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Introduction

Literature

Early literature

In 1553 the French physician-naturalist Pierre Belon (Bellonius) described an African bovid from Asamia, possibly in present-day Morocco, that Brooke (1873) suggests may have been a buffalo. Belon called this animal a little ox. Its horns, however, are described as ringed like those of gazelles and raised upon the frontal bones. Could it have been, not an "ox," but an antelope such as a hartebeest (*Alcelaphus buselaphus*) or a related type, for example, *Damaliscus* sp.? We cannot be sure, as no specimen remains, and furthermore Belon may have obtained the geographic locality only by hearsay (Figure 1.1).

There are a few mentions of the buffalo in the writings of seventeenth- and eighteenth-century Dutch settlers in southern Africa, for example, in van der Stel's narrative of his journey to Namaqualand (English trans. Waterhouse, 1932). Such descriptions contain little information other than indications of the buffalo's former range. Until about the middle of the nineteenth century there is only a trickle of new information on the African buffalo, mostly of a superficial nature. It consists mainly of notes relevant to taxonomy (e.g., Sparrman, 1779, 1785; Thunberg, 1811; Smith, 1827, 1850; Smuts, 1832; Smith, 1834; Gray, 1837, 1843; Hodgson, 1847) and of hunters' accounts (e.g., Cornwallis Harris, 1840).

In the second half of the nineteenth century the trickle increases substantially. For example, the subject index of the proceedings of the Zoological Society of London for 1830–60 has only one entry dealing with the African buffalo, but in the following 30 years there are over 60 such entries. Most of these deal either with the acquisition of live and dead specimens or with taxonomy. Papers that appeared during the

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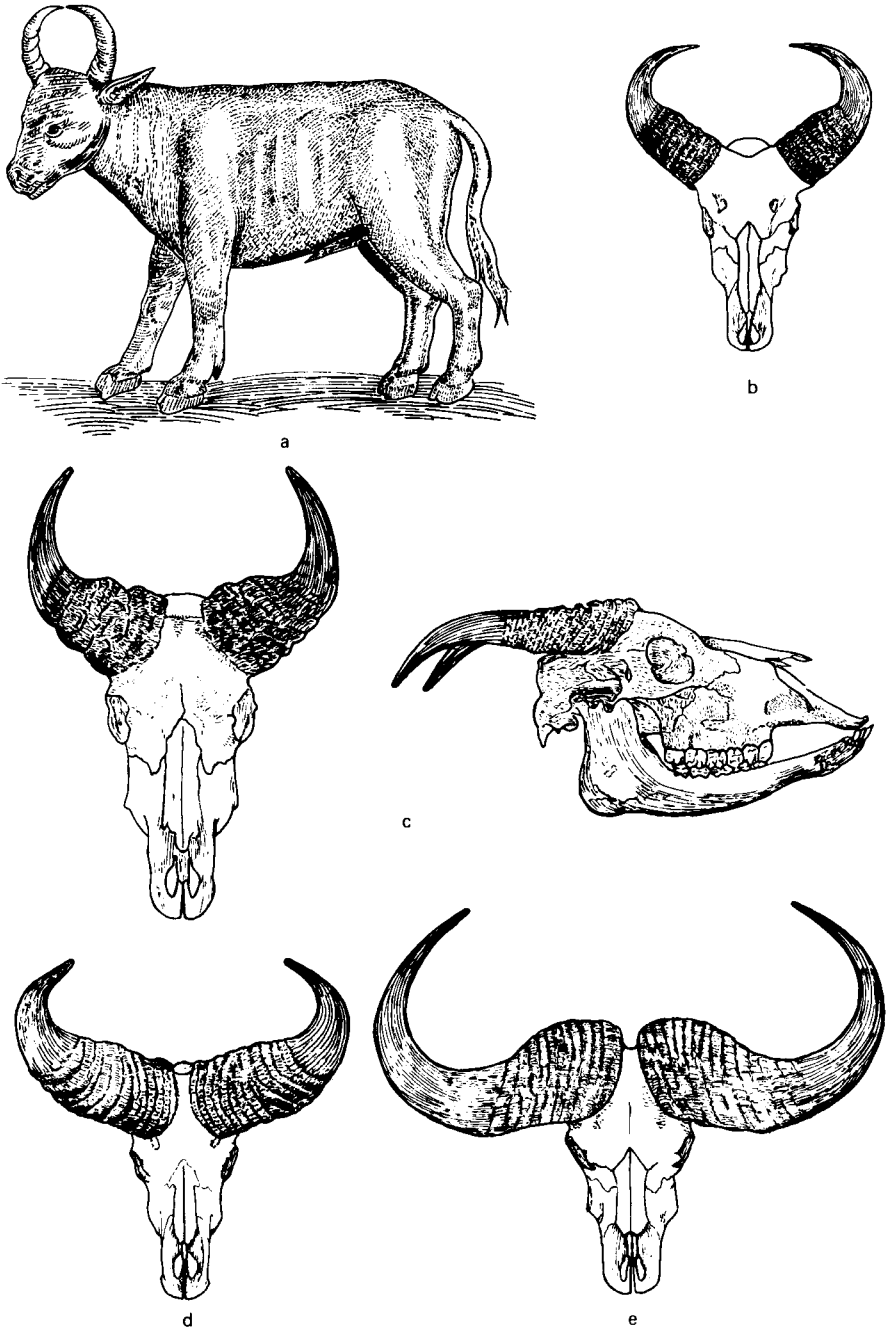

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same period in the French bulletins of the Société Philomatique de Paris and of the Société Nationale d'Acclimatisation, in the German *Zoologisches Jahrbuch*, and in the notes of the Leyden Museum and others also deal mainly with points of taxonomic interest. Among the authors are Sclater (1864), Kirk (1864), Blyth (1866), Gray (1872), Brooke (1873, 1875), Johnson (1885), Rochebrune (1885), Cincinn (1887), Schlegel (1880), and Pechuel-Loesche (1888).

Some comment on the distribution of the African buffalo also begins in the second half of the nineteenth century (e.g., Temminck, 1853; Buckley, 1876).

Occasionally, useful accounts of the buffalo occur in explorers' and hunters' narratives of that period, for example, Livingstone (1857, 1865), Holub (1881), Selous (1881), and Bryden (1899). Most of the early notes on African buffalo behavior and social structure that may merit attention occur in such accounts. The value of these sources is very unequal. Some of the notes, especially those by Selous, simply report direct observations of buffaloes and contain a fair amount of detail, but some others appear overinterpreted or too fragmental. A few of these accounts, for example, von der Decken's *Travels in East Africa* (1869), have been edited to a damaging extent by persons without direct experience of the subject matter. Lydekker (1898, 1904, 1906, 1910, 1913, 1926) may have done most to launch the modern trend in African buffalo systematics.

Twentieth-century literature

African buffalo systematics were discussed and revised during and after Lydekker's time by a number of other authors. Contributions in

Figure 1.1 Some historic buffaloes: (a) This may be the first picture of an African buffalo to appear in a natural history text. It accompanies the description by Pierre Belon, a sixteenth-century French physician-naturalist, of a small buffalo claimed (with questionable accuracy) to have come from northern Africa. The illustrator may have seen an authentic *Syncerus* hide, to judge by the deep wrinkles on the neck and an indication of hairy tufting in the ear. The horns, if drawn from a specimen, may have belonged either to a *Syncerus caffer* of the *brachyceros* or *nanus* variety, or to an alcelaphine antelope, although the body is clearly meant to appear cattlelike. The depicted skulls, redrawn from Brooke (1873), were used in the early studies of the species by Sir Victor Brooke and others. (b) A female skull brought by a Captain Clapperton from central Africa in the 1830s (greatest horn spread about 51 cm); (c) two aspects of a male skull obtained by Brooke from E. Gerrard in 1872 (greatest horn spread about 69 cm); (d) a male skull brought by Sir Samuel Baker from Sudan or Ethiopia in the 1860s (greatest horn spread about 64 cm); (e) a male *S. c. caffer* skull represented in Brooke's paper and described as a "very fine specimen of the horns of *Bubalus caffer*" (Brooke 1873, p. 481) (greatest horn spread about 104 cm). It is now known that the span of such horns can slightly exceed 142 cm.

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this field were made by Schwartz (1920), Christy (1929), Malbrant (1936), Schouteden (1945), Blancou (1954), Dalimier (1955), and Grubb (1971). Grubb, besides expressing his own views on African buffalo speciation, contributes a good review of the literature on this subject. Comments on Grubb's paper can be found in Groves (1975). A substantial paleontological contribution to the field of African buffalo speciation is found in Gentry (1979).

There exist a few brief studies, notes, and communications, mainly in French, English, and German, which have a local character and usually deal with more than one aspect of the buffalo. They may yield useful bits of information, depending on the reader's special interest, and some of them are cited in various parts of this work. Among those cited the most valuable are a paper by Pienaar (1969a) concerning the buffaloes of the Kruger Park, South Africa, and a paper by Henshaw and Greeling (1973) that describes the buffaloes of Yankeri Game Reserve, northeastern Nigeria, and reviews some relevant literature. Local studies that are not directly mentioned elsewhere in the present work but must not be overlooked include papers by Leuthold (1972) on a buffalo herd in the Tsavo Park, Kenya; Grimwood et al. (1958) on Zambian buffaloes; Baudenon (1952) on Togo buffaloes; and Monard (1935) on Angolan buffaloes.

The largest recent contribution is Sinclair's (1977) study of the buffaloes of the Serengeti region, northern Tanzania. This work contains a long list of references. There is a substantial body of literature dealing with parasitological and pathological conditions affecting the African buffalo, and much of this is listed in Sinclair (1977).

Finally, much varied information is contained in the annual and other reports of several African government game or wildlife departments. These sources, however, may be difficult to reach and tedious to search.

Biogeography

General notes

The main study areas are located on or near the great high plateau that covers roughly one-third of the African continent (Figure 1.2). This plateau occupies most of Africa south of the equator and in the east extends far into the northern hemisphere. The plateau with its margins probably comprises the entire geographic range of the largest races of the African buffalo, for example, *capensis* and *radicliffei* (the largest buffaloes found outside this region are of the slightly smaller *aequinoctialis* type).

This great highland is topographically diversified and includes flat to

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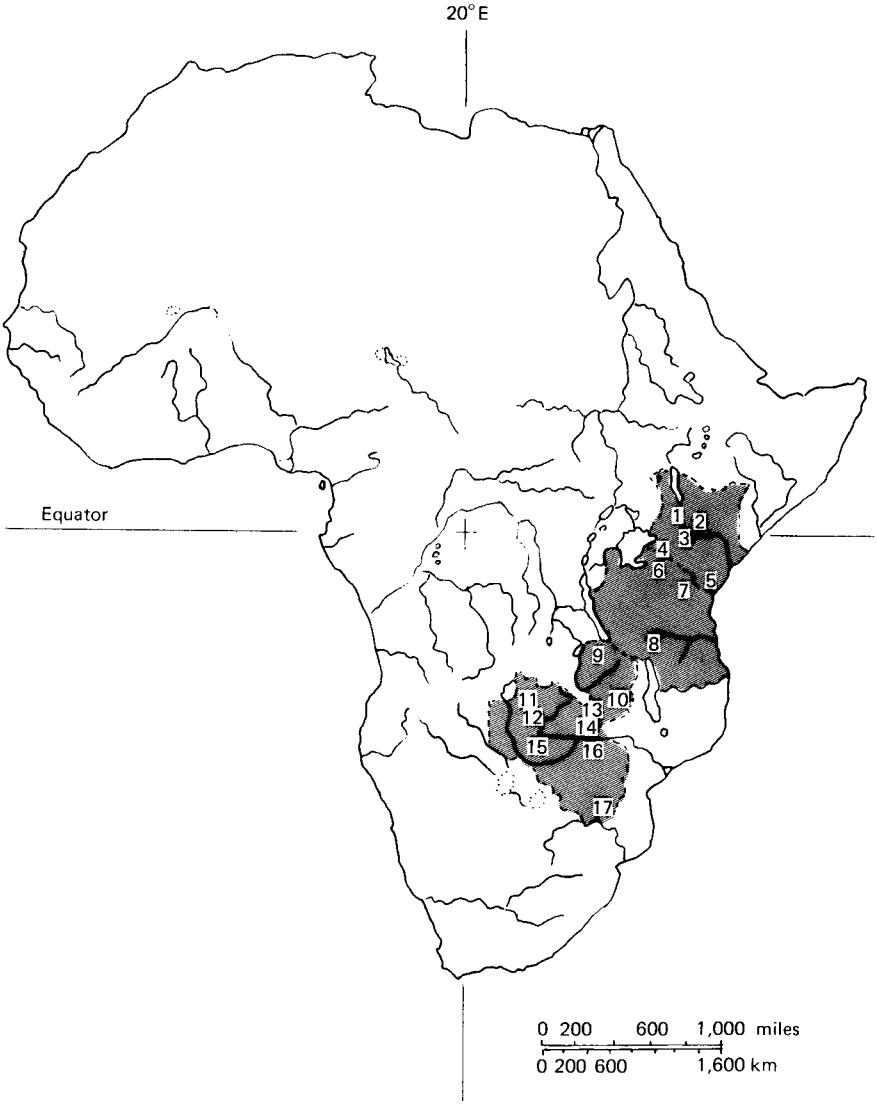

Figure 1.2. Study area. Shading indicates in general where most of the author's own observations were made. Localities considered particularly useful to the study are indicated. These do not always coincide with the largest remaining buffalo concentrations. Key: (1) Marallal–Baragoi; (2) Archer's Post–Samburu Game Reserve; (3) Mt. Kenya–Abardares; (4) Narok District (Lolgorien, Loita); (5) Coastal hinterland–Tsavo National Park; (6) Serengeti N.P.; (7) Ngurdoto Crater; (8) Ruaha N.P.; (9) Mporokoso–Sumbu; (10) Luangwa Valley; (11) Lukwakwa–W. Lunga N.P.; (12) Busanga and adjacent area; (13) Mkushi–Muchinga escarpment; (14) Zambezi Valley, north bank; (15) Nanzhila; (16) Zambezi Valley, south bank; (17) Gona-Re-Zhou G.R. (Mabalauta).

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rolling plains, hilly areas, a few mountain chains (e.g., the Ethiopian mountains, the Ruwenzori, and the Drakensberg), and some isolated high mountains (e.g., Kilimanjaro, Kenya, and Elgon). There are also present very large elongated tectonic depressions known as rift valleys. Most of the high plateau is between 1,000 and 2,000 meters above sea level (a.s.l.), but on mountains elevations attain up to 5,895 meters a.s.l. (Kilimanjaro). Extensive floodplains occur along many larger rivers and around some lakes. Around the plateau margins occur large embayments of ground well below 1,000 meters a.s.l.

The surface rocks are largely Precambrian metamorphics and Paleozoic and Quaternary sedimentary formations. Mesozoic rocks also outcrop, but over smaller areas. Intrusive complexes and extrusive volcanic rocks are exposed in many places.

The main soil types of the great African high plateau are, in the north and south, the chestnut and brown soils typical of semiarid grasslands and the red to yellow savanna/rain forest ferrisols in the middle portion. On this background occur a few patches of dark gray to black subtropical vertisols. An area of montane soils is found in the Ethiopian part of the highland. A large expanse of red and gray desert soils occurs in the far southwest of the highland plateau, over the Kalahari area. The major soil types do not demarcate the plateau but extend into the neighboring lowlands.

The plateau is drained by several large river systems. The Orange, Cunene, and Cuanza systems empty directly into the Atlantic. The Limpopo and the great Zambezi system flow in the opposite direction into the Indian Ocean. Also important are two northwesterly flowing major tributary subsystems of the Congo river – the Kasai and the Lualaba – and so is the drainage northward into the Nile. The Ethiopian, Kenyan, and Tanzanian highlands are partly drained by several major streams which empty into the Indian Ocean – the Shaballe, Juba, Tana, Ruaha, and Ruvuma rivers. A large number of seasonal and some permanent streams flow into all these major rivers, which also collect the water of numerous surface and near-surface seepage lines, such as those called *dambos* in Zambia and Zimbabwe, and swamps. All the great African lakes, with the exception of Lake Chad, are located in this highland region, some of them occupying low ground within it and some occurring at relatively high elevations.

Mean annual rainfall over the high plateau varies between about 200 millimeters and a little under 2,000 millimeters. In the savanna areas it is of the order of 600 to 800 millimeters. The mean monthly temperatures vary between about 8 and 30°C. The most common temperatures are around 20°C.

The high plateau is covered mainly by savanna and arid land vegetation in its northern and southern parts and by dry deciduous wood-

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land and savanna woodland in its middle portion. Patches of montane forest and meadow occur locally, particularly in a few localities between northern Ethiopia and the northern end of Lake Malawi. A few small patches of rain forest occur, for example, the Kakamega forest in western Kenya, the montane rain forests on Mount Kenya and the Ruwenzori range, and the Tsitsikama forest in the Cape Province of South Africa. Arid-land vegetation occurs in much of northern Kenya, in the Kalahari area, and elsewhere.

The savanna and deciduous woodland areas – the most common vegetation assemblages on the plateau – typically have one or two closely spaced rainy seasons annually. These coincide with the growth of grasses and are slightly preceded by the appearance of new leaves on deciduous trees. A large proportion of the year is rainless, when the grasses stop growing and trees are mainly without leaves.

The savannas support a large variety of grasses, typically of tufted growth habit (see also Chapter 6). Except for relatively rare areas of pure grassland savanna, a tree cover occurs which varies in density between types where individual trees are several tens of meters apart and types where crowns of trees nearly touch. The latter types grade into woodlands. Many species of trees are found in various parts of the high plateau, largely belonging to the genera *Acacia*, *Brachystegia*, *Julbernardia*, *Isoberlinia*, *Terminalia*, and *Albizia*, though many others also occur. *Colophospermum mopane*, occurring either as mopane woodland or scrub in dry, hot, low valleys up to about 1,000 meters a.s.l., and *Adansonia digitata*, the baobab, are also important and occasionally characteristic.

Evergreen communities or individual evergreen trees are fairly common in areas which are broadly referred to as savannas and savanna woodlands or woodlands. For example, among 84 common trees of Zambia, not including palms and euphorbias, 32 percent are deciduous, 49 percent semideciduous, and 19 percent evergreen. Evergreens occur largely in riverine environments, gallery woodlands, and a few other relatively well-watered deep-soil situations. The genera represented include *Parinari*, *Trichillia*, *Diospyros*, *Syzygium*, *Baphia*, *Cryptosepalum*, and others.

Deciduous and semideciduous thickets are common. Among the many genera of small trees and shrubs found in thickets are *Combretum*, *Commiphora*, *Balanites*, *Pseudoprosopsis*, *Bussea*, and *Pseudolachnostylis*. In wetter areas, evergreen thickets occur.

The region is of course famous for the diversity of its vertebrate fauna: Over 115 major mammal species, not counting mice, squirrels, and bats, many hundreds of bird species, and a fair number of reptilian and amphibian species occur on the plateau. Bovids are represented by about 50 species. The buffalo is found in all types of habitat, with the exception of large waterless tracts.

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It is not clear to what extent the distribution of vegetation on the high plateau has been affected by man-made fires. Burning may have gone on, by design or semiaccident, for as long as man has known fire, and this may have been an important modifying factor in the size and distribution of grasslands and therefore in the ecology of grazing animals.

Specific areas

Three study areas are particularly often mentioned in the chapters that follow: Lolgorien, Kenya; Busanga, Zambia; and Mabalauta, Zimbabwe (Rhodesia). All three furnished important data, and they represent three very different buffalo habitats. Later comments may be more meaningful if these areas are summarized at the start. There will follow a few very brief notes on the other areas of study.

Lolgorien. Lolgorien is situated in the extreme west of the Kenya Maasai lands, 25 kilometers due west of the Mara river and 22 kilometers due north of the Tanzania border. It is located on a belt of Precambrian metamorphic rocks sculptured by erosion to form a number of 135- to 165-meter-high hills strongly elongated in a northwesterly direction and often topped with forest. Strips of forest also grow along watercourses in the bottoms of valleys as well as in the vicinity of the not distant and perennial Migori river. The long hill slopes that comprise most of the area are grass-covered, with small patches of forest, often only a few tens of meters in diameter, scattered over the grassland.

Some 3 kilometers east of Lolgorien and extending to the Mara river is a relatively high lava flat – the Isuria Plateau – overgrown by a patchwork of forest and grassland. From this lava flat the hills around Lolgorien are seen from slightly above. About 2½ kilometers south of Lolgorien and trending parallel to the Tanzania border, that is, along a northwest line, commences a large granite area. The landscape over the granite near Lolgorien consists of low rolling hills and depressions without any definite trend, covered by grassland and shrubs with occasional woodland patches and strips of riverine forest. Bounding the Lolgorien area on the west and north sides, 6½ to 11 kilometers distant, is the curving Migori River.

At the time of the study (1964–67) the human element consisted only of a small police post, a store catering mainly to the pastoral Maasai, a small government infirmary, and a small primary school. Several pastoral Maasai compounds separated from one another by a kilometer or so were scattered over some of the area. A handful of other people, unconnected with the above, and usually fewer than 10, inhabitated the location more or less intermittently.

The fauna in general was rich. The bird and reptilian faunas were

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large and biogeographically typical. The abundance of the larger mammalian fauna was very evident. Besides buffalo, resident bovids included topi (*Damaliscus korrigum*), kongoni (*Alcelaphus buselaphus cokei*), waterbuck (*Kobus ellipsiprimnus/defassa*),[1] impala (*Aepyceros melampus*), reedbuck (*Redunca redunca*), bushbuck (*Tragelaphus scriptus*), oribi (*Ourebia ourebi*), red and Grimm's duiker (*Cephalophus natalensis* and *Sylvicapra grimmia*), and roan antelope (*Hippotragus equinus*). Eland (*Taurotragus oryx*) often passed through. Conspicuously absent were Thomson's and Grant's gazelles (*Gazella thomsoni* and *G. granti*), wildebeest (*Connochaetes taurinus*), and giraffe (*Giraffa camelopardalis*), four very common species on the east bank of the Mara River.

The area may have been the westernmost bastion of the black rhino (*Diceros bicornis*) in Kenya. Seven rhinos were resident within easy walking distance and others occurred in the vicinity. Zebras (*Equus burchelli*) and warthogs (*Phacochoerus aethiopicus*) were common. Elephants (*Loxodonta africana*) were usually present, especially just to the east and northeast of Lolgorien, and were occasionally seen browsing next to Maasai cattle when the latter grazed near trees.

Hyena (*Crocuta crocuta*), leopard (*Panthera pardus*), lion (*P. leo*), and cheetah (*Acinonyx jubatus*) were either resident or common visitors. Wild dogs (*Lycaon pictus*) also visited the area, and I observed them raising pups there. Serval (*Felis serval*), common and large-spotted genet (*Genetta genetta* and *G. pardina*), civet (*Viverra civetta*), side-striped jackal (*Canis adustus*), baboon (*Papio anubis*), and a number of small mammal species were also seen.

The Lolgorien area merited the status of a game reserve, open to cattle grazing and a few other activities, along the lines of Ngorongoro or the Maasai–Mara reserves. It was, however, one of the gazetted shooting blocks.

Busanga. The Busanga flats are situated in northwestern Zambia some 65 kilometers south of Kasempa and are mostly within the Kafue National Park. Even outside the national park boundaries the region is very sparsely populated and the land is a game management area.

The Busanga area includes woodlands and *dambos* but consists very largely of the vast floodplain of the Lufupa and Lushimba rivers which drain into the Kafue, and thus eventually the Zambezi.

The reader is referred to Chapter 12 for details on this area, where it is compared to the habitat of the Asiatic buffalo (*Bubalus bubalis*) resettled in Australia.

The Busanga area supports a large bird, reptilian, and amphibian fauna and a highly diversified medium-density mammalian fauna.

[1] Individuals resembling either species occurred.

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During my working visits and stays in the Busanga area, between 1970 and 1978, I positively indentified many mammal species. Within the confines of the floodplain, including a thicket and several isolated "palm mounds," I encountered in different seasons the following species, besides the prominent buffalo:

Puku (*Kobus vardoni*), red lechwe (*K. leche*), roan antelope (*Hippotragus equinus*), situtunga (*Tragelaphus spekei*), reedbuck (*Redunca arundinum*), wildebeest (*Connochaetes taurinus*), eland (*Taurotragus oryx*), zebra (*Equus burchelli*), hippopotamus (*Hippopotamus amphibius*), warthog (*Phacochoerus aethiopicus*), bushpig (*Potamochoerus porcus*), rhinoceros (*Diceros bicornis*), elephant (*Loxodonta africana*), side-striped jackal (*Canis adustus*), wild dog (*Lycaon pictus*), hyena (*Crocuta crocuta*), lion (*Panthera leo*), leopard (*P. pardus*), cheetah (*Acinonyx jubatus*), serval (*Felis serval*), caracal (*F. caracal*), honey badger (*Mellivora capensis*), spotted-necked otter (*Lutra maculicollis*), clawless otter (*Aonyx capensis*), civet (*Viverra civetta*), genet (*Genetta genetta*), marsh mongoose (*Atilax paludinosus*), banded mongoose (*Mungos mungo*), other types of mongoose, cane rat (*Thryonomys swinderianus*), and vervet monkey (*Cercopithecus aethiops*).

On the periphery but overlapping with the floodplain I identified (besides many of the above species): oribi (*Ourebia ourebi*), Grimm's duiker (*Sylvicapra grimmia*), yellow-backed duiker (*Cephalophus sylviculltor*), waterbuck (*Kobus defassa*), sable antelope (*Hippotragus niger*), hartebeest (*Alcelaphus lichtensteini*), and Cape hare (*Lepus capensis*).

In woodland adjacent to the floodplain (again besides many of the species named above) I identified: kudu (*Tragelaphus strepsiceros*), bushbuck (*T. scriptus*), impala (*Aepyceros melampus*), baboon (*Papio cynocephalus*), wild cat (*Felis lybica*), antbear (*Orycteropus afer*), blue duiker (*Cephalophus monticola*), grysbok (*Raphicerus sharpei*), squirrel (*Heliosciurus* spp.), and porcupine (*Hystrix africae-australis*).

The Busanga flats and vicinity are one of the important remaining wildlife areas of Central Africa.

Mabalauta The Mabalauta area is situated in the far southwest of Zimbabwe, near the intersection of the Mozambique border with the Nuanetsi River. It is not on but peripheral to the African high plateau, in the so-called *lowveld*.

At the time of the study (1972) the area was a part of the Gona-Re-Zhou Game Reserve and uninhabitated except for the sector headquarters compound. Visitors were rare.

The area is largely underlain by crystalline rocks. During the dry season the streams dry out, with the possible exception of a few pools in the Nuanetsi riverbed and a few *pans* in relatively impervious depressions. The country is flat to hilly scrubland with some deciduous

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