An Introduction to the Ecology and Zoo-Geography of the Okavango Delta

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The Okavango Delta comprises three major ecoregions, distinguished by their low, open, or abundant, of water. These are:

1. the permanent swamp, with perennial surface water up to 4 m deep;
2. seasonally-inundated areas, the extent of which varies to a large degree, depending on the magnitude of the annual flood from Angola and the amount of local rainfall;
3. the higher, dry land masses, of which there are three major examples: Moremi Wildlife Reserve, Chief’s Island and the Western sand-void tongue.

Within these three broad divisions is an interlocking mosaic of habitat types, which contributes most to the diversity of the Delta’s wildlife spectrum at all phylogenetic levels. Most of the conspicuous wildlife species utilise the last two zones to varying degrees, but the first provides suitable habitat for comparatively few large wild animals.

The permanent swamp extends from approximately half-way down the “pan-handle” to cover large areas in the north-west of the Delta. It penetrates further down the eastern drainage systems of the NgColes, Meonchosira and Sauterduide then down the western rivers, such as the Thaong and Marsebe, while the centrally-situated Xudum and Boro show an intermediate phase.

It is characterised by deep, perennally-flowing channels and lagoons, with extensive beds of papyrus (*Cyperus papyrus*) and reeds (*Phragmites spp.*). Other conspicuous plants are bulrushes (*Typha spp.*), hippo grass (*Vossia cuspidata*) and water lilies (*Nymphaea caerulea*), with the date palm (*Phoenix reclinata*) and gomoti (*Fissu verrucosus*) among the most characteristic trees.

Islands occur throughout this zone with increasing frequency towards the south. They may be simply classified according to their size. The smaller islands (up to 100 m diameter) are normally covered by dense riparian woodland in which the dominant species are large trees, eg. mopane (*Mathostrachys lepcha*) and mopane (*Mopane lepcha*), lead-wood (*Ceratonia imbecillus*), knobthorn (*Acacia nigrescens*), with the palm (*Hyphaene boennigru*) often the most numerous species centrally.

The larger islands in this zone usually consist of a fringe of similar riparian woodland which is succeeded centrally by an area of “island grassland” often dominated by *Sporobolus spadix* or couch grass (*Sporobolus decipiens*).

The second and largest zone is one of larger islands divided by melapo which are wide (up to 500 m), shallow, grass and sedge-covered flood plains. These are often branched and form drainage lines, either open-ended from one river system to another, or closed, the water penetrating the melapo from the river and receding as the flood diminishes. These melapo may be conveniently divided into two classes: “primary” floodplain, ie. regularly inundated in a year of average flood, and “secondary” floodplain, which is inundated less frequently, when the flood is higher than average. The “primary” floodplain vegetation is dominated by sedges, particularly *G. meunierii*, *Sporobolus spadix* and *Fimbristylis complanata*. This vegetation type is very dense and forms thick mats of mostly dead material when dry. The mean vegetation height is approximately 75 cm, and these are flooded for a major part of each year, often to a depth of half a metre or so.
"Secondary" floodplain is characterised by tall grasses, such as Imperata cylindrica, Setaria viridis, Cenchrus ciliaris, Eragrostis hirsuta and Panicum repens. The last-named grass may be strongly dominant locally. This vegetation category is found near the edges of the floodplain between the "primary" category and permanently dry ground, or it may cover a smaller melapo completely. The vegetation height is approximately one metre and it rarely floods to more than 10 cm in depth. Extreme examples occur of "secondary" floodplains, which have not received flood water for many years and which have been colonised by woody species, such as Acacia tortilis, until a subsequent year's higher flood has inundated the area again, causing the death of the trees, which are sometimes as much as 20 years old.

The islands in this zone also show the typical fringe of riparian woodland and central areas of "island grassland." The latter, however, are often very extensive and broken up by patches of dry woodland and patches of vigorously colonising forbs, such as Phaseolus virgatus. The dry woodland patches vary from Acacia/terminaria-dominated sandveld, to dense shrub consisting of, e.g., Dioclea adhatoda ensora and Acacia spp., and in some less sandy areas, pockets of mopane (Colophospermum mopane) woodland occur.

The large dry land masses comprise mainly areas of mopane woodland with frequent pans. Interpersed with these are large patches of deep sandveld where the dominant trees are either Terminaria sericea or Acacia greggii, or a mixture of both together with other species, Lousiacarpus velutina and Combretum spp. Conspicuous areas of scrub occur particularly in the mopane woodland, where the plant apparently does not grow beyond approximately 1 m in height. These areas of inhibited growth have not yet been adequately explained, but the result may be a combination of factors, such as soil, drainage and fire. Much of the mopane woodland may be regarded as a monotypic for long periods of the year, the only other plants being annual grasses in evidence during the rainy season.

Another important component of the Okavango's physical environment is the large number of wetlands which occur throughout the Delta. Widespread in the dry areas, they are of some importance to various animals as either vantage points or convenient breeding sites. In the area of permanent swamp, they provide sites for colonisation by woody species forming a category of very small islands and increasing the diversity of that zone. Here again they provide vantage points, and lying-up places, for recce in particular. It is, however, in the zone of seasonal flooding where they are most important. As well as performing the functions described above, they have been attributed with having a substantial effect on regulating the flow of the floodwaters and initiating the formation of new islands. There are frequent examples of the entrances to narrower melapo having been obstructed by a series of terrateria, which, after being built up, have been partially eroded, causing the water to flow into the melapo. As a consequence, the melapo eventually becomes permanently dry and woody vegetation colonises the former floodplain.

The input of water to the Delta is biphasic. Each year the Okavango floods, of Angolan origin, provide water at a time when the residue of the single annual rainy season is diminishing and has disappeared. Precipitation normally occurs between November and March, with the bulk of the rain falling in January and February. Annual amounts vary between 200 mm (1933) and 1200 mm (1974), with an average of 560 mm. In a normal year, the rainfall in pans, melapo and other areas of impeded drainage has disappeared by July. The coincidences with the high point of the annual flood in the central Delta. Water begins to rise in the Okavango River in mid-January and peaks at Xaxaba in May and at Maun in August. Conversely, as the water in the melapo recedes to a minimum towards the end of the year, rainfall normally begin to fill the pans. This is of crucial importance to the majority of larger wild animals.

Every year most of the Delta is burned (possibly up to 75%). Nearly all the burning is deliberately caused by humans. These burns often begin as early as the end of May and have considerable effect on the local movements of animals. Where melapo are burned, the progress of the rising flood is accelerated due to the removal of much of the vegetation, which acts as a barrier. For the same reason, burning also helps the water to reach areas it would otherwise not have reached.

The Delta can boast an extremely wide variety of large wild animals, ranging from those which are almost totally aquatic, such as the crocodile (Crocodylus niloticus) and hippopotamus (H. amphibius), semi-aquatic species, such as sitatunga (Tissulaphus schupei) and lechwe (Kobus leche), many water-dependent species, and a few which are totally independent of water, such as the gemsbok (Oryx gazella) and aardvark (Orycteropus afer), which reflects the Delta's proximity to the arid region of south-western Africa.

The permanent swamp sustains only three species of large wild animals: the crocodile, hippopotamus and sitatunga, although it is not a completely discrete zone, lechwe do occur in some areas and occasionally leopard (Panthera pardus) may be found. In the northern region, in addition, other species may traverse sections of this zone, notably elephants (Loxodonta africana) and buffalo (Syncerus caffer).

The Delta's populations of crocodile and hippopotamus both show indications of being considerably depleted, although for the crocodile, on which some recent work has been carried out, there are some signs of partial recovery. This species was hunted extensively on a commercial basis between 1955 and 1968 and an estimated 50 000 crocodiles were killed. Local tribesmen, however, show little interest in hunting crocodiles except where they have threatened livestock. In 1973, a pilot-poaching scheme in the Okavango "panhandle" was started by Botswana Game Industries. The annual quota was set at 500, but the project was abandoned in 1974 as uneconomic, under the conditions imposed by the Department of Wildlife and National Parks of the Botswana Government.

As far as the hippopotamus is concerned, there is very little information. No surveys have been attempted, but superficially it appears that much of the habitat suited to the animal is relatively unused. Like the crocodile, it occurs throughout the Delta, but has its stronghold in the area of permanent swamp. School of 20 or more are rare in the Delta, although they are numerous in the associated waters of the Selinda/Queen Olifants/Lammasi system to the north-east. It is apparent from long-standing local residents' reports that these animals were hunted extensively in the past. Their meat is highly prized and they are also considered a threat to local river traffic, particularly dug-out canoes (makoro). Another factor contributing to their assumed decline in numbers was, no doubt, the widespread use of hippopotamus carcasses as crocodile bait by commercial hunters. The species now enjoys full protection, although some poaching still occurs in remote areas.

The sitatunga is the only true example of a large mammal which is confined to the permanent swamp zone. Its numbers are unknown, but the species is exclusively to the permanent swamp zone. Its numbers are unknown, but the species is exclusively to the permanent swamp zone. Its numbers are unknown, but the species is exclusively to the permanent swamp zone.
habitat onto the higher dry land, eg. in the early part of 1975 to the "panhandle."

It is, however, in the last mosaic of channels, meispo and islands together with the large dryland that the large variety of the Okavango wildlife resource becomes apparent. It is here that the unique alternating floods and rains characterise the seasonal distribution of most of the large fauna. There are 20 species of large herbivore, ranging in size from the steenbok (Raphicerus campestris), weighing 10 kg, to the elephant, which may weigh 6000 kg. On the basis of biomass, the buffalo (Syncerus caffer) is by far the most prominent, approximately 20 000 animals are to be found in the Delta for most of the year. They normally occur in large herds of 70 to 200 animals, and often form congregations of up to 1 000 individuals prior to the rains. Their preferred habitat is the sandveld and during the period December to May, they are to be found mainly in the three large land masses where they utilise the numerous rainwater pans. The nutritious grazing available, in that habitat during the rainy season is responsible for their fairly strict seasonal breeding. The vast majority of calves are born between January and March, and the gestation period is approximately 11 months. As the grazing deteriorates and the pans begin to dry up, the buffalo herds move to the edges of the dry land masses, using the meispo for both water and night-time grazing. Towards the end of the dry season they are found roaming in large concentrations in the mosaics of islands and meispo which makes up the seasonal swamp. They utilise the islands mainly for shade and cover during the day and the floodplains for grazing from dusk until 2 or 3 hours after dawn. The much coarser grasses of the floodplain, which are increasingly utilised towards the end of the dry season, lead to a loss in condition, which can amount to 250 kg in a large bull, ie almost 25% of the total body weight.

Exercises in which ever 600 buffalos have been marked in Ngamiland, show that animals utilising the eastern floodplains of the Khwai during the dry season are generally during the rains and can be found up to 100 km to the north-east of the Delta. Similarly, animals from north-west of the Delta have moved up to the Conzalo, and those on the west move out to the south and west when conditions are suitable, although this last movement has been curtailed in recent years, due to the more intensive human settlement along the Thaive. There is no evidence that the "western" and "eastern" buffalo mix to any extent, although the populations must meet along the Boro drainage.

Other species range outside the Delta too, particularly elephants, but also zebra (Equus burchelli) and wildebeest (Connochaetes taurinus). These latter two large grazing herbivores utilise, in general terms, similar habitats to those described for the buffalo, and their seasonal movements are also similar but less well defined. Their combined populations total approximately 12 000 animals, with zebra slightly more numerous in the Delta. In exceptionally dry years, such as 1973, spectacular herds of over 2 000 zebra and wildebeest may be seen concentrated on the floodplains near permanent water. It is likely, however, that under such circumstances the normal Delta populations of these highly mobile species have been reinforced by the influx of herds normally resident outside the Delta.

Elephants are now numerous in the Okavango, although in the dry season, fairly large herds may be seen, particularly around Khwai, Moremi and Maxwee. Like other elephant populations in Botswana, they are characterised by their small tusks and apparently unusually large body size. At any time, the Delta's present elephant population does not exceed 2 000, though indications are that the area could support considerably more.

The habitat with the most pressure exerted on it, and therefore the most limiting, is the ecotone consisting of the woodland/grassland fringes of the larger islands and dryland mass. Here, the diversity of browsing and grazing animals on a year-round basis has resulted in locally-evident browse lines and patches of overgrazing. The grazing phase of this ecosystem receives protection to a varying degree from the rising floodwaters. As the grasses grow through the water, only the lechwe feed on them in any quantity and recent work has shown that even they spend more time feeding out of the water. Obviously at the time of peak flooding, there is the least available floodplain grazing, most of the animals' feeding being confined to a narrow strip against the island woodland. Later, as the floodwaters recede, progressively more of the freshly-growing grasses and sedges in the meispo become available to more species, such as tsessebe (Damaliscus lunatus), warthog (Phacochoerus aethiopicus), impala (Aepycerus melampus) and reedbuck (Redunca arundinum) as well as those already mentioned.

Browsing animals utilising this zone include the impala, kudu (Tragelaphus strepsiceros), bushbuck (T. svaleri) and giraffe (Giraffa camelopardalis), all of which also penetrate the dry woodland, except for the exception of the bushbuck, which is seldom found far from water. Another conspicuous resident of this zone is the baboon (Papio anubis), which feeds on many of the large fruit-bearing trees, which are common in the riparian woodland. Although figures are not available, there is little doubt that the baboon and impala form a conspicuous and considerable fraction of the total biomass of the Delta.

Other large herbivores are abundant locally, eg, sable (Hippotragus niger) and waterbuck (Kobus ellipsiprymnus) in the north and east, particularly along the Khwai River, and occasionally roar (H. equinus) may be seen. Genet and are often found in the lower portion of the sandveld in the western Delta.

Large predators are abundant, but the brown hyena (Hyaena brunnea) is the most in evidence (Acinonyx jubatus) and wild dog (Lycaon pictus) are widespread and the leopard undoubtedly occurs throughout the Delta. The brown hyena (Hyaena brunnea) has been recorded on the western fringes in the Nokhang area.

Domestic animals are limited in their distribution, mainly to the western edge of the swamps and to the south-east around Maun and other centres of human population. The steenbok (Raphicerus campestris) has prevented livestock and human settlement from encroaching much into the Delta, but it is now the subject of an intensive eradication campaign which may open up large areas of the Delta for cattle production within 5 or 6 years.

Leaving aside the crocodile, which has already been discussed, reptiles are significant mainly through their rather poor representation in the Delta. The two large monitor lizards (Varanus niloticus) and (V. albigularis) are conspicuous and occur throughout, but most other groups of lizards are lacking, there being remarkably few geckos, although the skinks are more common.

There is a wide variety of snakes, but their populations appear to be lower than could be expected. The largest snake in the Delta is the African python (Python sebae) which is very common. Other non-venomous snakes include the mole snake (Pseudaspis cana), which is common on the estuaries of the Delta and on the larger islands. Several species of blind snakes (Typhlops spp.) occur, as well as three genera of water snakes (Philothamnus sp., Lamprophis sp. and Lycodonomorphus sp.).

The most conspicuous back-fanged snake is undoubtedly the boomslang (Dispholidus typus), which is common throughout, as are the sand snakes (Ophisaurus sp.). The large snake (Tecolobus s. lenzhauensis) is fairly common in the northern part of the Delta. The bird snake (Thelotornis sp.) and the herald snake (Cnemophis sp.) are also collected regularly.

Three cobra occur commonly: the Egyptian cobra (Naja haje haje) and the darker Anchieta's cobra (N. h. anchieta), with the spitting cobra (N. nigricollis mossambica)
occurring most frequently. Equally abundant is the black mamba (*Dendroaspis polyplepis*).

The three common species of vipers are the puff adder (*Bitis arietans*), the night adder (*Causus rhombeatus*) and the mole viper (*Atractaspis bibroni*).

As in most other groups the fish fauna of the Okavango appears less rich than might be anticipated, as the lack of commercial fisheries demonstrates. Eighty-two species of fish are recorded from the Okavango System, including Lake Ngami, of which 19 may be of some commercial value, the remainder being too small or too scarce. Predators predominate, of which the most widespread is the Kafue pike (*Hepsetus*) occurring in channels, lagoons and molapos. The sporting tiger fish (*Hydrocynus vitatus*) is very common in the rivers and channels of the permanent swamp. Catfish (*Clariidae*) are the most important predators, due to their wide distribution and abundance. Together with three species of *Tilapia*, the catfish are also the most important component of catches for local human consumption, although fair quantities of *Serranochromis spp.* are also netted. For these cichlids and clarids the shallow *melapo* at high flood are prime breeding sites. Very little is known of the feeding behaviour and population dynamics of fish in the Okavango and the first major studies are only now beginning.

A similar situation exists regarding the avifauna of the Delta. Although a checklist of the birds of Botswana has been compiled, very little systematic work has been done in the Okavango. There is a variety of birds and more than 400 species have been recorded.

The area of permanent swamp is relatively poor in bird life, with a notable lack of sites suitable for waders. The reed and papyrus beds contain a great number of warblers at certain times of the year, and the palm trees and gomoti provide important roosting sites for several storks, notably the marabou (*Leptoptilus crumeniferus*) and the wood ibis (*Ibis ibis*). In addition, a nesting colony of the pink-backed pelican (*Pelecanus rufescens*) is located near the base of the “panhandle” and a series of deepwater lagoons on the Ngokha has large heronries from which 24 species of herons, storks and ibises have been recorded. Wildfowl are poorly represented on the whole, although good numbers of spurwing geese (*Plectropterus gambensis*) and white-faced duck (*Dendrocygna viduata*) occur. Raptors are fairly well represented, the most noticeable being the fish eagle (*Haliaeetus vocifer*) which is common throughout the area. At present, some work is being carried out on the fishing owl (*Scofa pelia peli*) on the Okavango River.

Lake Ngami, when it contains water, is one of the major habitat areas for water birds in Southern Africa. Eleven species of waterfowl, 19 waders and 43 other water birds have been recorded in the area. The most notable are the concentrations of pelicans and flamingoes, which may be found there periodically. Up to 100,000 greater flamingoes (*Phoenicopterus ruber*) and 10,000 white pelicans (*Pelecanus onocrotalus*) were estimated in December 1971.

Overall, the Okavango Delta sustains a wide variety of wildlife at most levels, exceptions such as some birds, reptiles and small mammals being due largely to a paucity of certain niches caused by the frequent flooding of huge areas. In general, population levels are surprisingly low, but may be explained in terms of fairly low primary productivity, owing to very poor-quality soils and extremely low nutrient inputs into the system — the Okavango River carrying almost no mineral or organic matter. It is, however, one of the few major wildlife areas remaining in Africa that combines such a high degree of natural beauty with viable populations of many major species. Until recent years, the Delta’s ecology has been self-maintaining, but now demands upon it are increasing to the extent that active management should be introduced with the minimum delay, in order to keep open development and conservation options.