

Chapter I

General introduction to the Kalahari natural environment, its ecological challenges and the research objectives

I. The beginning

“But when did it begin? Did it begin with the first expansion of modern humans out of Africa, 200–45 thousand years ago (kya), or 12–10 kya during the Neolithic Revolution when human populations began to increase rapidly as a result of the development of agriculture, or did it begin much more recently, even as late as during the 19th century industrial revolution?” (Cowie et al., 2022).

All three milestones seem to have contributed to the biodiversity crisis Earth is currently facing due to human-induced global changes, many considering it as the beginning of the Sixth Mass Extinction (Barnosky et al., 2011; Butchart et al., 2010; Cowie et al., 2022). For thirty years this has been acknowledged, yet changes to try and modify the trajectory are slow, stumbling over political, economic and cultural obstacles. Hence, let it be redundant claiming that effective conservation efforts and land use management measures, amongst other avenues, are urgently needed to halt the current biodiversity loss and mitigate its foreseen impacts on ecosystem function, and therefore humankind ultimately.

So then why Botswana, amongst all other lands? Beside my own life path leading me there, the region hosts some impressive natural assets. About forty percent of Botswana have been dedicated to wildlife and its habitat since 1966, covering and connecting various ecosystems (Cooke, 1985; Parry & Campbell, 1990). In fact, Botswana's Kgalagadi Transfrontier Park (KTP) and Central Kalahari Game Reserve (CKGR), together with the unfenced rangelands connecting these two Protected Areas (PAs), comprise what is possibly one of the largest free-ranging wild ecosystem remaining south of the Sahara (WCS & CIESIN, 2005) (**Figure 1-1**). This is certainly unique, and forms the major part of the Kalahari “Desert” of Botswana. However, as elsewhere in the world, this region has not escaped conservation challenges, of which major ones are ecosystem degradation, human-wildlife conflict and illegal hunting in and around wildlife areas following the expansion of human settlements and related activities (Carlsson, 2005; CI, 2010a; Fynn & Bonyongo, 2011; Parris & Child, 1973; Senyatso, 2011; Verlinden, 1997). Ecological changes in response to anthropogenic development have been accelerating especially in

the last 150 years (Campbell, 1981, 1997; Campbell & Child, 1971). But even over a decade, I could witness some changes, particularly the spatial expansion of livestock grazing lands. So, that is how the present research began to take shape, driven by a desire to help preserve these stunning lands.

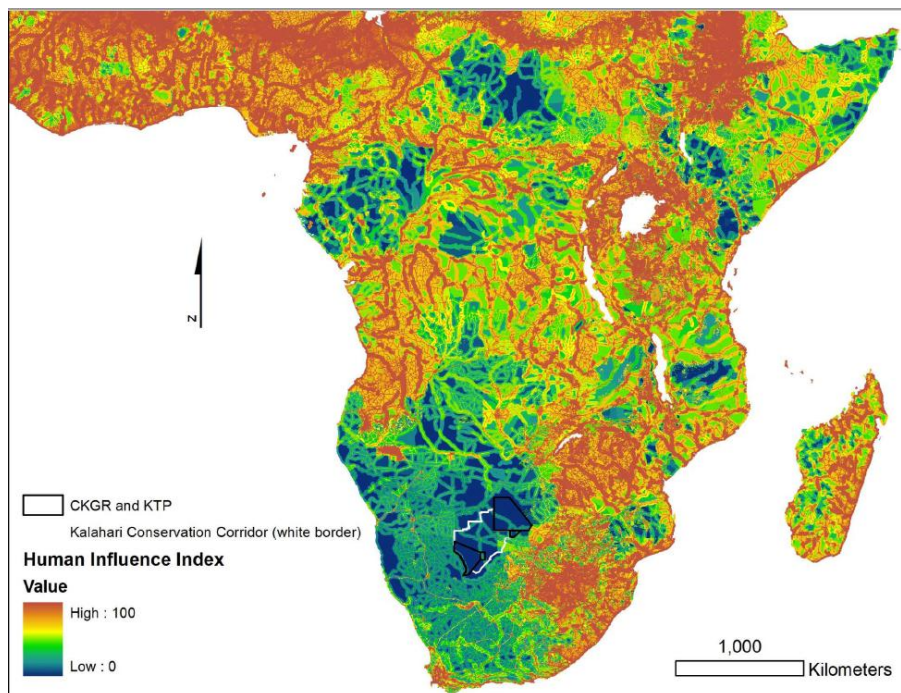


Figure 1-1 The location of the Central Kalahari Game Reserve (CKGR), the Kgalagadi Transfrontier Park (KTP) and the unfenced rangelands (i.e. conservation corridor) connecting them, in relation to the Human Influence Index (HII) in sub-Saharan Africa. The HII is a measure of direct human influence on terrestrial ecosystems using the best available data sets on human settlement (population density, built-up areas), access (roads, railroads, navigable rivers, coastline), landscape transformation (land use/land cover) and electric power infrastructure (night-time lights). Dataset from WCS & CIESIN (2005), adapted by D. Keeping and reproduced with his permission.

2. The wild lands of Botswana

2.1. A brief overview

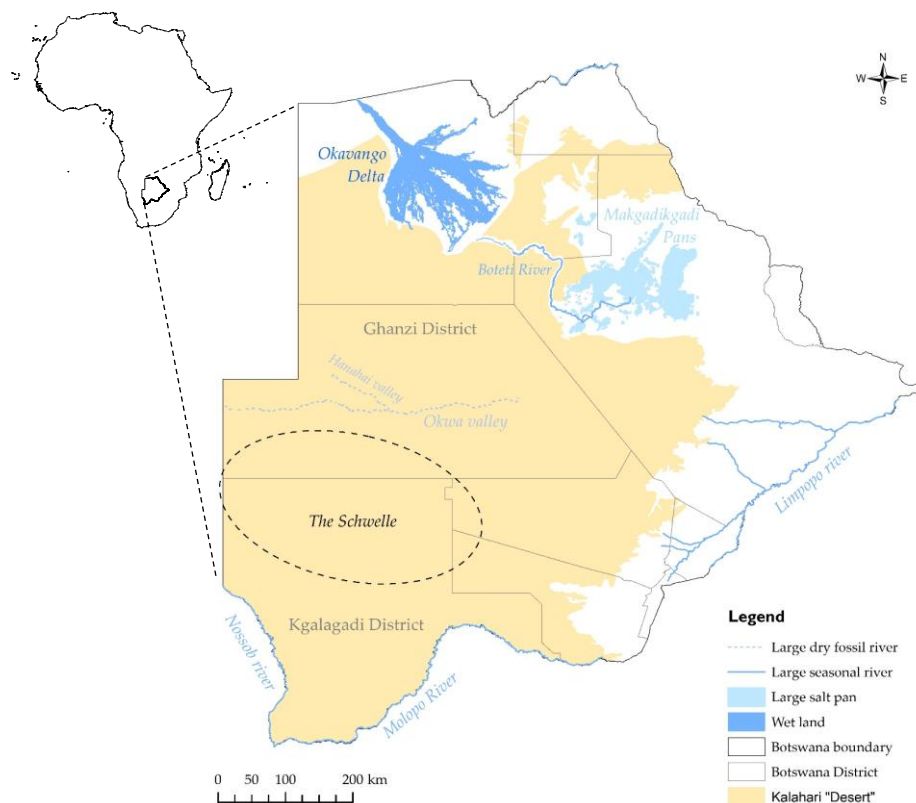


Figure 1-2 Botswana's location in the centre of the southern African continent.

In the north and northeast of the country lie the Makgadikgadi Pans, seasonally connected to the Okavango Delta by the Boteti River, which provides an essential water source for wildlife –seasonally for the pans and year-round for the delta. The Okavango Delta transitions into the Kalahari "Desert", which spans the remaining two-thirds of the country, encompassing the entirety of the Ghanzi and Kgalagadi Districts. The major landforms of the Kalahari "Desert" include dry fossil valleys and the Schwellie, which is characterised by a high concentration of large pans. Source: Representations of the Kalahari "Desert" extent vary slightly between authors. The above representation reflects the boundaries of the Kalahari xeric savanna and acacia woodlands ecoregions (Resolve, 2017) of the [Greater Karoo & Kalahari Drylands bioregion](#) (One Earth, 2023). Reproduced with permission.

Botswana is landlocked in the centre of Southern Africa, bordered by Namibia, Zambia, Zimbabwe and South Africa (**Figure 1-2**). Covering 581,730 km², it is slightly larger than France, yet it hosts only 2.4 million people (World Bank, 2021), ranking it within the last quarter of the least populated countries in the world (Worldometer, 2022). Mostly flat, Botswana is nevertheless far above sea level, located on a plateau on average 1000m in elevation. Due to its unique topo-geographical features, the region hosts several contrasting ecosystems, with two primary ones being the wetlands of the Okavango Delta and the Boteti/Makgadikgadi Pan system, as well as the Kalahari "Desert" (**Figure 1-2**).

2.2. The Kalahari

"Kalahari" appears to be derived from the Sekgalagadi words *Kgala* or *Kgalagale* (known as *Kgalagadi* in Setswana), which means "drying" or "always dry". The term refers to an area with boundaries that vary by context, often causing confusion. The Kalahari Basin, also referred to as the "Mega Kalahari," is characterised by the Kalahari group of sediments and extends across most of Botswana and parts of Namibia, South Africa, Angola, Zimbabwe, Zambia, the Democratic Republic of Congo, the Republic of Congo, and Gabon (Thomas & Shaw, 1991). The Kalahari "Desert," which is the focal area of this thesis, represents a smaller region within this basin, though its exact boundaries also vary slightly among authors. For clarity, I delineate the Kalahari "Desert" based on both physical and environmental factors, restricting it to the Kalahari xeric savanna and acacia woodlands ecoregions (see [Greater Karoo & Kalahari Drylands bioregion](#)), characterised by a semi-arid climate and lack of permanent surface water (see estimated outlines in Botswana in **Figure 1-2**).

The Kalahari "Desert" is a vast, sand-covered plain characterised by gentle undulations and a relatively well-developed vegetation cover. While the term "desert" may be somewhat misleading, the region certainly experiences harsh climatic conditions. Temperatures can exceed 40°C during summer heatwaves and drop below freezing on some winter nights, with typical day-to-night variations of 15–20°C. Rainfall occurs primarily during the wet season from November to April (summer) and, rarely, as brief showers in the dry season from May to October (winter). Annual rainfall is spatially unpredictable, ranging from about 150 mm in the southwest to 500 mm in the northeast (DHV, 1980). Such conditions still qualify the Kalahari as a thirland, better described as a semi-arid environment (Grove, 1969; Ngwamotsoko, 1985; Thomas & Shaw, 1991). To avoid misconceptions, I will simply refer to it as "the Kalahari" from here on.

A key topographic feature of the Kalahari is the Bakalahari Schwelle (Passarge, 1904). Covering the western central Kalahari, it extends north-west to south-east between 25°S and 23°S in latitude (**Figure 1-2**). This slightly more elevated region acts as a natural division between two hydrographic systems, relics of a much more humid and cool climate in the past, now largely fossilised (Boocock & Van Straten, 1962). To the north-east of the Schwelle, fossil valleys such as the well-known Okwa and Hanahai valleys penetrate the Kalahari (**Plate 1-1**), remnants of ancient tributaries of the Palaeo-Makgadikgadi Mega Lake, whose vestiges are the current Makgadikgadi Pans. In the south, the usually dry beds of the Nossob and Molopo rivers can be found, though flow still occurs in the upper reaches of the Molopo during the rainy season (DHV, 1980; Grove, 1969; Riedel et al., 2014).



Plate 1-1 Section of the Okwa Valley

Photo credit: Marie-Charlotte Gielen

The Schwelle itself is characterised by its concentration of major pans (>500 m in diameter) (**Plate 1-2**). These are shallow sub-circular to sub-elliptical depressions of a relatively high silt and clay soil content that temporarily hold small amounts of water after rains. Their size can vary from a few hundred meters to four kilometres across, and their surfaces range from grass-covered to completely bare clay (Grove, 1969; Lancaster, 1974). In the Schwelle, in



Plate 1-2 Example of a pan, visible in the centre of the photograph, characterised by short grasses (light brown in this case) and mineralised soil.

Photo credit: Nicolas Schtickzelle

absence of any drainage system, pans appear to have been created and maintained by wind erosion, attested by the dunes found south of the pans (Grove, 1969). Larger pans could be of tectonic origin, enhanced by deep weathering involving ground water activity (Thomas & Shaw, 1991). In some other places in the Kalahari, where pans are laid in belts, they could be the remnants of sand-choked old drainage lines (Boocock & Van Straten, 1962). Pans are of particular importance for the Kalahari fauna, playing a critical role regarding availability of surface water after rains (**Plate 1-3**), nutrient-rich vegetation, and mineral licks (CI, 2010a; Parris, 1976; Parris & Child, 1973; Verlinden, 1998).



Plate 1-3 Natural pan filled with rain water in the Kalahari.
Photo credit: Marie-Charlotte Gielen

The vegetation in the Kalahari generally evolves along an axis running roughly in a north-east to south-west direction, which also correlates with the rainfall isohyets (Skarpe, 1986). It extends from a complex woodland savanna in the north to shrub savanna with scattered trees in the drier west and centre, becoming progressively more open towards the south-west (**Plate 1-4**). A field layer of mainly perennial grasses, along with low shrubs, stabilises the sandy soils and occasional dunes. The vegetation physiognomy is fairly homogeneous over large areas, with the exception of pans hosting a specific plant community (Cooke, 1985; Skarpe, 1986; Weare & Yalala, 1971).



Plate 1-4 Examples of vegetation structures found in the western central Kalahari, arranged from least to most dense from top to bottom.

Photo credit: Marie-Charlotte Gielen

2.3. Lands for Kalahari wildlife conservation

Geographically, the Kalahari today encompasses the two largest PAs of Botswana: the CKGR and KTP. These are interconnected by a series of Wildlife Management Areas (WMAs), collectively forming the “Western Kgalagadi Conservation Corridor” (WKCC) (CI, 2010a) (**Figure 1-3**). This permeable landscape traverses the Schwelle, considered key to its ecological integrity (DHV, 1980). Remaining unfenced, the corridor allows free-ranging wildlife to move between essential resources.

Historically, the establishment of these conservation areas emerged from a slow awakening of the importance of rangeland and wildlife preservation. This shift followed the extensive commercial exploitation of these resources through cattle farming and hunting during the nineteenth century - a period marked by the introduction of large numbers of firearms and increased

political stability, particularly under growing European influence (Campbell, 1997; Campbell & Child, 1971; Cooke, 1985).

Between 1885 and 1966, Botswana was a British Protectorate, known as the Bechuanaland. Before the 1960's, wildlife was reportedly prolific throughout the country, although certainly declining, remaining vital for local subsistence. However, cattle farming firmly established as the backbone of the country's economy, while wild animals were largely regarded as having little value, but for sport hunting and derived products (Campbell, 2004; Cooke, 1985). It was not until 1938 that legislation finally provided for the establishment of Game Reserves.

The first Game Reserve was the Nossob River Game Reserve. Its creation followed the one of the Kalahari Gemsbok National Park in South Africa in 1931, situated just across their shared boundary. This initiative by the South African Minister of Lands was driven by concerns over the scarcity of game in the region. Bechuanaland then promulgated the Nossob River Game Reserve in 1938, which was later renamed the Gemsbok Game Reserve. Following the Independence of Botswana in 1966, it was enlarged to its present extent and its status was upgraded to the Gemsbok National Park in 1971. In 2000, the South African and Botswana National Parks officially became a single unit co-managed by both countries, which was renamed the KTP (Campbell, 2004; Sanparks, 2022).

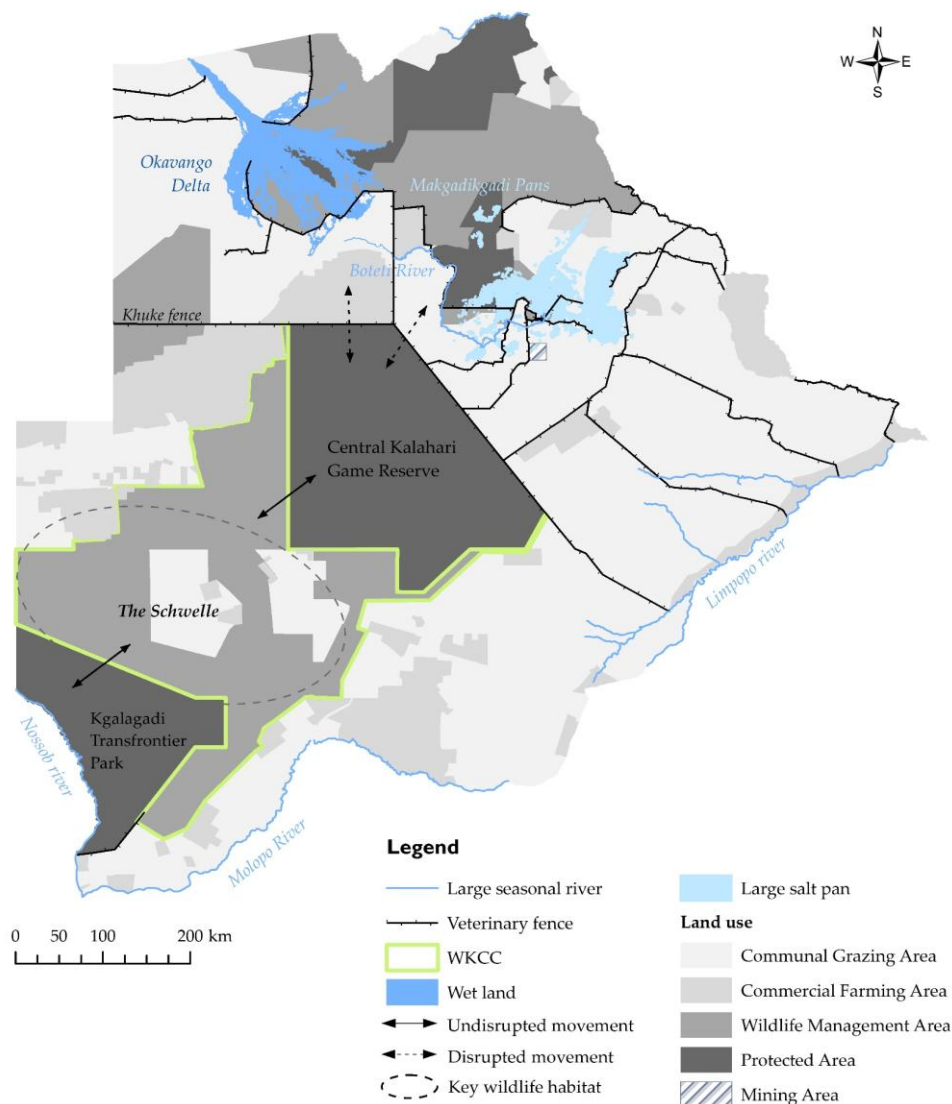


Figure 1-3 The “Western Kgalagadi Conservation Corridor” (WKCC) and wildlife movements in and out the Kalahari in relation to human developments.

The WKCC is formed by a succession of Wildlife Management Areas interconnecting the Central Kalahari Game Reserve and the Kgalagadi Transfrontier Park. This free-ranging landscape is running through the “Schwelle”, a key wildlife habitat of the Kalahari. Movements are still free-ranging between the Schwelle and the CKGR/KTP (continuous arrow), while they are disrupted between the Kalahari and Okavango-Boteti-Makgadikgadi systems (dashed line arrows), due to the erection of veterinary fences and expansion of agricultural lands.

The CKGR was promulgated later, in 1961, originally to secure land for the San (also known as “Bushmen”) on a permanent basis. These Indigenous Peoples of the Kalahari were known for their nomadic gathering and hunting lifestyle. Surveys conducted in the 1950’s highlighted the difficulties San faced in their interactions with other groups, particularly their inability to retain land rights. As a result, the CKGR was established where the San were intended to continue their traditional way of life. Simultaneously, it aimed to protect wildlife and preserve unique ecological features, such as pans and fossil valleys (Campbell, 2004; Hitchcock, 2002). However, in 1997, the residents of the CKGR started to be relocated outside. This followed nearly two decades of intense political wrangling opposing Botswana Government and CKGR resident representatives, which even involved the international community (Hitchcock, 2002). At present time, a few hundred residents still live in the CKGR under certain rights (Hitchcock et al., 2020). Regarding land use, the CKGR is now designated exclusively for photographic tourism, as is the KTP.

The concept of WMAs arose as a new land use category in the early 1980’s, after the state interest and investment in wildlife conservation notably increased in the 1970’s following Botswana Independence (Campbell, 2004; Cooke, 1985). The first President of Botswana, Sir Seretse Khama, voiced concerns about the country rangeland management in a speech in 1975:

“The time has come to tackle a subject about which there has been a lot of talk but no action - the better use and development of our land. As our human population and the numbers of our cattle and other livestock increase there is a growing danger that grazing will be destroyed by uncontrolled use of communal grazing areas by ever growing numbers of animals. Once grazing has been destroyed it is extremely difficult to get grass re-established. And under our communal grazing system it is in no one individual’s interest to limit the number of his animals.” (Frimpong, 1995)

As a result, the ambitious Tribal Grazing Land Policy (TGLP) was released the same year, aiming to overcome social inequalities and counteract rangeland degradation caused by cattle grazing pressure by improving land use management practice (Government of Botswana, 1975). It rezoned the tribal communal lands (i.e. most areas outside the PAs) in three categories: Commercial Farming Areas, Communal Grazing Areas and Reserved Areas. Amongst other uses, the Reserved Areas aimed to spare some lands for wildlife utilisation. A land use planning exercise started, from where the zoning of the WMAs emerged around 1980, to be officially embraced in the Wildlife Conservation Policy of 1986, with a delineation largely unchanged to

this day (Government of Botswana, 1986). Their intention was to secure the continued existence of game resources and to integrate wildlife in the rural economy of Botswana.

WMAs were meant to shift the emphasis of conservation for its own sake (i.e. total preservation already endorsed by National Parks and Game Reserves) onto conservation of game stocks for sustained hunting or cropping. Therefore, wildlife utilization is to be WMAs' primary form of land use. Other forms of land use are permitted provided they do not prejudice the wildlife populations and their utilisation (DHV, 1980; Government of Botswana, 1986; Parry & Campbell, 1990). In this regard, WMAs correspond to game rich habitats outside Parks and Reserves. Some act as buffer zones to prevent conflicts between the latter and agricultural areas. Others aim to protect known wildlife movement corridors as most large mammals are nomadic and spend extended periods outside PAs (Government of Botswana, 1986; Parry & Campbell, 1990). Within the WKCC, their spatial sequence forms three corridors between CKGR and KTP, allowing wildlife movements around livestock farming areas (CI, 2010a). However, some of these WMAs have yet to be gazetted, mainly due to the pressure of the cattle lobby (Thomas & Shaw, 1991), which make them vulnerable to rapid change in land tenure categories.

Today, Botswana is divided into four main categories of land use: PAs and WMAs, both dedicated to the protection or utilisation of wildlife; Commercial Farming Areas (CFAs) as fenced farms primarily used for livestock farming, though some game farming also occurs; and Communal Grazing Area (CGAs) as unfenced areas used for livestock farming, arable activities, or residential purposes (villages and townships). A fifth category exists as Mining Areas, although accounting for a small fraction of the land (**Figure 1-3**).

3. The ecological challenges of the Kalahari in history

"There are few areas in the world which contain so many exciting components as the Kalahari ecosystem: the historical and alas diminishing migratory movements of its animals, its remarkable sand-dunes, its survival problems, its underground plant food, its underground animal community, its remarkable micro-ecosystems, its [...] territorial man; apparently unattached components but [...] This is how we must regard the Kalahari: one ecosystem, one giant organism, the parts of which compete with each other but also live together in harmony." (Eloff, 1984)

In light of the previous section, one might ask: what are the actual challenges the Kalahari faces, given the extensive measures implemented over the past 50 years and the vast areas of land allocated to wildlife resources? Unfortunately, as is often the case, theory diverges from practice. History leaves scars, and old cultural traditions are difficult to revive or reconcile with contemporary management approaches.

3.1. Early human expansions

Modern human presence in the Kalahari is as old as the origins of *Homo sapiens sapiens* itself. The Paleo-Makgadikgadi Lake margins has been identified as the possible homeland of humanity 200,000 years ago (Chan et al., 2019). The direct descendants of the oldest human lineage found to date, the Khoisans, still live in the Kalahari sandveld. They are more commonly known as the “San” or “Bushmen”, which I will introduce in more detail later on (see Chapter 2). Their traditional nomadic lifestyle allowed them to live in a sustainable relationship with their environment, practicing gathering and subsistence hunting (Silberbauer, 1965; Tanaka, 1974) (**Plate 1-5**).



Plate 1-5 Groove on a flat stone of the Okwa valley, Ghanzi District. These cupules were likely made and used by ancient inhabitants to sharpen tools or hunting implements and are at least several thousand years old.
Photo credit: Marie-Charlotte Gielen

Evidence of pastoralism exist throughout the last two millennia (Denbow & Wilmsen, 1986), and as early as 2000 years ago (Robbins et al., 2008), brought by small groups intermittently entering and settling in Botswana riverine sites. It is only in the 18th century that the first large wave of Bantu-speaking farmers came to settle in Botswana, fleeing South Africa, where tribal conflicts and migration, known as the *Difaqane*, were intensifying. Europeans first ventured in the Kalahari in the early 19th century, primarily through the activities of Christian missionaries, hunters and traders. A well-known figure among these early travellers is David Livingstone. When the

region reached political stability in the second half of the 19th century, coinciding with the creation of the Bechuanaland Protectorate in 1885, human populations began to increase rapidly, leading to an intensification of agriculture (Campbell & Child, 1971; Thomas & Shaw, 1991).

3.2. The wildlife plunder of the 19th century

In the 19th century, old writings (Campbell, 1997; Campbell & Child, 1971) and recent climate reconstructions (Nash, 2017) suggest that the Kalahari experienced wetter habitat conditions than it does today. The southern Kalahari, particularly along the headwaters of the Molopo and Nossob rivers, and further inland during the wet season, once supported water-dependent animals such as buffalos (*Syncerus caffer*), rhinoceros (*Diceros bicornis* and *Ceratotherium simum*), elephants (*Loxodonta africana*), zebras (*Equus quagga*), giraffes (*Giraffa giraffa*), and even hippopotamus (*Hippopotamus amphibius*). Similarly, elephants, buffalos, rhinoceros and zebras were also wandering the central Kalahari, where the Ghanzi District is now located. Wildlife appeared to be plentiful, and with the arrival of foreigners and firearms in the region, animals began to be heavily hunted for both sport and commercial gain. So much that, by then end of the 19th century, game herds in Botswana have been visibly greatly diminished (Campbell, 1997).

In the first half of the 20th century, consideration for wildlife started growing slowly with the establishment of temporary hunting bans, wildlife product trade rules, and the first Game Reserves, allowing wildlife to increase again in areas with low human density (Campbell, 1997, 2004; Spinage, 1991). However, some areas have seen species disappear forever, such as the water-dependent rhinoceros, buffalo, or hippos in the southern and western Kalahari. Overexploitation is surely one cause (Campbell, 1997), but changing environmental conditions are another, as natural springs in the Kalahari became depleted due to human settlement around them (Campbell, 1981, 1997), aided by a climate that already started to become drier (Nash, 2017).

3.3. Fences and artificial waterpoints

Since the establishment of the Bechuanaland Protectorate, the economical emphasis has been strongly put on to the development of the cattle industry. By the 1950's, the number of cattle had exceeded one million heads (Campbell, 1978). About that time, foot and mouth disease (FMD) was also raging in the region, mainly in the north of Botswana, threatening the national cattle herd. In response, a network of veterinary cordon fences was established across Botswana starting in 1954 (**Plate 1-6**). It aimed to prevent the movement of

sick animals across areas, but also, in the northern regions of Botswana, to prevent the transmission of FMD to cattle by wildlife (Raborokgwe, 1997). Buffalos were believed to be the main natural reservoir transmitting the virus widely. However, it now appears that such transmission to cattle is rather occasional and cattle themselves can very much be a reservoir (Brito et al., 2016; Omondi et al., 2020). In any case, fencing was considered necessary to control the spread of livestock diseases to meet the sanitary requirements of the European Union market, where Bechuanaland beef was exported (Darkoh & Mbaiwa, 2002).



Plate 1-6 Typical game fence in Botswana.
Photo credit: Marie-Charlotte Gielen.

As a result, by 2002, the Kalahari had been cut off from the adjacent northern Okavango Delta, north-eastern Makgagakadi Pans-Boteti River, and eastern Limpopo River basin (**Figure 1-3**). These are dry season refuges representing the only perennial surface water available for Kalahari large ungulates. Although Kalahari wildlife is well adapted to dry conditions, during severe drought years, the most water-dependent species, such as blue wildebeests (*Connochaetes taurinus*), would undertake one of the largest animal treks in the world, leaving the Kalahari in search of greener grazing and surface water. So, while some have argued for the effectiveness of the fences in disease control, reducing predation on livestock and keeping livestock away from the PAs (Raborokgwe, 1997), they have unfortunately also been severely undermining critical wildlife movements (Campbell, 1981; Williamson & Williamson, 1984). First, the Khuke fence (**Figure 1-3**), built in 1958, channelled Kalahari animals on the move towards the north-eastern part of Botswana where surface water and grazing were already exploited by

human and cattle. This resulted in massive die-offs such as in Lake Xau (a few km south-west of Makgadikgadi Pans) in the 1960's and 1980's droughts (Child, 1972; Parry, 1987; Williamson & Mbano, 1988). The same fence also excluded water-dependent species such as zebra and buffalo from the northern Kalahari (Williamson & Williamson, 1984), confining them to the northern and north-eastern wetlands of Botswana. Later on, once the construction of the eastern fence of the CKGR began in 1993 (Hitchcock, 1999), any connectivity between the Kalahari and these wetlands disappeared. Finally, fences have garnered a bad reputation for causing the death of animals that become entangled in them, or for facilitating illegal hunting along their lines (Campbell, 1981; Kalikawe, 1997).

As an alternative to the loss of dry season refuges, permanent artificial water points (**Plate 1-7**) were available to wildlife within the CKGR and KTP starting in the late 1980's. However, some of which were of poor water quality (Bonifica, 1992; Knight, 1995; Selebatso, Maude, et al., 2018). Such permanent water provision also raised concerns with respect to altering the behaviour and resilience of wildlife species. Provided all year round it fosters sedentary behaviour, and in case such water provision is not maintained, the loss of adaptative strategy can be fatal for wildlife (Selebatso, Bennitt, et al., 2018). Also, the placement of some water points in wildlife wet season range will attract animals there during the dry season as well. Consequently, the use of the same resources all year round could locally exhaust food reserves necessary to survive the winter months (Knight, 1995). Perkins (2019) extensively lists the pros and cons of artificial waterpoints in the Kalahari.

Fortunately, south and west of this network of fences, wildlife is currently still free ranging over 168 000 km² within the Kalahari. More sedentary water-independent species have been less affected, and smaller seasonal movements can still happen in and out the "Schwelle", from and to the CKGR and KTP, mostly through the use of the WMA network (**Figure 1-3**) (Carlsson, 2005; CI, 2010a; Verlinden, 1998).



Plate 1-7 Examples of artificial waterpoints in a protected area of the Kalahari, Botswana.

Both photos were taken in Khutse Game Reserve, which borders the Central Kalahari Game Reserve. The left image shows a waterpoint visited by elephants during the dry season, while the right one captures African wild dogs during the wet season. Water is supplied all year round.

Photo credit: Marie-Charlotte Gielen – Leopard Ecology & Conservation.

3.4. Boreholes and human settlements

In the course of the 19th century, pastoralism became widespread across Bechuanaland Protectorate, especially in eastern regions. With the political stability settling at the end of the century, many pastoralists started to trade nomadism for permanent homes, naturally seeking the most resourceful lands for themselves and their cattle. In the Kalahari, that was the vicinity of pans and fossil valleys still offering natural springs or water accessible through shallow wells, along with nutritious pasture (Campbell, 1981). Herds were still nomadic in the rainy season but returned to these permanent homes in the dry season, starting to put pressure on the limited surface water and grazing.

With access to only little water during the dry season, the Kalahari still was unsuitable for intensive pastoralism as cattle are highly water-dependent. Eventually, the milestone that opened the Kalahari to the cattle industry was the introduction of a major borehole drilling program by the Protectorate in response to the 1930's drought, which was intensified after 1956 (**Plate 1-8**); groundwater reserves are now available throughout the year, bringing new human populations and their livestock to areas where before they had been

only transitory (Campbell, 1981; Cooke, 1985). The lack of informed land use planning at the time resulted in the mushrooming of more settlements in the resourceful areas of high value for wildlife, such as the Schwelle. Consequently, now sedentary cattle herds soon overgrazed their fragile grazing resources, and wildlife access to such key habitats has been increasingly denied, with added disturbance through hunting, illegal or not.



Plate 1-8 Example of a borehole extracting underground water using either a solar power system (as in this case) or a fuel-powered engine.

Photo credit: Alessandro Araldi – Leopard Ecology & Conservation

The advent of borehole technology and government support allowed the cattle population to grow rapidly after the 1960s drought, reaching up to 3 million heads before the 1980s drought (not including small livestock), which is over double the present number (Statistics Botswana, 2021a; Vossen, 1988).

3.5. Cattleposts and their impact on the ecosystem

Rangeland degradation caused by cattle overstocking and grazing mismanagement has long been recognised in Botswana (Abel & Blaikie, 1989; Cooke, 1985; Parris & Child, 1973; Ringrose & Vanderpost, 1997), with evidence of overgrazed lands as early as the end of the 19th century in eastern Botswana (Campbell & Child, 1971), and effects on the vegetation still visible after decades (Parris & Child, 1973; Skarpe, 1986). The TGLP of 1975, while promising in addressing the issue, ultimately fell short of meeting its objectives (Cooke, 1985; Frimpong, 1995; Makepe, 2006). By establishing fenced farms for owners of larger herds in newly designated CFAs, the policy sought to reduce livestock pressure in CGAs and empower small-scale

farmers. However, amongst other issues, farmers often did not manage their herd as intended, failing to confine their cattle within the ranch boundaries or engaging in overstocking.

That is in fact of cultural essence: cattle-keeping in Botswana has traditionally been based upon a free-ranging system, first nomadic, then later sedentary around what is called “cattleposts” (**Plate 1-9**). Cattleposts, made of one or more wooden enclosures and herder huts, are centred on a water point supplied by underground water pumped from a nearby borehole (Perkins, 1996). From there, cattle often roam freely across the landscape, returning to access water. As opposed to fenced farms in CFAs, cattleposts dominate the unfenced CGAs and surround the settlements within WMAs. Settlements in WMAs have been allocated a 20km radius Remote Area Dwellers (RADs) development zone for exclusive use, which has been mostly utilised for developing cattleposts (Ministry of Local Government, 2009). Beyond these zones, the land remains reserved for wildlife use. Collectively, the traditional cattle sector, represented by cattleposts, raises approximately 80% of Botswana’s cattle numbers in recent years (Statistics Botswana, 2018).



Plate 1-9 Example of a cattlepost.

The photograph on the left depicts wooden enclosures or “kraals”, while the one on the right shows the reservoir containing water pumped from underground.

Photo credit: Alessandro Araldi - Leopard Ecology & Conservation.

Over the last 50 years, the growing human population has led to cattleposts being established progressively farther from villages - often at the very edge of the 20km development zone of WMA villages - and increasingly closer to the boundaries of WMAs and PAs when in CGAs. As a result, free-ranging cattle frequently enter wildlife-designated areas while grazing, as there are no physical boundaries and herding practices are mostly absent (Van der Weyde, 2019; pers. obs.).

Such encroachment of the cattle industry into WMAs in particular has now become a major threat to the integrity of the Kalahari ecosystem. For instance, the effect on vegetation condition and structure has been shown to exist up to 10 km from the livestock water points (Skarpe, 1986; Verlinden et al., 1998), and sometimes up to 25 km when several water points were found clustered in some areas (Verlinden, 1997). Changes in the distribution of large game species have also been reported, with a rare presence within 10 km from the villages (Bergström & Skarpe, 1999; Verlinden, 1997). Negative effects on gemsbok (*Oryx gazella*) presence were even detected up to 45-50 km from cattleposts (Verlinden et al., 1998).

Several explanations for wildlife decline around human settlements and cattleposts have been proposed. One is the direct competition for resources caused by livestock, further exacerbated by habitat degradation and fragmentation (Blaum et al., 2007; Cooke, 1985; Moleele & Mainah, 2003; Parris & Child, 1973; Perkins, 2018; Verlinden, 1997). Unsustainable illegal hunting by villagers and herders appear to be another non-negligible factor (Brett, 2000; Campbell, 1981; Senyatso, 2011; Thouless, 1998; Verlinden et al., 1998; Märtha Wallgren et al., 2009). For carnivores, lethal removal following predation events on livestock is another driver (CI, 2008; Klein, 2013; Schiess-Meier et al., 2007).

3.6. Illegal hunting

Over the last century, hunting has sparked significant debate, between those practicing it as part of their traditional lifestyle, others wanting to shoot for sport, trade or protecting their livestock, and some wanting to curtail its use in favour of wildlife protection (Spinage, 1992a, 1992b). It is a complex matter, which I feel first needs a differentiation between its subsistence and commercial components. In comparison to hunting for sport or commercial gain, subsistence hunting has long played an important role in local communities of Botswana (Campbell, 1997; Campbell & Child, 1971; Parris & Child, 1973), and for times immemorial among the oldest residents such as the San (Liebenberg, 2006; Tanaka, 1974). Hitchcock (1996) defines subsistence hunting as “the customary and traditional use of wild animals for food, raw material, social, and ceremonial purposes”. Until recently, some remote rural populations still depended to a significant degree on wild resources, especially in the Kalahari (Parry & Campbell, 1990).

Historically, regulations towards the use of game species were of dual nature, applying differently to “natives” under the customary authority of Chiefs, and “foreigners” under statutory laws of the Protectorate (Spinage,

1991). After its independence, in an effort to regulate hunting in all forms, Botswana produced statutory game laws universally applicable to all people, citizen or not, known as the Fauna Conservation (Unified Hunting) Regulations of 1979 (Government of Botswana, 1979). They included Special Game Licenses (SGLs) allowing local communities depending on wild resources in remote areas to continue practicing subsistence hunting (Hitchcock, 1996; LaRocco, 2020). In the 1990's, concerns grew regarding the sustainability and possible abuse of such SGL based-hunting on wildlife population numbers, which have been further declining since the 1970's. SGL's were also seen by some as an unfair privilege available to only part of the Botswana population. Consequently, the granting of SGLs decreased from 1996 onwards, until a complete national hunting moratorium was implemented in 2014 until 2019 (Hitchcock, 1996; Hitchcock et al., 2020). Nowadays, commercial hunting is currently reopened for trophies under certain quotas, and citizen hunting licenses are available through a lottery system provided the winner pays for the license won, which is likely to be financially out of reach for remote local community members (LaRocco, 2020). Currently, all forms of hunting requires a licence issued by the government and is otherwise considered as illegal, with the exception of hunting on privately owned lands (Government of Botswana, 1992).

While some express outrage at the denial of subsistence hunting as a violation of human rights (Hitchcock, 2002; Hitchcock et al., 2020), others warn that an increase of human population and evolution of hunting methods would render even that form of hunting unsustainable in the long-term. The increase of road networks, motor transportation, horses, donkeys, dogs, and firearms at settlements and cattleposts simplify and improve efficiency of hunting trips, compared with traditional methods on foot using spears, bow and arrows (Campbell, 1981; Cooke, 1985; Spinage, 1998). In addition to pure subsistence hunting, illegal bushmeat hunting for commercial gain (i.e. for selling meat or valuable body parts) is also a reality in Botswana, particularly in the Okavango Delta (Lindsey et al., 2013; Rogan et al., 2015). It is more largely pointed as a major threat to mammal populations worldwide (Ripple et al., 2016).

In the Kalahari, illegal hunting, for subsistence or commercial purposes, has also been assumed by several authors to still be common practice (**Plate 1-10**), and contributing to the decline of the wildlife populations (Brett, 2000; Campbell, 1981; Senyatso, 2011; Thouless, 1998; Verlinden et al., 1998; Märtha Wallgren et al., 2009). Poaching incidents are indeed reported by the Botswana Government every year; gemsbok and eland (*Taurotragus oryx*) seem to be favoured species, and blue wildebeest, kudu (*Tragelaphus strepsiceros*) and springbok (*Antidorcas marsupialis*) are also targets (Statistics Botswana, 2005, 2015; Thouless, 1998). Away from iconic species such as elephant or rhinoceros, anti-poaching operations in the Kalahari are limited due to the vastness of the area relative to available resources (Thouless, 1998; USAID, 1988).



Plate 1-10 Empty shotgun shells found along the gravel road of GH11 WMA in the Ghanzi District at the end of October 2021, outside the legal trophy hunting season.
Photo credit: Marie-Charlotte Gielen

3.7. Human-wildlife conflict

Habitat degradation, competition for resources, and illegal hunting are not the only challenges posed by cattle farming in the Kalahari; human-wildlife conflict is another (**Plate 1-11**). Carnivores, especially large predators such as leopards (*Panthera pardus*), lions (*Panthera leo*), cheetahs (*Acinonyx jubatus*), African wild dogs (*Lycaon pictus*), and hyenas (*Hyena brunnea* and *Crocuta crocuta*), are essential in keeping ecosystems functional. The survival of most of these species relies on their ability to exist outside PAs, but this often brings them into conflict with humans and their livestock (Gross et al., 2021; Kent, 2011; Klein, 2013; Winterbach et al., 2014). These conflicts are widespread across the whole Kalahari, where the farmer tolerance levels are generally low. This is largely because the potential benefits of coexistence with carnivores is generally poorly understood or experienced by livestock

owners. Although trophy hunting is now active again, the non-consumptive tourism industry is undeveloped in the area. A compensation scheme exists for livestock losses, but a lack of resources often prevents government officers from assessing kills on-site (LeFlore et al., 2019; pers. obs.).



Plate 1-11 Consequences of human-wildlife conflict.

a) A cow predated on by a lion, b) a gin trap - an illegal method used to capture and often lethally remove predators in farming areas, c) a lion killed in retaliation for predation, d) a leopard captured and being relocated in response to predation events. Photo credit: a), b) and d) Leopard Ecology & Conservation. c) Credit withheld.

Predation on livestock by predators often leads to the lethal control of the animals perceived as the source of conflict (Kent, 2011; Klein, 2013), whether legally or illegally. In this regard, the Wildlife Conservation and National Parks Act of 1992 stipulates:

"[...] the owner or occupier of land, or any agent of such owner or occupier may, subject to the provisions of this Act, kill any animal which caused, is causing or threatens to cause damage to any livestock, crops, water installation or fence on such land." (Government of Botswana, 1992)

Although lethal removals must be reported and the animal trophies delivered to the Government, there are reasons to assume that in practice a number of such events are not officially documented. Due to the absence of compensation for some species, late discovery of the damage (distorted evidence), lack of response or resources from Government officers, or large distance to the nearest reporting office, some conflict animals are not reported as causing damage (Karunya Consulting et al., 2020; LeFlore et al., 2019; Mmopelwa & Mpolokeng, 2008). In such cases, the problem may be dealt with separately than through the Government agency.

In the Kalahari, the impacts of human-wildlife conflict (as the proportion of livestock holdings lost) appear more severe in cattleposts within WMAs compared with other land-use types such as CGAs and CFAs, particularly when located near PAs (CI, 2008; Karunya Consulting et al., 2020; Klein, 2013). This aligns with the generally higher abundance of wildlife observed in PAs and WMAs (CI, 2010a; DWNP, 2015, 2018).

3.8. Current status of wildlife in the Kalahari

Botswana is reported to have lost only two medium- to large-bodied animal species in recent history: the white rhinoceros and the black rhinoceros, due to hunting and poaching. Both species have since been restocked from South Africa (Du Plessis, 1969; Marks, 1993; Maron, 2020). While this can be regarded as an achievement, it conceals a less optimistic reality. In light of the aforementioned historical events, it is evident that Botswana's wildlife populations have experienced a significant decline over the past 200 years.

Historically, the Kalahari once supported more diverse wildlife populations than it does today, partly due to the availability of natural surface water. Over time, these water sources have either disappeared or been rendered inaccessible by Man. As a result, the contemporary Kalahari wildlife community predominantly consists of species adapted to arid conditions, thanks to physiological or behavioural mechanisms enabling them to make optimum use of the available moisture (Parris, 1971).

Writings from early travellers and oral testimonials provide a fascinating glimpses into the Kalahari as it was, for instance, in the 1850's:

"[...] the pan at Ghanzi was "hemmed in with thorn-coppice, intersected by numerous foot-paths, the work of those huge creatures, the elephants and the

rhinoceros". He goes on to state that both were numerous and that he counted 20 rhinos in one night" (Campbell & Child, 1971)

Spinage (1992c) further reports:

"[...] in 1921-1922 from Sekgoma (Sekoma) to Kgokong and Dukwe (Dutlwe), you could travel for 40-60 miles (64-96 km) 'and never be out of view of game' trekking south-west or north-east. Although the species are not mentioned they would have been wildebeest, hartebeest, and perhaps eland Taurotragus oryx."

Even as recent as the 1960's, wildlife still appeared to be abundant, though likely as a fraction of the numbers that had existed in the previous century. According to skins and other wild animal products purchased by local traders in the Kalahari:

"The 1965-67 records of trophy dealers in southwestern Botswana [...] in that period they had bought skins of 40 080 springbok, 155 lions, 131 leopard, 40 cheetah, 10 445 bat-eared fox, 15 231 other small furs, 185 fur karosses, together with 6 009 ostrich eggs and 900kg of ostrich feathers. This, of course, reflects legally bought products, it does not even consider the purchases of numerous unlicensed trophy dealers, or domestically used products." (Von Richter, 1970)

Today, just over 20,000 springboks roam the Kalahari (DWNP, 2018); half of the numbers "harvested" in three years' time half a century ago. Similarly, about the same number of both wildebeests and hartebeests inhabit the area (DWNP, 2018), while they were each estimated at over a quarter of a million heads in 1979 (DHV, 1980).

It is important to note, however, that the Kalahari is an extremely dynamic ecosystem, where wildlife populations fluctuate naturally. These fluctuations are largely driven by a drought cycle of quasi-18 years, alternating above average rainfall (wet) and below average rainfall (dry) years spells (Tyson, 1980). The natural climatic conditions are therefore responsible for temporary wildlife decline during droughts, to which Kalahari wildlife is once again adapted. For example, female blue wildebeests show a higher survival rate than males during droughts, which allows populations to recover quicker once wetter years return (Child, 1972). As a result, the severe drought of the 1960's did not decimate herds as much as the 1980's did, the latter causing massive and widespread mortality with a low recovery rate (CI, 2010a; Parry, 1987). So, what happened? Human activity reached a tipping point.

Major changes have intensified in between the two drought periods, as described in the previous sections: the erection of veterinary cordon fences disturbed wildlife movements, while artificial water points were not provided yet; the expansion of cattle farming and human settlements through deep borehole drilling caused wildlife habitat loss due to competition with livestock, land degradation from overstocking in a sedentary farming system, and intensified human-wildlife conflict; hunting (illegal or not) remained prevalent with the growing human population, better techniques, and improved access to wilderness through new boreholes and roads. These factors, combined with the severe drought of the 1980's and a less severe one in the early 1990's, caused several ungulate populations in the Kalahari to decline to a mere fraction of their historical numbers, yet without proper recovery. The estimated depletion for some species such as blue wildebeests, red hartebeests (*Alcelaphus buselaphus caama*) and springboks, is greater than 80%, over half a century from now (Bonifica, 1992; DG Ecological Consulting, 2010; DHV, 1980; DWNP, 2015, 2018; Thouless, 1998).

Aerial surveys have been used by the Botswana Government to monitor wildlife populations both countrywide and at regional level since 1987. Although their reliability for large carnivores is limited due to their mostly nocturnal and elusive nature, they serve as a valuable tool for long-term monitoring of population trends in large herbivores across the entire unfenced Kalahari. In the last 30 years, following the major decline depicted above, large antelope populations have been stable or increasing in the Kalahari, with the exception of springbok which is on the decline (DWNP, 2015, 2018). The Kalahari currently supports the majority of the country's free-ranging eland, gemsbok, hartebeest, and springbok populations, with the numbers of wild herbivores in the WMAs regularly exceeding those inside the PAs of CKGR and KTP (DWNP, 2018; Perkins, 2019). Notably, Kalahari WMAs are home to Africa's largest recorded free-ranging eland population (Keeping, Keitsile, et al., 2018). This is an important indicator that the Schwelle remains a core free-ranging wildlife area in the Kalahari, with extensive use of the WMAs corridor in between CKGR and KTP.

Several authors have emphasised both the wildlife declines and ecological importance of the area over the past decades (Bonifica, 1992; CI, 2010a; Verlinden, 1994). However, these "old" reports appear forgotten by some, likely overshadowed with the belief that the Kalahari is irreparably encroached and fragmented by cattle expansion, with no major movement occurring outside of the KTP or CKGR anymore. Added to the continuing increase in the human population, the younger generations' demand for new grazing lands (citing the degradation of current ones), and the economic

underutilisation of WMAs, this may explain why some Kalahari WMAs have now started to be fully or partly converted to CFAs for cattle ranching (Department of Lands, 2009). Accordingly, Thouless (1998) warns:

“In the long term, the greatest threat to wildlife in unprotected parts of the Kalahari may well be habitat loss, and there is continuing pressure to erode the Wildlife Management Areas in favour of cattle ranching. However, it appears that even if wildlife habitats are secured, recovery of populations in these areas will be inhibited unless illegal hunting can be controlled.”

The current picture is therefore not an encouraging one, but the wild Kalahari is not yet lost. The recently created Ghanzi and Kgalagadi Integrated Land Use Management Plan (ILUMP) (Tshukudu, 2024), aimed at improving ecosystem connectivity and facilitating wildlife-based livelihoods for rural communities, still offer hope.

4. Research objectives

“Any system of utilizing these herds [the large herbivores] in the Kalahari should be designed so as to allow for movement, as this movement is essential for the survival of large wildlife populations under these conditions.” (Parris, 1971)

Although already suggested by USAID (1988), Conservation International (2010a) has more recently promoted three suitable wildlife corridors running through the WMAs between the CKGR and KTP, collectively forming the free-ranging WKCC. These corridors allow wildlife movements between the two PAs, provide wildlife access to the Schwelle, and support key wildlife habitats. Recommendations were made to raise the protective status of key WMAs essential for ecosystem preservation, along with the creation of a management plan for the entire area. However, due to the lengthy process of implementation or delays caused by conflicting interests from various economic sectors, “business as usual” has mostly prevailed on the ground with continued encroachment of human and livestock into these WMAs.

Therefore, the region is confronted with a complex set of challenges where wildlife conservation, human-wildlife coexistence, and socio-economic issues are deeply intertwined. As anthropogenic development continues to expand, wildlife faces growing threats from both human activities and climate change, compromising long-term population viability. The hoped-for coexistence between humans and nature is further undermined by high conflict levels, particularly with large carnivores, driven by the dominance of the agricultural

sector. Additionally, the sedentarisation and shift in the lifestyles of Indigenous groups —whether voluntary or not— has led to their dependence on government, Bantu and European groups, contributing to the gradual erosion or change of traditional knowledge and cultural practices (du Plessis, 2004; Liebenberg, 2021; Twyman, 2000). Beyond their negative impact on overall ecosystem functioning and the natural legacy for future human and non-human generations, these issues also undermine the development of sustainable livelihoods based on natural resources. As a result, they hinder the economic upliftment potential of local communities.

In the 21st century, the first comprehensive assessment of wildlife, human-wildlife conflict, and socio-economic conditions in the WKCC at a landscape scale was conducted in 2010 (CI, 2010a and associated reports). A more recent wildlife landscape connectivity analysis, based on animal track data up to 2018, was completed in 2022 (Keeping et al., 2022a, 2022b). It served as the foundation for the ILUMP for the Ghanzi and Kgalagadi Districts, which was finalised in 2024 (Tshukudu, 2024). However, systematic large-scale wildlife monitoring has not been regularly scheduled post-2018, particularly efforts that involve Indigenous community members and integrate their traditional knowledge. While regional and national aerial surveys are conducted by the Botswana Government, they have become increasingly infrequent (the last survey dates back to 2018, as of 2025) and are carried out by professionals from outside the communities. Follow-up research, ideally at a finer scale where possible, is essential for the continuous monitoring of ecosystem health, especially as anthropogenic development in the region continues to expand without any moratorium. Integrating local community members into this effort could provide multiple benefits across ecological, cultural, and economic dimensions (Keeping, Burger, et al., 2018; Liebenberg et al., 2017; Lilleyman et al., 2022). In this context, animal track surveys (detailed in Chapter 2) serve both purposes, offering a promising approach for reliable wildlife monitoring through traditional tracking knowledge (Keeping, Burger, et al., 2018). However, the method could benefit from further parametric refinements.

Building on the observed challenges and research gaps, this thesis explores the overarching question: **What is the current status of large wildlife species populations within the WKCC, and can track surveys serve as a reliable wildlife monitoring method while also promoting coexistence and conservation?** By addressing this question, the ultimate goal is to inform strategies and provide recommendations for future land-use planning that support the long-term functionality of the WKCC, considering both ecological and socio-economic factors. Additionally, this research seeks to highlight

alternative track-based livelihood opportunities for local communities, fostering benefits for both wildlife and people.

Due to logistical constraints, this question focuses on the northern part of the WKCC, specifically four WMAs in the Ghanzi District (GH3, GH10, GH11, and GH13), which collectively cover a substantial area of 22,000 km² (see Chapter 2, **Figure 2-1**). However, given the interconnectedness and similarities among WKCC regions, the findings of this thesis remain relevant to the southern parts of the WKCC as well.

To address this question, my research is structured around two main Working Packages (WPs) (**Figure 1-4**). The first, **WP1**, focuses on validating and improving the methodology of track surveys - particularly the Formozov-Malyshev-Pereleshin (FMP) formula approach - as a reliable and cost-efficient wildlife data collection method for the region. In more detail, I study its two detectability components: the probability of track detection by observers (Chapter 3) and individual animal detectability, which refers to the probability of intersection between an animal's movement path and the transect (Chapter 4). The latter specifically involved improving a key FMP parameter - the average daily travel distance estimate of the species, i.e. how far an animal moves within a 24h period. The findings of WP1 aim to ultimately enhance the accuracy of wildlife density estimates derived using the FMP formula approach. The second work package, **WP2**, builds on WP1 by utilising track surveys and WP1's findings to assess the current status of 13 large carnivore and herbivore species (see Chapter 2, **Table 2-1** and **Table 2-2**) in terms of abundance, density distribution, movement routes, and their environmental drivers. WP2 corresponds to Chapter 5 of this thesis.

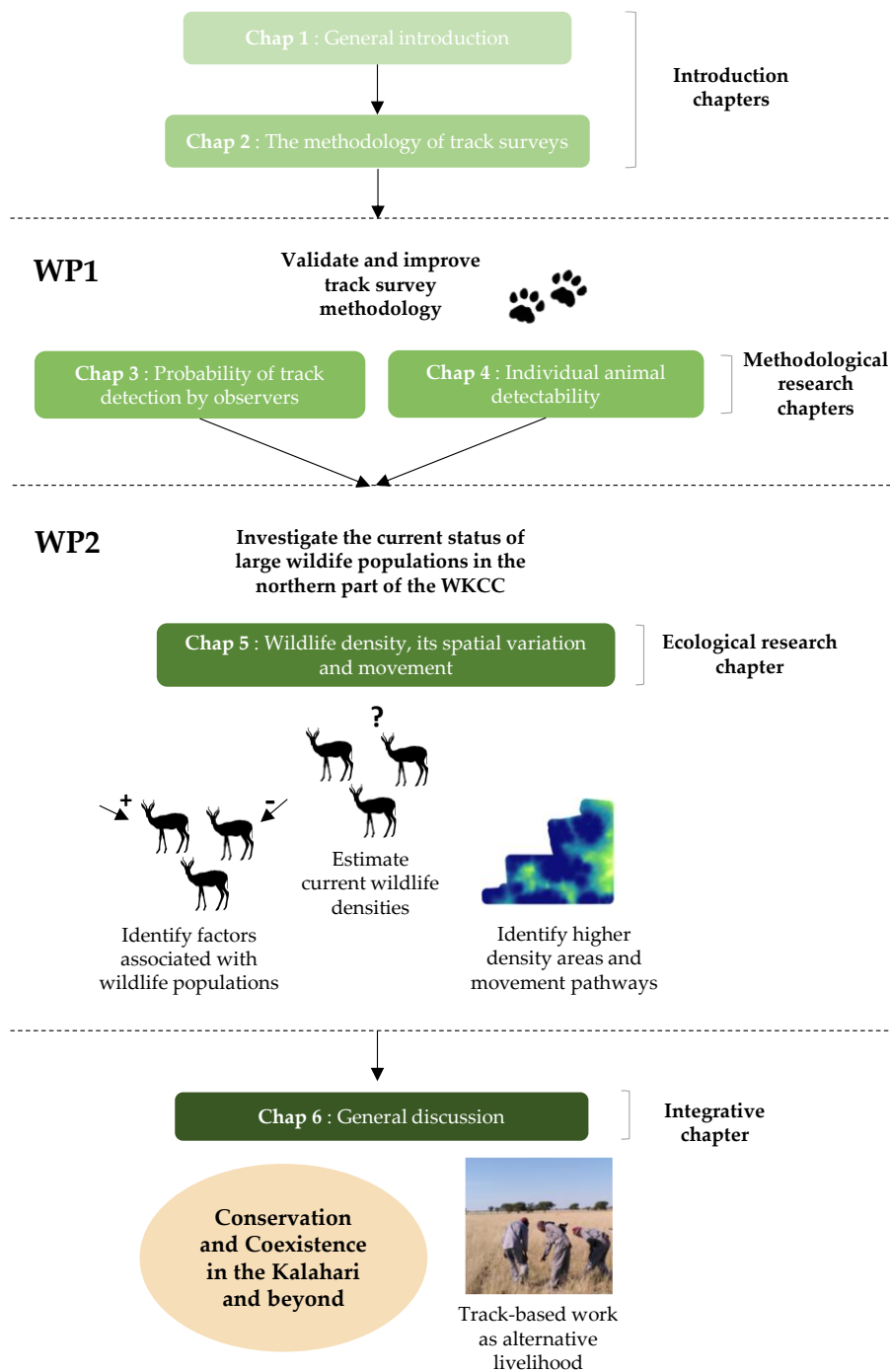


Figure 1-4 Schematic illustration of the thesis work packages (WPs) and chapter structure.

For **WP1**, the set of specific research questions and associated hypotheses are listed below, per Chapter. Detailed scientific literature related to these questions is provided within the respective chapters.

Chapter 3 – Probability of track detection by observers:

- What is the probability of track detection in driven track surveys, and does it vary across observers and sampling conditions (i.e. the type of transect substrate, the density of livestock tracks on the transect, the age of track, the crossing behaviour of the species)?

I hypothesise that the probability of track detection is imperfect in driven surveys, mainly due to the speed at which the vehicle is moving. Measuring this probability is therefore important for correcting density estimates derived from the FMP formula approach accordingly. I suggest that this probability may also vary depending on sampling conditions. However, if observers are highly trained and the survey speed is adjusted to suit the sampling conditions, the probability of track detection is more likely to remain relatively constant across different conditions.

- Are there disagreements between observers on the species identification and ageing of tracks? If yes, what characterises disagreements ?

I hypothesise that disagreements in track identification and ageing should be minimal among highly trained observers. However, when species identification disagreements do occur, they are likely to involve species with very similar tracks or tracks of poor quality (e.g., older tracks or those found on substrates with reduced visibility). Additionally, disagreements in track ageing may be more frequent on highly erodible substrates.

Chapter 4 – Individual animal detectability:

- How can the accuracy of empirical estimates of the species' average daily travel distance be improved?

As an alternative to GPS telemetry, I hypothesise that animal trailing (i.e. following the footprints of an individual or group to reconstruct its movement path across the landscape) has strong potential to yield robust empirical estimates of average daily travel distance of large wildlife species. With highly trained observers, it could serve as a cost-efficient data collection method within a flexible spatial and temporal framework,

potentially providing a greater number of independent samples (i.e. different individual animals or groups) than other techniques.

- How can the accuracy of allometric estimates of the species' average daily travel distance be improved?

Where empirical daily travel distance data are unavailable for certain species, allometric estimates can be derived using the body mass–daily travel distance relationship. Furthermore, these estimates must be adjusted, as Kalahari species travel greater distances daily than their counterparts in other regions where this relationship has been established, due to the sparse and patchy distribution of resources. However, I hypothesise that the adjustment needed may vary across species groups, depending on their foraging strategies.

Likewise, for **WP2**, the set of specific research questions and associated hypotheses are:

Chapter 5 – Wildlife density, spatial variation and movement:

- What is the current population size of 13 large herbivore and carnivore species in the northern part of the WKCC?

I hypothesise that track surveys using the FMP formula approach can provide reliable estimates of population densities for all studied species. Although no direct baseline comparison is available, the methodological refinements introduced in Chapters 3 and 4, along with survey repetition, are expected to improve the accuracy of these estimates. Given the increasing anthropogenic pressures, a decline in some species over this three-year period would not be surprising. Yet, such trends should be interpreted with caution, as wildlife populations in the region are subject to significant fluctuations due to drought cycles and possible changes in anthropogenic activities.

- Which environmental factors are associated with wildlife population density?

I hypothesise that proximity to cattleposts, and to a lesser extent fenced farms, are negatively associated with most large wildlife species densities. In contrast, proximity to pans and fossil valleys is expected to be positively associated with large herbivore densities, which may, in turn, draw large carnivores that primarily prey on large species or use valleys

as travel corridors. Additionally, areas with higher rainfall, greater vegetation productivity, and recent burn scars —promoting green grass sprouts— are likely to be positively associated with large herbivore densities. Higher large herbivore density is also expected to be positively associated with the density of large carnivores that predominantly hunt large prey. Association with vegetation cover is expected to vary among species based on their ecological traits and feeding habits. Regional variations in species distribution are possible, particularly for rare or specialised species.

- Can areas of higher densities and potential movement pathways be identified for each of the 13 largest wildlife species, as well as for each guild (herbivores vs carnivores)?

I hypothesise that, overall, the highest density patches and potential movement pathways are located farthest from human settlements and cattleposts, though species-specific variations are expected based on ecological traits and resource requirements. More generalist species, such as brown hyena, leopard, kudu, and ostrich, may exhibit a more widespread distribution. Most animal movements between the eastern (GH3-GH10 WMAs) and western (GH11-GH13 WMAs) parts of the study area are likely confined to a narrow corridor across the tar road, where human influence is lower —or may be entirely absent for some species. Previously identified movement corridors to the Kgalagadi WMAs are likely still functional but increasingly at risk due to the increasing development of the livestock industry.