decreased, reaching near modern conditions around 60 kyr (Cohen et al., 2007; Scholz et al., 2007), the development of large savanna-type grasslands allowed for an expansion of the ES cluster around 50 kyr (Van Hooft et al., 2002; Smitz et al., 2013) or 80 kyr (Heller et al., 2012; de Jager et al., 2021). Another, non-exclusive hypothesis is that the expansion could have followed the extinction of the giant long-horned buffalo (*Peloveris antiquus*), which dominated savannas until the late Pleistocene, as supported by fossil data (Kingdon, 1982; Klein, 1995; Van Hooft et al., 2002; see Chapter 2). This expansion was concurrent with the expansion of humans between 80 and 10 kyr (Heller et al., 2012). It therefore refutes an adverse ecological effect of Palaeolithic humans (Heller et al., 2012). Finally, it is worth pointing out that the finding of *Syncerus*-like fossil records in Southern Africa pre-dating this expansion (Porat et al., 2010) might indicate multiple colonization–extinction events in the region, following habitat suitability (Smitz et al., 2013). Local loss of populations in Southern Africa and subsequent recolonization from an East core was also suggested for the hartebeest *Alcelaphus buselaphus*, the topi *Damaliscus lunatus* and the giraffe *Giraffa camelopardalis* (Arctander et al., 1999; Pitra et al., 2002; Brown et al., 2007).

Following this expansion phase, a strong signal of population decline was identified within the ES cluster, in the order of 75–98 per cent (Heller et al., 2008, 2012). This major decline was not detected in the studies of Van Hooft et al. (2002) and Smitz et al. (2013), although discrepant demographic signals can be obtained from different types

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of molecular markers and databases. This major bottleneck occurred around ~5000 years ago (Heller et al., 2008, 2012). The mid-Holocene aridification, marked by a pronounced transition from warm and wet (the Holocene Climatic Optimum – DeMenocal et al., 2000) to drier conditions around 4500 years ago (Marchant and Hooghiemstra, 2004; Burroughs, 2005; Kiage and Liu, 2006), was identified as a possible driver of the effective population size decline. In addition to the climate-mediated decline hypothesis, the explosive growth in human population size and their domestic bovines (the Neolithic revolution – Finlay et al., 2007; Scheinfeldt et al., 2010) and correspondingly rapid decline in buffalo populations from 5 kyr onwards, could represent an alternative explanation (Heller et al., 2012). Together, they could have driven humans, domesticated cattle and large savanna mammals into closer contact around remaining water sources, leading to ecological competition and possible spill-over of exotic diseases from cattle to buffalo. This two-phased dynamic (expansion/decline) was also observed in other drought-intolerant species, such as the savanna elephant *Loxondonta africana* and baboon *Papio cynocephalus* (Storz et al., 2002; Okello et al., 2008), indicating a community-wide collapse.

Various studies indicate that the African buffalo from Southern Africa have relatively high frequencies of deleterious alleles throughout their genome, which negatively affect male body condition and disease resistance (Van Hooft et al., 2014, 2018, 2019, 2021). These high frequencies are attributed to an underlying sex-ratio meiotic gene-drive system. Meiotic drivers are selfish genetic elements that, by distorting meiosis, favour transmission of the chromosome on which they reside. In the case of sex chromosomes, this results in distorted primary sex ratios, as observed in KNP and HiP (Van Hooft et al., 2010, 2019). High frequencies of deleterious alleles indicate that environmental stressors such as drought and diseases have been consistently acting as selective agents for long periods of time. Despite this, most populations of African buffalo seem to have been large in the recent evolutionary past and to be stable after their recovery from the rinderpest pandemic of 1889–1895. This seems to support the view, advocated by some population geneticists, that deleterious alleles and genetic diversity in general play a smaller role in ecology, at least with respect to demographics, than one might expect (Agrawal and Whitlock, 2012; Teixeira and Huber, 2021).

Note that overall, less is known for the WC cluster because available studies are limited by the sampling size and geographical coverage for this region, as well as by the type of DNA marker investigated, limiting

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the possible inferences (Van Hooft et al., 2002; Smitz et al., 2013). To our knowledge, two ongoing studies involving the investigation of genome-wide single nucleotide polymorphism (SNP) data and whole genomes (WGS) undertaken by the research teams of L. Morrison (University of Edinburgh) and of J. Michaux (University of Liège) might uncover some additional events which shaped the evolutionary history of the WC cluster.

Population Genetic Structure at Local Scale and Linked to Recent Events

The African buffalo has suffered important population losses during the last century, impacting all of the subspecies mentioned above. Of the more than 3 million buffalo that roamed the continent in the nineteenth century (Lessard et al., 1990), only around one million presently survive (Chapter 4).

Habitat loss and poaching are the main challenges currently threatening the species. Habitat loss can be due to anthropogenic factors (Alroy, 2001; Godfrey and Jungers, 2003; Surovel et al., 2005) or to climatic changes (Meijaard, 2003; Barnosky et al., 2004; Lovett et al., 2005; Vanacker et al., 2005), as for example the increasing drought observed in Africa since the 1990s (rain is the ecologically most important climate variable in most of Africa). The African buffalo, a species highly sensitive to drought (Ogutu et al., 2008), exhibits important climate-mediated population decline as demonstrated by a decrease in the Masai Mara population from 10,000 to 2400 individuals during the severe drought of 1993–1994 (East, 1999). This last factor was associated with other drivers like enhanced encroachments of pastoralists/cattle and commercial farms and changes in governance systems, which further aggravated the situation (Chapter 12).

Fragmentation of the natural habitat into small patches also endangers the populations by increasing genetic drift, resulting in loss of genetic diversity and consequently leading to a reduction in the evolutionary potential of the species (Frankham et al., 1999; Hedrick, 2005). For example, around 75 per cent of all buffalo (estimated to be around 900,000 animals) are currently located in protected areas (i.e. national parks (NPs) and game reserves; East, 1999), with many populations completely isolated each from another (Chapter 4). These reduced population sizes due to human-induced population fragmentation have a strong impact on local genetic diversity. In Kenya and Uganda, a significant correlation

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between park area and microsatellite heterozygosity (fraction of individuals with two different alleles per microsatellite) was observed, with populations in small parks (<400 km^2) having a genetic diversity reduced by ~5 per cent compared to the population of the Masai Mara–Serengeti ecosystem (Heller et al., 2010). This amount of reduction in genetic diversity was also observed among the buffalo from the Ngorongoro Crater, Tanzania (Ernest et al. 2012). In South Africa, genome-wide diversity in the populations from HiP (~4500 buffalo) and Addo NP (~800 buffalo) is 19 per cent and 31 per cent smaller, respectively, in comparison to the KNP population (~40,900 buffalo) due to historical population bottlenecks (de Jager et al., 2021). Other small isolated populations with reduced genetic diversity are those in Arusha NP (Kenya, ~1800 buffalo in the early 1970s; Ernest et al., 2012) and Campo-Ma'an (Cameroon, <100 buffalo; Bekhuis et al., 2008), which show ~15 per cent reduction in mtDNA diversity compared to nearby populations (Smitz et al., 2013). It is therefore safe to assume that genetic drift affects population in smaller conservancies more rapidly than in larger ones. It is also expected that this genetic erosion will become significantly more progressive in the near future (Heller et al., 2010). Suppression or restriction of gene flow by confinement into small areas could also have an ethological impact, disturbing the behaviour of natural dispersion in response to seasonal variations in food availability (Sinclair, 1977; Halley et al., 2002; Ryan et al., 2006; Heller et al., 2010).

The introduction of non-native species, such as domestic cattle, besides generating direct competition for natural resources, also poses severe problems due to the introduction of pathogens. Indeed, domestic cattle and African buffalo are related closely enough to cause considerable challenges in terms of disease transmission. It was notably the case of the rinderpest morbillivirus introduced in 1889 by a colonial military expedition to Ethiopia (Branagan and Hammond, 1965; Sinclair, 1977; Prins, 1996). The African buffalo has probably been one of the African species that has suffered most from this disease (extreme regional reductions in population density, paired to many local extinctions; Wenink et al., 1998), with the most severe collapse occurring in the 1890s when mortality rates estimated between 90 per cent and 95 per cent were registered over the continent (Mack, 1970; Sinclair, 1977; Plowright, 1982; Prins and Van der Jeugd, 1993; Shigesada and Kawasaki, 1997; O'Ryan et al., 1998; Winterbach, 1998).

Some studies investigated the impact of rinderpest epidemics on the genetic diversity of the African buffalo. Results contrasted between no

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reported genetic signature of a recent bottleneck (Simonsen et al., 1998; Van Hooft et al., 2000; Heller et al., 2008) to the observation of a population decline caused by the rinderpest epidemic (Heller et al., 2012; de Jager et al., 2021). Nevertheless, all studies still reported high genetic diversities (O'Ryan et al., 1998; Simonsen et al., 1998; Wenink et al., 1998; Van Hooft et al., 2000, 2002; Heller et al., 2008, 2012; Smitz et al., 2013; Smitz et al., 2014a; de Jager et al., 2021). Even though the continent-wide pandemic reportedly caused important buffalo mortalities (with death rates in some localities possibly as high as 90 per cent; Lessard et al., 1990; Estes, 1991; Prins, 1996; O'Ryan et al., 1998), the absence of a pronounced effect on the genetic diversity might result from a possible overestimation of the severity of the pandemic in terms of population decline, but also from a rapid population regrowth combined with high interpopulation gene flow, reintroducing rare alleles and distorting the genetic signal of bottleneck (Van Hooft et al., 2000; Heller et al., 2008). This is supported by the observation that survivors recolonized their range, being so productive that by 1920 the species was again numerous (Sinclair, 1977; Estes, 1991). For example, in the KNP, area survival estimates were off by at least a factor of 10, considering the high number of mitochondrial and Y-chromosomal haplotypes observed in the present-day population.

High genome-wide nucleotide diversity in KNP is indicative of a large long-term effective population size of ~48,000 individuals (de Jager et al., 2021). Because within-population nucleotide diversity is largely determined by the total size of a metapopulation, this effective population size is probably indicative for the subspecies as whole (Strobeck, 1987). The aforementioned linear relationship between genetic and geographic distance (Figure 3.1) indicates that this effective population size varies little between the different savanna-dwelling subspecies. However, effective population size is probably considerably smaller for the small *S. c. nanus* subspecies, considering the relative isolation and small sizes of the forest-dwelling populations as indicated by the relatively large genetic distances observed with microsatellites.

Conclusion

The evolutionary history of the African buffalo began a long time ago, between one million and 500,000 years ago. It started with an expansion throughout sub-Saharan Africa, probably during cool and dry phases (interpluvials/glacial) as these periods favoured the development of more

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constant savanna environments. Later, around 130–300 kyr, population isolations in savanna refugia led to an allopatric differentiation and to the appearance of two main genetic lineages (the WC and EC clusters). These lineages spread again from Central African refugia, in sub-Saharan Africa during the late to middle Pleistocene along different routes: into the forest belt and the Western Sahel regions, for the WC cluster, and in the south of the continent for the EC one. Following this expansion phase, a strong signal of population decline was identified within the ES cluster around ~5000 years ago. This decline could be linked to the mid-Holocene aridification of Africa, but also to the explosive growth in the population sizes of humans and their domestic bovines (the Neolithic revolution), which also happened during this period. In more recent times, during the last century, the African buffalo also suffered important population losses. Habitat loss and poaching are the main challenges currently threatening the species. Habitat loss can mainly be due to anthropogenic factors or, to a lesser degree, climatic changes. Other aspects like the introduction of non-native species, such as domestic cattle, besides generating direct competition for natural resources, also had a deep impact on the Africa buffalo's survival due to the introduction of pathogens.

Concerning the taxonomic aspect, genetic studies tend to propose either two (*S. c. caffer* of the East and Southern African savanna and *S. c. nanus*, in Western and Central Africa), or three (*S. c. caffer* of the East and Southern African savannas; *S. c. nanus* of the West and Central African rain forests; and *S. c. umarii* in the savanna buffalo of the West and Central African savannas) subspecies. However, irrespective of subspecies designation, which appears quite subjective, the Eastern and Southern populations, the West and Central African forest buffalo and the West and Central African savanna buffalo should be recognized as three separate Conservation Units. Indeed, the global conservation status of the West Central African forest buffalo is not as good as that for the West Central African savanna buffalo (Chapter 4). Its conservation context is also quite distinct from that of the West Central African savanna buffalo. A particular conservation status for the forest buffalo group is therefore needed.

From a genetic point of view, the main challenges for the conservation and management of the African buffalo are the development of new genetic markers, such as the study of whole-genome sequences, which will give an even more precise information concerning the evolutionary history of the African buffalo and the relationships among the different

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conservation units. The comparison of neutral as well as selective genetic traits will also help to better understand the impact of artificial hybridization among different African buffalo morphotypes, which are developed in some areas to obtain particular hunting trophies (in the frame of game farming activities). In a more general context, another important challenge will be to promote the integration of genetic studies in conservation practices (i.e. important to retain high genetic diversity and gene flow for long-term conservation – and better consider the impact of habitat fragmentation and land use and major drought events).

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