

17 • *Knowns and Unknowns in African Buffalo Ecology and Management*

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On Knowledge

The definition of ‘knowledge’ is ‘a justified true belief’. Philosophers of science took a few centuries to arrive at this definition. The reasoning on which it is based is that knowledge is a ‘belief’ because a belief is defined as ‘conviction of the truth of some statement’ and is related to the verb ‘to believe’, which means ‘to hold something as true’ or ‘to give credence that something is true’. Because science does not deal with revelations or their interpretation, the justification of holding a particular belief can only be found in evidence, which thus makes it a ‘true belief’. Finally, as many things are seen by people and taken as evidence (even if not true – think of Cold Fusion), the belief and the evidence for it must be ‘justified’. Justification is found in an entire corpus of other, related, evidence.

Ecologists have been studying the African buffalo in the wild for about 70 years. Before that time, most knowledge came from hunters, and with hindsight it is reasonable to assume that the information so gathered was often more closely related to storytelling than to what we consider science. Prins and Sinclair (2013) and Cornélis et al. (2014) provide good recent summaries of what we think we know about the African buffalo. New knowledge added since the publication of these works is reported in the different chapters of the present book. We dare to assert that with this book and all of the publications referred to in it, the African buffalo is now the best-known animal of all Bovidae, so even better known than the American bison (*Bison bison*), the European wisent (*B. bonasus*) or any antelope, wild sheep, or goat. Are there other terrestrial wild mammals that are better known than the African

buffalo? We believe that two or three species can compete for that honour, namely the red deer (wapiti, American elk; *Cervus elaphus*), the white-tailed deer (*Odocoileus virginianus*) and, perhaps, the mule deer (*O. hemionus*). The white-tailed deer is said to be the most studied large mammal in the world (Hewitt, 2011). Many books have been published on this species, but, like for the mule deer, most are on its management for hunting. However, the knowledge gathered on reindeer (*Rangifer tarandus*) (Leader-Williams, 1988; Forbes et al., 2006; Tryland and Kutz, 2019) and especially red deer has contributed much more to science, as exemplified by Clutton-Brock et al. (1982). The other mammal species that has been of great significance for science is the elephant seal (*Mirounga angustirostris*; Le Boeuf and Laws, 1994; Le Boeuf and Le Boeuf, 2021). Yet of all these species, the African buffalo may present the biggest challenge because of its intricate relationships with domestic cattle in its network of diseases and parasites.

However, after exulting and crowing about how good we, students of the African buffalo are and have been, we would like to identify the knowledge deficits that remain. Our aim is to bring our science of ‘nyatology’ (from ‘Nyati’ = buffalo in kiSwahili and other Bantu languages) to such a level that it morphs into deep-seated contributions to the theory of evolutionary ecology, behavioural ecology, functional ecology, disease ecology and, perhaps, biology. Too much of our ‘nyatology’ remains basically descriptive and is, at best, testing hypotheses derived from more general science. Yet we believe that this amazing species, comprising phenomenally robust and well-adapted individuals with a social organization so intricate that it approaches eusociality, has more in store for us to learn, and its students will be able to generate hypotheses that can be tested on other organisms. Indeed, the house mouse (*Mus domesticus*) or the fruit fly (*Drosophila* spp.) may be wonders of adaptation too, but they became model organisms probably more as historical accidents than because of their wonderful resistance against diseases, their enormous distribution associated with complicated clinal variations in (eco-)morphs and richness of genetic patterning, or their social organization. So, where are the knowledge deficits that we must fill? To identify the holes in our knowledge, we surveyed this book’s authors, who collectively may be the most knowledgeable group of scientists and practitioners concerning the African buffalo alive (Figure 17.1).

Former Secretary of Defence of the United States of America Donald Rumsfeld once made a famous distinction between the different sorts of knowledge that one has. He said on 12 February 2002, ‘There are



Figure 17.1 Four African lions about to kill a juvenile male of Cape African buffalo, Mana Pools National Park, Zimbabwe. © Alexandre Caron.

known knows; there are things we know we know. We also know there are known unknowns; that is to say we know there are some things we do not know. But there are also unknown unknowns – the ones we don't know we don't know ...it is the latter category that tends to be the difficult ones'. We scientists are very good at reporting on 'known knows'. This book and earlier publications such as those of Sinclair (1977), Prins (1996) and the many, many good papers on the African buffalo (check all references in this book) offer a wealth of information about what we know on African buffalo. However, what about the 'known unknowns' and 'unknown unknowns'? And we would like to add a category, namely, 'unknown knows' – which we posit refers to sound scientific knowledge that appears to have been forgotten. Too many scientists do not read scientific papers that are older than 10 years or so, or they only read abstracts, and knowledge that used to be in the scientific domain thus tends to fall out of it. This is called 'knowledge decay'. The term does not describe the process through which knowledge becomes outdated, but rather one through which knowledge is forgotten.

On purpose, we have not formulated ‘hypotheses’ in this chapter for several reasons. We believe that what we need most is ‘descriptive ecology’ and ‘natural history’ (see Prins and Gordon, 2014; Gordon and Prins, 2019), while the use of storylines (linked to the assessment of their plausibility) probably offers better heuristic tools to approach best understanding (see De Jong and Prins, 2023; Prins and Gordon, 2023). The following knowledge deficits were identified in a process of questioning the collective of authors who contributed to this book.

Known Unknowns – These Are the Next Research Questions Sitting in the Backs of Our Minds

These research issues represent, relatively speaking, low-hanging fruit – others already have given them much thought, allowing one to delve deeper. The following thoughts and ideas were shared among us, which we have collected under a suite of subsections.

Natural History, Climate Change and Conservation

1. As compared to the Cape buffalo from the area ranging between Kenya and South Africa, precariously little is known about the buffalo ranging between Senegal and Sudan. Perhaps the only exception is the work of Cornélis et al. (2011), and only little is known on forest buffalo despite the work of especially Korte (see Cornélis et al., 2014) but also of others (e.g. Bekhuis et al., 2008).
2. In a number of countries where African buffalo still occur or did occur in the recent past, the respective ‘departments of wildlife’ (whatever their name) are not allocated sufficient funds to survey animal populations on a regular basis. In some of these countries, trend analyses and/or population estimates are thus frequently not very reliable. Offtake quotas are ideally set on reliable and precise population estimates (from which reliable and trustworthy trends can be deduced), and thus may not be set correctly (see e.g. Hagen et al., 2014; Milner-Gulland and Shea, 2017; see also Pellikka et al., 2005; Morellet et al., 2007). Additionally, offtake quotas may be set on the wrong premise of population stability (Chapter 5). Does this uncertainty in the data and the application of the wrong models negatively impact some local populations of buffalo?

3. The IPCC (2022) predicts that temperatures will rise in coming decades over much of the African buffalo's range. Heatwaves are on the increase (ACSS, 2021), implying that heat stress for African buffalo (and other large mammals) may become severe. The search terms 'heat stress' associated with 'cattle' or 'water buffalo' yield thousands of publications. Much more research on the thermal ecology of the species is needed (see Hetem et al., 2009, 2010, 2013; Shrestha et al., 2012, 2014; Fuller et al., 2014, 2021; Strauss et al., 2016).
4. Increasing CO₂ levels could lead to a strengthening of the woody layer, resulting in an inexorable march to a thicker tree layer competing strongly with the grass layer (e.g. Bond and Midgley, 2000; Kgope et al., 2010), although the simplicity of the mechanism has been contested (Gosling et al., 2022; Raubenheimer and Ripley, 2022). Regardless, many former grasslands in African savannas have densified. In extreme circumstances where grazing pressure is high and the grass layer is stressed, a drought pushes grazers such as buffalo into a marginal space for survival. Most past research findings may hence no longer be applicable.
5. Even though there is much arm-waving about climate change and its impact, there is a significant lack of fundamental knowledge on the habitats of the African buffalo (in the Sahel, the savannas of East and Southern Africa, but also in the rainforests).
6. What are the exact workings of the transcription of DNA, the translation of RNA and the functionality of proteins in relation to the development and physiology of the African buffalo? In cattle, much progress has been made (see e.g. Drackley et al., 2006; Beerda et al., 2008; Kirkpatrick, 2015; Cesar et al., 2016; Barshad et al., 2018). There are some intriguing findings by Van Hooft et al. (2007) that have yet to be clearly explained (Van Hooft et al., 2018). Indeed, many techniques are already in place (see e.g. Smits et al., 2016) for tackling this.
7. For the forest buffalo, there may be more unknowns than for the Cape buffalo. As shown elsewhere in this book, it appears as if the forest buffalo evolved later than the savanna buffalo. Yet there are many gaps in our knowledge concerning gene flow between the different forms. Too much credit is given to subjective assessments of horn forms or the proportions of calves with reddish coats versus blackish ones. The exchange of individuals between groups of forest buffalo is an identified knowledge gap.

Ecology

1. Research is needed to understand the causal factors underlying behavioural avoidance between buffalo groups. Many studies have shown very little spatial overlap between neighbouring groups of buffalo, but the mechanism by which segregation is maintained remains poorly understood (scent marking, perhaps). Research is also needed that goes beyond mere speculation about the functionality of this spatial segregation of groups. One can think, of course, about competition for resources or the prevention of transmission of pathogens. However, exhaustive systematic reviews of the literature to discover whether competition has been proven show a lack of evidence for interspecific competition (Prins, 2016; Schieltz and Rubenstein, 2016) but good evidence for intraspecific competition (see e.g. Prins, 1989b).
2. Information is needed on male contact patterns – males could be important vectors of pathogens at the population level due to group affiliation behaviour between groups of females and bachelor groups. More work should focus on understanding the movements of adult males (e.g., how often they encounter mixed groups, how long and where). Such work also is needed to better understand the socioecological organization of the species (see also Prins, 1989a). For forest buffalo, this lack of knowledge is even more prevalent.
3. Research is needed on how extractive industries (notably, for instance, mining gold using mercury) might impact buffalo and their habitat across their range. It is known that extractive industries influence the habitat (e.g. Foster et al., 2019). In water buffalo, health effects have been measured (e.g. Singh et al., 2018), in cattle as well (e.g. Ranjan et al., 2008; Pati et al., 2020), and mining has been shown to have unexpected consequences for African elephant distribution (Sach et al., 2020). The effects of gold mining using mercury have been studied in South America (e.g. Markham and Sangermano, 2018), North America (e.g. Eagles-Smith et al., 2016) and the Arctic (e.g. Dietz et al., 2013). It appears that most problems can be expected in aquatic environments (Basu et al., 2018), but because buffalo are closely tied to water, the problem may be large.
4. The expansion of cotton growing (most of it *Gossypium hirsutum*, a native to Central America), especially in West and Central Africa (but also elsewhere in Africa), is a threat especially to the northern savanna buffalo because cotton appears to thrive where this buffalo form has its native range. Cotton growers rely heavily on

phytosanitary procedures, and the widespread use in Africa of highly dangerous chemicals prohibited by, for example, the Stockholm Convention since 2001 (see, for instance, Hagen and Walls, 2005) is putting at risk entire ecosystems but is very much understudied. The presence of these chemicals has been found in African animals living in ‘cotton regions’ (e.g. Aikpo et al., 2017; Houndji et al., 2020). Simple toxicology analysis would easily help to describe and measure the phenomenon, its magnitude, risk analysis, etc. (cf. Baudron et al., 2009).

5. Do buffalo use auditive clues in their communication? There is much we do not understand concerning hearing (see e.g. Benoit et al., 2020) in ungulates and there is much to learn about vocalization (e.g. Blank, 2021). Who would have thought that Sumatran rhinoceros (*Dicerorhinus sumatrensis*) have song-like vocalizations (Von Muggenthaler et al., 2003) or that giraffe (*Giraffa camelopardalis*) and okapi (*Okapi johnstonii*) use infrasound (Badlangana et al., 2011; Von Muggenthaler and Bashaw, 2013)? Given the fact that buffalo are generally so silent in the audible range for humans, one would not be surprised if they use infrasound too in their communication, especially in dense vegetation.
6. The mechanisms underlying collective movements, particularly at the time of group fission, are still unknown in buffalo. In other words, how do individuals decide to join one of the subgroups that form at the time of fission? The probability of following one of the subgroups could depend on the number of individuals already involved in the movement, regardless of their identity, social or affiliative relationships with individuals already moving or still at rest or their needs at the time. It would be interesting to examine decision-making during group fission in buffalo to measure the weight of social influence, compared to ecological influence (often examined), on group stability. This lack of knowledge appears to be even stronger in the forest buffalo.
7. Group decision-making has been studied in buffalo (e.g. Prins, 1996, p. 218 ff), but also in other mammals. Theory has been developed by for example Conradt and Roper (2003) and reviewed by Conradt and Roper (2005). See also Couzin et al. (2005). Much can be gained by further studying this under different ecological circumstances.
8. What is the effect of genetic relatedness on fission and fusion patterns (see Prins, 1996, p. 77 ff; p. 54 ff)?
9. What are the impacts of human disturbance on buffalo grouping patterns and social decisions? Do buffalo groups tend to be more

transient when encounters and disturbances from human activities are higher (human–wildlife interfaces versus within a park)? A testable idea could be that the higher the intensity and frequency of buffalo–human (including livestock) interactions, the higher frequency of the fission–fusion events, which would perhaps lead to smaller groups of buffalo closer to the borders of protected areas without fences (as compared to areas that are fenced). This ought to be controlled for possible competitive effects and poaching (see for instance Clegg, 1994; Leweri et al., 2022; cf. Dave and Jhala, 2011). One can also imagine that undisturbed animals maintain diseases within their own groups (e.g. Delahay et al., 2000), but disturbed animals do so less (cf. Smith and Wilkinson, 2003). Network analysis (e.g. Jacoby et al., 2012; Yin et al., 2020) will need to be applied to buffalo in disturbed and undisturbed situations.

10. What are the effects of poaching on social cohesion and fission–fusion patterns in buffalo? In the African elephant (*Loxodonta africana*), poaching has been shown to affect social patterns (e.g. Prins et al., 1994; Archie et al., 2008), but it is not known how poaching affects buffalo.
11. While more is understood about the functioning of key resource areas in animal migrations (e.g. Scholte and Brouwer, 2008; Moritz et al., 2010; Cornélis et al., 2011, 2014; Fynn et al., 2015; Moritz et al., 2015), much less is understood regarding how buffalo maintain themselves in areas without such green floodplains during the late dry season, for example in Kruger National Park (South Africa). Where do buffalo get sufficient (crude) protein and energy to support foetus development or peak lactation, which is even more demanding? Indeed, perhaps it can be found in the maintenance of grazing lawns (e.g. Vesey–FitzGerald, 1969; 1974; Cromsigt et al., 2013; Muthoni et al., 2014; Hempson et al., 2015). Gut morphology (e.g. Hofmann, 1973) is key to gaining a better understanding, as is the digestibility of the forage.
12. There is no understanding of the forage traits that buffalo select under different constraints and demands. In other words, the proximate factors in food selection are not understood, and a simple description, ‘roughage selector’, does not do justice to either the animals or the plants. What forage traits help buffalo to maximize intake of energy, protein and minerals for growth and reproduction, and what is the optimal height of the sward? What forage traits provide optimal reserves of forage for the early dry season, the late

dry season and during droughts? For example, we know that buffalo rather select for leafy, medium-height grasses such as *Themeda triandra*, *Digitaria eriantha* and the lawn-forming grass *Cynodon dactylon*, but what is it about these grasses that they like? Are the leaves more digestible, is it the leaf-to-stem ratio, is it the height and the bite size they offer for a tongue-sweeping forager, or some combination of the above? What are the traits of drought refuges – that is what level of leaf and stem toughness can they tolerate to avoid severe loss of body stores and starvation during droughts? See also below under ‘unknown knowns’, point ii.

13. Much modern buffalo research nowadays depends on darting animals, immobilizing them and fitting them with a measuring device (like a GPS collar). The assumption is that the animal, once given its antidote, ‘immediately’ reverts to its normal behaviour, finds its herd and assumes its normal social position. In human patients, the standards are set high, but much has still to be learned before one really knows what one does to memory (Borrat et al., 2018; Galarza Vallejo et al., 2019; Veselis and Arslan-Carlon, 2021). In companion animals, rather in-depth analysis is carried out to investigate what is done to the animals (e.g. Biermann et al., 2012; Reader et al., 2019; Abouelfetouh et al., 2021) and likewise in horses (e.g. Hubbell and Muir, 2006; Schaulvliege et al., 2019; Cock et al., 2022). Even in ruminants, precious little is known about the effects of key processes in the intact animal (e.g. Nicol and Morton, 2020; Waite et al., 2021). Research is urgently needed not only on the effects on the animals’ well-being, but also on their social behaviour and ranging behaviour.
14. Time series of total population alone may lead to erroneous predictions about the population without detailed knowledge of its age structure (Chapter 5). Without this detailed knowledge, incorrect deductions may be made about possible density-related effects or sustainable harvesting regimes. Nyatiologists need to find a way to more precisely identify the age of individuals in the field.

Disease

1. Some key resource areas, like floodplains, play a critical role in supporting buffalo over the late dry season. Yet, these areas also may harbour internal parasites, such as giant fluke (*Fasciola gigantica*) and the small fluke (*Dicrocoelium hospes*), and many other Platyhelminthes and Trematodes that can make cattle very sick if they are not properly

treated (e.g. Swai and Wilson, 2017). How do buffalo contend with liver flukes? Indeed, they are widely infected (Hammond, 1972), but in the Central African Republic, 12 of 33 inspected buffalo that were infested with both flukes had no apparent clinical signs (Graber et al., 1972). It is worrying to note that African buffalo that are not infected with such parasites are resistant to bTB (Ezenwa et al., 2010; c.f. Budischak et al., 2012), but it is gratifying to know that a grazing alternation between ruminants and hindgut fermenters may reduce parasite burdens (Odadi et al., 2011).

2. Do buffalo use natural plant chemicals to treat themselves for flukes and other parasites? Species that spring to mind are *Lippia javanica* and *Tarhonanthus camphoratus* (e.g. Koné et al., 2012; Kosgei, 2014; Hassen et al., 2022), and an evolutionary arms race may already have been on for a long time (see Beesley et al., 2017). By and large, however, evidence is scant and the literature abounds with ‘potential effects’ versus real ones, and ethnoveterinary storytelling instead of proven remedies.
3. What is the influence of group formation dynamics on pathogen dynamics in buffalo? Cross et al. (2004) and Wielgus et al. (2021) studied the influence of contact patterns within groups on pathogen dynamics. However, the aggregation of contact indices across time (e.g. per month) may lead to a misleading prediction of pathogen dynamics, as it ignores short-term interactions that change due to ecology and social behaviour (i.e. fission–fusion behaviour), which could have a significant effect on pathogen transmission patterns. See also Prins (1989a), Cross et al. (2012), Sintayehu et al. (2017a, 2017b) and Davis et al. (2018).
4. What are the veterinary standards for health, or good reproduction, in buffalo (or for other wild mammals)? Little is known about the normal parameter values of blood, liver or other tissue, and too often one must rely on cattle standards. However, African buffalo are not at all closely related to cattle or Asian buffalo (see Chapter 2), and it is thus not very plausible that cattle standards are informative for African buffalo.
5. More research is needed on foot and mouth disease (FMD), (bovine) tuberculosis ([b]TB) and brucellosis in free-ranging buffalo populations in unfenced ecosystems of central, eastern and western Africa; for the latter, these diseases pose public health problems as they are. Work on FMD in cattle in East Africa has shown how the model developed for this disease in southern Africa does not capture the whole story, nor do controls need to be so draconian with the options

of commodity-based trade. This potential for a different perspective in terms of management of landscape and animal agriculture/wildlife economy and tolerance/control of the disease needs to be investigated further. This will need an integrated programme of socioeconomic, cultural, environmental (including climate change), biodiversity, agricultural, political and ecological benefits of living with FMD. The work of Sintayehu (2017a, 2017b) provides good pointers.

6. Buffalo are resistant to a number of diseases, but the mechanisms for such resistances are not well known (for trypanosomiasis it remains quite unclear). Strikingly, even livestock-focused scientists have expressed little interest in understanding how to take advantage of such mechanisms in buffalo to apply to livestock production. Cases in point are: how are African buffalo capable of maintaining FMD on a permanent basis without expressing any symptoms (asymptomatic, or are they healthy carriers)? Applied to domestic artiodactyls, meat commercial trade rules would be reshuffled with new FMD policies. How do African buffalo resist African trypanosomes (genus *Trypanosoma*) and how can they live and thrive in areas that are heavily infested with the vector tsetse flies? What causes buffalo to be insensitive to CBPP (contagious bovine pleuropneumonia), Peste des petits ruminants (PPR), East Coast fever (ECF), heart water, babesiosis, streptothricosis/dermatophylosis and many other potential diseases which are so deadly for cattle? If we knew, we would not need to spend billions in yearly national cattle vaccination campaigns. Once again, African buffalo are probably not bovids (Chapter 2).
7. The role of closed (i.e. fenced) versus open (i.e. non-fenced) systems with bTB expression and prevalence needs further research, but again in areas other than the southern African region where much of the work has been done already. The nature of the force of infection in a mixed livestock–buffalo system needs to be explored in the context of different cattle breeds. The potential risks of buffalo zoonotic bTB transmission through hunting or sustainable use of infected buffalo herds (managed culling and processing) needs to be explored.

Management

1. What is the economic value of different land uses, namely, buffalo hunting (but also other species), agriculture (without buffalo but with livestock), conservation without hunting (but with buffalo) or any form of co-management including cattle and buffalo? Some work

has been done on this (e.g. Hearne et al., 1996; chapters in Hearne et al., 2000; Prins et al., 2000; Mayaka et al., 2005; Mwakiwa et al., 2016; Poshiwa et al., 2013a, 2013b; Mwakiwa, 2019). Yet these economic analyses seem to encounter difficulties in entering more freely formulated, data-free discourses espoused by many conservationists. The implications of this are severe (see e.g. Scholte et al., 2022). These economic value assessments could be placed in the context of climate change scenarios in the contexts of Africa too. This lack of knowledge is even more pertinent for the forest and northern savanna buffalo.

2. The often-positive role of controlled trophy hunting is insufficiently acknowledged by too many conservationists even though the Sustainable Use Principles of the Convention on Biological Diversity, in which its role is acknowledged, have been endorsed by all signatory States (COP Decision VII/12: see www.cbd.int/decision/cop/?id=7749). There is much disagreement between NGOs, but also for instance Kenya does not acknowledge the acceptability and effectiveness of hunting as a conservation tool (although it is under ministerial review). This contrast between different parties is intensified by a lack of reliable data on the impact of trophy hunting on wildlife. Much information on African trophy hunting is still available only as unpublished grey literature, and thus is difficult to access (for instance, Snyman et al., 2021; but see Baker, 1997; Hurt and Ravn, 2000; Lindsey et al., 2007; Schalkwyk et al., 2010) and more efforts should be done to collate information.
3. Even though theories of non-equilibrium dynamics were formulated some 40 years ago (e.g. Ellis and Swift, 1988) and have been tested for savanna systems (e.g. Gillson, 2004; Accatino and De Michele, 2016; Engler and von Wehrden, 2018), too much work on buffalo and their ranging still is not placed in that context. African rangelands necessitate management strategies that acknowledge the unpredictability of weather, markets and politics. Many pastoralists realize this (e.g. Mace and Houston, 1989; Mace, 1990), but many managers do not (e.g. Shawiah, 2016) and are thus overwhelmed by so-called black swan events. In modelling for game ranching, some progress has been made (e.g. Joubert et al., 2007; Dlamini, 2011), but this is still unsatisfactory. The collapse of live buffalo prices, for example, made many an enterprise in South Africa suddenly unprofitable, and the effects of drought reverberate for many years through a population's age structure (Chapter 5).

4. The effect of trophy hunting is contested, as evidenced by parliamentary debates in, for example, Great Britain in 2022. Intriguingly, parliamentary members from western countries allow themselves to take decisions that would affect an industry (and positive outcomes for local people) in Zimbabwe or Namibia without encouraging parliaments in those countries to discuss red deer (*Cervus elaphus*) hunting (a.k.a. ‘deer stalking’) in Great Britain. Much more research along the lines of Gandiwa et al. (2014) is called for to reveal the hypocrisy in this debate (c.f. Curtin, 1940, p. 162 ff). Yet typical examples of successful management, at least partly based on utilization, occurred in South Africa where trophy hunting has facilitated the recovery of bontebok (*Damaliscus dorcas*), black wildebeest (*Connochaetes gnu*), cape mountain zebra (*Equus zebra*) and, until recently, southern white rhino (*Cerathotrium simum*). Furthermore, in recent years, trophy hunting has also facilitated the recovery of the buffalo and its habitat in several hunting areas of Mozambique and South Africa. It can be thought, however, that trophy hunting has a negative impact on buffalo and other wildlife (cf., #2), and the necessary data should lead to clear evidence to move the debate away from only emotions.
5. The fact that large buffalo herds are mobile also means that they seldom ‘camp’ on a patch for a long period of time but are continually moving through different landscapes. This means that unlike selective water-dependent grazers, buffalo will utilize an area and then move on, thus reducing the chance of overgrazing (a function of time and not necessarily number – the vegetation needs rest according to a number of range ecologists). On fragmented (fenced) areas, excessive artificially supplied surface water results in high densities of sedentary water-dependent species (e.g. impala *Aepyceros melampus*) and less space for buffalo to move. So, where and when should animal control (including culling) be exercised? Even in unfenced areas, animal control may need to be implemented where water point provision has resulted in increased animal numbers due to their increased distribution, resulting in insufficient forage for animals during dry periods (obviously more critical in fenced or fragmented situations). The alternative is that the population is allowed to fluctuate with the prevailing resource conditions, that is a die-off in drought (of buffalo in a poor condition or recent weanlings). This may be appropriate in unfenced, ‘open’ situations, but is it acceptable in fenced areas where animals are unable to move widely? The tricky issue if the ‘laissez-faire’ option is pursued is the long-term effect on the

resources resulting from overgrazing (see Peel and Smit, 2020) apart from the ethical issues surrounding enclosing animals in fenced-off areas where droughts occur.

6. Horn size and horn shape drive much of the economics of buffalo breeding in South Africa and buffalo hunting. However, little is known about the genetics around the inheritance of horn size and shape. Equally little is known about the effects of levels of nutrition (macro- and micro-nutrients) or of hormones on horn growth. In other species, the situation is slightly better (e.g. big horn sheep *Ovis canadensis*: Reich, 2021; domestic sheep: Pan et al., 2018), but even in cattle this field is understudied.
7. What are the effects of nutrition on calving rate, calf birth and weaning weight, intercalving interval, milk production, and calf growth? Similarly, what are the effects of nutrition on milk composition? Milk quality comparisons should be carried out on the milk of wild buffalo and those living in different forms of captivity (game ranches, farms and zoos). Apart from the scientific importance of these questions, they could lead to the formulation of standards for the nutrient requirements for African buffalo based on real research on buffalo rather than on comparative nutrition from cattle or water buffalo (as done at present). This is a common problem in wildlife ecology, and nutritional knowledge is detailed enough only in deer to have proper feeding standards (e.g. Hynd, 2019, p. 263 ff; Anonymous, 2020; Kim et al., 2020; Bao et al., 2021).
8. The former Resource Ecology Group under H.H.T. Prins has most consistently reported on forage quality parameters as espoused by Peter Van Soest (so, apart from crude protein, potassium, phosphorus, digestibility parameters such as neutral digestive fibre (NDF) and acid digestive fibre (ADF), but also in-vivo digestibility using rumen fluid; Van Soest, 1994). An important caveat is that the rumen fluids came from domestic cattle, and that NDF and ADF calibration was never done with African buffalo (or other African large mammals with the exception of blue wildebeest). To really understand buffalo fitness or merely performance, it is of paramount importance to establish a captive group of buffalo on which depth nutritional measurements can be done. There is not much known about the need for micro-nutrients either, and there are no feeding standards.
9. The reliance on opioids for buffalo immobilization (and other large mammals) is still enormous. Veterinary authorities and regulators are making very little progress to get rid of these substances that are very

dangerous to animals and humans. Similarly, we know little of the health effects of the use of helicopters for the mass capture of buffalo herds, and we are not aware of reliable and stress-free alternatives under development.

Unknown Knowns – Evidence-Based Scientific Knowledge on Buffalo That We Appear To Have Forgotten

The collective of buffalo scientists did not signal many insights that were forgotten. Of course, this may simply mean that this older knowledge truly has been forgotten or, alternatively, that the corpus of knowledge that has been garnered over the last decades is well integrated into our present-day knowledge. Finally, it may indicate that we have collectively reached the verdict that much of the older knowledge does not meet our standards and is thus rejected. However, there are three knowledge domains that were flagged as probably forgotten.

- i. There was possibly good knowledge of pastoral systems in which buffalo also could find a place, or, alternatively, good knowledge of systems that could not accommodate buffalo. If this knowledge exists or existed, it is probably indigenous knowledge of integrated pastoral systems tolerant/intolerant of buffalo. If such indigenous knowledge (still) exists, it is extremely likely that it was never written down and thus would need a socio-anthropological approach. If this knowledge could be ‘tapped’, or somehow ‘resurrected’, it could provide valuable insights into future land use possibilities.
- ii. In contrast, the second field of knowledge that appears to have been forgotten can be found in the scientific literature. This relates to the bioenergetics of herbivores, including African buffalo. This field is, however, getting renewed attention (see e.g. Malishev and Kramer-Schadt, 2021). The great measuring systems of herbivores in metabolic chambers that were extremely important for understanding the physiology of ruminants (e.g. Blaxter, 1966; Moen, 1973) were hardly used for large African mammals. The great exception was the work of Martyn Murray. Careful feeding experiments of wild herbivores in captivity have been extremely rare (but see e.g. Murray and Brown, 1993) even though very important insights were obtained from shot individuals (e.g. Gordon and Illius, 1996). Much is known about domestic ruminants and small lagomorphs and geese, but we

know little about large tropical wild ruminants (see e.g. Illius and Jessop, 1996). Proper measurements of energy expenditure of wild ruminants are rare, and non-existent for African buffalo.

Work that was nearly forgotten concerned the horns of bovids as possible cooling organs (Taylor, 1966; see also Picard et al., 1999; Cain et al., 2006), which was not used in some important reviews on thermal adaptation (e.g. McKinley et al., 2018) or just mentioned in passing (e.g. Henning et al., 2018), and experimental evidence has hardly been collected since (see Knierim et al., 2015). Many other important works on thermoregulation and water usage from the early 1970s by scientists like Taylor (Taylor, 1969, 1970a, 1970b; Taylor and Lyman, 1972; Taylor et al., 1969) deserve to be integrated better into tropical ungulate ecology, and especially that of the African buffalo. The current generation is, however, exploring this (e.g. Hetem et al., 2009, 2010, 2013; Shrestha et al., 2012, 2014; Strauss et al., 2016).

Lastly in this category is the non-use of non-Anglophone published literature. A good case in point are the books of Riviere (1978), De Vries and Djitéye (1982) and Boudet (1984) on forage and foraging, and those on parasites (e.g. Troncy, 1982).

- iii. A third issue that has been flagged is the knowledge that is or was locked in the grey literature. Le Houérou's (1980) review of the knowledge on browse in Africa perhaps still has not been surpassed, but in July 2022 it had been cited only 149 times. Knowledge that remains hidden in the grey literature is especially relevant for wildlife inventories, game censuses and pest control reports in the archives of ministries or of consulting companies. All of this contributes to intergenerational amnesia and to the so-called 'shifting baseline syndrome' (e.g. Papworth et al., 2009; Soga and Gaston, 2009; Prins and De Jong, 2022).

Unknown Unknowns – Knowledge That, Once Obtained, Will Upset Our Present Thinking, Perhaps About African Buffalo, Perhaps About Ecology Evolution, or Aspects of Veterinary Sciences

We share these 'unknowns' without too much comment, but we hope that some of these thoughts may influence your own thinking and creativity.

Overarching in our thinking is Darwinism, which represents life as a continuous struggle, and which leaves scientists to think in terms of functionality and (negative) selection. To what extent does this paradigm cause us to overlook or misinterpret natural patterns and processes? The central tenet is that many features of an organism are not necessarily adaptive but may arise as a by-product of evolution, whatever their subsequent exaptive utility (Gould 1979; Gould and Lewontin, 1979). For example, it is assumed too easily that ungulates have coevolved with their food, yet the average duration of existence of a large mammalian chronospecies is about 1.5 million years (Prins and Gordon, 2023) while that of plant chronospecies is about 10 times longer (cf. Stanley, 1978). Plant families arise much slower than may be thought (see Harris and Davies, 2016). A trait-based approach may give false certainty (cf. Gordon and Prins, 2019), as many traits are interrelated and should not be viewed in isolation as promoted by the ‘adaptationists’.

Much selection took place during the bull market for ‘trophy animals’, where especially in South Africa much effort was spent on breeding bulls with massive horns. We know very little of the possible pleiotropic effects of genes (or of proteins; pleiotropy is the property of a single gene or protein to act in a multiplicity of ways). If these occur in African buffalo, they immediately throw a stark light on the basis of the selection for adaptability of traits (see previous paragraph). In cattle, these pleiotropic effects have now been discovered (see e.g. Bolormaa et al., 2014; Saatchi et al., 2014; Xiang et al., 2021). It is intriguing to learn that many QTL (quantitative trait locus, a section of DNA that correlates quantitatively with phenotype) effects are linked to weight at birth, age of weaning, weaning weight and carcass weight in cattle, and that pleiotropy is involved (Saatchi et al., 2014; Gershoni et al., 2021; Li et al., 2021; Tiplady et al., 2021; Widmer et al., 2021). One may also assume that these vital life-history parameters are governed in a similar way in African buffalo. With the effects of inbreeding on the genetic make-up of the species and calving and weaning percentages, the lack of connectivity between buffalo populations across the continent may thus affect the essential life history of the remnant populations. We would think that an effective and rapid first approach would be to assume that genes and QTLs that have been discovered in cattle could be looked for as candidate genes in African buffalo. A next question to address would be: after what level of ‘breeding’ is a buffalo no longer ‘natural’ and thus lost to conservation? (See Child et al., 2019). We thus advise much caution

when breeding for ‘maximum trophy value’, especially when the spill-back of animals into nature is not rigorously prevented.

Because African buffalo are very distantly related to other Bovini, and perhaps should not even be viewed as bovine but as boselaphine (Chapter 2), it is unlikely that ‘genetic pollution’ will occur at the level of interspecies hybridization. At the level of crossings between animals from widely different locations, as was done for the breeding of ‘better’ trophy buffalo (e.g. buffalo from Tanzania and Zimbabwe bred in South Africa), we know next to nothing. The genetic distance is not small (see Chapter 3). It is thus not clear really why IUCN voices concerns because the so-called intra-taxon biodiversity in reality may be minimal. Moreover, the suggested argument concerning the associated growing risk of diminishing the capacity of the taxon to resist ‘all sorts of shocks, either expected or not expected’ if buffalo from different regions within the same taxon (*Syncerus caffer caffer*) are crossed, is countervailed by concepts of hybrid vigour. In red deer (*Cervus elaphus*) this type of crossbreeding has been measured and evaluated (De Jong et al., 2020), but not in buffalo. We thus call for an in-depth evaluation of this issue, taking into account societal effects, conservation considerations and genetics.

This crossbreeding and ranching of African buffalo may, under as yet unknown circumstances, perhaps lead to a change of perspective of wildlife versus domestic animals. For 150 years, the Midwest of the United States was nicknamed the ‘Red Meat Republic’ (Specht, 2019; Dolan, 2021), yet it became possible to ‘bring back the bison’. What would happen if in some African cultures the societal perceptions of ‘bringing back the African buffalo’ took hold? Would that be possible through greater use of communal land rather than limiting protected areas? That would herald a societal earth slide away from seeing wildlife merely as ‘nyama’ (in kiSwahili, ‘game’ [alive] and ‘meat’ [the dead product]), towards a highly valued, iconic, cultural symbol for a form of African Renaissance. What if, as has rarely happened, an African leader actually embraced the conservation, sustainable use and pride of African wildlife?

This issue is important, because currently cattle populations are supplanting those of buffalo across much of Africa. In West and Central Africa this process nearly came to its fulfilment (Chapter 4; Scholte et al., 2022). The consequences of this replacement – from grazing by a once-dominant wild herbivore to its domestic surrogate – on soil, animal ecologies, resilience and animal and human health are totally unknown, although it has been speculated about through what was termed ‘holistic

management' (see Savory, 1983). Conversely, we also know next to nothing about the effects of compartmentalization of natural habitats and reinforcement (through protection) of buffalo enclaves on 'mini-ecosystems' (i.e. small protected or small game farms) from a variety of perspectives, including health and disease. There is much ecological thinking about the effects of isolation (and shrinking) of protected areas (based on Island Theory; e.g. Prins and Olf, 1998; Olf et al., 2002), but we are not aware of so-called 'before–after' evidence-based comparisons of ecosystem functioning during the process of this isolation and shrinking of protected areas with African buffalo.

The most extreme 'unknown unknown' could be this: what would happen if the proverbial black swan event occurred that conceivably could knock the whole wildlife system off its axis? From the experience of COVID-19, one may deduce that some horizon scanning to create anticipatory awareness (and perhaps the development of early warning systems) to build system recoverability after a major disturbance of nature and its wildlife is needed. Ecosystem managers should, we think, engage much more in scenario-thinking like big industry does (Chapter 18). We could possibly anticipate the effects of four major processes that take place in savanna Africa, namely rising CO₂ levels, changing weather systems, woody thickening which seem to suppress the grass layer and probably African buffalo numbers, and the human population explosion with associated land hunger and need for fuel wood. Buffalo may feature in the development of scenarios not only as a casualty but perhaps also as some ecosystem architect (Prins and Van Oeveren, 2014).

Perhaps one day we will finally come to grips with the fact that we do not know much about buffalo communication (Figure 17.2). We hardly understand their cognitive processes, cognitive maps, or communal decision making (cf. Prins, 1996). Like most mammals, it is very likely that their sense of smell is linked to their perception of other buffalo, the world, and their detection of predators and strangers. This world of pheromones and smells is for us a closed book, but the emergence of 'electronic noses' may open this world. Indeed, dogs have learned to understand our language (e.g. Grassmann, 2014; Reeve and Jacques, 2022), while we – with our 'superior' brains and AI tools – do not understand theirs (e.g. Harris, 2017). When will we then understand African buffalo?

The number of doctoral candidates needed to answer the research questions presented in this chapter must be in the order of 100 or more (as compared to the 30-odd so far); after they are done, we definitely will be closer to understanding this splendid species. But truly



Figure 17.2 Herd of West African savanna buffalo, Konkombri Hunting Area, Benin. © Christophe Morio.

understanding your partner and family takes a lifetime of study, and be honest – did you succeed?

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